Title

Interactions of Vegetation, Climate, and Ecosystem Services From Leaf to Landscape in U.S. Cities

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Interactions of Vegetation, Climate, and Ecosystem Services From Leaf to Landscape in U.S. Cities

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Peter Ibsen

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ABSTRACT OF THE DISSERTATION

Interactions of Vegetation, Climate, and Ecosystem Services From Leaf to Landscape in U.S. Cities

by

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Doctor of Philosophy, Graduate Program in Plant Biology
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Dr. G. Darrel Jenerette, Chairperson

Urban vegetation represents a novel ecosystem where classical theories of vegetation ecology interact with systems of management and control not found in wildland areas. These interactions between urban management and vegetation provide unique circumstances to test classical ecological constructs of how vegetation responds to climate, while under the influence of urban actors. As urban areas are often hotter than rural counterparts, include a globally diverse array of vegetation of native and horticultural varieties, and are consistently directly and inadvertently treated with additional resources of water and nitrogen; urban areas make for novel common gardens to examine vegetation ecology. Furthermore, understanding the nexus of urbanization, vegetation, and climate will aide in quantifying ecosystem services as well as provide insight into how a diverse array of vegetation responds to multiple stressors. The research contained within this dissertation aims to explore how the dynamics of cities influence vegetation responses to extreme climates. To capture the many possible interactions, I explore urban vegetation ecology at multiple levels of organization, including the organismal, community, and ecosystem scale. Moreover, these studies examine both within city and across city dynamics, comparing cities from different regional climates. I use a combination of ecophysiological traits, community diversity sampling, and remote sensor networks to understand interactions of cities, climate, and plant-based ecosystem services. Overall, I find that the abundance of water resources in arid cities cause urban trees to decouple their carbon and water-use strategies, and that decoupling is increased in desert climates. When comparing plant communities in parks in mesic and arid cities, taxonomic diversity was strongly driven by climate, but aspects of functional diversity were more determined by management practice. Across cities, the ecosystem service of vegetation-derived nocturnal cooling was tightly correlated to atmospheric aridity, highlighting the relationship between transpiration and ecosystem services. Taken together this dissertation connects how increases in water availability can result in shifts in plant function, community diversity, and resulting plant-derived ecosystem services

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Introduction

The interactions of urban vegetation, climate, and management are a key component in understanding how novel urban ecosystems function from the leaf to landscape-scale (Whitlow and Bassuk 1988, Kowarik 2011, Groffman, Cadenasso, et al. 2017). Human impacts are heightened in cities, ensuring urban vegetation depends on unique resource patterns compared to rural counterparts (Kaye et al. 2006, Grimm et al. 2008). Irrigation, both in arid and mesic cities, provides increased access to soil moisture (Bijoor et al. 2012). Urban vegetation can receive potentially greater nitrogen resources, provided purposely through horticultural fertilization, as well as unintended inputs of dry and wet nitrogen deposition (Fenn et al. 2003, Decina et al. 2020). Urban plant communities are also a novel conglomeration of diverse species, responding not only to natural ecological filters (Ackerly 2003) but also filters imparted by management practices (Aronson et al. 2016, Pearse et al. 2018, Andrade et al. 2021). Furthermore, the biological functions of urban vegetation provide valuable ecosystem services of surface and air cooling (Armson et al. 2013, Shiflett et al. 2017).

While the urban environment introduces many factors that influence plant function, relationships between vegetation, temperature, and water are primary drivers of urban vegetation dynamics. Increases in daytime air temperature positively correlate with daytime sap flux in urban trees, and the strength of that relationship is stronger than their rural counterparts (Winbourne et al. 2020). Across cities, climate, in particular minimum temperature and annual precipitation, are crucial determinants of urban forest species richness (Jenerette et al. 2016). Moreover, the ecosystem service of microclimate cooling is both a factor of urban vegetation moderating temperature through increasing latent heat flux (due to leaf transpiration) (Broadbent et al. 2018) and by reducing sensible heat flux (due to shading of surfaces) (Crum and Jenerette 2017). However, these biophysical responses to climate vary depending on vegetation type and local environment, adding uncertainty when modeling urban vegetation function and services (Heris et al. 2020).

Scaling organismal functions to ecosystem properties has long been a fundamental challenge in ecology (Levin 1992, Heffernan et al. 2014) and is exacerbated in urban areas (Borgström et al. 2006). In cities, functional properties of vegetation have been measured and modeled against climate variables (Leuzinger et al. 2010, McPherson et al. 2018, Borowy and Swan 2020). Yet, when attempting to understand the urban community's function, patterns of dispersal and competition can be altered by active planting or removal (Avolio, Pataki, et al. 2020). Scaling vegetation function to the community in cities has provided evidence for the phenomena of urban homogenization. Urban homogenization is what occurs when urban communities are more similar to each other than to their rural counterparts (Groffman et al. 2014, Padullés Cubino et al. 2018). Microclimate and natural resources, such as water and nitrogen, can be homogenized which adds to the uncertainty in determining vegetation responses to climate (Hall et al. 2016, Groffman, Avolio, et al. 2017, Trammell et al. 2020). To reinforce the biological foundations of urban vegetation ecology, studies need to address within and among-city variations in vegetation function due to species, functional type, and climate. Moreover, research must quantify what patterns of plant function and services are due to urban management plans and/or responses to climate.

Municipalities often highlight various ecosystem services of urban trees that are rooted in their physiological function, from removing airborne particulate matter, and cooling air and surface temperatures, to reducing flood risks (Bowler et al. 2010, Grote et al. 2016, Livesley et al. 2016). The value of these benefits is often derived from how the species would function in wildland areas, yet urban species are known to function differently than wildland counterparts. Recently, studies have shown urban tree species grow at advanced rates, and have greater risks of mortality, compared to their rural counterparts (Smith et al. 2019). Shifts in tree water-use may be due to differences in resource availability in urban areas (Winbourne et al. 2020). Services derived from urban vegetation also vary depending on the region (Shiflett et al. 2017), the arrangement of vegetation (Feyisa et al. 2014, Skelhorn 2014), vegetation type (i.e turf vs. trees) (Gómez-Navarro et al. 2021), and species present (Rahman et al. 2015, Litvak et al. 2017).

Advancing the understanding of how urban vegetation functions in response to urban management, and linkages to production of ecosystem services is a growing need, both in the field of urban ecology and in the realm of urban planning. Urban greening programs can cost millions of dollars in major metropolitan areas (Pincetl 2010). The benefits (carbon sequestration, pollution removal, heating reduction) of these large-scale greening programs themselves are valued in the tens of millions in Los Angeles alone (Nowak et al. 2010). The cooling benefits of urban trees can reduce heat-related illness in at-risk populations. Increasing the canopy cover of Philadelphia by 30% averts more than 400 deaths a year (Kondo et al. 2020). Cities can also act as hot-spots of biodiversity, conserving regional natives (Ives et al. 2016) and acting as arks of global diversity (Clarke et al. 2013).

Increasing ecosystem services and diversity are important goals for urban vegetation management, however, the benefits can come with significant trade-offs. The cooling services of urban vegetation are strongly associated with greater water-use (Vahmani and Jones 2017). In more arid cities, the "water-for-cooling" bargain is linked to socio-economic disparities, where the majority of cooling being provided is in higher-income regions (Shandas et al. 2019). This economic disparity is again found in urban biodiversity, where wealthier areas of a city exhibit greater biodiversity (Hope et al. 2008). This "luxury effect", has been evident in the size of trees, more so than the life stage of the individual (Avolio, Blanchette, et al. 2020).

Recent research has aimed to overcome some gaps in the field. However, past approaches have been limited in their scope. At the leaf level, urban ecophysiological studies that aim to resolve the interactions of vegetation function, climate, and urbanization have either focused on a few key species (Rahman et al. 2011, Sjöman et al. 2015, Sanginés de Cárcer et al. 2018), or spatially limited studies at single locations (Pataki et al. 2013, Savi et al. 2015). Research into the drivers of urban biodiversity has made broader steps into scaling-up results, with many multiple cities and global studies in the past decade (Nielsen et al. 2014, Dobbs et al. 2017, Kendal et al. 2018, Locke et al. 2018, Padullés Cubino et al. 2018). One limitation of many of these studies is the focus on one vegetation community (i.e. parks, residential yards, or street trees), one metric of diversity (i.e. taxonomic, functional, or phylogenetic), or one vegetation type (i.e. herbaceous lawns, park or street trees).

The primary goal of this dissertation is to provide a greater understanding of the nexus between urban vegetation function, climate, and vegetation-derived services, and to link these three factors together through the biophysical processes of urban vegetation. Through this goal, I aim to examine urban vegetation processes at organismal, community, and ecosystem scales of organization, from the micro to the continental-scale. This dissertation will address this goal by asking three primary questions corresponding to three chapters: 1) How do functional strategies of a diverse array of urban trees shift when soil moisture is not a limiting factor, and how do these functional strategies perform in extremely arid environments? 2) How do interactions of climate and management drive taxonomic and functional diversity of trees, turf, and spontaneous species in recreational parks of the United States? 3) How does atmospheric aridity determine the magnitude of vegetation-derived nocturnal cooling in multiple U.S. cities of different regional climates.

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Chapter 1
Increased resource availability reduces necessary trade-offs of ecological strategies in urban trees.

Abstract

Ecological strategies of carbon and water use are fundamental to predicting tree functional responses to changes in climate. However, these strategies themselves can be altered by environmental conditions, including water availability and heat and aridity. We ask how do suites of functional strategies in tree species shift in environments with reduced water limitations and high heat and aridity? We test the hypothesis that tree ecological strategies are rooted in water resource availability by measuring suites of functional traits associated with carbon and water-use strategies of multiple tree species in a novel common garden, planted throughout an irrigated urban area distributed across a prominent heat and aridity gradient. Our results show an overperforming of carbon-use strategies in water-rich environments, where the leaf economic spectrum of a global array of tree species skews more productive than in wildlands. Similar to studies done in irrigated greenhouses, we found a decoupling of carbon and water-use strategies among our sample species, with 36% percent of functional variation being explained by carbon-use traits, and 29% percent of variation being explained by water-use traits. We interpret these results as evidence that tree functional strategies themselves respond dynamically to a combination of environmental stress and resource availability. These results will aid in predicting shifts in global forest functions as a result of changing water resources and

climate, as we show interactions between soil moisture and atmospheric aridity driving tree productivity.

Introduction

We interpret these results as evidence that tree functional strategies themselves respond dynamically to a combination of environmental stress and resource availability. As climate change models predict increases atmospheric aridity in multiple forested biomes in the coming decades (Lickley and Solomon 2018, Grossiord et al. 2020), we find a need to discern extreme climate effects on the fundamental functional strategies of global forests. Trees species employ a spectrum of strategies to address the carbon/water use trade-off . As the leaf is the primary source for both the acquisition of carbon through leaf stomata (Ball et al. 1987, Medlyn et al. 2011), and the use of carbon through the photosynthetic machinery (Onoda et al. 2017), carbon use strategies lie along a leaf economic spectrum (LES) (Wright et al. 2004), which ranges from "fast" to "slow" carbon strategies. A "fast" carbon strategy allows for quicker resource acquisition, growth, and establishment, all at the risk of functional loss or mortality under low resource conditions (Reich 2014). The "slow" carbon strategy allows for greater functional stability in low resource and stressful environments at the cost of a weaker competitive advantage in high resource in environments (Reich 2014).

An analogous spectrum can be used when considering water-use strategies. More liberal water-use strategies allow for more water use as a resource for internal (photosynthetic processes, leaf turgidity), and external (leaf surface cooling) actions at the risk of hydraulic failure and leaf damage in times of soil and atmospheric drought

(Barber 2017, Drake et al. 2018, Zhu et al. 2018). Conservative water-use strategies reduce risk of hydraulic failure during droughts at the cost of reduced rates of photosynthesis (McDowell 2011). The anatomical basis for these water-use strategies is found in how plants regulate their stomata under drought conditions. As VPD increases, plants respond by regulating transpirational water loss in proportion to the potential failure of their xylem, and soil drought (Sperry et al. 2016). Species that display isohydric behavior respond to water deficit by quickly closing stomata, limiting water loss through transpiration at the cost of carbon uptake (Tardieu and Simonneau 1998). Conversely, anisohydric species maintain stomatal conductance under limited water availability, losing more internal water through transpiration, but maintaining active photosynthesis (Skelton et al. 2015). The degree to which tree species regulate water loss remains a matter of debate regarding whether a hydraulic strategy is more strictly evolutionary- based (Tardieu and Simonneau 1998), or a spectrum that varies with exposure to the environment (Hochberg et al. 2018a, Grossiord et al. 2020).

While carbon and water use traits are connected at the leaf level, how these processes are connected as whole-plant strategies, and as indicators of stress responses, remains uncertain (Blonder et al. 2014, Sack et al. 2014, Pappas et al. 2016, Grossiord et al. 2020). Stomatal openings provides a physiological link between carbon and water-use strategies at the leaf level. The classical model of stomatal behavior describes a strategy of optimizing carbon gain for water loss (water-use efficiency) (Farquhar and Wong 1984, Jones 1998, Santiago et al. 2004). The more recent LES also hypothesized that water-use traits were connected on the same “fast” and “slow” spectrum as carbon-use traits (Reich 2014, Jiang et al. 2020). However, certain environmental conditions can cause in carbon and water-use strategies to decouple from each other (Urban et al. 2017). Should water limitations be reduced, through either less competition or plentiful soil moisture, stomatal strategies can adjust to maximize carbon gain against any water costs (Wolf et al. 2016). Decoupling of carbon and water-use may allow a greater freedom to acclimate to extreme changes in climate (Li et al. 2015). Photosynthetic rates in trees can also be decoupled from transpiration rates during heat waves (Drake et al. 2018), allowing individuals to reduce leaf temperatures, both by slowing photosynthetic processes and by increasing transpiration to the leaf surface. However, a major factor with the potential to decouple carbon gain and water loss constraints in plant photosynthetic systems may be access to abundant water resources. An ecosystem scale study found no decoupling in Australian forest communities, implying the previous decoupling found by Drake et al (2018) was likely due to their study species tapping into moisture deeper in the soil profile (De Kauwe et al. 2019). Thus, water resource limitations may be an overlooked, but key factor in determining whether carbon and water strategies are decoupled in high heat environments.

Increased aridity can have significant effects on tree physiological functions and has been correlated with reductions in tree growth in wildland (Williams et al. 2010) and urban areas (Nitschke et al. 2017). With increasingly arid conditions trees can shift ecological strategies of carbon acquisition and water usage (Drake et al. 2018). High aridity can stress trees past their hydrological limits, causing loss of productivity and increased mortality (Greenfield and Nowak 2013, Choat et al. 2018). However, these ecophysiological responses do not necessarily follow the same patterns for all species. Aridity correlated growth changes vary by species (Sanginés de Cárcer et al. 2018), and while some tree species increase their usage under high aridity, others may become more water-use conserving (Pivovaroff et al. 2016). As heat and aridity are projected to increase in multiple biomes, understanding how carbon usage of multiple species is linked to water resources in the context of climate change is key to predict future global forest productivity.

We address uncertainties of how carbon and water use strategies will shift in trees under the stress of high VPD, but supplied with the artificially high resource availability found in urban ecosystems. Urban forests in certain regions of mild to warm climates are populated with tree species representing a broad swath of global genetic diversity (Jenerette et al. 2016). Maintained urban forests receive an abundance of additional resources through regular irrigation and fertilization (Bijoor et al. 2012), but how such resources liberate species from fundamental trade-offs or push species beyond their normal functional constraints is unknown. Furthermore, the biodiverse urban forest of Southern California, stretches across a dynamic coast-to-desert climate gradient. Using the urban trees of Southern California as our study system we ask, **how will a diverse arrangement of trees experience carbon and water use strategies in an environment of low resource limitation such as urban areas, and how will tree carbon and water use strategies shift in low resource environments when exposed to extreme climates?** From these two research questions we have developed three main hypotheses. First, we hypothesize trees will shift to a greater carbon-use strategy in urban areas due to regular irrigation reducing the need to regulate stomata. Second, tree carbon gain and water loss strategies will become more “fast” and “liberal” in extreme climates with otherwise low resource limitation, due to abundant soil moisture and profligate leaf gas exchange. Finally, carbon gain and water loss will be decoupled due to relaxed stomatal restrictions under high resource availability. Through tests of these hypothesis we will help resolve the question of how tree carbon and water-use strategies are connected through water resource limitations and predict how these relationships will shift in a future climate of greater aridity.

Methods

Study system

The Los Angeles Megacity is one of the largest urban populations in the United States. Located in southern California, the LA conurbation include over 17.5 million residents, includes towns from five counties, and is highly urbanized from the coastal to the Coachella Valley desert (Figure 1.1) (Tayyebi and Jenerette 2016). Along that urban expanse are multiple Köppen climate types. Moving from coast to desert one finds, semi-arid steppe with summer fog, semi-arid steppe, Mediterranean/hot summer, semi-arid steppe/hot, and arid low latitude desert/hot (https://www.coastal.ca.gov/). Aridity itself can be measured as vapor pressure deficit (VPD), the difference between atmospheric-saturation water vapor pressure and actual water vapor pressure in the air. a leaf. Maximum summer temperatures and VPD can range from ~24.5 °C and ~1.4 kPa on the coast, to ~41.0 °C and ~6.1k kPa in the desert (30-yr climate normal, 1980-2010, PRISM

Climate Group, Oregon State University). For this study we use VPD as our primary climate variable, as temperature and VPD are tightly correlated in this region (Shiflett, SA., et al. 2017). As the urban forest extends for coast to desert, we are able to create space-for-time substitution in examining both inter and intraspecific effects of extreme heat and aridity on tree species.

Selection of trees and traits.

To study the function of urban trees within the LA megacity, we selected 30 focal tree species (Table 1.1) represent some of the most common tree species found in southern California (including 8 out of 15 of the most common street trees in Los Angeles, Orange, and Riverside counties) (Avolio et al. 2015), and 17 of our species are from the City of Los Angeles Approved Street Tree list (https://www.marvista.org/productphotos/LA-City-Approve-Street-Trees.pdf). Our study species comprise 15 different families and 7 biomes of origin.

We clustered the sampled traits into three specific suites that described the overall ecological strategy represented by the chosen traits (Table 1.2). The "Carbon-use" suite is comprised of three leaf traits, specific leaf area (SLA), percent of leaf nitrogen by mass (%N), and leaf laminar thickness (LT). These traits serve as proxy indices for allocation to maximum carbon gain potential, which in turn is associated with their position on the leaf economic spectrum, varying from fast to slow return on investment in carbon to photosynthetic structures (Cornelissen et al. 2003, Wright et al. 2004). The "Water-use" suite is comprised of stomata guard cell length (GCL), stomata density (SD), and wood density (WD). Greater GCL, SD, and lower WD are associated with rapid water transport and loss from leaves (Santiago et al. 2004, Sack et al 2003).

Data collection and identifying study species with citizen scientists

We located sample individuals through a collaboration with Earthwatch, a non-profit that provides citizen science engagement. Local citizen scientists were trained on how to identify our species of interest and take an environmental identify of the tree's condition and nearby environment. In the field when volunteers would ID a potential study species, they were trained to record the GPS location of the individual, measure the trunk diameter to prevent including saplings in the study, provide a qualification of the tree's condition, measure the canopy size, and estimate the percentage of surface around the tree that is permeable to water.

Leaves and stems were sampled over the summer (July-Sept) month of 2016-2018. We sampled southern exposed portions of the tree crown, avoiding any leaves growing in the shade of other leaves. Leaves were removed from trees using pole pruners up to 5m in length. Post removal, leaf samples were placed in plastic bags with a damp paper towel to prevent desiccation, then kept in the dark in a cooler for transport out of the field. We collected wood core samples from the trunk of the tree using an increment borer, following the methods described in the section "Addition useful methods from forestry" (Cornelissen et al. 2003). To derive the hydraulic strategy of a species we sample pre-dawn and mid-day leaf water potential of a southern exposed leaf with a Scholander Pressure chamber (PMS Instruments, Corvallis, OR, USA). To highlight comparisons between climate extremes, leaf water potential was only collected in the coast and desert regions, and only for species which we could be found in both regions (21 out of 30 study species). A minimum of three individuals per species per region were sampled for water potential measurements.

Sampling Processing

A total of three leaves from each individual tree were processed for trait values. While still fresh, each leaf was scanned into an 8-bit image of leaf surface. These scans were the analyzed with imageJ (http://rsbweb.nih.gov/ij/) software to calculate leaf area, to be used in the calculation of SLA. LT was determined using a micrometer, where three measurements were taken per leaf and averaged. Leaves were then processed for SD and GCL through creating stomatal peels using the methods described in Franks et al. (2009), where a thin layer of acrylic polymer (clear nail polish) is applied to the abaxial side of the leaf, allowed to dry, transferred to clear cellophane tape, and affixed to a microscope slide creating an impression of the stomates (Franks et al. 2009). Stomatal trait parameters were determined using a microscope at 400x magnification. Leaves were then dried in a 60 °C oven for three days and then weighed to determine dry matter content. SLA was derived as the ratio of leaf area to dry matter content. All leaf measurements were then averaged to the individual level for analysis. Wood density was determined by a volumetric displacement method. Following determination of volume, wood cores were then dried in a drying oven at 60 °C for four days and WD was expressed as the ratio of wood core volume to dry weight.

Statistical Analysis

To compare our carbon and water-use strategies to established ecological strategy trade-offs found in wildlands, we collected trait values representing the leaf economic spectrum (SLA and %Leaf N) and a spectrum of water-use (pre-dawn leaf water potential and wood density from the TRY database (Kattge et al. 2020). We determined the comparison spectrum by deriving the linear equation of the relationship and the 95% confidence interval. These wildland strategy spectrums were then used as the baselines to compare our strategies.

Relationships between traits, and between traits and VPD, at both the inter and intra specific level were determined using Pearson correlations. To view the full trait space occupied by our urban trees we conducted an ordination using a principle components analysis (PCA). We applied a Box Cox transformation to each category of functional trait to maintain an assumption of normality. Traits were z-transformed to a mean of zero and standard deviation of 1. We removed any sampled individual that did not have a full set of associated traits. Significant axes were determined to have eigenvalues > 1.

We calculated our metric of hydraulic strategy as the delta of mid-day and pre-dawn water potential. Shifts in hydraulic strategy were determined as the difference between the delta water potential at in the coast region to that of the desert region. Increases in delta water potential were taken to imply a shift to a more isohydric or “conservative” water-use strategy. Decreases in water potential imply a shift to a more anisohydric or “liberal” water use strategy (Klein 2014). The significance of hydraulic shifts was determined by ANOVA (alpha = 0.05) of the coast and desert leaf water potential measurements for each species.

Results

We collected leaf and stem traits for 30 species of urban trees planted across Southern California representing 17 different families and 11 different biomes of origin (Table 1.1). Out of those thirty species we collected the pre-dawn and mid-day water potential of 21 urban tree species that were able to be sampled with replication in coast and desert locations. When comparing carbon-use and water-use strategies to wildland baselines, we found that our sampled trees showed greater leaf N per unit SLA compared to the global pattern (Figure 1.2a). Our results also showed greater predawn leaf water potential per unit wood density (Figure 1.2b), indicating that urban trees appear to overperform relative to wild plants in natural ecosystems in terms of carbon-use strategy, and did not present a statistical tradeoff of water-use strategies (Figure 1.2).

Overall Functional Characteristics of Study Species

The two main PCA axes comprised approximately 61 % of variation (PC axis 1 = 36.54% variation, PC axis 2 = 29.57% variation) (Figure 1.3). PC axis 1 was most heavily drive by carbon use traits (SLA – loading value: 0.58, %N – loading value: .39, LT – loading value: -0.64). PC axis two was most strongly driven by water use traits (GCL – loading value: -0.42, SD – loading value: 0.69, WD – loading value: 0.53).

Interactions of Among Species, Traits, and Climate

When performing correlation analyses of all functional traits we found significant correlations among traits organized by their ecological strategies. Carbon economy traits were significantly (alpha = 0.05) correlated with each other (SLA – % N = 0.34, SLA – LT = -0.66, %N – LT = -0.12). Water use traits were mostly significantly correlated (SD – GCL Pearson coefficient = -0.2, GCL – WD Pearson coefficient = 0.23), though no significant correlation was observed between SD and WD (Figure 1.4). All carbon economy traits were significantly correlated with leaf morphology traits. Carbon economy and leaf morphology traits were partially correlated with water use traits.

When comparing sampled functional traits to the local maximum aridity of sampled tree locations two carbon-use traits were significantly correlated (VPD – SLA Pearson coefficient = 0.22, VPD – N Pearson coefficient = 0.13).We found more correlations between traits and the local climate when restricting the correlation analysis within individual species. Across all data, there was no singular trait ~ VPD relation which was significant for all studies tree species. Similarly, there was no species with significant correlations between all traits ~ VPD. Twenty tree species in the study exhibited significant correlations between traits and climate (though not all species were able to be sampled across the entire coast to desert range) (Figure 1.5). All within species significant correlations between carbon economy traits and VPD were positive, while all other correlations of traits as a function of VPD varied between significantly positive and negative depending on the species.

Hydraulic Characteristics of Urban Tree Species Across a Climate Gradient

We found significant shifts in intraspecific hydraulic strategy across the southern California climate gradient. Out of the initial 30 species in the study, we restricted the hydraulic portion of the study only to species that could be found in abundances large enough to allow for statistical analysis (n=6) in both coastal and desert regions, leaving 21 species. Using the difference in delta leaf water potential between coastally planted individuals and desert planted individuals. 11 out of 21 species experienced a significant shift in mean delta leaf water potential between urban coast and urban desert. 10 out of those 11 experienced a shift to a more anisohydric strategy in desert conditions (Figure 1.6). Only *Ficus macrocarpa* experienced a significant shift to a more isohydric strategy.

Discussion

Our work highlights resource limitation as a foundation for carbon and water use strategies in trees. We found evidence of abundant water resources driving changes in carbon and water-use strategies. With soil water in unlimited supply trees are able to increase their carbon gain potential, shifting to a strategy of carbon maximization with little regulation of water loss. While carbon-use strategies of urban trees outperform the LES, trait-based water-use strategies lose their significance in a non-water limited context. The combination of overperforming carbon strategy and weakened water strategies results a decoupling of carbon and water-use strategies in an environment with minimal water limitation. The interactions of increasing aridity and ample soil moisture appear to increase the potential for decoupling of strategies.

Setting our results in context to carbon and water-use strategies (Figure 1.2) provides an important juxtaposition between our resource rich study and natural ecosystems. Within wildlands resource limitation and resource competition set the boundaries for the trade-offs which define these strategies, while resource rich urban environments appear to allow species to extend beyond the constraints posed by resource supply in nature. The carbon economic over performance of resource saturated trees compared to wildland, resource-limited species, in our studies is similar to the “live fast die young” results found in other urban forests (Smith et al. 2019). When tree species in cities have abundant access to water resources, through irrigation and through tapping into sewer and water lines (Randrup et al. 2001), increased urban heat also may be providing additional resources increasing carbon economy (Hardiman et al. 2017). In addition to the abundance of water and heat resources, the urban environment also supplies higher resources of CO^2 and nitrogen (Idso et al. 2001, Decina et al. 2017). Within these high resource environments, there may be little incentive for trees to conserve water resources.

We find that in a high resource input environment, the stressors that could reduce carbon use strategies may actually be doing the opposite. Our measurements of SLA and %N, both carbon use traits, positively correlated with VPD across all species, and we saw a general trend of intra-specific positive correlations as well (Figures 1.3 & 1.4). Yet, increases in VPD have been often correlated with a global loss of terrestrial carbon gain (Yuan et al. 2019), as well as with reduced growth in individual tree species (Sanginés de Cárcer et al. 2018). These negative relationships of aridity and carbon-use indicate an overall coupled strategy of carbon-use and water-use, hypothesized as the WUE strategy (Farquhar and Sharkey 1982, Wolf et al. 2016)). However, when soil moisture is no longer limiting, stomatal control is lessened (Sperry et al. 2016), potentially allowing for a "faster" carbon economy in environments of higher VPD but plentiful water resources. While we did see a general trend of increased carbon-use strategy under higher VPD, at the intra-specific level only certain species appear to be able to take advantage of this ability, as 11 out of 30 species experienced at least one carbon-use trait increase with VPD.

At the intraspecific level water-use strategy shift to a more anisohydric strategy in arid environments for a number of our study species (Figure 1.6). This shift implies a reduction of stomatal regulation to aridity in areas with plentiful water resources. With constant access to abundant soil moisture, certain tree species do not have the ecological necessity to conserve internal water. This hydraulic response mirrors what Is mechanistically expected by Wolf et al (Wolf et al. 2016), where under well-watered conditions species that favor water-use-efficiency strategies, and plants that favor carbon-maximizing stomatal strategies will act in the same manner. This result is further emphasized by the species that did not shift to an anisohydric strategy in the desert, also (except for *Ficus macrocarpa*) shift to a more water-conserving isohydric strategy. Without the resource limitation constraining the linking between carbon-use and water-use strategies, tree species experienced a decoupling of strategies. Seen in Figure 1.2, carbon and water-use strategies deviate from their respective norms in different ways, carbon-use strategies overperform and water-use strategies are reduced. These separations of strategies create this decoupling, which is seen in the separation of PCA axis 1 vs. axis 2 in Figure 1.3. Similar decoupling of carbon and water strategies has been seen in tropical and subtropical trees (Li et al., 2015). Furthermore, when exposed to elevated resources of CO_2, some water-use traits, such as stomate density, become more associated with the LES (Blackman et al. 2016). We expect carbon and water-use traits to experience a greater decoupling under higher VPD, where the shift to more anisohydric strategies allows for the increase in carbon-use strategies at the expense of maintaining water-use efficient goals.

We were able to test the hypothesis of how resource abundance affects ecological strategies in conjunction with aridity by using an urban forested ecosystem. With a removal of soil water limitation, urban trees have the capacity to present an interesting hydraulic responses to extreme heat and aridity. Not only do our results add evidence to urban tree physiology being a novel “without limits” hydraulic response to extreme VPD, but these results also build the case that hydraulic strategies in general are more responsive to the environment than they are innate. Plant hydraulic strategy has developed from a view that species could be classified into binary categories of how a plant control their stomata under stress from soil and atmospheric drought (Tardieu and Simonneau 1998). Understanding of these hydraulic strategies has advances into viewing them as a spectrum across which species fall (Klein 2014), as species specific yet variable depending on environment (Franks et al. 2007, Hochberg et al. 2018b), and as response to both seasonal and rapid changes in weather as well as a heritable trait (Guo et al. 2019). An irrigated urban forest in a desert region follows the trends describing hydraulic strategy as an environmental trait, and one that will maintain stomatal conductance under high aridity resulting in more liberal water usage.

As we are seeing, irrigated urban tree species are generally using more water in hotter arid environments, therefore there are implications for how urban planners decide what species to use in arid cities. Urban policy and research have put out calls to increase the planting of "drought-tolerant" species in arid cities (Konijnendijk et al. 2005, Mcpherson and van Doorn 2017, McPherson et al. 2018, Vogt 2020). Yet, if cities are not changing their irrigation practices, these "drought-tolerant" species may actually end up using more water than they need. In fact, out of the 11 species that showed a shift to more liberal water-usage in the desert, 6 of them are considered drought tolerant by the Urban Forest Ecosystems Institute (https://selectree.calpoly.edu/). When preparing sustainable urban forest planning for a hotter and drier future, urban planners need to consider that species planted in a resource rich environment may not function the same as their native counterparts.

Conclusion

The next decades will see a changing in resource availability across the globe. Through our study we have found evidence that when water-resource limitation is reduced, tree species of diverse origins experience a decoupling of carbon-use and water-use strategies. Where overall, the trade-off that underlie the leaf economic spectrum are over-emphasized. Species tend to maximize carbon gain with less regard for water loss. This effect is emphasized in arid conditions, where abundant water resources allow for species to shift their hydraulic strategies to one of more liberal water usage, with less risk of hydraulic failure.

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Tables

Table 1.1 Table of all study species, respective families, and native biomes. Traits are mean values collected across all individuals of noted species. Standard deviations are in parentheses.

			Mean /Functional Trait Values							
Species	**Family**	**Native Biome(s)**	**Specific Leaf Area**	**% Leaf Nitrogen**	**Wood Density**	**Guard Cell Length**	**Stomate Density**	**Leaf Area**	**Dissection Index**	**Leaf Thickness**
Olea europaea	Oleaceae	Hot Summer Mediteranian	40.42	2.41	0.73	21.56	341.01	4.31	1.89	0.45
Quercus agrifolia	Fagaceae	Temperate grassland	57.44	1.48	0.62	16.55	356.33	6.94	1.33	0.24
Arbutus unedo	Ericaceae	Hot Summer Mediteranian	62.82	1.38	0.61	28.02	236.59	22.68	1.47	0.25
Platanus racemosa	Planatanaceae	Temperate Riparian Woodlands	97.99	1.66	0.51	29.95	208.70	144.03	2.49	0.18
Populus freemontii	Salicaceae	Temperate Riparian Woodlands	80.99	3.04	0.43	23.49	189.71	49.04	1.67	0.24
Chitalpa tashkentensis	Bignoniaceae	Hybrid	116.95	3.10	0.45	30.83	176.88	24.52	1.90	0.21
Quercus engelmanii	Fagaceae	Hot Summer Mediteranian	62.65	2.69	0.72	18.91	530.79	5.42	1.41	0.25
Pistacia chinensis	Anacardiaceae	Humid SubTropical	78.69	2.73	0.71	15.60	578.76	123.57	5.81	0.19
Cinnamomum camphora	Lauraceae	Temperate deciduous forest	109.79	1.92	0.57	21.30	325.18	16.21	1.79	0.19
Koelreuteria bipinnata	Sapindaceae	Temperate deciduous forest	94.74	2.33	0.64	16.43	722.80	746.06	12.47	0.15
Lagerstroemia indica	Lythraceae	Temperate deciduous forest	76.34	1.55	0.61	18.86	448.41	10.58	1.25	0.24
Liquidambar stryaciflua	Hamamelidaceae	Temperate deciduous forest	98.22	1.77	0.51	28.22	248.34	43.57	3.04	0.19
Magnolia grandiflora	Magnoliaceae	Temperate deciduous forest	56.09	1.85	0.56	27.24	274.41	78.92	1.37	0.37
Celtis laevigata	Cannabaceae	Temperate deciduous forest / Temperate grassland	82.03	2.36	0.59	18.00	512.32	20.45	1.44	0.18
Gleditsia triacanthos	Fabaceae	Temperate deciduous forest / Temperate grassland	92.92	2.21	0.66	28.51	151.00	33.69	5.28	0.21
Ulmus parvifolia	Ulmaceae	Temperate deciduous forest / Tropical rainforest	71.15	2.29	0.69	25.67	414.36	5.49	1.54	0.26
Jacaranda mimosifolia	Bignoniaceae	Temperate grassland / Tropical grasslands	94.72	2.12	0.53	12.79	249.37	282.09	9.59	0.16
Dalbergia sissoo	Fabaceae	Tropical dry deciduous forest / Desert	105.15	3.81	0.61	17.99	286.05	14.55	2.86	0.20
Lophostemon confertus	Myrtaceae	Tropical grassland	56.51	1.30	0.58	18.57	302.60	39.97	1.56	0.31
Tipuana tipu	Fabaceae	Tropical grassland / Chapparal	95.79	3.01	0.56	14.55	63.06	131.17	5.28	0.20
Eucalyptus sideroxylon	Myrtaceae	Tropical grassland / Tropical rainforest	59.30	1.42	0.76	24.90	139.58	14.54	2.09	0.31
Brachychiton populneus	Malvaceae	Tropical grassland/ Temperate grassland	107.22	2.15	0.43	16.56	364.75	18.73	1.84	0.20
Melaleuca ericifolia	Myrtaceae	Tropical rainforest	63.51	1.61	0.58	21.81	374.05	5.21	1.66	0.37
Tabebuia impetiginosa	Bignoniaceae	Tropical rainforest	93.64	3.08	0.74	20.92	260.13	84.06	4.20	0.19
Grevillea robusta	Proteaceae	Tropical rainforest / Temperate grassland	74.64	1.41	0.53	23.68	250.07	100.89	11.11	0.20
Ficus microcarpa	Moraceae	Tropical rainforest / Tropical dry deciduous forest	77.59	1.52	0.65	19.62	260.70	10.69	1.48	0.29
Fraxinus uhdei	Oleaceae	Tropical rainforest / Tropical dry deciduous forest	67.36	2.05	0.58	24.32	247.35	141.24	4.06	0.21
Afrocarpus falcatus	Podocarpaceae	Tropical rainforest / Tropical grassland	61.98	1.36	0.52	23.64	122.65	1.45	2.43	0.35
Rhus lancea	Anacardiaceae	Tropical rainforest / Tropical grassland	71.50	2.25	0.68	23.93	299.50	19.05	4.08	0.27
Schinus terebinthefolius	Anacardiaceae	Tropical rainforest / Tropical grassland	96.43	1.79	0.55	21.42	301.23	43.06	4.40	0.25

Table 1.2 Functional traits sampled along with what ecological strategies the trait acts as a proxy for. Intraspecific trait variation provided by the mean coefficient of variation from all species as well as the total variation of all traits across species.

Trait	Units	Ecological Strategy	CV (within species)	CV (across species)
Specific Leaf Area (SLA)	$cm^2 g^{-1}$	Carbon use	21.77	33.49
%Leaf Nitrogen (N)	na	Carbon use	29.39	42.60
Leaf Thickness (LT)	mm	Carbon use	16.19	34.56
Guard Cell Length (GCL)	µm	Water Use	12.58	27.93
Stomate Density (SD)	$cm\ mm^{-2}$	Water Use	20.71	53.03
Wood Density (WD)	$mg\ cm^{-2}$	Water Use	11.68	18.66

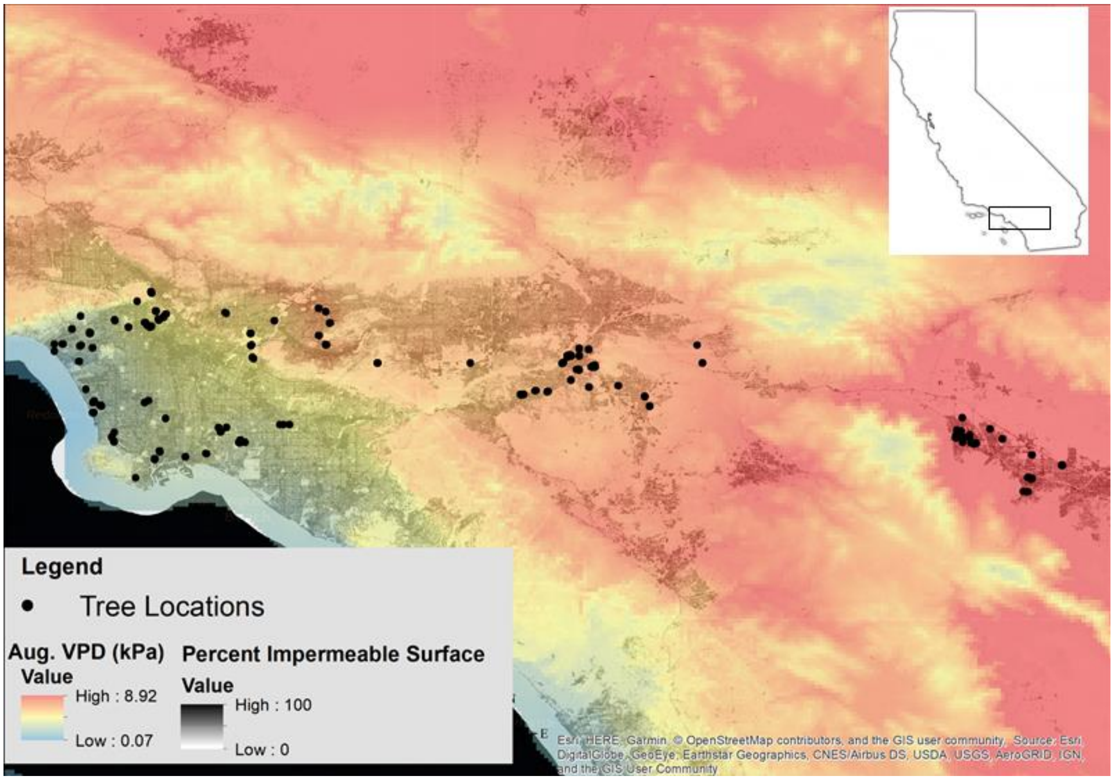

Figure 1.1: Site locations of sampled trees across the Southern California urban climate gradient. Urban area is represented as percent impervious surface and climate is represented as a gradient of VPD (kPa).

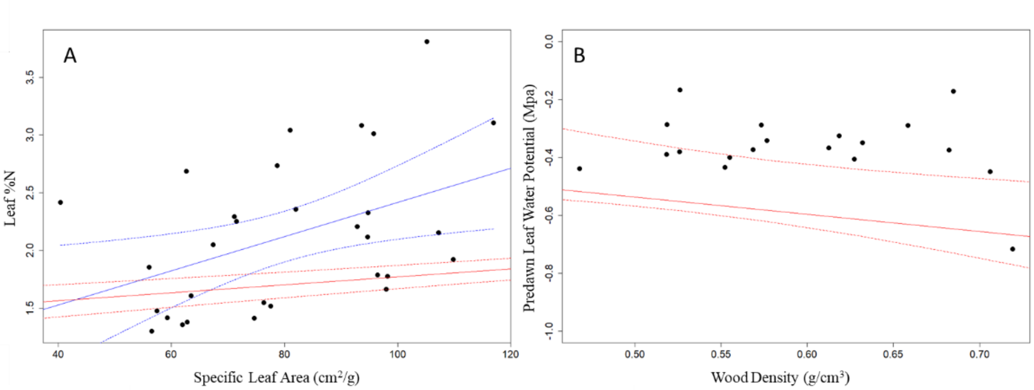

Figure 1.2: Relationships of traits which underlie (A) carbon-use and (B) water-use ecological strategies, found in our samples of urban tree species. Carbon-use strategy (A) is represented as the relationship between specific leaf area (SLA) and percent leaf N by mass (%N). Water-use strategy (B) is represented as the relationship between wood density and predawn leaf water potential. Blue solid and dashed lines represent the linear regression and 95% confidence interval of study data when linear regression is significant (alpha < 0.05). Red solid and dashed lines represent the linear regression and 95% confidence interval of data derived from tree species in the Try Database, representing the baseline of ecological strategies (alpha < 0.05).

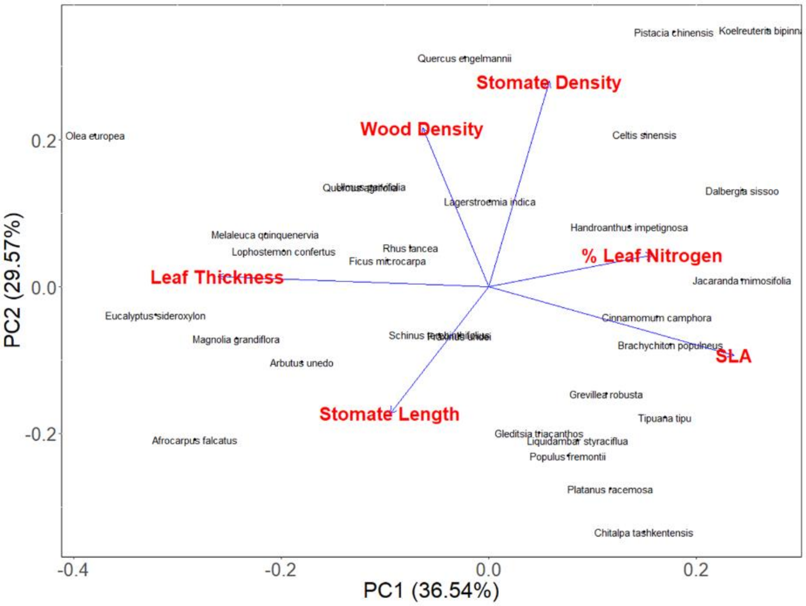

Figure 1.3: Principle components analysis (PCA) of trait variation in all study species. Traits were box cox transformed and z-transformed before analysis to conform to assumptions of normalcy and comparable ranges. Percentage next to the axis label indicates the percentage of variation in trait values determined by that axis.

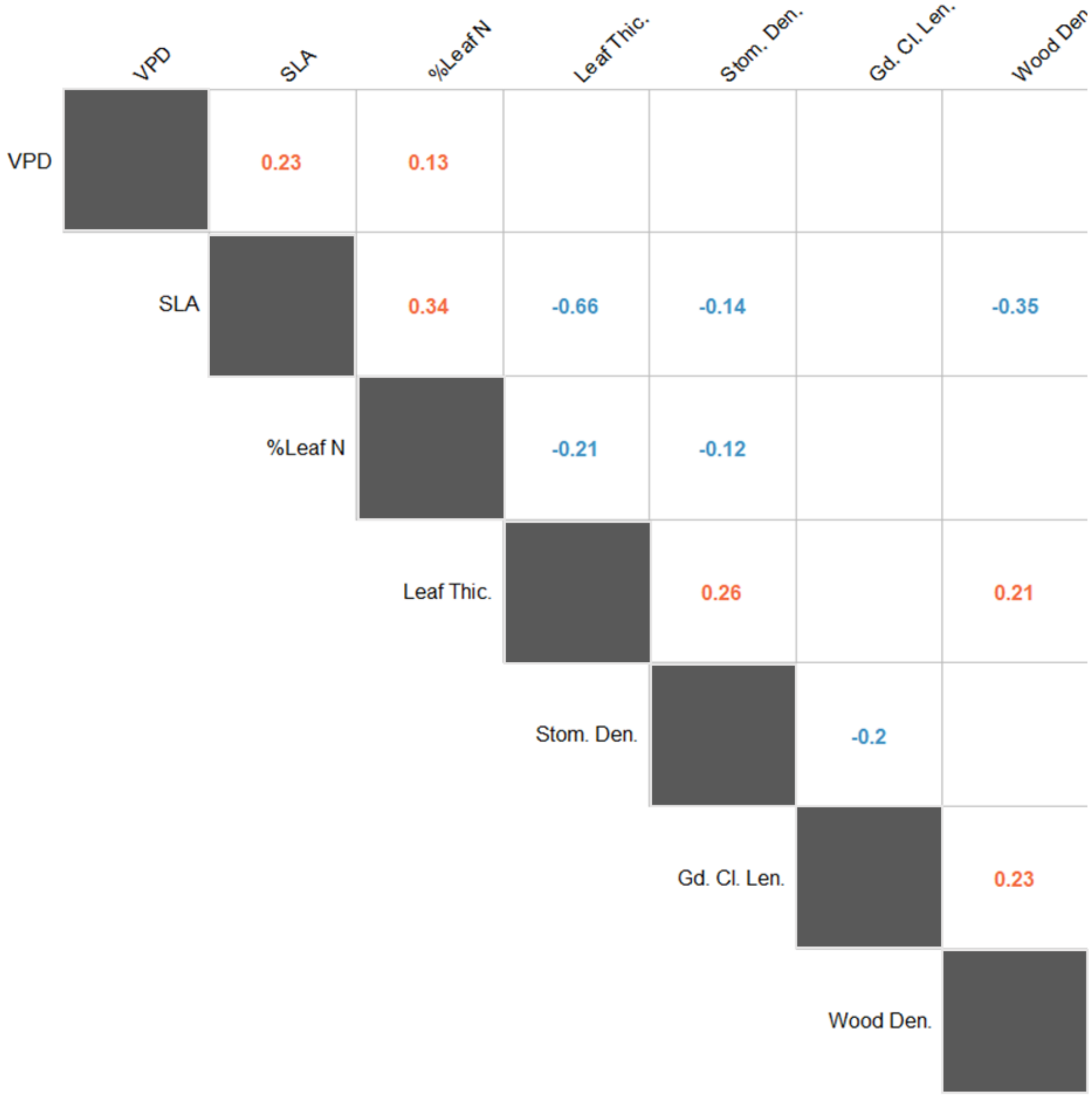

Figure 1.4.: Correlation matrix of interactions of individual traits and climate (here as VPD) across all sampled individuals. Only significant correlations are represented. Non-significant relationships are left blank.

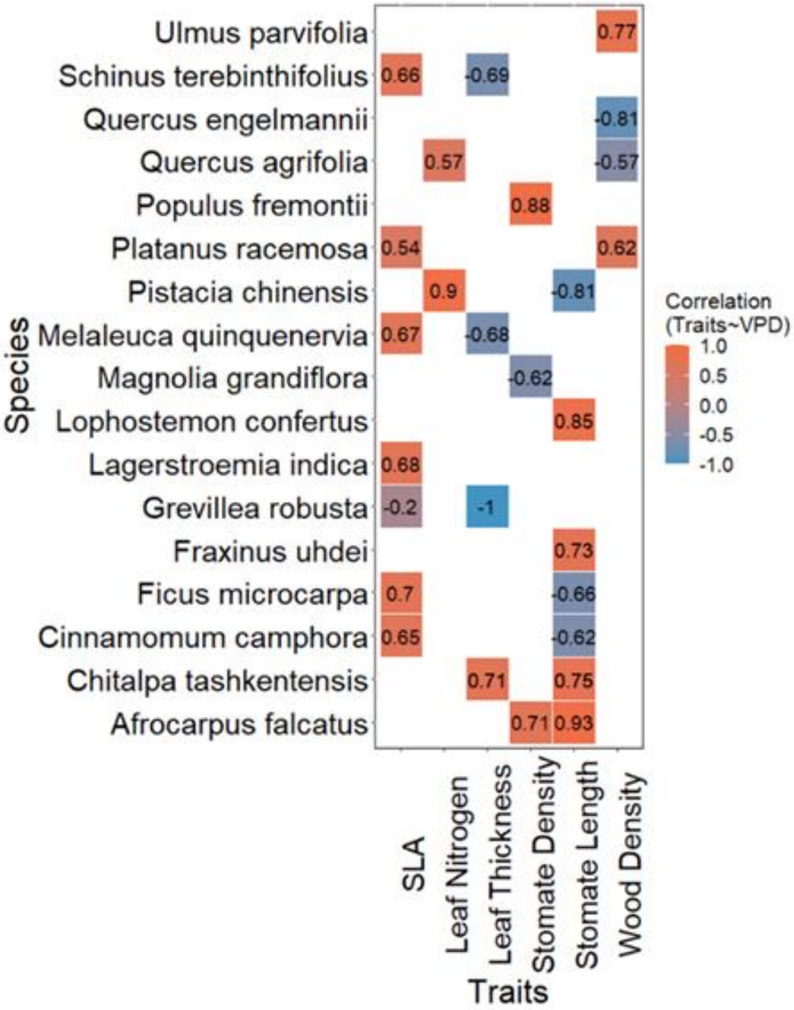

Figure 1.5: Significant Pearson correlations between functional traits and VPD, restricted to intraspecific variation within each study species. Asterix indicates alpha level of significance 0.05 > * > 0.01 ; 0.01 > ** > 0.001

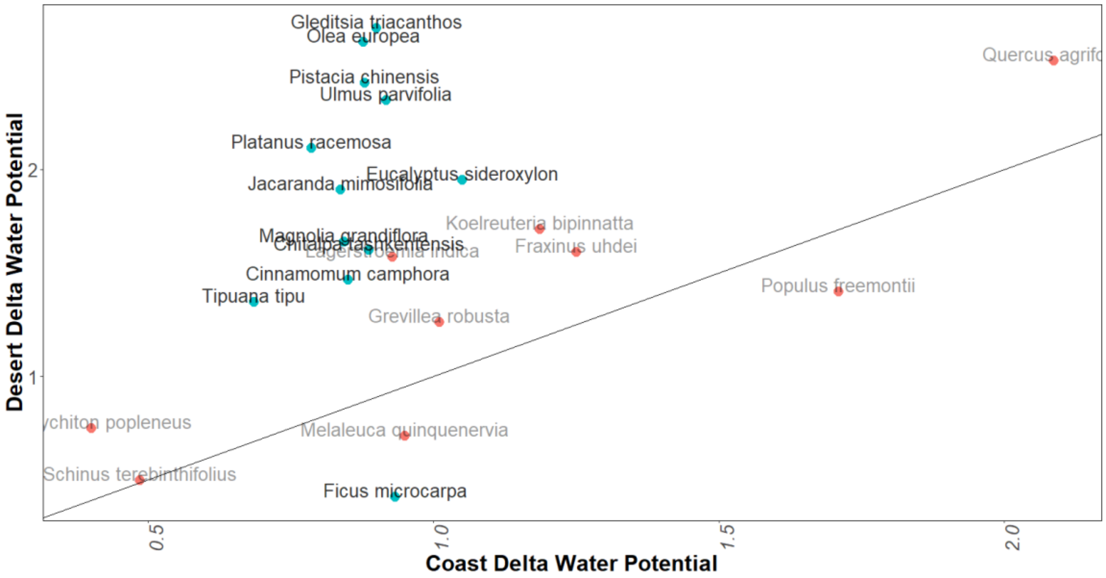

Figure 1.6: Comparison of hydraulic function in urban tree species planted near the coast versus the desert. Hydraulic function is derived as the delta leaf water potential (midday leaf water potential – predawn water potential). 1:1 line indicated no difference between coast or desert hydraulic function. Species with red points and greyed names were not significantly different between locations.

Chapter 2

Influence of Climate and Management on Patterns of Taxonomic and Functional Diversity of Recreational Park Vegetation

Abstract

Recreational urban parks support diverse assemblages of plants that through their functions, contribute beneficial services to billions of individuals throughout the world. Drivers of vegetation-derived services in parks are complex, as climate and park management interact with the functioning of multiple species of vegetation types. Yet, informal observations suggest that recreational parks are constructed consistently to specific principles of landscape design. Here we ask: what are the patterns of functional traits and vegetation diversity in cities of varying climate in the United States, and how do these patterns result in a consistent typology of recreational park? We hypothesized that increased aridity would exclude species not adapted to warm, dry climates, thereby reducing local, or alpha, taxonomic diversity and shifting community composition. However, a similar preference of park managers in the United States for suites of service-based functional traits leads to similarity of mean values of services traits in recreational parks among cities, regardless of climate differences. We tested this hypothesis by surveying lawn species, comprised of herbaceous turf and spontaneous plants, and woody species in fifteen recreational parks across Baltimore MD, Riverside CA, and Palm Springs CA, three cities that contain multiple parks but differ in regional climate. With increasing aridity, taxonomic alpha diversity decreased and plant physiology shifted, yet no differences were observed among most service-based functional traits. Among the cities surveyed, no significant differences were observed in functional dispersion of woody and spontaneous species or most service-based traits. Taxonomic composition differed in each city for all vegetation types, while suites of service-based traits differed between Baltimore and the two more arid cities of Riverside and Palm Springs. Our results suggest that across the U.S., service-based functional traits are consistent, even when arising from unique compositions and abundances of species in recreational parks. We interpret these results as an interaction between climate and the preferences of recreation park managers for services, creating a pattern of vegetation diversity where taxonomic alpha and beta diversity vary among regions while specific suites of services remain available.

Introduction

Urban vegetation comprises novel ecosystems by bringing together native and non-native plant species of no natural analog (Hobbs et al. 2014, Aronson et al. 2017). In cities across climates and cultures, one finds novel vegetation arrangements within recreational parks (Threlfall et al. 2016, Weems 2016, Talal and Santelmann 2019). Recreational parks are a public form of green infrastructure that provides services to individuals through access to recreation, cooler temperatures, and improvement to overall health (Bolund and Hunhammar 1999, Larson, Jennings, et al. 2016, Ayala-Azcárraga et al. 2019). These urban greenspaces contain multiple species of trees planted to provide aesthetic benefits and shade as well as large expanses of green turf for recreation and gathering (Tinsley et al. 2002, Pataki et al. 2013, Talal and Santelmann 2019). However, specific services provided to individuals and neighborhoods by planted vegetation may be contingent on the diversity of species and vegetation function (Larson, Nelson, et al. 2016, Vieira et al. 2018).

Taxonomic and Functional Diversity in Recreational Park Vegetation

Examining patterns of taxonomic and functional diversity among communities allows us to understand the drivers behind local species assembly and functioning (Anderson et al. 2011, Johnson et al. 2015). What drives urban diversity is a blend of biophysical and social factors (Padullés Cubino et al. 2018). Climate and management preferences can determine the expression of plant functional traits in parks, from the physiological of leaves to aesthetic characteristics preferred by people (McCarthy et al. 2011, Pataki et al. 2013, Avolio et al. 2018). Vegetation physiological function has also been linked to the provisioning of ecosystem service-based traits (Pataki et al. 2013, Swan et al. 2016). The influence of climate and management preference can vary depending on the type of vegetation studied (Nielsen et al. 2014a). A meta-analysis of species richness in urban parks found out of ten studies focused on vascular plants, seven studies restricted results to only woody species (Nielsen et al. 2014a). Other recent studies in urban green systems focus only on trees (Avolio et al. 2015, Gillespie et al. 2017, Kendal et al. 2018), or herbaceous turf and weedy species (Knapp et al. 2012, Wheeler et al. 2017, Padullés Cubino et al. 2018). To understand the causes of vegetation diversity in an urban plant community, we need to know how regional (climate) and local (management) influence different vegetation types in a specific urban community (Aronson et al. 2016), such as recreational parks.

Building on the framework of environmental filtering of communities (Ackerly 2003, Spasojevic and Suding 2012, Kraft et al. 2015), extreme aridity reduces physiological niche space, thus reducing taxonomic diversity and shifting physiological function of park vegetation (Spasojevic et al. 2014, Kraft et al. 2015, Pearse et al. 2018). Cities of extreme climates generally have lower species richness of urban trees and lawn vegetation compared to milder climates (Jenerette et al. 2016, Padullés Cubino et al. 2018). Within lawn communities, these patterns may arise due to differences in irrigation practices across cities, as well as differences in turf varietals (Kendal et al. 2018, Pincetl et al. 2019). Cities in more arid climates, such as Los Angeles and Phoenix, irrigate their lawns, while more mesic cities have both irrigated and non-irrigated lawns (Wheeler et al. 2017). Warmer climates also allow land managers to plant species of turf which use the C4 photosynthetic pathway, which can maintain productivity under high temperatures and aridity, while C3 turf species are more physiologically restricted, making them a poor choice for hot and dry cities environments (Wherley and Sinclair 2009, Beard 2013). Furthermore, lawn communities are often colonized by spontaneously growing herbaceous species that has a greater range of functional properties compared to turf, potentially allowing more spontaneous species to pass through environmental filters that limit turf species (Robinson and Lundholm 2012).

Services Preferred by Recreational Park Management

While taxonomic composition and physiological functions are strongly driven by climate, similar preferences for suites of traits related to specific service-based functions among urban residents may decrease functional diversity of urban plant communities (Fukami et al. 2005, Larson, Nelson, et al. 2016). The service-based traits chosen for recreational parks reflect how park managers design park vegetation, where the park tree composition can provide services such as shade and visual aesthetics not found in the local native communities (Avolio et al. 2018). Lawns provide similar services across cities, such as vibrant greenness and resiliency to active use (Larson, Nelson, et al. 2016). However, the effect of preference in parks on service-based traits can differ depending on the plant community and type of trait. In warmer cities, there can be an increase in service-based traits relating to showy flowers and fruits; however across a gradient of aridity, differences in tree heights or leaf areas have not been identified (Jenerette et al. 2016, Pearse et al. 2018).

Service-based functional traits can have distributions less limited by climate compared to ecophysiological traits. For example, aesthetic flower production is a valued service trait not limited by climate due to seasonally available flowering species in most regions (Konijnendijk et al. 2005, Threlfall et al. 2016, Goodness 2018). However, aesthetic fall foliage is prevalent in broadleaf deciduous species, which are likely to be found mostly in biomes like temperate deciduous forests. Preferences allow for similarity of aesthetic flower traits across climates while having fewer effects on traits of aesthetic fall foliage. Alternatively, spontaneous vegetation is not actively planted, making its dispersal more limited than horticultural vegetation (De Wet and Harlan 1975). After undergoing selection by dispersal and environmental filters, the selected traits of spontaneous species in recreational parks are those that can overcome mowing, weeding, and physical dispersal barriers. Overall, these at times independent variations of taxonomic, ecophysiological, and service-based diversity implies multiple drivers may determine the pattern of diversity in urban park vegetation.

While visually one can see that recreational parks appear similar in form to one another regarding their design, the question remains who controls that typology and the diversity found within? Urban park tree diversity has been found to respond to different physical and social drivers compared to residential yards and street trees (Kendal et al. 2012). What vegetation is found in recreational parks is ultimately a function of the park managers who decide what is planted. A recent study based in Portland OR found the reasons behind vegetation design in recreational parks are often a function of economics, maintenance of the park environment from human disturbance, and a desire to provide beneficial services for visitors (Talal and Santelmann 2020). Similar management desires for economy of maintenance were found in surveys of park managers in Hong Kong (Chan et al. 2014). The differences between park visitor preferences and manager preferences can often be due to budget constraints (Baur et al. 2013), where park visitors may desire an increase in colorful foliage and more flowers, managers are looking for ways to improve maintenance on a restricted budget (Talal and Santelmann 2020). While park managers may have similar goals in different countries, the species diversity found in parks is often determined by national and local horticultural trends (Pincetl et al. 2013, Nielsen et al. 2014a, Roman et al. 2018), as well as regional climate (Jenerette et al. 2016).

To better understand how climate and management preferences influence the distributions of recreation park diversity, we ask: how do park biodiversity, community composition, and values of service-based traits differ among three mid-sized U.S. cities of varying climates? We predict that alpha diversity will vary among recreational parks in arid and mesic cities due to the physiological tolerances of vegetation, and that each city will have a unique taxonomic beta diversity. Functional diversity and service provisioning, however, will not differ across climates owing to the preference of park managers for a specific typology of vegetation composition and provided services within recreational parks. To resolve the gap spanning multiple vegetation types within the same community, we focus on three different vegetation types, including horticultural woody species and lawn communities comprised of turfgrass and spontaneous herbaceous vegetation. By quantifying patterns in taxonomic and functional diversity and their relationship to services provisioning in recreational parks, we describe how broad-scale climatic variables interact with the preferences of recreational park managers to influence park vegetation diversity and function.

Methods

Study System

We assessed climate and park managers preference as drivers of park vegetation biodiversity by sampling 15 recreational parks located in three cities within the United States: Baltimore MD, Riverside CA, and Palm Springs CA (Figure 1, Table 1). Cities were selected to represent a gradient of aridity (measured as the vapor pressure deficit, VPD). Baltimore (mean summer VPD: 0.89 kPa) is in a temperate humid climate characterized by the regular precipitation events throughout the growing season.

Riverside (mean summer VPD: 2.7 kPa) is in a Mediterranean climate of intermediate aridity and Palm Springs (mean summer VPD: 6.2 kPa) is in a desert climate of extreme aridity, and both cities are characterized by seasonal precipitation during winter and early spring with very little precipitation during summer and fall. Within Riverside and Palm Springs, urban vegetation health is maintained through regular irrigation throughout the year. In each city, we selected five recreational parks. We focused only on highly managed recreational parks, rather than natural parks or parks with remnant natural areas, to highlight effects of park managers' preferences for recreation. Recreational parks are characterized by large lawn areas with multiple species of planted, maintained woody species. Lawns, along with spontaneous species found within the lawn, are the only herbaceous species present in the park and no area is unmanaged. To test whether species-area relationships influence diversity (Nielsen et al. 2014a, van der Maarel and Franklin 2015), our parks represented a range of areas, from 10,000 m^2 to 300,000 m^2. Park size was determined via ArcGIS 10.6 (ESRI, Redlands, CA) polygon delineation (Table 1). Our field sampling protocol was designed to collect all taxonomic data for the five parks within each region over seven days of field work in each city. To assess climate as a driver of physiological function, parks were sampled during mid-afternoon in peak summer months. Our experimental protocol is designed to be transferrable to other cities to characterize recreational park vegetation can within a approximately five days.

Field Sampling Protocol

We assessed entire woody species assemblages in each park. We sampled herbaceous species by generating four randomized points within the mowed lawn areas of each selected park. From each point, we randomly placed a 0.5 x 0.5 m quadrat in each cardinal direction. We calculated the total cover of all species in the quadrat using a modified Braun-Blanquet method (Braun-Blanquet and J 1932, van der Maarel 2007), which included the following cover classes: (0) absent, (1) >1% (individual), (2) 1–5%, (3) 5–10%, (4) 10-25%, (5) 25–50%, (6) 50–75% and (7) 75–100% cover. This methodology resulted in a total of 16 sample quadrats per park. Sports fields within parks (e.g. baseball diamonds, soccer fields, etc.) were not included in quadrat surveys. We identified all herbaceous species in each quadrat and classified them as turf or spontaneous species.

Functional Trait Analysis

Our research protocol is designed for maximum repeatability, even by researchers without access to physiology wet labs. To that end we collected functional data *in-silico*, using trait databases and primary literature. To incorporate functional diversity metrics into our analysis of recreational park species, we used the BIEN database (Maitner et al. 2018), the Global Wood Density Database (Chave et al. 2009) and primary literature to assemble average ecophysiological (EP) traits for each sampled species (Table 2). Following Westoby's leaf-height-seed plant ecology strategy scheme, we included traits that relate to a holistic ecological strategy: Specific Leaf Area, Seed Dry Mass, and Height (Westoby 1998). To incorporate traits that relate to hydraulic architecture in stems, we included wood density as an additional trait (Swenson and Enquist 2007, Chave et al. 2009) for woody species. To analyze influences of park manager preference, we included a series of service-based traits for woody species (ES). These traits are based on desired attributes found in nursery stock (Avolio et al. 2018). We included traits reflecting shade and fruit provisioning, as well as flower, fruit, foliage, and bark aesthetics. While there are many service-based traits found in horticultural vegetation, such as carbon capture (Pataki et al. 2006), pollution and dust mitigation (Wang et al. 2019), and microclimate regulation (Shiflett et al. 2017), we chose to focus on traits that were more associated with attributes preferred by urban residents and urban land managers (Pataki et al. 2013, Larson, Nelson, et al. 2016) We used horticultural sources to determine ES traits for each woody species (Table 2). ES traits were analyzed as presence/absence, where if a horticulture record listed a trait as associated with the species, that trait was given a value of 1 and if no record of the traits was found, we recorded a value of 0. We only used species that had records for all trait factors for subsequent analyses. As there was an unequal number of species containing all ES and all EP traits, we separated woody species into two categories to capture all species with a full spectrum of service-based traits, and all species with a full spectrum of EP traits. We analyzed herbaceous species as a lawn, encompassing all herbaceous species, as well as separated by functional groups of turf species or spontaneous species. As turf and spontaneous species were all herbaceous, we did not include wood density as an EP trait and focused only on those traits in the Leaf-Height-Seed strategy. ES traits were not calculated for turf or spontaneous species. Turf is selected based on its ability to persist; thus if turf is present a singular selectable service is being provided (Christians et al. 2016). Spontaneous species are not preferentially selected for planting. We filled gaps in trait data through searches of primary sources (Table 2).

Statistical Analysis

We conducted all statistical analyses in R (R Core Team. 2019). For each vegetation type we created a site by species matrix, each site being one sampled recreational park. Taxonomic alpha diversity of vegetation types in parks was represented by the Shannon-Wiener index calculated in the *vegan* package in R (Oksanen et al. 2008). Statistical significance was determined using one-way ANOVA calculated for each cover type; differences among cities were determined with a Tukey's HSD post-hoc test. Taxonomic beta diversity between any two parks was calculated using Brey-Curtis distance, and visualized through Principle Coordinates Analysis (PCoA). Within-city beta diversity was defined as the Euclidean distance to centroid, and significance was determined through a PERMANOVA, while differences in composition were determined using a pairwise PERMANOVA in the *RVaideMemorie* package in R (Maxime 2019). To examine differences in beta diversity, we calculated dissimilarity matrices between all parks in the study, using both taxonomic and functional characteristics. Functional beta diversity was calculated using Gowers distance. Any trait distribution that did not fit a normal distribution was log-transformed and all trait data were z-transformed before any multivariate analysis was completed. Using PERMANOVA, we tested for compositional shifts in taxonomic and functional diversity for all vegetation types, and visualized results by the PCoA. The dissimilarity matrices allowed us to calculate homogeneity of variance through PERMANOVA and we identified compositional shifts in taxonomic and functional diversity.

Functional alpha diversity was defined as the functional dispersion (FDis) of each park. FDis is an abundance-weighted measure of the distribution of functional traits in a community and quantifies the range of functional strategies within a community (Laliberte and Legendre 2010). To quantify individual functional metrics, we calculated community weighted trait means (CWM) for each trait. CWM values provide a single-trait metric that is weighted by species abundances within a sampled community (Zuo et al. 2016). FDis and CWM analyses were completed using the *FD* package in R (Laliberté et al. 2015).

Results

Across all cities, a total of 187 woody species, 9 turf species, and 44 spontaneous species were identified. Of the 187 woody species, we obtained physiological traits from databases for 107 species and service-based traits for 178 species. Woody species with no available trait information were removed from functional analyses. We obtained EP traits for all turf varieties and 36 of the 44 spontaneous species. Turf species included cool- and warm-season grasses that commonly comprise grass seed mixtures for lawns: *Festuca arundinacea* (C3), *Poa annua* (C3), *Agrostis palustris* (C3), *Lolium perenne* (C3), *Poa pratense* (C3), *Paspalum notatum* (C4), *Buchloe dactyloides* (C4), *Stenotaphrum secundatum* (C4), *Eremochloa ophiuroides* (C4), and *Zoysia spp*. (C4).

Taxonomic and Functional Alpha Diversity

Taxonomic and functional alpha diversity was first analyzed to determine if park area acted as a significant driver. Park area was not correlated with either taxonomic or functional alpha diversity. We then conducted subsequent analyses investigating city-wide climate as a primary driver of diversity metrics.

For both woody and turf vegetation, taxonomic alpha diversity, measured as Shannon-Weiner diversity, was lower in recreational parks of Palm Springs compared to the more mesic city of Baltimore (Woody species EP traits, p = 0.011; woody species ES traits, p = 0.021; turf species, p = 0.008). Differences in Shannon diversity of woody vegetation between Riverside and either Baltimore or Palm Springs were not detected. Differences in lawn taxonomic diversity were observed between the mesic Baltimore and the two drier cities of Riverside (p = 0.050) and Palm Springs (p = 0.010). However, when isolating turf and spontaneous species, the turf in Palm Springs was different compared to the other two cities (Palm Springs – Riverside p = 0.024, Palm Springs – Baltimore p = 0.008) and no differences were found when comparing spontaneous species assemblages (p = 0.115) (Figure 2A).

Functional alpha diversity, FDis, of both EP and ES traits in woody species were not significantly different among the three cities (EP p = 0.487; ES p = 0.659) (Figure 2B). Likewise, FDis of all lawn species and only spontaneous species were not significantly different across cities (p = 0.247). Within turf species, there was a significant difference in city-scale FDis means (p = 0.034). No significant difference of FDis means was found between Baltimore (mean FDis = 0.206) and Riverside (mean FDis = 0.200), however Palm Springs (mean FDis = 0.047) values were significantly lower than Baltimore (p = 0.050) (Figure 2C).

Functional Traits

Woody EP traits all showed shifts in CWM across cities. The three traits associated with the Leaf-Height-Seed strategy all decreased from Baltimore to Riverside and Palm Springs (SLA: Baltimore – Riverside $p < 0.001$, Baltimore - Palm Springs $p < 0.001$; Height: Baltimore – Palm Springs $p = 0.002$; Seed Dry Mass: Baltimore – Riverside $p < 0.001$, Baltimore – Palm Springs $p < 0.001$) . Wood density increased from Baltimore to Riverside and Palm Springs (Baltimore – Riverside $p = 0.031$, Baltimore – Palm Springs $p = 0.001$) (Figure 3A). Overall values of woody ES traits display little dissimilarity among cities. Shade and fruit provisioning, and aesthetic traits of flowers, fruit and bark were not different across our study cities. In each city, the highest value for any service-based trait was that of shade provisioning. The lone service functional trait which exhibited differences among cities was that of aesthetic fall foliage; more trees associated with the fall foliage trait were found in Baltimore compared to Riverside and Palm Springs (Baltimore – Riverside $p < 0.001$, Baltimore – Palm Springs $p < 0.001$) (Figure 3B).

Within lawn species, only seed dry mass differed across cities, with Palm Springs having significantly lower values than Baltimore ($p = 0.031$). Similar results were observed in spontaneous species, where seed dry mass was higher in Baltimore compared to Riverside and Palm Springs (Baltimore-Riverside, $p = 0.016$; Baltimore-Palm Springs, $p = 0.012$). Turf species in Riverside showed larger specific leaf area compared to Baltimore ($p = 0.021$), while vegetation height in all herbaceous vegetation groups was not different among cities. (Figure 4).

Composition / Beta Diversity

All cities displayed a significant difference in taxonomic composition from each other except in lawn species composition between Riverside and Palm Springs (Figure 5 A, p values displayed in Table 3). In a pairwise PERMANOVA, we found no difference between all lawn and only spontaneous functional composition among cities; woody ES and EP and turf composition were significantly different in Baltimore compared to both Riverside and Palm Springs but not between the two more arid cities (Figure 5, Table 3B). No differences were found in the distance to centroid of taxonomic compositions among the cities or vegetation types. Regarding functional composition, only woody physiological composition showed a significant difference in variance around the centroid between parks in Baltimore and Palm Springs (Table 3A).

Discussion

Regional Climate as a Driver of Park Diversity

The decrease of taxonomic alpha diversity with increasing aridity is consistent with our hypothesis of climate filtering. In arid cities like Palm Springs, the number of woody and turf grass species that can withstand physiological stress is limited compared to the horticultural species found in more mesic cities (Pearse et al. 2018) (Figure 2). In recreational parks, taxonomic diversity is further filtered by park planners selecting species that provide specific desired services (Talal and Santelmann 2019). The increased selection pressure of park management combined with extreme aridity could explain why we found a decrease in diversity while other studies found a positive correlation between species diversity of all urban trees and warmer climates (Jenerette et al. 2016). Conclusions based on broad sampling of urban vegetation differ when confining studies to a specific type of green infrastructures, such as residential lawns or recreational parks as in this study, where management practices regarding planting and watering are more specialized (Pearse et al. 2018). As increasingly arid climates appear to reduce species diversity within recreational parks, differences in climate also result in unique taxonomic and functional composition in recreational parks across cities (Figure 5).

All vegetation types in recreation parks have unique compositions among our study cities. We hypothesized that to achieve desired services, the taxonomic composition will vary with minimal effect on the values of service-based traits. Unique taxonomic compositions can vary across cities due to climate-driven changes in the availability of urban vegetation (Jenerette et al. 2016), temporally through variability of nursery offerings (Pincetl et al. 2013), or depending on local consumer preferences (Conway and Vander Vecht 2015, Roman et al. 2018). While many species found in recreational parks are not native to the region (Wheeler et al. 2017, Talal and Santelmann 2019), the lower Shannon diversity in Palm Springs and the difference in composition among all cities, explain how horticultural vegetation physiologically responds to the native climate.

For recreational parks to maintain healthy vegetation, planted vegetation must be able to functionally acclimate to regional climate. Lower specific leaf area is often connected to adaptations that confer tolerance to drought, such as reduced wilting and ability to maintain photosynthesis in extremely arid environments (Poorter et al. 2009, De Micco and Aronne 2012). The higher wood density seen in arid urban park trees can lower cavitation risk, and mortality caused by extreme aridity may be better avoided by these species than by species of lower wood densities (Wright et al. 2004, Savi et al. 2015). However, resistance to drought is likely a co-benefit as park managers are more concerned with planting for ease of maintenance and economic reasons, and high wood density is associated with long lived trees which would need to fewer replacements (Díaz et al. 2015, Talal and Santelmann 2020). This ecological tradeoff between stress tolerance and growth is also found in the trait of seed dry mass. Species adapted to arid regions generally have seeds with lower dry mass to prevent desiccation before precipitation brings on germination (Westoby 1998). Recreational park tree species found in arid regions exhibit adaptations to reduce heat and drought stress by having lower specific leaf area, seed dry mass, and higher wood density. Variation in functional traits (Figure 3A) among cities will result in park visitors in Baltimore experiencing a different functional composition than in Riverside and Palm Springs (Figure 5B).

The photosynthetic pathway of C4 turfgrasses allows for continuous transpiration during extreme heat and aridity, and in a well-irrigated Palm Springs park there is plenty of water for turf to maintain productivity. In a mild city like Baltimore, there are better conditions for C3 turf to highly productive year-round. However, while the physiological traits of the C3 turf in Baltimore and the C4 turf in Palm Springs were similar, the range of trait values was smaller in Palm Springs. This result is indicative of fewer varieties of C4 turf grass for planting compared to C3 varieties in nurseries throughout the country (Trammell et al. 2019).

Spontaneous species are not subject to the same environmental or preferential drivers as turf species (Niinemets and Peñuelas 2008, Knapp et al. 2012). Yet, many varieties of spontaneous species persist in cities and are of similar functional type (Wheeler et al. 2017), resulting in similar physiological traits and taxonomic diversity. Spontaneous species maintained distinct compositions among cities, while the turf species were less dissimilar (Figure 5A). However, unlike turf composition, spontaneous functional composition was not significantly different across cities. For spontaneous species to be found within a recreational park lawn, the species must disperse and germinate within the climate of the city, and then establish despite management and recreational activities enacted on lawns (Abu-Dieyeh and Watson 2005, Anderson and Minor 2019). Adaptations to regional climate may explain the variety in lawn taxonomy that we observed, while the adaptation to intense human impacts could explain the lack of difference in functional composition.

Management Preference as a Driver of Park Diversity

Depending on the specific functional trait, management preference or climate can be a greater influence on park plants. The functional responses specific leaf area in turf and seed mass in spontaneous species are potential evidence of aridity creating regions of unique taxonomic and functional compositions (Figure 4). Regarding suites of service-based traits, Baltimore’s climate allows for a greater abundance of species with the highly valued trait of aesthetic fall foliage, as evidenced by the Maryland Department of Natural Resources’ weekly fall updates tracking the changing of the leaves (Maryland

Department of Natural Resources 2019). This unique difference in a single climate driven trait can drive significant changes in total service-based trait composition in recreational parks (Figure 5B). Similarly, while fruit production is not a preferential service-based trait by park managers, we did find a greater abundance of fruit trees in the Palm Springs and Riverside regions, which could be indicative to the legacy of citrus in southern Californian agriculture (Farmer 2013).

In recreational parks, woody species are generally planted to provide valued service traits of shade, and aesthetic appreciation (Pataki et al. 2013, Avolio et al. 2018) and turf is planted to provide the service of vegetative greenness and recreational play areas (Ayala-Azcárraga et al. 2019). Park trees are spaced far enough apart for aesthetics to be appreciated while providing copious but fragmented shaded areas, creating a physical arrangement of vegetation where similar service traits are available across cities (Goodness 2018, Talal and Santelmann 2019). While regional aridity is correlated with park vegetation physiology, the preference for specific values of ES traits is generally similar across urban regions. Similarity of service-based traits in recreational parks allows park visitors, who value certain services, to have similar experiences in cities regardless of regional horticulture. While our study cities exhibited a unique functional composition of woody EP and ES traits, we found no differences in FDis or compositional variation (Figure 2B, Table 3A). We suggest this pattern represents an example of park managers' preference for a similar arrangement of function in recreation parks across cities, despite a regionally varying species diversity. Parks in Palm Springs achieve a comparable range of functional breadth to milder cities while exhibiting a unique taxonomic and function composition and a significantly smaller taxonomic diversity (Figures 2,3,5).

One of the defining characteristics of woody species in recreational parks is that they are not a monoculture; there is generally a variety of tree species (Jim and Chen 2008, Nielsen et al. 2014a). Moreover, surveys of urban residents have identified specific highly valued service-based traits in trees, such as shade, beauty, and fruit production (Avolio et al. 2018). Variation in the desires of urban residents result in a large variety of species that can provide these specific services (Avolio et al. 2018, Talal and Santelmann 2020). Therefore, a wide variety of woody species will result in a similar FDis of physiological traits, even when the distribution of species is different. While parks may provide varying amounts of services, the similarity of dispersion of service-based traits in cities with differing Shannon diversity implies management practices that select for a specific range of service functions in a park.

Woody species may not be a monoculture, but our results show that planted turf acts like a plantation. We interpret this result as evidence that the highest value service trait is that it remains green and usable for recreation and is easily maintained (Christians et al. 2016, Larson, Nelson, et al. 2016). If a minimal number of species available can achieve this goal, there is little need to expand planting to species with unique functions. Maintenance regimes can be standardized to the similar taxa, which fits with the stated desires of park managers to minimize maintenance costs (Chan et al. 2014, Talal and Santelmann 2020). There are other varieties of native grasses or sedges that are viable in regions of high aridity, yet these varieties are not commonly cultivated as turf.

Urban Form as a Driver of Diversity

Interestingly, we did not find significant relationships between park area and alpha diversity, either taxonomic or functional. This is in contradiction to the recent review of diversity drivers in urban parks (Nielsen et al. 2014b). The discrepancy between our study and current literature could arise from our focus on urban recreational parks, where the entire park area is actively managed only for recreation (Weems 2016). Conversely, the review by Nielsen and colleagues (2014b) includes parks managed for recreation, agriculture, and natural areas. Including multiple varieties of urban park incorporates multiple habitats as well, which influence species-area relationships.

While we used observations of urban park vegetation as evidence of management preferences, there are other management interactions outside of vegetation preference that can influence the diversity in a community. Fertilization, pesticide application, prioritizing play equipment, and access to local nurseries can all lead to variations in taxonomic and functional vegetation diversity (Kjelgren and Clark 1993, Politi Bertoncini et al. 2012, Chan et al. 2014, Cavender-Bares et al. 2020). Urban soil profiles can be both heterogeneous within and among cities (Crum et al. 2016, Herrmann et al. 2018). Regional climate and human facilitation are major filters leading to taxonomic and functional diversity (Aronson et al. 2016, Pearse et al. 2018), however future work would be inclined to explore other potential narrower urban filters on recreational park diversity.

Conclusions

Climate and management preferences both play key roles in determining recreational park structure and composition, through driving differences in taxonomic alpha and beta diversity while maintaining similarity in the value and distribution of service-based traits. We show that regional climate drivers affect the taxonomic diversity and composition of each city's parks. Furthermore, the number of functional strategies also reflects a stabilization of FDis among cities. By showing how Shannon diversity of woody and turf species both responds to climatic shifts, FDis of woody species and turf species diverge in this regard, we can infer woody species FDis is influenced by park management preference while turf has a strong limitation to extreme climates. Integrating woody, turf, and spontaneous vegetation with multiple metrics of diversity allows for these results and answers a call for work to incorporate multiple functional types within a singular study (Nielsen et al. 2014a). To develop a comprehensive diversity framework for entire cities, future work should incorporate more cities to represent more regional climates and differences in local horticultural preference.

Following the paradigms of urban ecology "in", "of", and "for" the city, our hypothesis required a synthesis of both climate drivers and the influence of park managers' preference to understand the patterns of recreational park diversity (Pickett et al. 2016). Our study synthesizes a biotic (ecology "in" the city) and a social-ecological (ecology "of" the city) influencer of diversity and our results provide a rationale for why specific vegetation types and functions are more influenced by either climate or preference. Our results show the influence of management preference guiding diversity in recreational parks, where service-based traits and FDis (excepting turf) does not change while taxonomic alpha diversity decreases into arid regions. Using our approach, we can identify functional co-benefits that could enhance the selection of park vegetation to provide climate resiliency along with traditional park management. The baseline days of extreme heat in Palm Springs are projected to increase from 135 to 179 days > 35°C by the end of the century (Sun et al. 2015), creating opportunities for the current stewardship for service-based function to shift in these extreme cities as the availability of viable vegetation decreases. By incorporating the results of this study with local urban park planning are cities at risk of extreme heat, we can move to practicing ecology “for” the city as well.

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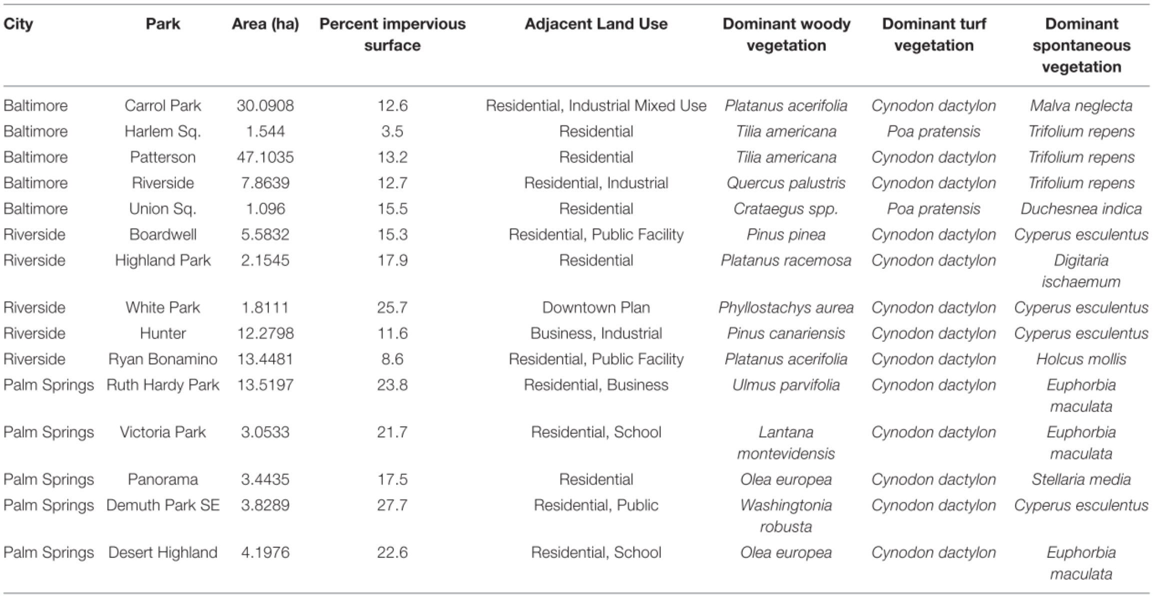
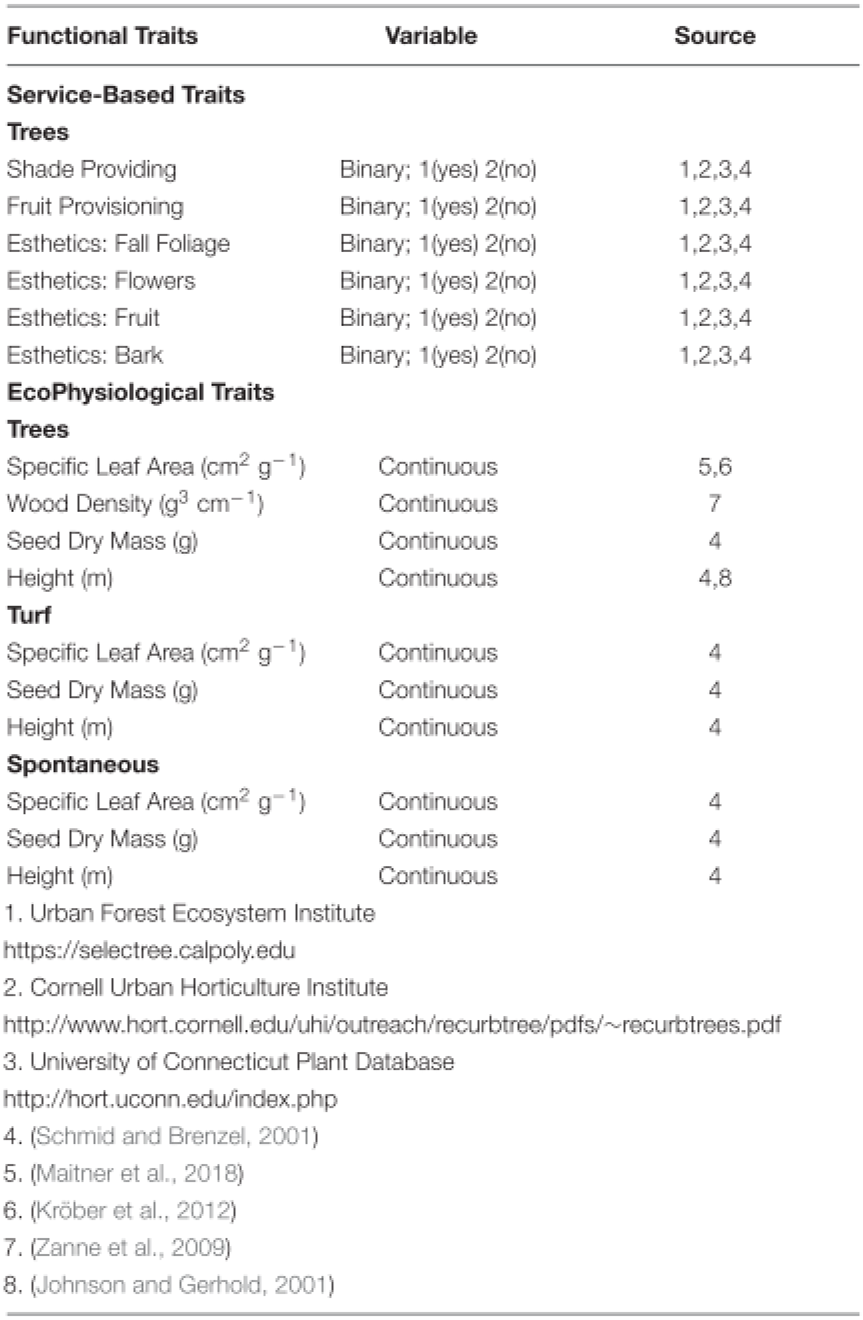
Tables

Table 2.1: Descriptions of urban form and dominant vegetation in each park. Park area was determined through ArcGIS, percent impermeable surface was determined from the 2016 National Land Cover Database (Homer et al. 2012), and adjacent land use was determined through county zoning maps of each city.



City	Park	Area (ha)	Percent impervious surface	Adjacent Land Use	Dominant woody vegetation	Dominant turf vegetation	Dominant spontaneous vegetation
Baltimore	Carrol Park	30.0908	12.6	Residential, Industrial Mixed Use	*Platanus acerifolia*	*Cynodon dactylon*	*Malva neglecta*
Baltimore	Harlem Sq.	1.544	3.5	Residential	*Tilia americana*	*Poa pratensis*	*Trifolium repens*
Baltimore	Patterson	47.1035	13.2	Residential	*Tilia americana*	*Cynodon dactylon*	*Trifolium repens*
Baltimore	Riverside	7.8639	12.7	Residential, Industrial	*Quercus palustris*	*Cynodon dactylon*	*Trifolium repens*
Baltimore	Union Sq.	1.096	15.5	Residential	*Crataegus spp.*	*Poa pratensis*	*Duchesnea indica*
Riverside	Boardwell	5.5832	15.3	Residential, Public Facility	*Pinus pinea*	*Cynodon dactylon*	*Cyperus esculentus*
Riverside	Highland Park	2.1545	17.9	Residential	*Platanus racemosa*	*Cynodon dactylon*	*Digitaria ischaemum*
Riverside	White Park	1.8111	25.7	Downtown Plan	*Phyllostachys aurea*	*Cynodon dactylon*	*Cyperus esculentus*
Riverside	Hunter	12.2798	11.6	Business, Industrial	*Pinus canariensis*	*Cynodon dactylon*	*Cyperus esculentus*
Riverside	Ryan Bonamino	13.4481	8.6	Residential, Public Facility	*Platanus acerifolia*	*Cynodon dactylon*	*Holcus mollis*
Palm Springs	Ruth Hardy Park	13.5197	23.8	Residential, Business	*Ulmus parvifolia*	*Cynodon dactylon*	*Euphorbia maculata*
Palm Springs	Victoria Park	3.0533	21.7	Residential, School	*Lantana montevidensis*	*Cynodon dactylon*	*Euphorbia maculata*
Palm Springs	Panorama	3.4435	17.5	Residential	*Olea europea*	*Cynodon dactylon*	*Stellaria media*
Palm Springs	Demuth Park SE	3.8289	27.7	Residential, Public	*Washingtonia robusta*	*Cynodon dactylon*	*Cyperus esculentus*
Palm Springs	Desert Highland	4.1976	22.6	Residential, School	*Olea europea*	*Cynodon dactylon*	*Euphorbia maculata*

Table 2.2: Functional traits used for analysis, grouped into “Service-based trait” and “EcoPhysiological” suites. Trait values are determined from cited sources.



Functional Traits	Variable	Source
Service-Based Traits		
Trees		
Shade Providing	Binary; 1(yes) 2(no)	1,2,3,4
Fruit Provisioning	Binary; 1(yes) 2(no)	1,2,3,4
Esthetics: Fall Foliage	Binary; 1(yes) 2(no)	1,2,3,4
Esthetics: Flowers	Binary; 1(yes) 2(no)	1,2,3,4
Esthetics: Fruit	Binary; 1(yes) 2(no)	1,2,3,4
Esthetics: Bark	Binary; 1(yes) 2(no)	1,2,3,4
EcoPhysiological Traits		
Trees		
Specific Leaf Area (cm^2 g^{-1})	Continuous	5,6
Wood Density (g^3 cm^{-1})	Continuous	7
Seed Dry Mass (g)	Continuous	4
Height (m)	Continuous	4,8
Turf		
Specific Leaf Area (cm^2 g^{-1})	Continuous	4
Seed Dry Mass (g)	Continuous	4
Height (m)	Continuous	4
Spontaneous		
Specific Leaf Area (cm^2 g^{-1})	Continuous	4
Seed Dry Mass (g)	Continuous	4
Height (m)	Continuous	4

1. Urban Forest Ecosystem Institute
https://selectree.calpoly.edu
2. Cornell Urban Horticulture Institute
http://www.hort.cornell.edu/uhi/outreach/recurbtree/pdfs/~recurbtrees.pdf
3. University of Connecticut Plant Database
http://hort.uconn.edu/index.php
4. (Schmid and Brenzel, 2001)
5. (Maitner et al., 2018)
6. (Kröber et al., 2012)
7. (Zanne et al., 2009)
8. (Johnson and Gerhold, 2001)

Figures

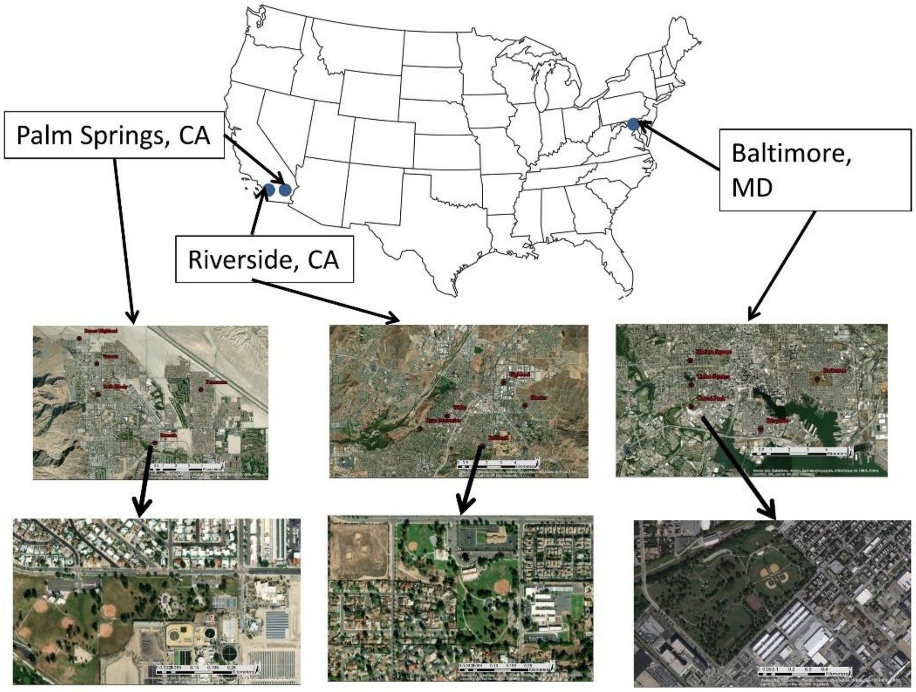


Figure 2.1: Study area of cities of interest. Five recreational parks were sampled in each city. All parks are representative of a recreational park typology, comprising expansive lawns and individually planted trees. Images are sourced from Google Earth Pro.

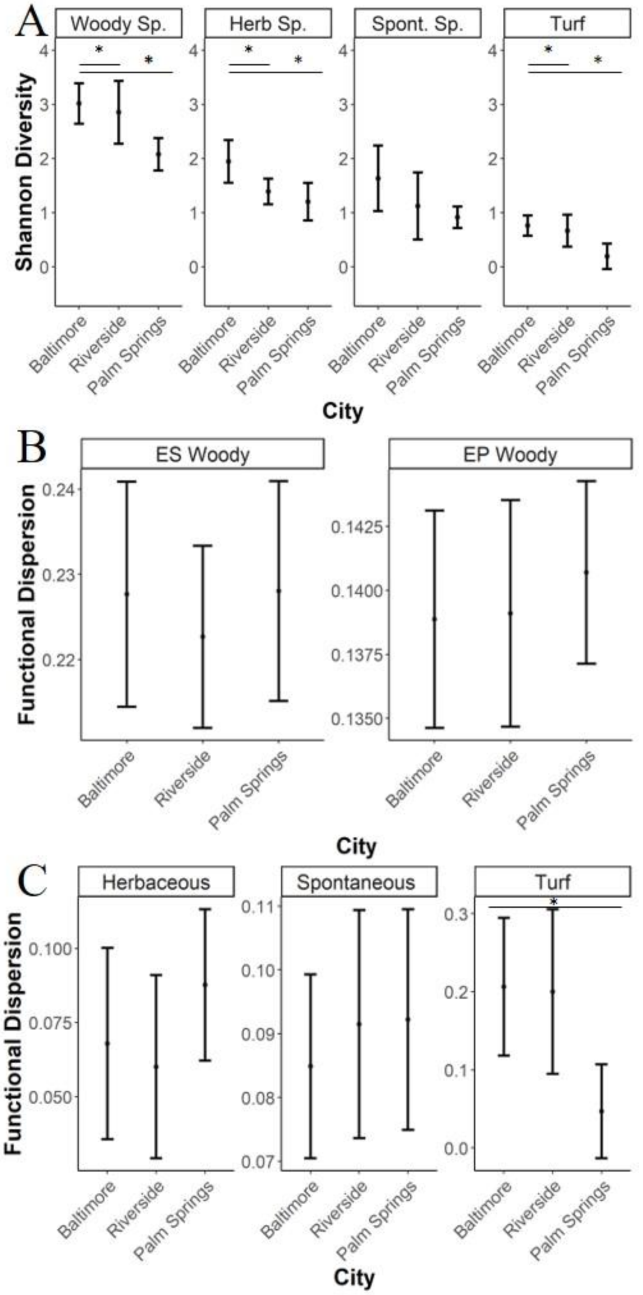


Figure 2.2: : Metrics of alpha diversity for each vegetation type (mean and standard deviation). Asterix refer to significant differences between groups tested through ANOVA with a posthoc Tukey HSD test (* 0.001<p<0.05). Herbaceous species are both spontaneous and turf species A: Taxonomic alpha diversity was measured by Shannon-Weiner Diversity, B: Functional alpha diversity (FDis) of woody species, C: FDis of herbaceous type species. FDis was measured by Functional Dispersion, an abundance weighted metric of functional trait ranges.

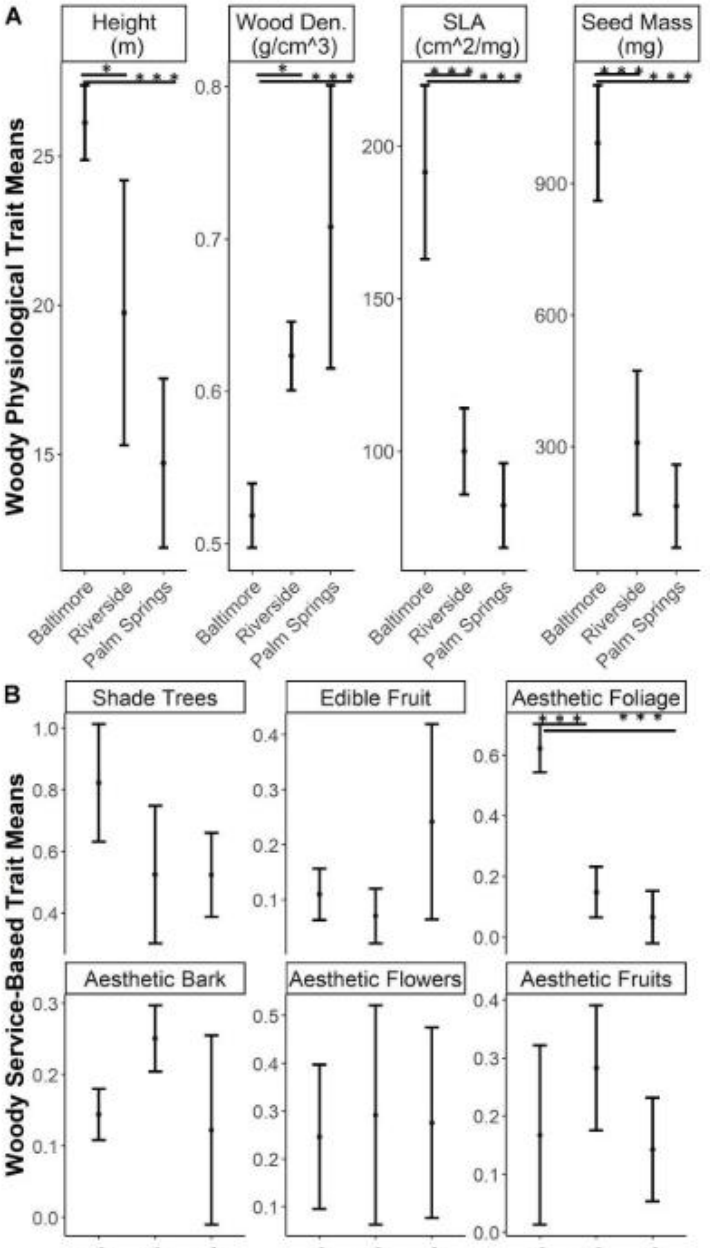


Figure 2.3: . Community weighted means (CWM) of woody functional traits (mean and standard deviation). Asterix refer to significant differences between groups tested through ANOVA with a posthoc Tukey HSD test (* 0.001< p <0.05,, *** p<0.0001). A: Traits related to ecophysiological characteristics; B. Traits related to service-based functional trait characteristics.

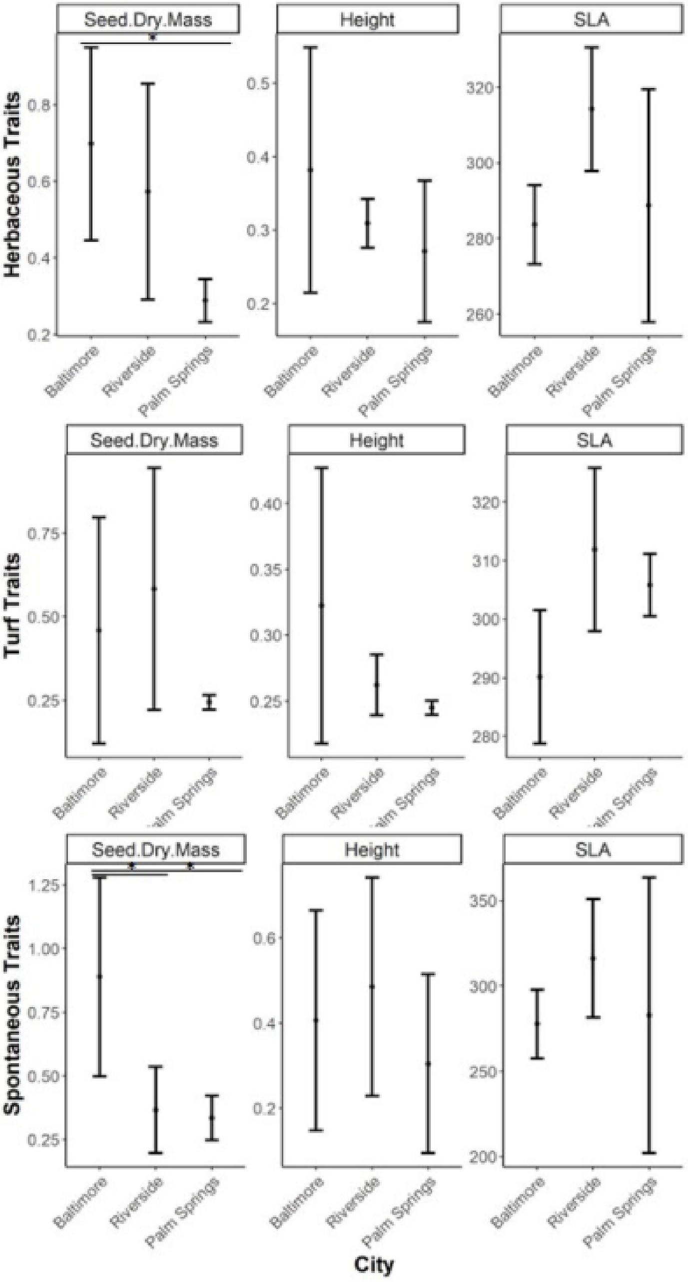


Figure 2.4: CWM of ecophysiological traits of herbaceous, turf, and spontaneous species (mean and standard deviation). Asterix refer to significant differences between groups tested through ANOVA with a posthoc Tukey HSD test(* 0.001< p< 0.05). Observe that y-axis varies for each trait type.

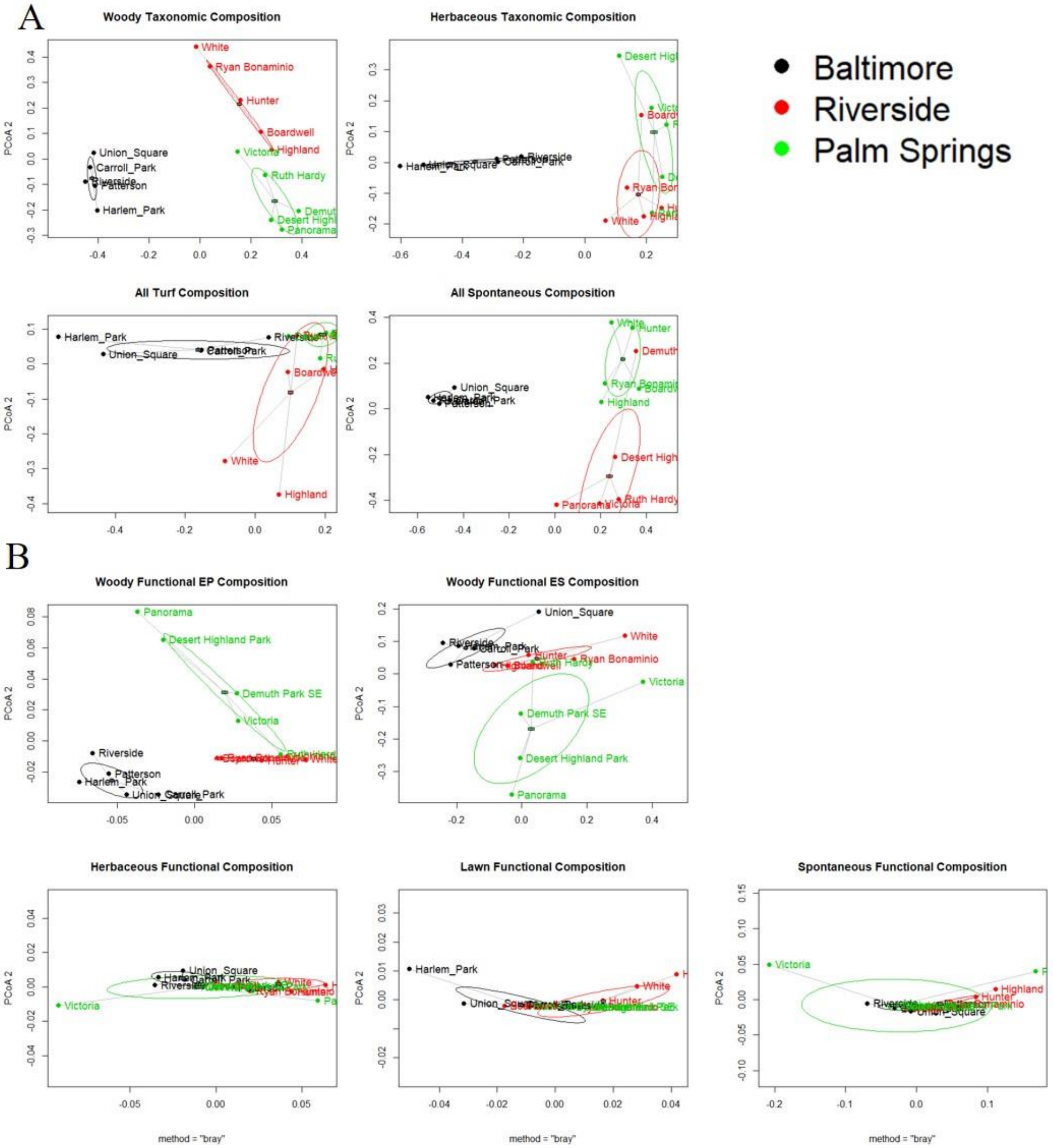


Figure 2.5: Principal Coordinates Analysis of Beta Diversity for A: Taxonomic Diversity, and B: Functional Diversity, for all vegetation types. Point represent a sampled park and are colored and labeled based on city of location. Difference of points is calculated as bray-curtis distance. Ellipses are one standard deviation of the data.

Chapter 3

Greater Aridity Increases the Magnitude of Urban Nighttime Vegetation-Derived Air Cooling

Abstract

High nighttime urban air temperatures increase health risks and economic vulnerability of people globally. While recent studies have highlighted nighttime heat mitigation effects of urban vegetation, the magnitude and variability of vegetation-derived urban nighttime cooling differs greatly among cities. We hypothesize that urban vegetation-derived nighttime air cooling is driven by vegetation density whose effect is regulated by aridity through increasing transpiration. We test this hypothesis by deploying microclimate sensors across eight United States cities and investigating relationships of nighttime air temperature and urban vegetation throughout a summer season. Urban vegetation decreased nighttime air temperature in all cities. Vegetation cooling magnitudes increased as a function of aridity, resulting in the lowest cooling magnitude of 1.4 °C in the most humid city, Miami, FL, and 5.6 °C in the most arid city, Las Vegas, NV. Consistent with the differences among cities, the cooling effect increased during heat waves in all cities. For cities that experience a summer monsoon, Phoenix and Tucson, AZ, the cooling magnitude was larger during the more arid pre-monsoon season than during the more humid monsoon period. Our results place the large differences among previous measurements of vegetation nighttime urban cooling into a coherent physiological framework dependent on plant transpiration. This work informs urban heat risk planning by providing a framework for using urban vegetation as an

environmental justice tool and can help identify where and when urban vegetation has the largest effect on mitigating nighttime temperatures.

Introduction

Average nighttime air temperatures (T_{air}) have been steadily increasing across the U.S. in recent years, with implications for reduced human health and well-being (Zhang et al. 2014, Hondula et al. 2015)**.** Rising nighttime T_{air} is especially important for heat vulnerability during summer months when heat waves intensify heat-related health effects, and are also a major global cause of weather-related mortality (Johnson et al. 2005, Brooke Anderson and Bell 2011, Laaidi et al. 2012). Urbanization exacerbates T_{air} increases through the urban heat island (UHI)effect, which describes how nighttime T_{air} in cities increases relative to non-urban locations through increased daytime heat storage (Oke 1982). With increasing urbanization, more people are becoming vulnerable to inequitable distributions of heat risk and increased cooling costs (Harlan et al. 2006, Chakraborty et al. 2019). Within cities, developed areas with little vegetation result in hot spots where local temperatures are substantially greater than the city-wide average, exacerbating UHI effects (Pincetl, Prabhu, et al. 2013, Shiflett et al. 2017, Moffett et al. 2019). Not only does urban warming elevate health risks, high temperatures also increase energy costs due to air conditioning (Akbari et al. 2001, Harlan et al. 2006). While a variety of aspects of urban form can influence urban temperatures such as cool pavements, green roofs, and urban wetlands (Taleghani et al. 2016, Palta et al. 2017), the cooling capacity of urban vegetation may be a key factor determining the health and well-being of a neighborhood (Jenerette et al. 2016). Increasing urban vegetation density has been proposed as an adaptation approach for mitigating urban nighttime temperatures and resulting heat-related vulnerabilities (Jenerette et al. 2011, Wang et al. 2016, Crum et al. 2017). However, recent work has revealed substantial variability in the magnitude of vegetation-derived nighttime cooling (Delta T_{veg}). In Madison, WI, recent work only 1 °C air cooling associated with urban vegetation, while studies in Los Angeles and Palm Springs, CA, reported a mean 2.5 °C and 4.9 °C Delta T_{veg}, respectively (Shiflett et al. 2017, Crum et al. 2017, Ziter et al. 2019). In Salt Lake City, UT, nighttime Delta T_{veg} in vegetated parks reached up to 3.3 °C (Gómez-Navarro et al. 2021). A more comprehensive evaluation of Delta T_{veg} is needed, both within and among cities.

Variability in vegetation-derived cooling may reflect multiple physiological mechanisms responsible for air-cooling effects. Urban cooling can occur through shading and by transpiration, both of which alter the urban energy balance by moderating sensible and latent heat fluxes (Pataki et al. 2011, Rahman et al. 2015, Wang et al. 2018). While atmospheric factors such as irradiance intensity and windspeed also influence latent and sensible heat flux (Kjelgren and Montague 1998, Arnfield 2003, Ballinas and Barradas 2016), the positive effect of atmospheric aridity on transpiration indicates that humidity and temperature may influence energy dynamic (Litvak et al. 2012, Winbourne et al. 2020). Atmospheric aridity can be measured as the Vapor Pressure Deficit (VPD), which describes the difference between the amount of water pressure the atmosphere can hold (saturation vapor pressure) and the total amount of water pressure at a specific temperature (actual water vapor pressure) (Yuan et al. 2019). Transpiration reduces heat by increasing latent heat flux as energy is used to evaporate water from leaves (Oke 1982). While vegetation rooted in dry soils can limit water loss by closing leaf stomata, transpiration from urban vegetation can be maintained even in high heat and aridity because regular irrigation mitigates physiological responses to water limitation (Drake et al. 2018, Winbourne et al. 2020). In both urban and natural settings, the tight coupling of VPD and plant transpiration has been well established (Sulman et al. 2016, Litvak, McCarthy, et al. 2017), as are the positive correlations between VPD and Delta T_{veg} within certain cities (Konarska, Uddling, et al. 2016, Lindén et al. 2016). However, the direct linking of VPD at the air cooling potential of urban vegetation has not been shown across multiple cities of varying climates and mean summer VPD values.

While Delta T_{veg} exhibits a relationship with VPD, the high variation among results of prior studies investigating urban Delta T_{veg} in different climate regions reveals a gap in our understanding of key drivers for the cooling capacity of urban vegetation (Shiflett et al. 2017, Crum et al. 2017). **To reconcile differences among the estimated Delta T_{veg}, we ask, how does the magnitude of vegetation-derived cooling vary within and among cities of the United States? We hypothesize that Delta T_{veg} is predominantly affected by VPD and other atmospheric processes that influence vegetation transpiration.**

We test this transpiration hypothesis by measuring the variation of nighttime T_{air} across a vegetation gradient within and among cities representing a range of aridity. By using a novel network of microclimate sensors in eight U.S. cities, we predict that daytime VPD, windspeed, and solar irradiance will be positively correlated with Delta T_{veg}, with daytime VPD having the strongest effect. Among cities, we anticipate that Delta T_{veg} will be greater in cities with higher VPD, and within cities we predict great Delta T_{veg} during weather patterns that increase aridity. The high temporal resolution, spatial extent, and seasonal extent of the sensor networks provided opportunities to observe heat wave events in each city and temporal shifts in local climates such as heat waves and monsoons, which allowe multiples tests of predictions on the importance of atmospheric drivers of transpiration influencing the magnitude of Delta T_{veg}.

2. Methods

Study sites

Our study took place within eight major U.S. cities that span a gradient of aridity from Miami (mean August VPD: 0.67 kPa) to Las Vegas (mean August VPD: 5.86 kPa) (Figure 1). Each study city was selected based on metro area populations larger than 1,000,000 people and providing a representation of a continental aridity distributions. Each city exhibited a wide range of vegetation density from urban cores to lush parklands (Table 1). Sensor distribution within each city was stratified across a gradient of urban vegetation in each city, which was measured spectrally using the normalized difference vegetation index (NDVI). NDVI is a widely used metric of vegetation and encompasses all photosynthetically active vegetation such as trees, grasses, and shrubs (Tucker 1979). Sensors were deployed in the core of each metropolitan area and the surrounding environs. The extent of deployment differed slightly for each city. All climate data were derived from the nearest airport weather station through the National Centers for Environmental Information (https://www.ncdc.noaa.gov/cdo-web/datatools/lcd). Across cities, midday VPD ranged from 0.0 kPa to 9.4 kPa, and nighttime cooling magnitude ranged from -0.6 °C/NDVI to 8.3 °C/NDVI.

Data Acquisition and Sensor Deployment

To test the relationship of vegetation cover, T_{air}, and VPD, we deployed 100 microclimate sensors that logged data at 60-minute intervals (Maxim Integrated Products, Inc., iButton Thermocron DS1921 & DS1922L) in each city (100 sensors/city, total 800 sensors). This style of sensor has a history of being used for rural and urban microclimate analyses (Meineke et al. 2016, Scott et al. 2017, Shiflett et al. 2017). Each sensor was shielded from direct solar radiation in the manner of Crum et al. (2017), encased in a breathable mesh and housed in custom polystyrene cylindrical white cups (Crum et al. 2017). While the precision (+/- 1 °C) of iButtons is coarser than a more commonly used instruments such as Campbell Scientific HMP60-L (+/- 0.6 °C), to assess the potential discrepency in our sensors, we validated our sensors for bias and sensitivity against an HMP60-L sensor (See Supplemental Appendix for more detail). The low cost of iButtons allowed for a large spatial distribution within and among cities throughout the United States to create a continental scale network of city-scale networks collecting *in-situ* data.

We determined values of NDVI with Landsat 8 imagery of each study city, retrieved for cloud-free days during the study period. Using NDVI as our metric of urban vegetation allowed for the required broader comparisons of within and among city cooling, as NDVI quantifies the variety of vegetation found at the continental scale. NDVI was calculated with Landsat 8 bands 4 (Near Infrared) and 5 (Red), using the equation NDVI = (Band 5 – Band 4)/(Band 5 + Band 4) in the Raster Calculator function of ESRI ArcGIS 10.6.1. We used the aggregate function of the Spatial Analyst extension in ESRI ArcMap to scale the native Landsat 8 resolution of 30m per pixel to a coarser 90m per pixel, which has been identified as an appropriate spatial scale to observe the signal of vegetation induced cooling (Crum and Jenerette 2017, Ziter et al. 2019). Sensors recorded T_{air} and relative humidityevery hour of every night during summer months in one year (i.e., ~June through September, varying slightly for each deployment) (Table 1). The exact time of deployment varied by city, but was between early to late June with sensors recovered in late August to early September (Table 1). Locations of sensor deployment were determined by randomly selecting 20 locations within five binned categories of NDVI values spanning the range of NDVI within each city. Binning the distribution of sensors allowed us to capture the full NDVI gradient within each city while also randomizing the sensor placement. Random selection of sites was conducted using the ArcGIS extension Sampling Tool 10 (Buja and Menza 2009), and potential deployment locations were derived as the global positioning system coordinates in the center of a single 90m pixel (Crum et al. 2017, Ziter et al. 2019). Deployments occurred in 2017, 2018, and 2019. Deployments in each city took approximately 3-5 days, where potential sites for each sensor were located and sensors were affixed to the nearest tree with a full canopy. Sensors were affixed at ~2 m height from the surface, and the location was recorded. For areas in which no suitable tree location could be found near the randomized point, the next nearest location with a similar vegetation density was used. To reduce shading and reflected radiation from nearby structures, trees located next to buildings were not used as sensor sites. Across all cities, ~18% of sensors were lost due to equipment error and/or vandalization.

Data Analysis

Data were downloaded from each sensor and restricted to measurements recorded at 01:00 local time, which was approximately five hours past sunset when UHI effects are estimated to be strongest (Oke 1982). To assess vegetation's influence on T_{air}, we first spatially detrended T_{air} patterns within each city of the study. This procedure was needed to remove temperature variation associated with geographic factors such as maritime effects in Los Angeles and Baltimore that were unrelated with vegetation cooling. For each city, the detrending process isolated residuals from a linear trend-surface regression of the NDVI at sensor location against the sensors recording over the entire city (T_{air}~ Lat $_{cityA}$ + Lon $_{cityA}$). The residuals from the regression are the T_{air} values with regional spatial drivers of T_{air} removed and were used as detrended sensor values of T_{air} for subsequent analyses. Vegetation-derived cooling magnitude was then determined by linear regression analysis, regressing citywide NDVI against detrended sensor T_{air} at 01:00 local time. Significant regression slopes were used as a metric of the vegetation cooling magnitude (°C/NDVI) and used for final analysis (Shiflett et al. 2017, Crum et al. 2017). The regression slope is a singular point of citywide Delta T_{veg} for each day of study deployment. The remaining data analysis and presentation uses the significant slope of the regression of NDVI on T_{air} as the primary metric of Delta T_{veg}.

Heat waves were defined as five continuous days where the daily mean maximum temperature is 5 °C above the normal mean maximum temperature, calculated from 30-year normals derived from PRISM climate data (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 27 Sep 2019) (63). To determine the significance between heat wave and post-heat wave cooling, we conducted a bootstrap randomization procedure where each cooling magnitude was shuffled and resampled with replacement. We ran 1000 variations of resampling, thereby building a data set of heat wave cooling magnitude and post-wave cooling magnitudes. Monsoon season was determined using the pre-2009 National Weather Service definition, which begins an Arizona monsoon season following three continuous days averaging a dew point > 12.2 °C (https://climas.arizona.edu/rgbo/rio-grande-bravo-outlook-june-2017/monsoon-2017).

Differences between resulting slopes of the regression of site NDVI and heat-wave T_{air} of each city were determined with an analysis of variance (ANOVA) and subsequent pair-wise city differences were determined with a Tukey's post-hoc test. This method was repeated for analyzing heat waves and monsoonal effects. All statistical analyses were performed in R version 3.60 (R Core Team, 2019).

Results

Within all study cities, increased NDVI was significantly correlated with reduced nighttime T_{air} (cities ordered from least arid to most: Miami: $p = 0.002$, $r^2 = 0.14$, Baltimore: $p < 0.001$, $r^2 = 0.63$, Los Angeles: $p < 0.001$, $r^2 = 0.27$, Portland: $p < 0.001$, $r^2 = 0.22$, Denver: $p < 0.001$, $r^2 = 0.39$, Tucson: $p < 0.001$, $r^2 = 0.23$, Phoenix: $p < 0.001$, $r^2 = 0.48$, Las Vegas: $p < 0.001$, $r^2 = 0.40$) (Figure 2A). We computed Delta T_{veg} magnitudes as the slope of T_{air} and NDVI relationship, which generates a standardized metric of the change in air temperature across a one-unit change in NDVI (i.e., bare ground to full vegetation). Among cities, the mean cooling magnitude varied, exhibiting a 4.5 °C/NDVI range (mean slope and standard deviation of Delta T_{veg} for each city ordered from least arid to most: Miami: mean = 1.41, sd = 0.30, Baltimore: mean = 1.64, sd = 0.74, Los Angeles: mean = 1.65, sd = 0.61, Portland: mean = 1.85, sd = 0.64, Denver: mean = 2.45, sd = 0.95, Tucson: mean = 4.12, sd = 1.64, Phoenix: mean = 4.25, sd = 1.91, Las Vegas: mean = 5.08, sd = 1.27) (Figure 2B). When comparing citiwide Delta T_{veg} across the mean August VPD of each city, the mean effect of vegetation on cooling was significantly greater ($p < 0.05$) in the more arid cities (i.e., Denver, Tucson, Phoenix, Las Vegas) compared to the mesic cities (i.e., Miami, Baltimore, Los Angeles, and Portland).

When comparing Delta T_{veg} to the mean midday VPD, calculated using dry bulb T_{air}, relative humidity, and air pressure at the local 13:00 hour at the nearest airport weather station, we found signification correlation with the magnitude of vegetation cooling the following night ($p < 0.001$, adj $r^2 = 0.62$) (Figure 3). Yet, within each city, the midday VPD effect varied with no relationship observed in Miami or Tucson ($p = 0.965$ and $p = 0.237$, respectively) (Supplemental Figure 1). Increases in ambient daytime T_{air} also increased Delta T_{veg} across regions, and this effect was smaller than that of VPD alone ($p < 0.001$, adj $r^2 = 0.47$). Daytime windspeed had no significant relationship with Delta T_{veg} among cities, but nighttime windspeed correlated with greater air cooling; however, model fit was low ($p < 0.001$, adj $r^2 = 0.03$). Direct solar irradiance also had a significant positive correlation with Delta T_{veg} magnitudes and model fit was also low ($p < 0.001$, adj $r^2 = 0.08$). (Supplemental Figure 2). A multiple linear regression of possible parameters, including VPD, direct irradiance, and nighttime windspeed had a slightly higher model fit than VPD alone (adj $r^2 = 0.62$).

Temporally, the regional weather patterns differed from the mean atmospheric conditions during the study in two major ways: heat waves and seasonal monsoons. During the study, all cities experienced at least one heat wave in which the daily mean T_{air} was 5 °C above the summer average for four consecutive days. Compared with the average cooling magnitude in days following heat waves, Delta T_{veg} magnitude increased in all cities during heat waves. Delta T_{veg} increases ranged from 0.8 °C in Miami to 3.9 °C in Phoenix. Delta T_{veg} increases during heat waves also significantly scaled with the citywide mean VPD during heat waves within each city ($p = 0.035$, adj $r^2 = 0.46$) (Figure 4a). Two cities (Phoenix and Tucson) experienced a shift from a dry pre-monsoon climate to a more humid monsoonal climate. Ambient T_{air} and VPD decreased during Phoenix's monsoon season (T_{air}: $p < 0.001$, VPD: $p < 0.001$). In Tucson, ambient T_{air} during the monsoon was consistent with pre-monsoon temperatures ($p = 0.3$), but VPD decreased from pre-monsoon to monsoon season ($p = 0.005$). Transitioning into the monsoon, the magnitude of vegetation cooling in Phoenix decreased from a mean of 8.1

°C to 4.6 °C ($p < 0.001$), whereas in Tucson, the magnitude of Delta T_{veg} decreased from a mean of 5.0 °C to 4.0 °C ($p < 0.01$) (Supplemental Figure 3).

4. Discussion

Increases in urban vegetation cover decrease nighttime T_{air} in cities throughout the United States; nevertheless, the magnitude of cooling varies dramatically among and within cities. Furthermore, not only was higher aridity during heat waves associated with greater cooling, but a consistent pattern also occurred in the two cities that experienced a shift between a hot and dry pre-monsoon and a more humid monsoon weather pattern. The intra-urban temporal changes in Delta T_{veg} are consistent with the patterns observed among cities with respect to the role of daytime transpiration in nighttime cooling. Our results, spanning spatial scales of intra-urban to continental and temporal scales from individual evenings to the summer season, suggest widespread urban vegetation cooling that is consistently sensitive to aridity, implying greater latent heat fluxes in more arid cities at the same levels of vegetation coverage. The strong correlation between aridity (VPD) and the magnitude of Delta T_{veg} is consistent with the hypothesis of transpiration as a primary influence on cooling.

The dependence of Delta T_{veg} on VPD helps reconcile the large variation observed in the magnitude of vegetation cooling observed in modeling studies, surface temperature observations, and T_{air} measurements within individual regions. Our results provide needed validation that explains differences in vegetation cooling among cities using regional climate (Georgescu et al. 2014, Krayenhoff et al. 2018) and microclimate

(Middel et al. 2014) models that show varying cooling effects among cities and within neighborhoods. Similarly, our results indicating a strong influence of VPD on Delta T_{veg} are consistent with evaluations of satellite-derived land surface temperatures (Jenerette et al. 2011, Zhou et al. 2017), which also show increased daytime surface cooling in more arid conditions. Importantly, these findings suggest the large variation in observed vegetation cooling effects on urban nighttime T_{air} in varying climates may reflect a consistent underlying cause. Recent work quantifying T_{air} over vegetation gradients within individual cities reported a mean Delta T_{veg} magnitude of 5.9 °C in Palm Springs, CA (Crum et al. 2017), 3.1 °C in Los Angeles, CA (Shiflett et al. 2017), and a Delta T_{veg} range of 0.5 to 1.1 °C in Madison, WI (Ziter et al. 2019). When factoring the mean summertime VPD of Palm Springs, Los Angeles, and Madison into our results (5.4 kPa, 1.8 kPa, and 1.28 kPa respectively), we find these cooling magnitudes consistent with the results presented here that indicate a linear trend of Delta T_{veg} in response to aridity. This linear relationship between VPD with Delta T_{veg} provides a coherent transpiration-based hypothesis for extending studies within individual regions, satellite observations, and modeling approaches.

Atmospheric drivers of Vegetation-Derived Nighttime Cooling

The transpiration hypothesis for regulating Delta T_{veg} suggests the importance of physiological interactions between vegetation and the urban environment. Not only is VPD a key driver of transpiration, but it also strongly correlates with Delta T_{veg} as irrigated vegetation may maintain open stomata in high VPD conditions (Winbourne et al. 2020). Vegetation stabilizes surface temperature in high heat and aridity through maintaining transpiration (Leuzinger et al. 2010). As daytime VPD increases, urban vegetation increases transpiration, which in addition to increasing immediate latent heat flux, reduces leaf surface temperature and eventual re-radiation of stored heat energy. The combination of these modifications to the surface energy balance are the potential causes for our observed correlation between daytime VPD and Delta T_{veg}.

As aridity increases, plants in natural areas generally exhibit a saturating relationship between transpiration and ambient VPD (Pataki et al. 2011, Chen et al. 2012), where leaves restrict their stomatal conductance in response to atmospheric drought to limit risks of xylem cavitation. However, transpiration for urban trees is less limited by high VPD relative to their rural counterparts (Winbourne et al. 2020). Transpiration rates are also dependent on local soil moisture, which is generally elevated through irrigation in cities (Litvak, Manago, et al. 2017, Hochberg et al. 2018). We found a linear relationship between daytime VPD and Delta T_{veg}, which implies that irrigated urban vegetation experiences fewer limitations to transpiration even in conditions with high atmospheric demand. The increased transpiration resulting from irrigated vegetating experiancing high VPD could cause cooling when combined with higher wind speeds, and our results also indicated a significant, though weak, effect of nighttime wind speed on cooling (Supplemental Figure 2). Wind-induced air cooling is generally caused by a thinning of the leaf boundary layer that increases latent heat flux (Wolf et al. 2016); however in practice, correlations between instantaneous wind speed and air cooling are weak (Kjelgren and Montague 1998, Leuzinger and Körner 2007). At the continental scale, aridity appears to be the primary dtiver of changes in cooling magnitudes.

In addition to among-city differences in Delta T_{veg}, within-city temporal differences in Delta T_{veg} during changing weather patterns are also consistent with a hypothesized transpiration mechanism. During heat waves, plants may maintain transpiration rates (Drake et al. 2018), thereby increasing energy lost to the latent heat of evaporation and resulting in potentially greater localized air cooling. Both Phoenix and Tucson experienced greater nighttime cooling before their monsoon periods, but the effect was highest in Phoenix. Phoenix's midday VPD and T_{air} were both significantly higher than during the monsoon. However, while Tucson's daytime VPD was higher pre-monsoon, daytime air temperature was not significantly different (Supplemental Figure 3), which was a trend consistent with the hypothesis that VPD is a stronger driver of transpiration derived cooling compared to air temperature alone. With continued irrigation, the strength of the cooling-VPD relationship could increase with climate change in many arid regions that are projected to become more arid (Overpeck and Udall 2020).

Using urban vegetation to reduce heat-related health risks

Our study highlights the potential benefits of urban vegetation for mitigating extreme urban heat scale across cities of dramatically different climates. The linear relationships between vegetation and air temperature in all cities (Figure 2A) imply that adding vegetation in these cities results in a continuous cooling effect. During periods of high heat, people require a cooler nighttime temperature to sleep and reduce stress on the body (Luther et al. 2016, Chakraborty et al. 2019). Reducing summertime nighttime urban heat can reduce heat stress and the need for medical treatment due to heat-related symptoms (Luther et al. 2016, Petitti et al. 2016). Mitigating high nighttime T_{air} is important for all urban residents; however, heat-associated health effects are unevenly distributed. In the U.S., lower income and non-white racial-ethnic groups more often live in areas with less vegetation and more impervious surfaces, which is associated with hotter temperatures (Nesbitt et al. 2019). Conversely, individuals with higher incomes more frequently live in areas with greater vegetation cover that they can afford to irrigate, which keeps local microclimates cooler (Hope et al. 2008, Tayyebi and Jenerette 2016). Households with higher incomes can also more readily often afford air conditioning during extreme heat conditions (Kurn et al. 1994, O'Neill et al. 2005). These inequalities may be exacerbated in the future as mean nighttime air temperatures are projected to increase even more than daytime temperatures (Donat and Alexander 2012). For economically- and racially-marginalized groups living in areas of minimal urban vegetation, heat risks (e.g., exposure to high nighttime T_{air}) may lead to greater vulnerability to health impacts when no coping methods (e.g., air conditioning or denser vegetation) area available.

Municipal policies considering increasing urban vegetation to mitigate heat vulnerability should also consider key trade-offs in achieving cooling. Our results show a strong influence of aridity on the magnitude of vegetation cooling; thus, in order to maintain Delta T_{veg} as an urban ecosystem service, vegetation needs to maintain transpiration. As transpiration is highly correlated to soil moisture, and irrigation practices in many cities determine soil moisture, maintaining Delta T_{veg} highlights a trade-off between cooling services and urban water use (Jenerette et al. 2011, Ellison et al. 2017). The magnitude of Delta T_{veg} and expected corresponding transpiration rates are highest in cities where municipal water use concerns are of high priority. Poorly planned and extensive tree planting campaigns in arid cities may exacerbate local water shortages through increasing irrigation costs (Roman et al. 2020). The water-for-cooling trade-off does have potential for mitigation through adaptive urban management policies of refocusing irrigation and promoting more water-conservative vegetation. In Phoenix, modeling assessments suggest nighttime air cooling could be increased with only a 2.6% water increase by shifting irrigation from areas of dense vegetation to those wish sparse vegetation coverages (Gober et al. 2010). The trade-off between air-cooling and urban water use can also be lessened by shifting vegetated land-cover from primarily turf to trees and shrubs that are adapted to the local climate. For example, in the arid climate of southern Israel, the cooling efficiency of trees with no surrounding grass is 27.5 times higher than exposed turf (Shashua-Bar et al. 2009).

Directly addressing the cost-benefit of implementing urban heat-risk management is a key goal of urban sustainability solutions (Georgescu et al. 2015). Directed urban greening projects also need to be developed for specific cities. Based on our results, greening a downtown block in Baltimore (~NDVI = 0.09) so it resembles more of a tree-lined residential street next to a park (~NDVI = 0.46) would reduce nighttime air temperature by approximately 0.60 °C. The same greening program in Phoenix would result in approximately 1.3 °C of cooling. The scaling of cooling is city-specific, but discrete increases in urban greening can result in significant nighttime cooling benefits depending on the aridity of the city. Partitioning the relative cooling potentials of vegetation types beyond the total greenness metric of NDVI, in both arid and mesic cities, is a necessary next step in resolving the nexus of urban vegetation, water use, and cooling benefits. Using NDVI as a greenness metric allowed this study to compare vegetation broadly across multiple cities addressing a gap in the research of studies examingn the within and among city variation in vegetation derived cooling. While some research has begun partitioning out the amount of cooling provided through shade and transpiration of urban trees (Rahman et al. 2018), identifying cooling rates for different types of urban vegetated parcels (Konarska, Holmer, et al. 2016), or modeling the potential cooling benefits of lawns and trees in a city (Wang et al. 2016), a multi-city empirical study of vegetation cooling effects delineated by vegetation type should be the next research gap addressed. Future studies should explore other covarying mechanisms of Delta T_{veg} such as the interactions of urban vegetation, albedo, and other reductions in radiant temperature through shading. Albedo can have a significant negative correlation with nighttime surface temperature (Jenerette et al. 2016), and urban trees directly reduce surface temperatures through reducing incoming radiation (Thom et al. 2016). Land surface cooling is a key component of urban heat health issues and while out of the purview of this study of air temperatures, should not be ignored in future urban heat mitigation plants.

Our results emphasize the need for city-specific plans focused on urban vegetation as a tool to mitigate high temperatures and region-specific water limitations. Policies must be city-specific, as we have seen that increasing greening by the same amount in Las Vegas and Miami will result in significantly more cooling benefits and subsequent health benefits in arid Las Vegas. Urban stakeholders across regions can use our results to identify areas that would likely receive the most cooling benefit from increases in vegetation, especially as the negative health effects caused by urban heat are not equally distributed. Many cities have developed large scale urban forestry projects (McPhearson et al. 2010, Pincetl, Gillespie, et al. 2013), but without directing greening initiatives to certain areas of cities, there may be overall increases in cooling that do not address urban heat inequities. To directly address the inequity of urban heat, rather than to focus on large city-wide greening efforts, policy makers should consider focusing urban greening to areas with the least amount of existing vegetation while also minimizing gentrification and displacement (Wolch et al. 2014, Goodling et al. 2015). As people continue to move to cities, using urban vegetation to reduce inequities in heat exposure can contribute to a more sustainable future.

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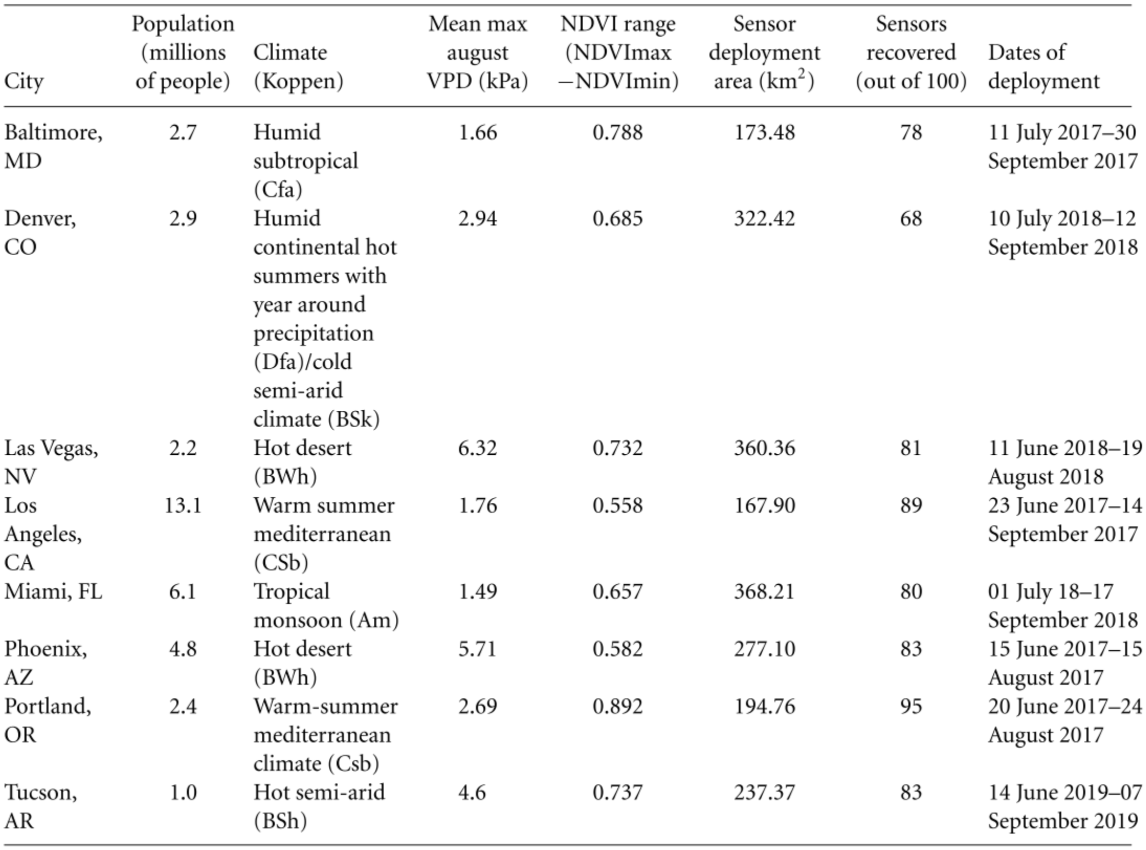
Tables

Table 3.1: Metadata for each study city. Including population, Koppen Climate Classification, mean summer VPD, range o fNDVI (max pixel NDVI − min pixel NDVI) for city extent, the area of each city covered by our recovered sensors, the number of sensors recovered from initial deployment of 100 and dates of sensor deployment.



City	Population (millions of people)	Climate (Koppen)	Mean max august VPD (kPa)	NDVI range (NDVImax −NDVImin)	Sensor deployment area (km^2)	Sensors recovered (out of 100)	Dates of deployment
Baltimore, MD	2.7	Humid subtropical (Cfa)	1.66	0.788	173.48	78	11 July 2017–30 September 2017
Denver, CO	2.9	Humid continental hot summers with year around precipitation (Dfa)/cold semi-arid climate (BSk)	2.94	0.685	322.42	68	10 July 2018–12 September 2018
Las Vegas, NV	2.2	Hot desert (BWh)	6.32	0.732	360.36	81	11 June 2018–19 August 2018
Los Angeles, CA	13.1	Warm summer mediterranean (CSb)	1.76	0.558	167.90	89	23 June 2017–14 September 2017
Miami, FL	6.1	Tropical monsoon (Am)	1.49	0.657	368.21	80	01 July 18–17 September 2018
Phoenix, AZ	4.8	Hot desert (BWh)	5.71	0.582	277.10	83	15 June 2017–15 August 2017
Portland, OR	2.4	Warm-summer mediterranean climate (Csb)	2.69	0.892	194.76	95	20 June 2017–24 August 2017
Tucson, AR	1.0	Hot semi-arid (BSh)	4.6	0.737	237.37	83	14 June 2019–07 September 2019

Figures

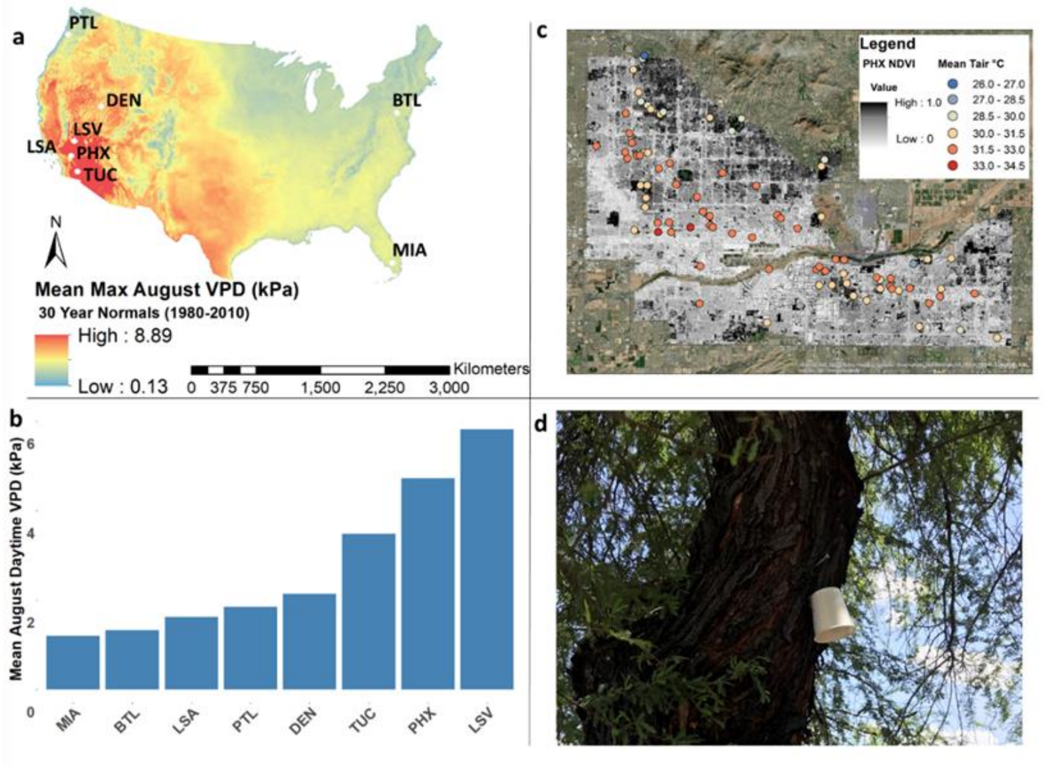


Figure3.1 a. Continental extent of study cities. Each city is located across a gradient of aridity. b. Mean maximum summer Vapor Pressure Deficit of each study city. City names are: MIA-Miami, BTL – Baltimore, LSA – Los Angeles, PTL – Portland, DEN – Denver, TUC- Tucson, PHX - Phoenix, LSV – Las Vegas. c. Phoenix deployment of sensors. Map is coloured by NDVI derived from Landsat 8 imagery. Each sensor location is indicated by the average nighttime T_{air} recorded during deployment. d. Example of sensor and shielding affixed to a tree.

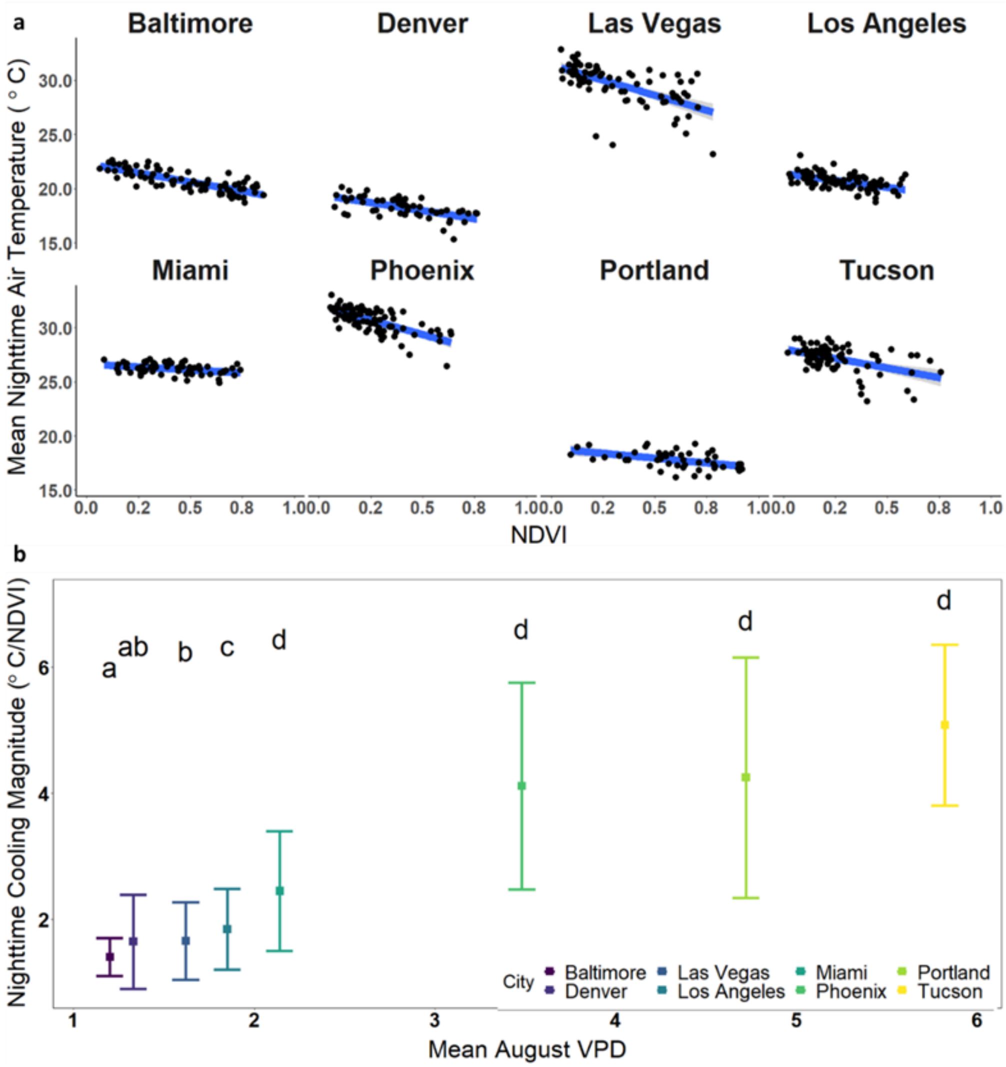


Figure 3.2: a. Average nighttime cooling of each study city. Cities are coloured by most mesic city to most arid. Each point is the mean T_{air} at 0100 hours, at that sensor locations NDVI Linear regressions plotted for significant relationships. Shading on regression lines represents standard error. b. Mean nighttime vegetation derived cooling magnitudes for entire study. Error bars represent standard deviation. Differences between means represented by differing letters. Significance determined by ANOVA. X-axis units are the significant regression slopes of T_{air} ~ NDVI (°C/NDVI) and is a singular measurement of nighttime vegetation-derived cooling for every night of sensor deployment.

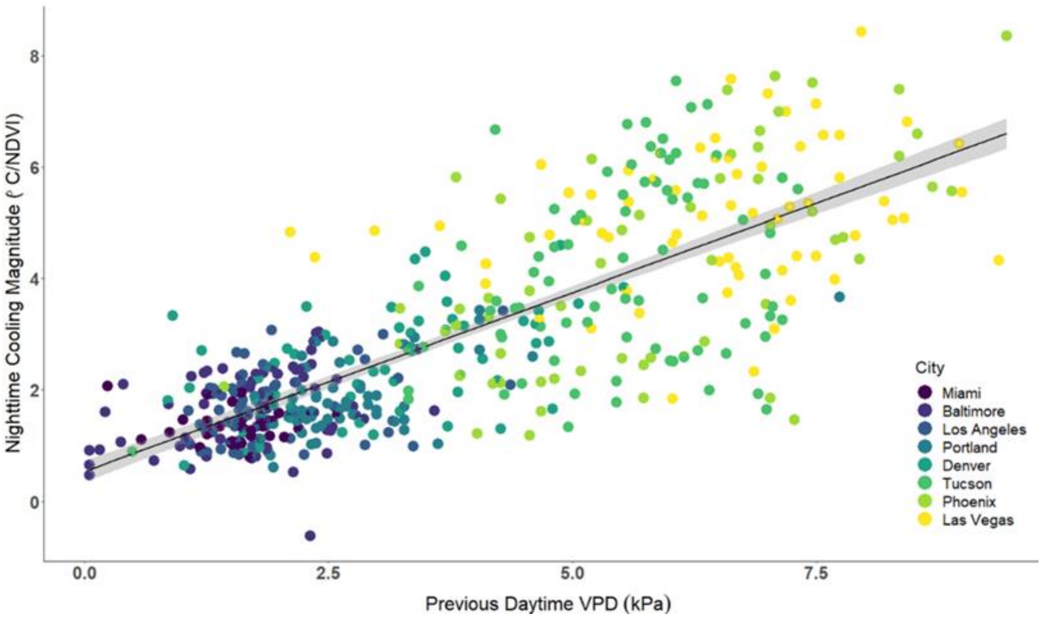


Figure 3.3: Nighttime cooling magnitude as a function of the previous days VPD ($p < 0.001$, adj $r^2 = 0.62$), Shading around regression line represents standard error. Points are coloured to indicate the regional climate of the city, from mesic to arid. Individual points are the significant regression slopes of T_{air} ~ NDVI (°C/NDVI) and is a singular measurement of nighttime vegetation-derived cooling for every night of sensor deployment, i.e., one point is equal to the citywide vegetation cooling effect at 01:00 for a single night.

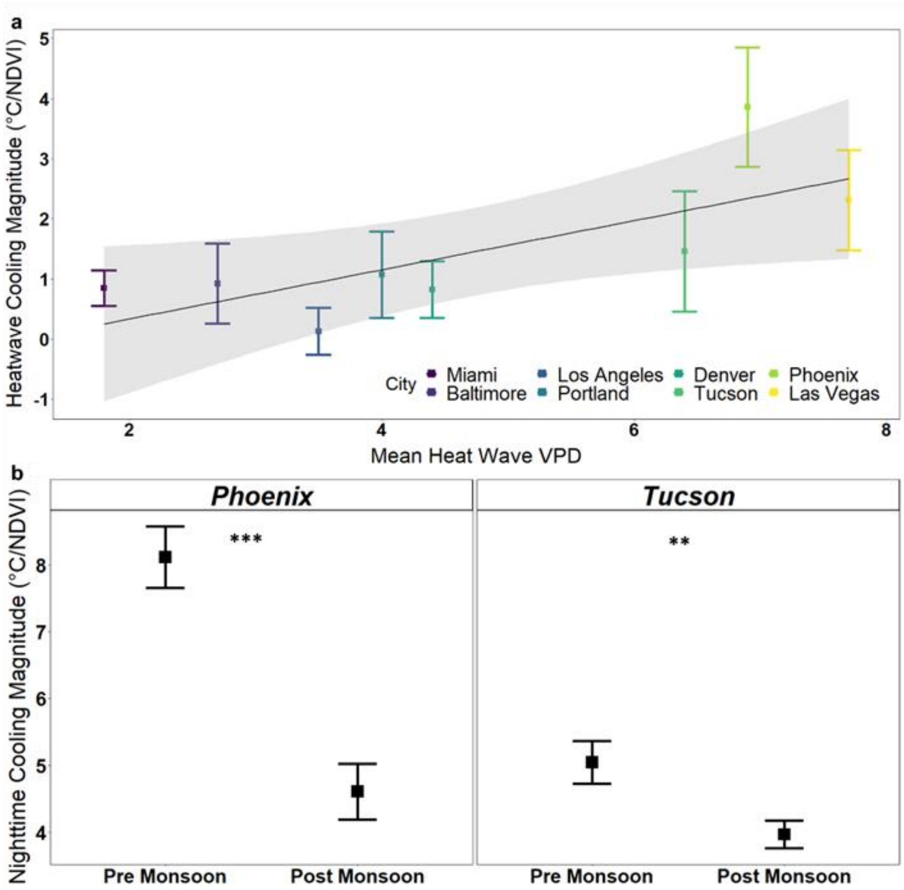


Figure 3.4: a: Mean difference of cooling magnitude between four days of heat waves (Tair > 90th% of study) and four days post heat wave, as a factor of regional city mean maximum August VPD ($p = 0.035$, adj $r^2 = 0.475$). Means were determined through bootstrapping differences of 1000 random selections of pre- and post-heat wave events. Regression line shading represents 95% confidence interval of regression. b. Nighttime vegetation-derived cooling before and during monsoon season for Phoenix and Tucson. Significance indicated by 0.001 < ** < 0.01, 0.001 < ***. X-axis units of A and B are the significant regression slopes of T_{air} ~ NDVI (°C/NDVI) and is a singular measurement of nighttime vegetation-derived cooling for every night of sensor deployment.

Supplemental Text and Figures

ST: **Sensor Validation.** While many studies have been published using Thermochron sensors to study microclimates (Hall et al. 2016, Shiflett et al. 2017, Crum et al. 2017, Meineke and Frank 2018), these sensors can introduce bias in measurement accuracy based on the shield type and placement, primarily associated with effects from radiation (Terando et al. 2017). We tested sensor accuracy through a preliminary study from 08/09/2018 to 08/14/2018. We attached shielded iButtons to a mobile meteorological tower that fitted with a temperature sensor in a ventilated shield (Campbell Scientific, HMP60-L). iButtons were shielded by a polystyrene cup measuring 47 mm wide and 30 mm deep. The shielded sensors were attached to the reference meteorological tower and placed in an area of both high and low vegetation density (30 m NDVI pixel derived from Landsat 8 imagery, high NDVI = 0.405 and low NDVI = 0.062), and following our deployment, both sensors and reference were placed under dense tree canopy. We gathered data over 5 nights in mid-July with clear skies and average heat. To test for differences in sensitivity, we used linear regressions of our sensor data compared with the reference towers' at 01:00 and compared that to a 1:1 line. Bias was calculated following Terando et al (2017), where bias is the sum of temperature differences between the sensor and weather station readings, all divided by total observations. Both bias and sensitivity were confirmed with an analysis of covariance (ANCOVA).

At both high and low NDVI there was no difference between sensor sensitivity and the reference for nighttime temperatures. At high NDVI we found a bias of 0.98 °C in our sensors compared to the reference. At low NDVI we found a bias of -0.20 °C. These sensor biases imply T_{air} under high NDVI conditions is lower than we recorded, and a smaller reverse effect in low NDVI conditions. and we are slightly underestimating our results. This bias is potentially related to an insulating effect of our shielding, which may prevent heated air molecules from fully dissipating during the night (Terando et al. 2017). Rather than applying a correction factor to all our results (which would increase the magnitude of cooling effects), they are presented here as more conservative estimates of vegetation cooling magnitude (Supplemental Figure 4).

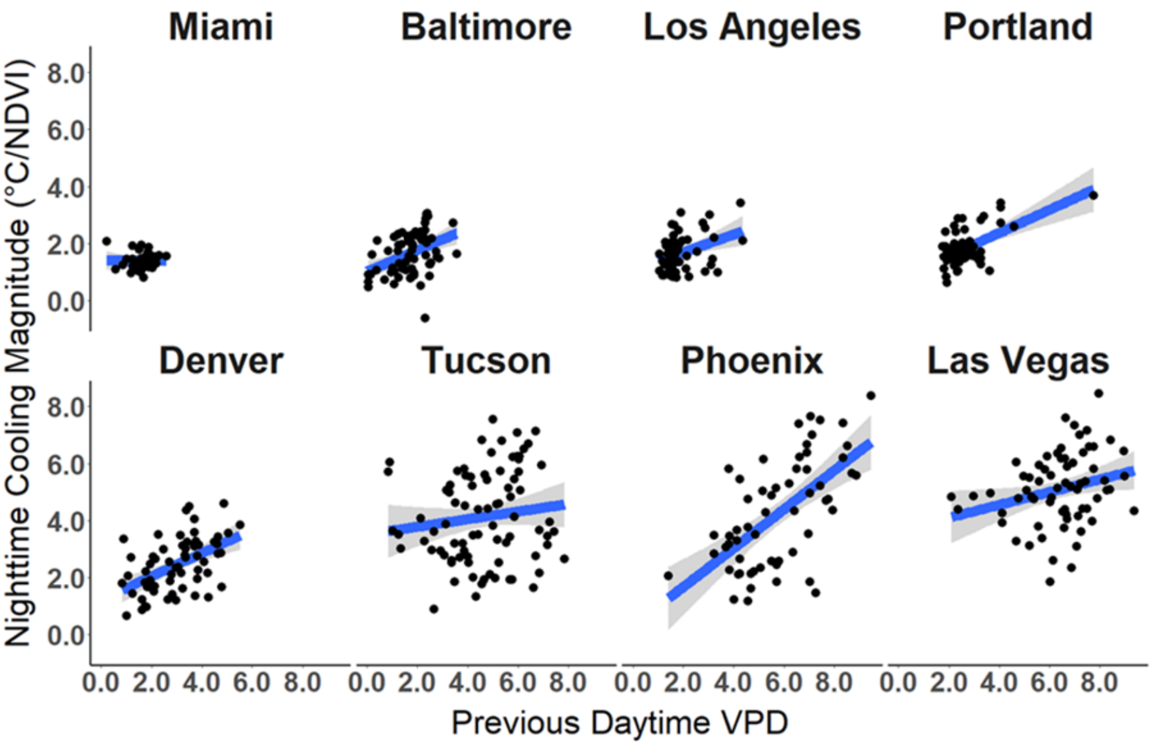


Figure 3.S1: Nighttime vegetation-derived cooling magnitude, binned by city mean maximum august VPD. Fitted with linear regression, shaded area represents standard error. X-axis units are the significant regression slopes of T_{air} ~ NDVI (°C/NDVI) and is a singular measurement of nighttime vegetation-derived cooling for every night of sensor deployment.

Conclusion

Synthesis and Contribution to Theory

My dissertation explored interactions of urban vegetation, climate, and management practices, from organism to ecosystem-level processes, within and among cities in different regional climates. At the organism scale, my study determined carbon and water-use strategies become decoupled in a water-resource-rich environment. When examining the response of functional traits to increasing VPD, I found the only two traits that significantly correlated with VPD, were the carbon traits of specific leaf area and leaf nitrogen. Similarly, intraspecific carbon-use traits generally trended positively with VPD. These results led to our conclusion that with abundant availability of water-resources, trees increase their carbon-use strategies, as opposed to reducing them to conserve water. Increased exposure to high VPD resulted in shifting to a more anisohydric water-use strategy in approximately half our study species, adding evidence that the combination of high aridity and copious soil moisture allows trees to keep stomates open and active longer than expected (Ch.1).

At the community scale, I determined regional climate is a strong driver of both taxonomy diversity and composition of tree and turf species in recreational parks while not affecting weedy species. However, the functional dispersion and aesthetic services provided by tree species did not vary much across cities. These results imply that while climate is a major driver of what species are found in cities, urban management provides a key role in determining the functional roles of vegetation in parks (Ch.2).

Finally, at the ecosystem scale, we discovered not only are nighttime air temperatures a function of vegetation density but that as regional aridity increases there are respective increases in the overall cooling potential. Furthermore, the vegetation-derived cooling magnitude is also a function of local day-time aridity. These results highlight the mechanism of transpiration as a driver of vegetation-derived cooling, as transpiration increases with VPD (Ch3).

Placing the biophysical mechanisms of urban vegetation as the foundation of examining urban vegetation ecology is a necessary task. The ecosystem services that are valued so highly, are derived from the physiological responses of urban plants. Linking ecophysiology to urban plant communities and ecosystem services allows for a mechanistic understanding of urban vegetation processes. My studies resolve uncertainties of how urban plants are functionally altered by an urban environment, at the species level, where individual trees function differently than wild counterparts, and at the community level, where novel urban plant communities are the result of the inadvertent collaboration between regional climate and urban park managers. The results from my first chapter also directly inform the mechanisms behind the third chapter's hypothesis, as well as add evidence to recent results from more temperate climates (Winbourne et al. 2020), that increased water resources results in greater transpiration under high VPD.

This dissertation also was able to address multiple areas of urban ecology which fit into the "in, of, and for" the city framework put forth by Steward Pickett (Pickett et al. 2016). This framework describes three paradigms around which the scope, theory, method, and application of future urban ecosystem studies can be grounded. The first chapter of this dissertation focuses on ecology "in" the city. This chapter's scope is primarily on the biotic processes which occur within a city environment, built from classical resource dynamic theory, using a common garden approach within a novel system, where the results can be applied to further both future theory and planning of urban forests. My second chapter described the ecology "of" the city by employing a more socio-ecological scope and theory, while the approach used sources from the planning and horticultural field, with an application both in urban planning and ecological design. Like the framework described in Pickett 2016, my third chapter integrates approaches of the "in" and "of" paradigm, but describes a more complex system connecting citywide planning, vegetation-derived services, and potential resulting inequities. Our results inform more than just urban vegetation management, but urban resiliency and equity applications.

Future Directions

While my dissertation research spans scales of ecological organization, as well as spatial scales, three key future directions would be to quantify the direct influence of urban water on vegetation-derived ecosystem services, to examine the relative contributions of a variety of vegetation cover classes to cooling benefits and to link soil moisture effects on plant function to remotely sensed indicators of plant performance. All chapters in this dissertations are studies of how changes in available water drive functional (and functionally related ecosystem services). However, in these chapters, the variable of water has been assumed (as in the sampling protocol of chapter one) or addressed by proxy (as in the relationships between atmospheric aridity and water demand). Directly quantifying soil moisture's effect on vegetation cooling, by expanding my sensor network, would increase our understanding of the “water-for-cooling” trade-off. Similarly, resolving uncertainty about the effect size of vegetation-derived ecosystem services by their cover classes is a key need. Chapter three was able to provide evidence of vegetation cooling writ large. Discerning differences between turf, shrubs, and trees will advance the theory of urban vegetation ecology beyond metrics of NDVI, to more applicable results at the micro-scale. Finally, while NDVI has proved very useful for identifying vegetation broadly, applying more high-resolution spectral measurements can prove useful in identifying stress-responses of urban vegetation remotely. A focus of on-the-ground urban forestry is the philosophy of “right tree right place” (Morakinyo et al. 2020). However, as we have seen throughout this dissertation, the place where a tree is planted can be altered through urban management. The use of remotely sensed metrics of plant function could serve as a testing ground of how established vegetation shifts functional responses under differing management protocols.

Morakinyo TE, Ouyang W, Lau KKL, Ren C, Ng E (2020) Right tree, right place (urban canyon): Tree species selection approach for optimum urban heat mitigation - development and evaluation. Sci Total Environ 719:137461. https://doi.org/10.1016/j.scitotenv.2020.137461

Pickett STA, Cadenasso ML, Childers DL, Mcdonnell MJ, Zhou W (2016) Evolution and future of urban ecological science: ecology in, of, and for the city. Ecosyst Heal Sustain 2:e01229. http://doi.wiley.com/10.1002/ehs2.1229

Winbourne JB, Jones TS, Garvey SM, Harrison JL, Wang L, Li D, Templer PH, Hutyra LR (2020) Tree Transpiration and Urban Temperatures: Current Understanding, Implications, and Future Research Directions. Bioscience 70:576–588.