Variation in arthropod hydration across US cities with distinct climate

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Abstract

Increasing evidence suggests that altered environmental conditions within cities (e.g. temperature) can have strong effects on the biology and ecology of animals. Moreover, multiple abiotic (e.g. soil moisture, distributions of water bodies) and biotic factors (e.g. plant and animal communities) may be more similar among cities in distinct climate regions as compared to outside cities. But the mechanisms behind these patterns are unclear. We suggest that animal physiological condition responds to urbanization and may become more similar with urbanization among cities. As a first attempt at assessing this possibility, we measured hydration (water content) of field-collected arthropods, across variation in urbanization (impervious surface), in three US cities with distinct climate. We found that seasonal variation, regional context and impervious surface are strongly associated with arthropod hydration. Moreover, mean arthropod hydration decreases with urbanization in a moist city with moderate temperatures (Raleigh, NC), while increasing with urbanization in cities in hot regions (Phoenix, AZ and Orlando, FL) during certain seasons, leading to greater similarity in mean hydration among cities with increasing urbanization (convergence). However, variance in hydration was greater among cities vs. undeveloped areas in some seasons, contrary to expectations. Impervious surface, region and season were better predictors of arthropod hydration than measured soil moisture, humidity, or temperature—suggesting landscape management may influence effects of climate on arthropod hydration. To understand the mechanisms behind these patterns and the implications for urban ecosystems, will require additional testing. But we offer the first evidence that animal water balance may be influenced by urbanization.

Key words: impervious surface, water content, soil moisture, desiccation, convergence, homogenization

Introduction

As the earth's population urbanizes (>50% of global population resides in cities, United Nations 2012), understanding ecological processes in cities becomes increasingly important, due to the potential to affect human livelihoods (Grimm et al., 2008; Pickett et al., 2008; Roy et al., 2012). Although regional context (e.g. climate) may play an important role in the ecology of cities (Diamond et al., 2014), evidence is accumulating that human landscape management also has strong effects (Chown and Duffy 2015; Dale et al., 2016) and may homogenize abiotic and biotic characteristics of cities in distinct climate regions (McKinney 2006; Groffman et al., 2014). Among multiple cities, urbanization tends to increase the similarity of maximum temperature, humidity, soil moisture and the distribution of water bodies, compared to undeveloped locations (Brazel et al., 2000; Imhoff et al., 2010; Groffman et al., 2014;

Steele et al., 2014). Plant communities among cities are also more similar than natural areas outside of cities (McKinney 2006). Thus, abiotic and vegetative conditions among cities tend to converge, but does animal physiology and ecology reflect this?

Previous research has suggested urbanization may homogenize urban animal communities (Jokimaki and Suhonen 1993; McIntyre 2000; Blair 2001; Blair 2004; Holway and Suarez 2006; McKinney 2006), but mechanisms are not always clear. Studies have shown that aspects of urbanization (e.g. temperature, food subsidies, reduction of predators) can have consistent, strong, positive effects on certain animals, including birds (e.g. rock doves, house sparrows), small, open-habitat associated ground beetles (Martinson and Raupp 2013) and arthropod pests (McIntyre 2000; McKinney 2006; Menke et al., 2007; Bang and Faeth 2011; Bang et al., 2012; Meineke et al., 2013; Dale and Frank 2014b). Other studies have shown consistent negative effects on other animals, such as certain butterflies (Blair and Launer 1997; McIntyre 2000), birds (Blair 2004), spiders (Shochat et al., 2004), or large, predatory, or forest-dwelling ground beetles (Niemelä and Kotze 2009; Martinson and Raupp 2013) and concomitant declines in diversity (Blair and Launer 1997; Blair 2004; Shochat et al., 2004; McKinney 2006; Niemelä and Kotze 2009; Bang and Faeth 2011; Martinson and Raupp 2013; Aronson et al., 2014). A few studies have specifically documented homogenization of animal communities. For instance, bird and butterfly communities in urban areas of California and Ohio are more similar to one another than outlying areas (Blair 2001; Blair 2004).

Following others (Chown and Duffy 2015), we propose that shifts in animal communities with urbanization may be partly driven by physiological responses to particular characteristics of urban habitats. More specifically, we predict that individual physiological states (arthropod hydration) will reflect differences in environmental conditions, such as temperature, as well as landcover, such as impervious surface. We focus on arthropod water content because it is likely affected by environmental conditions altered by urbanization, like temperature, humidity and soil moisture (Hadley 1994; Sabo et al., 2008; McCluney and Sabo 2009; Chown et al., 2011; Chown and Duffy 2015), and it has direct fitness consequences for animals. Severe arthropod dehydration typically results in death, even though desiccation limits may vary by species (Hadley 1994). Chronic, sublethal dehydration can also have negative consequences, damaging physiological processes and reducing growth rates (McCluney and Date 2008). Thus, avoiding desiccation is paramount; but desiccation can happen quickly, especially for small animals like arthropods (Hadley 1994; Woods and Smith 2010; Chown et al., 2011). Therefore, alteration of temperature and moisture associated with urbanization could lead to changes in arthropod hydration that result in differential mortality among taxa in different cities: taxa that are poor water conservers (e.g. those with few waxes in their cuticle) may decline in abundance in the hotter, drier parts of mesic cities (e.g. high impervious surface areas of Raleigh, NC) or may become more abundant in the wetter parts of xeric cities (e.g. residential neighborhoods in Phoenix, AZ).

Arthropod hydration is also relevant because it may have consequences for food webs and ecosystems; dehydrated animals may maintain water balance by altering foraging behavior (Sabo et al., 2008; McCluney and Sabo 2009). For example, recent research suggests that rates of herbivory and predation can increase substantially under moderately dry conditions, because animals are consuming moist food to meet water demands rather than energy or nutrient demands (Sabo et al., 2008; McCluney and Sabo 2009; McCluney et al., 2012). Thus, variation in animal water content may influence food web properties and community composition in important ways that could have

consequences for ecosystem services and disservices (plant pest damage, refuse removal, pollination).

Here, we take the first step in examining how animal water balance may be affected by urbanization by exploring patterns in arthropod water content within and among cities with distinct climates. We also examine relationships with local environmental and habitat variables like temperature, impervious surface and soil moisture. Because urbanization may increase the similarity of these factors between cities, we expect that mean animal hydration will converge (become more similar) among cities (McKinney 2006; Groffman et al., 2014). Moreover, we expect that the pooled variance in hydration among cities will decline with urbanization, as hydration becomes more similar between these cities. However, on average, we expect higher variation in hydration among sites within a city than outside, due to the considerable variation among locations within cities, with respect to temperature, impervious surface, plant diversity and density (Hope et al., 2003; Martin et al., 2004; Schwarz et al., 2015), and other factors. For example, mesic cities are warmer overall than adjacent natural areas, but within cities the extent of warming can vary by several degrees at 100–1000 m scales (Oke 1973; Dale et al., 2016). Variation in temperature is driven largely by features such as impervious surface cover, which also can vary from less than 10% to 80% over small scales (Dale et al., 2016). These small scale changes are biologically meaningful to many arthropods such as hemipterans (Meineke et al., 2013; Dale and Frank 2014b; Dale and Frank 2014a), parasitoids (Meineke et al., 2014), bees (Youngsteadt et al., 2015a) and ants (Pećarević et al., 2010; Menke et al., 2011; Savage et al., 2015; Youngsteadt et al., 2015b). Thus, we predict that variation in hydration will be higher within a city compared to adjacent undeveloped areas, even as mean hydration becomes increasingly similar between cities and pooled variance among cities declines with urbanization. To test our predictions, we measure arthropod water content (hydration) across urbanization gradients in cities in three climate regions of the US. To our knowledge, this is one of the first investigations of widespread geographic patterns in animal water content, inside or outside of cities.

Methods

Study sites

We selected three major cities in distinct climate regions varying in temperature and precipitation: Raleigh, NC, Orlando, FL and Phoenix, AZ (Table 1). Within each city, we used a grid (5 km per cell) to select specific sites. We numbered and then randomly selected 8 grid cells. Within each selected grid cell, we chose a suitable low impervious surface and a high impervious surface sampling location nearest to the center of the grid cell based on satellite imagery. This ensured relatively unbiased sampling of the city. We compared these locations to three undeveloped reference sites outside of each city, within natural areas, for a total of 19 sampling sites per city. Most of our sites were located in public parks, medians, or rights of way (publicly-owned land along the edges of private property). In Raleigh, we used an existing network of research sites that resulted in a greater sampling of rights of way in residential neighborhoods, compared to public parks in the other two cities, but sites were otherwise comparable. Post-hoc, we quantified the amount of impervious surface in 30 m radius circles around each sampling location using the 2011 National Land Cover Dataset (NLCD) and ArcMap 10.3. We chose to focus on 30 m radius circles because we wanted to understand how landscape management directly near each location influenced

Table 1. Climate and demographic data for each city included within this study

City	2013 Early growing season sampling max temperature	2013 Late growing season sampling max temperature	2013 Early growing season sampling total precipitation	2013 Late growing season sampling total precipitation	Historical range of mean high temperatures from march to october	Historical range of mean precipitation from march to october	Mean measured soil moisture (range)	Köppen climate classification	2013 Estimated human population size (metropolitan area)
Raleigh, NC	26–32 °C (9 days, May 28–Jun 5)	27–32 °C (5 days, Aug 21–25)	14.2 mm (9 days, May 28–Jun 5)	0.3 mm (5 days, Aug 21–25)	17.7–31.6 °C	76–114 mm	15.0% (0–38%)	Humid subtropical	1.21 million
Orlando, FL	28–32 °C (6 days, May 10–15)	33–35 °C (8 days, Aug 13–20)	0.0 mm (6 days, May 10–15)	40.4 mm (8 days, Aug 13–20)	25.2–33.2 °C	63–222 mm	9.2% (0–68%)	Humid subtropical	2.27 million
Phoenix, AZ	24–34 °C (6 days, Apr 17–22)	36–46 °C (15 days, Jun 30–Jul 14)	0.0 mm (6 days, Apr 17–22)	0.0 mm (15 days, Jun 30–Jul 14)	24.9–41.2 °C	1–27 mm	3.5% (0–34%)	Hot desert	4.40 million

Data from www.wunderground.com/history, www.usclimatedata.com, and factfinder.census.gov.

hydration and circles of this radius most closely matched our *a priori* site selection methods (i.e. many of the public parks we used were in the range of 60 m x 60 m). Moreover, Dale et al. (2016) found significant effects of impervious surface on scale insect abundance in Raleigh, NC when impervious surface was calculated at similar scales.

Sampling and hydration determination

We sampled arthropods at each site by sweep netting one tree and one shrub. The tree was chosen based on our ability to reach the branches without a ladder and we chose a shrub nearest to the tree (when multiple suitable trees were present, we chose haphazardly, but with preference for trees that were more representative of the overall site conditions). We swiped six times, vigorously and continuously, for each sample. Sampling was conducted once during the day and once at night, during two different parts of the growing season (late spring/ early summer, hereafter referred to as 'early season' and late summer, hereafter referred to as 'late season'). We measured soil moisture during sampling, taking 3 readings near each tree and shrub, with a delta-T SM150 with an ML3 ThetaProbe (Dynamax, Inc, Houston, TX), as well as temperature and humidity with a handheld weather meter (Aosong model AH8002, Aosong (Guangzhou) Electronics Co., Ltd., Guangzhou, China). We also noted the flowering condition of each sampled plant and any other visible flowering in the area.

Arthropod water content was determined gravimetrically using a Sartorius Cubis MSA with readability to the nearest µg. Upon collection, arthropods were knocked out with CO_2 and sorted into multiple pre-labelled, pre-weighed, airtight vials (Pelco Mini-vials). Multiple tiny individuals (e.g. aphids, flies) were combined into a single 0.3 ml vial due to analytical limits of the balance and procedures. Larger individuals were placed separately into vials, with larger 1.6 ml vials used as necessary. Sealed samples were stored in a cooler or portable refrigerator in the field and frozen as soon as possible (within 12 hours). In the lab, samples were defrosted, weighed, dried at 50 °C for at least 48 hours, and reweighed to determine wet and dry mass of the samples and calculate water content.

Data processing and statistics

Vial hydration was calculated as the mass of water divided by the total wet mass (proportion water). To get mean water content per sample (multiple vials), we calculated dry biomass-weighted means (individual-weighted means were not possible since very small individuals were grouped in vials). Despite our efforts (e.g. handling with gloves, extra weight stabilization time), some vials contained too little material to accurately determine hydration and thus many small samples had obvious errors (i.e. greater than 100% hydration or less than 0%). Therefore, although the results we report in the body of the paper include all the non-negative data (assuming errors were unbiased), we also performed analyses using only vials with wet masses greater than 0.7 mg (the value at which obvious errors were minimized, Supplementary Figure S1) and report those results in the appendix (Supplementary Table S1). The two analyses mostly agreed and differences did not alter our interpretations of the data.

Statistical analyses were conducted using site averages rather than individual samples (site = our experimental unit). We averaged sites by taking the simple mean of samples collected from the tree, shrub, day and night collections. Therefore, statistical models used a single estimate of the mean hydration for
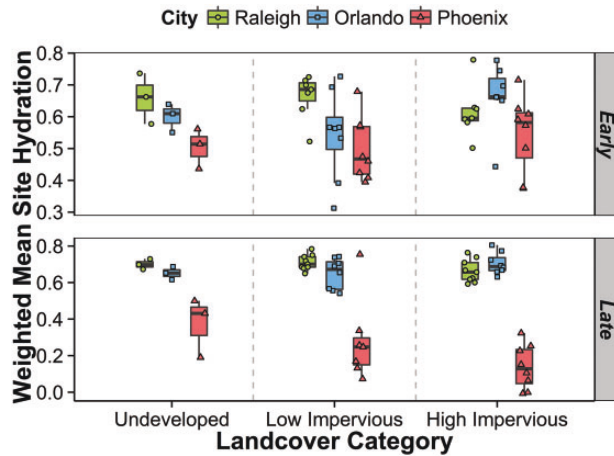
Figure 1. Differences in arthropod hydration between regions within landcover categories and within seasons (Table 2). In the early growing season, the difference in arthropod hydration between regions is greater in undeveloped areas and lesser at locations with high impervious surface. But there is a narrower range of hydration within and among undeveloped vs. developed landcover categories.

each site, during each season (simple mean of all samples taken from a site, with each sample represented by a biomass-weighted mean of all vials collected for that sample).

We analyzed three sets of potential predictors of arthropod hydration: (1) our *a priori* categorization of land cover along with region and season, (2) our *posteriori* measurements of impervious surface (within a 30 m radius) along with region and season, and 3) measured 'environmental' variables (temperature, soil moisture, relative humidity, flowering). In this way, we assess which types of factors best predict urban arthropod hydration among multiple cities with distinct climate.

Due to our repeated sampling of the same locations in the early and late growing season, as well as an unbalanced design, we used mixed effects models to examine how arthropod hydration related to site characteristics. In these analyses, we followed procedures outlined by Bolker et al. (2009), including iterative likelihood ratio tests, starting with the full model and testing the effects of dropping terms, one at a time. We also used Akaike Information Criterion (AIC) metrics to compare the relative explanatory ability of models based on our three sets of potential predictors (see above).

We primarily assessed convergence of hydration by comparing the degree to which mean hydration in different cities becomes more similar with increasing impervious surface (*sensu* Brazel et al., 2000; Groffman et al., 2014). Essentially we asked if the slope of the relationship between impervious surface and hydration differed between cities.

Previous authors (McKinney 2006; Steele et al., 2014) have assessed urban homogenization or convergence by comparing the relative degree of variation in some metric among locations within cities vs. among locations outside cities (lower variation among multiple cities vs. outside = homogenization). Thus, we calculated variance (and CV), pooled among cities, within each landcover category. No statistical tests were possible for these comparisons ($n = 1$).

We also assessed differences in variance (and CV) between each landcover category across regions. In this case, we had three calculations within each landcover, one for each city, which allowed us to test for differences in variation in hydration between undeveloped sites and each urban category using

Table 2. Effects of each factor on site-averaged, dry mass-weighted arthropod water content, shown as the effect of removing each term from the full model (likelihood ratio tests)

Model component removed	df	ΔAIC	LRT (χ^2)	P-value
Analysis of Land Cover Categories				
Season*LandCover*Region	4	−3.96	4.04	0.401
Season*Region	2	32.47	36.47	**<0.000**
Region*LandCover	4	2.97	10.97	**0.027**
Season*LandCover	2	−0.39	3.61	0.164
Analysis of Impervious Surface				
Season*%Impervious*Region	2	0.55	4.55	0.103
Season*Region	2	30.51	34.51	**<0.000**
Region*%Impervious	2	3.35	7.34	**0.025**
Season*%Impervious	1	2.00	4.00	**0.045**
Analysis of Environmental Variables				
SoilMoisture*RH*Temperature*Flowers	1	−1.64	0.36	0.548
SoilMoisture*RH*Temperature	1	−1.86	0.14	0.712
RH*Temperature*Flowers	1	−1.86	0.14	0.712
SoilMoisture*Temperature*Flowers	1	−1.76	0.24	0.626
SoilMoisture*RH*Flowers	1	−1.83	0.17	0.676
SoilMoisture*RH	1	−1.97	0.03	0.863
SoilMoisture*Temperature	1	0.66	2.66	0.103
SoilMoisture*Flowers	1	−1.80	0.20	0.655
RH*Temperature	1	1.07	3.07	**0.080**
RH*Flowers	1	−1.93	0.07	0.795
Temperature*Flowers	1	0.01	2.01	0.157
SoilMoisture	1	2.04	4.05	**0.044**
Flowers	1	0.14	2.14	0.144

t-tests ($n = 3$). Since variation in hydration within urban areas would be expected to match variation in temperature, soil moisture and humidity, we followed the same procedures as those outlined above, but to test for patterns in variation in these environmental factors rather than hydration. To appropriately compare estimates of variation between a smaller number of undeveloped sites ($n = 3$) and a larger number of low and high impervious surface sites ($n = 8$ for each type), in each city, we resampled the data to calculate unbiased metrics based on equal sample sizes ($n = 3$), using the mean of the estimate of variance of every possibly combination of sub-samples.

Since our goal was to detect patterns rather than test hypotheses, we used alpha = 0.1 as our cut-off for evaluating statistical significance, realizing that generating a greater understanding of these patterns will require additional work. Data were logit transformed to improve the normality and equal variance of the residuals, following Warton and Hui (2011).

Results

Landcover types

Overall, the effects of landcover and season on arthropod hydration differed by region (Fig. 1, Table 2). In the early season, hydration increased at high impervious sites in both Phoenix and Orlando and decreased at those sites in Raleigh—arthropod hydration at high impervious sites was less different than undeveloped sites (Fig. 1). In the late growing season, Phoenix showed the opposite of the early season trend—a decrease in hydration at the high impervious sites. Raleigh also showed this pattern, as it did during the early growing season (Fig. 1). Arthropods in Phoenix also tended to be less hydrated overall in the late growing season, than the early growing season, while arthropods in Raleigh and Orlando tended to be more hydrated

during this period. During the late growing season, all sites in all regions tended to be hotter, but especially Phoenix (Table 1), and Orlando experienced higher rainfall during this period than during the early season (Table 1).

Low impervious surface sites did not show the same patterns as high impervious surface sites (Fig. 1). Generally speaking, the only major trend for low impervious surface sites was that arthropods in Orlando were least hydrated at these low impervious sites.

Percent impervious

Arthropod hydration was significantly correlated with the *a posteriori* calculated percent of impervious surface within a 30 m radius around each site, within each city (Fig. 2, Table 2). In Raleigh, the relationship was negative in both seasons, with lower hydration arthropods occurring in sites with more impervious surface. In Orlando, the relationship was positive in both seasons, with higher hydration arthropods occurring in sites with more impervious surface. These opposite slopes led to a convergence of mean hydration at intermediate to high levels of impervious surface (Fig. 2). The relationship in Phoenix changed seasonally—a positive relationship occurred during the early growing season and a negative relationship occurred

Figure 2. Relationship between arthropod hydration and % impervious surface, in each city, in each season. There are significant effects of impervious surface, city and season (Table 2). The mean hydration of Raleigh trends towards converging with Orlando (both seasons) at intermediate levels of impervious surface and Phoenix during the early growing season at high impervious surface.

during the late growing season. The positive slope in the early growing season in Phoenix and the negative slope in both seasons in Raleigh meant that at certain times of year, higher impervious parts of Phoenix have arthropods with a hydration more similar to higher impervious parts of Raleigh. More generally, we note that all three cities had sites where most arthropods we well hydrated.

Environmental factors

Temperature, relative humidity and soil moisture all had significant effects on arthropod hydration (Fig. 3, Table 2). Temperature and humidity had an interactive effect, while soil moisture had an additive effect. Examined individually, hydration was negatively correlated with temperature and positively correlated with relative humidity and soil moisture. Flowering did not show a significant effect on hydration in this analysis. Notably, variation in arthropod hydration was wide at low soil moistures and relative humidity, but was reduced and generally high at high soil moisture and humidity (Fig. 3). Region (city), season and % impervious surface at 30 m radius were each significant predictors of temperature, relative humidity and soil moisture, sometimes interacting, sometimes additive (Table 3).

Comparisons among models

The model involving our *a posteriori* measurements of impervious surface, region and season best predicted site arthropod hydration (Table 4). The evidence for this model was substantially higher than the one involving our *a priori* classification of land cover categories, both had much higher evidence than the one involving only the environmental variables, and all had much greater evidence than the null model.

Variance patterns

Pooled variance within land cover categories among cities showed higher values in cities for arthropod hydration and temperature, in both seasons (contrary to expectations), but showed lower values in cities for relative humidity during both seasons and for soil moisture during the late season (matching expectation for convergence; Fig. 4; Supplementary Table S2). No statistical test is possible for differences in variance pooled among cities ($n = 1$).

On average, variance in hydration among sites within high impervious urban landcover was higher than within undeveloped areas (Fig. 4, Supplementary Table S2), matching our expectations based on high heterogeneity within cities. But there were no significant differences in variance of soil moisture, humidity, or temperature during this period and no significant differences in CV. In the late season, there was no significant
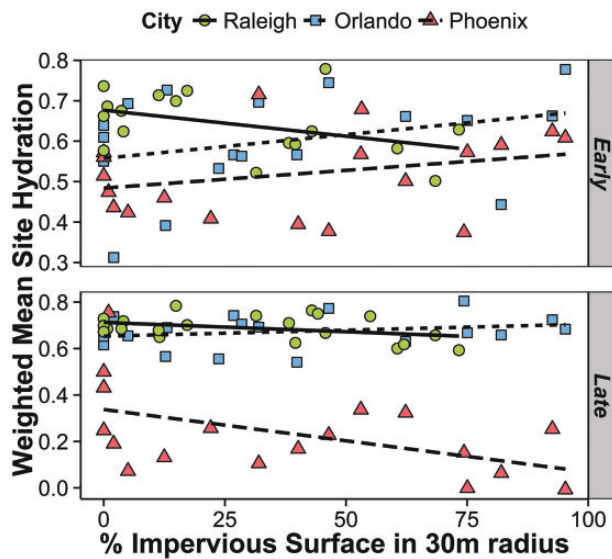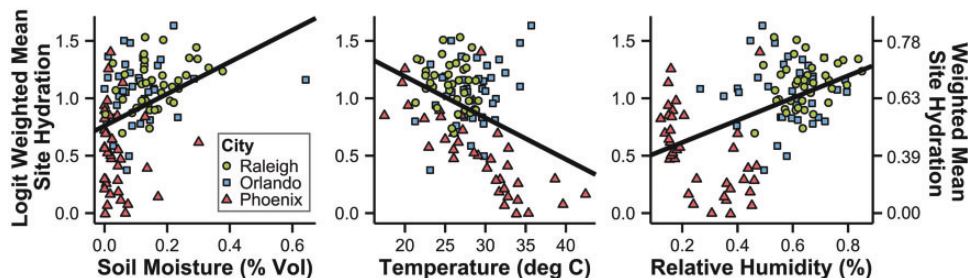

Figure 3. Statistically significant relationships (Table 2) between arthropod hydration and mean measured soil moisture (left), temperature (middle), relative humidity (right).

Table 3. Effects of region, season and impervious surface on soil moisture, relative humidity and temperature, shown as the effect of removing each term from the full model (likelihood ratio tests)

Model component removed	df	ΔAIC	LRT (χ^2)	P-value
Predictors of Soil Moisture				
Season*%Impervious*Region	2	1.10	5.10	**0.078**
Predictors of Relative Humidity				
Season*%Impervious*Region	2	−2.88	1.13	0.570
Season*Region	2	12.57	16.57	**<0.000**
Region*%Impervious	2	0.03	4.03	0.133
Season*%Impervious	1	−0.49	1.50	0.220
%Impervious	1	4.54	6.55	**0.010**
Predictors of Temperature				
Season*%Impervious*Region	2	−3.45	0.55	0.758
Season*Region	2	51.04	55.04	**<0.000**
Region*%Impervious	2	−2.34	1.66	0.435
Season*%Impervious	1	−0.11	1.89	0.169
%Impervious	1	1.07	3.07	**0.080**

Table 4. Multi-model comparison of the three best models from each analytical approach

Model	K	AICc	ΔAICc[a]	Likelihood	Weight	LL
Impervious (Season*Region + Region*%Impervious30m + Season*%Impervious)	12	15.17	0.00	1.00	0.94	5.99
Site Type (Season*Region + Region*LandCover)	14	20.57	5.40	0.07	0.06	5.88
Climate (Relative Humidity*Temperature + Soil Moisture)	7	45.70	30.53	0.00	0.00	−15.31
Null	3	100.77	85.61	0.00	0.00	−47.28

[a]Greater than 3 units indicates substantially more support.

difference in variance of hydration, but variance in relative humidity and temperature among sites within high impervious urban landcover was higher than undeveloped areas, matching our expectations.

Discussion

Here, we show that although regional and seasonal context plays a fundamental role in determining the physiological state of arthropods, urbanization can also have a large influence, and can lead to increasingly similar mean arthropod hydration (convergence) in cities in distinct climate regions, during certain time periods. Essentially, our results show that average arthropod hydration can be higher with urbanization in warm cities like Orlando, FL and Phoenix, AZ, but lower in milder cities, like Raleigh, NC. Thus, consistent with the findings of others (Groffman et al., 2014), human desires for similar aesthetics across cities in distinct climate regions can lead to more similar ecological conditions—here arthropod water content.

As expected, variability of arthropod hydration was higher among locations within cities than undeveloped areas (in the early season). At small scales, cities can exhibit substantial variability in temperature, soil moisture, or other factors, due to differences in landscape management practices within each city (e.g. irrigation, impervious surface amount or color, canopy cover)—especially between medians, public parks, (Pećarević et al., 2010; Menke et al., 2011; Savage et al., 2015; Youngsteadt et al., 2015b) and residential yards (e.g. see maps of surface temperature in Phoenix and Raleigh from Brazel et al. 2000, Meineke et al. 2013). Arthropods are likely to be particularly prone to respond to variation at these small scales (e.g. Dale et al., 2016).

Patterns of pooled variance did not match expectations. Based on the work of others (Groffman et al., 2014; Steele et al., 2014), we expected higher variance in arthropod hydration among undeveloped areas pooled across the three regions, vs. within cities. This would be expected if environmental conditions in undeveloped areas are very different between the three regions, but are less dissimilar within the cities in the three regions. Here, we find that despite increasingly similar mean arthropod hydration among the three cities with urbanization (Fig. 2), the variability of hydration was still greater between urbanized parts of the three cities than undeveloped parts of the three regions (Figs. 1 and 4). We propose two possible explanations. First, it is possible that arthropods living in undeveloped areas in each location are well-adapted to regulating hydration regardless of local environmental pressures, whereas arthropods living within cities may be less capable of regulation, either because they are not locally-adapted taxa, or because certain parts of cities expose arthropods to especially extreme conditions. Secondly, whether or not one should expect a reduction in pooled variance with urbanization is likely driven by the balance between (a) the difference in mean conditions among regions and (b) variability in conditions within cities. Reductions in pooled variance among multiple cities with urbanization is more likely to be produced when variability in conditions within cities is smaller than differences in mean conditions between regions. Pooled variance should not decline with urbanization when variability in conditions within cities is higher than differences in means between regions, even if means converge among cities. This is the pattern we observe in this data set (Figs. 1 and 2).

Our comparison among models suggested that the percentage of impervious surface within a 30 m radius of each site was a stronger driver of mean arthropod hydration than either our *a priori* categories of land cover or environmental factors like temperature, humidity, or soil moisture (Table 4). The fact that impervious surface, region and season were better predictors of arthropod hydration than temperature, humidity and soil moisture suggests that arthropod hydration is not directly reflecting our point-measurements of temperature, humidity and soil moisture at the time of collection, but rather there are additional factors associated with impervious surface, region, or season that are influencing hydration. The simplest explanation is that arthropod hydration responds to temperature, humidity and soil moisture over longer time periods than represented by our measurements and that impervious surface, region and season better predict those longer-term patterns. Alternatively, there could be another factor that varies with impervious surface, region, or season that alters arthropod hydration, such as variation in physiological traits among taxa (*sensu* Chown and Duffy 2015). For instance, impervious surface may influence the relative abundance of sap-feeding insects (Meineke et al., 2013; Dale et al.,2016) or other taxa that have traits that allow them to maintain high water content (i.e. low water loss rates or the ability to find and access overlooked water sources). To gain a better understanding of the mechanisms behind the patterns observed here will require future testing of these and other hypotheses.
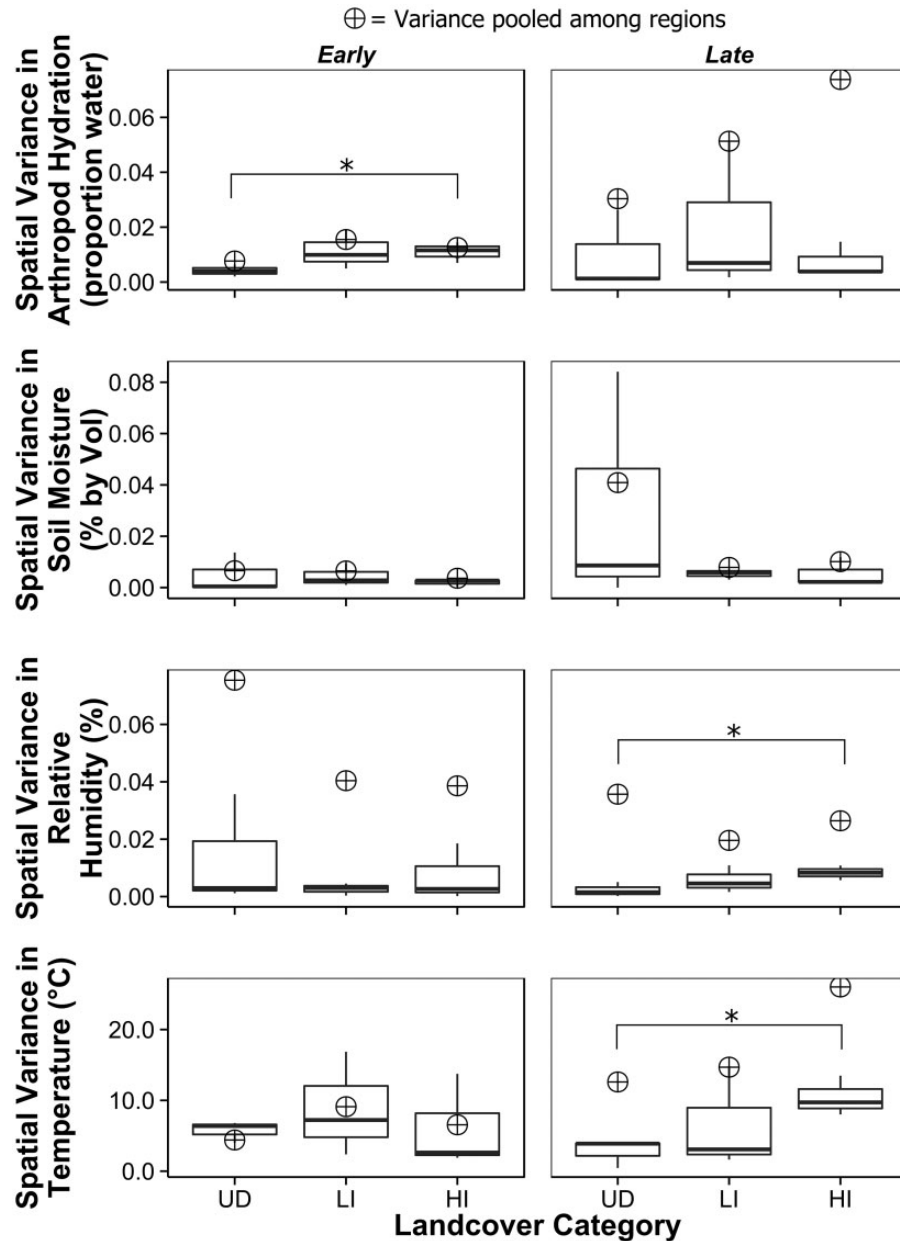
Figure 4. Box plots ($n = 3$ cities) of unbiased (resampled) estimates of variance within each land cover category (HI = High Impervious, LI = Low Impervious, UD = Undeveloped). Starred brackets indicate significant differences at $\alpha = 0.1$. Variance of early season hydration and late season temperature is higher within cities than outside cities. Pooled variance in hydration across the three regions is lower among undeveloped than developed locations.

Overall, our results point to the importance of impervious surface as a predictor of arthropod hydration. Impervious surface could increase local temperatures (Yuan and Bauer 2007 and Table 3) and higher temperatures may lead to higher rates of water loss and also dehydration (Hadley 1994; Chown et al., 2011), especially in non-sap-sucking arthropods. Moreover, greater amounts of impervious surface could reduce access to moist soils or limit the amount of moist plant material available (by reducing pervious surfaces conducive to plant growth). On the other hand, impervious surface could be related to higher soil moisture or moist plant materials in situations where urbanized areas are heavily landscaped and irrigated, and this could increase arthropod hydration (*sensu* Menke et al., 2007). The relative importance of these two mechanisms may differ between cities depending on the frequency of irrigation and

ambient temperatures, with hot cities (Phoenix, Orlando) more frequently irrigating landscaped urban areas. The interactive effect of region, season and impervious surface on soil moisture (Table 3) supports this possibility, but more careful examination is warranted.

We did not expect the relationship between impervious surface and hydration in Phoenix (hot, dry) to reverse seasonally. This seasonal effect may be due to the extreme temperatures observed later in the growing season, which may have been magnified by impervious surface. It is possible that when temperatures become exceptionally high (range of max air temperature during late growing season in Phoenix: 36–46 °C) irrigation does little to increase hydration.

We note that our measurements of arthropod water content represent only several snapshots in time within each city. In

reality, arthropod water content likely varies continuously over time with fluctuations in antecedent rainfall, soil moisture, temperature, and humidity. Thus, continuous sampling of arthropod hydration might reveal periods of time when differences between cities are stronger or weaker than those we observed.

Overall, our results suggest that impervious surface is a strong predictor of physiological condition of shrub and tree-dwelling arthropods across cities, but that effects differ between regions and seasons. Climatic factors could partly underlie these regional and seasonal effects. However, the importance of impervious surface in our analysis is particularly relevant, since it suggests that landscape management could exacerbate or mitigate the consequences of climate change for arthropods. For instance, surface temperature, humidity and soil moisture could be influenced by irrigation, soil amendments or coverings, or plant choice and density. Thus, urbanization, climate change, and landscape management may interact to influence the physiological condition of beneficial arthropods, pests and those of conservation concern.

As one of the first large-scale efforts to examine patterns in the hydration (water content) of field-collected arthropods, this study generates many additional questions. For instance, what is the relative importance of water loss vs. water gain in driving these patterns? If water gains are responsible, what are the routes for water acquisition (e.g. moist soil vs. moist leaves)? Do effects differ between arthropods occupying different habitats or with different functional traits? Additionally, how does the variation in hydration we observed influence arthropod health? Are there effects on growth, survival, or reproduction? Moreover, what are the ecological consequences of the measured variation in arthropod water content? Does lower arthropod hydration lead to declines of certain taxa over others? Does altered arthropod hydration lead to differences in rates of herbivory (sensu McCluney and Sabo 2009) or pollination? Future research is needed to delineate mechanisms behind the patterns we report here, and their consequences. Our work represents a step in linking local climate, urbanization and landscape management to variation in animal water balance and then to changes in communities and food webs. Elucidating these linkages could provide us with a better understanding of the potential role of arthropod water balance in moderating ecosystem services and disservices (e.g. pollination, pest damage to urban trees or crops) in diverse locations and climates.

We received permission to sample from: Phoenix Parks and Recreation Department; Maricopa County Parks and Recreation Department (to CAP LTER); City of Orlando Parks and Forestry; Orange County Parks and Recreation; Bureau of Land Management; Florida Department of Environmental Protection (to Joshua King); Raleigh Parks, Recreation, and Cultural Resources Department; North Carolina Division of Parks and Recreation; Knightdale Parks and Recreation; and Town of Cary Parks, Recreation and Cultural Resources.

Data availability

Data is available in the supplementary materials.

Supplementary material

Supplementary material is available at *Conservation Physiology* online.

Conflict of interest statement. None declared.

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