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# Water availability influences arthropod water demand, hydration and community composition on urban trees

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## Abstract

The drive for animals to regulate their water content can have significant consequences for food webs in xeric ecosystems. But the importance of animal water balance (gains vs losses) for mesic food webs has not been explored. Impervious surfaces in cities absorb and re-radiate solar radiation, raising local temperatures. Higher temperatures lead to greater rates of organismal water loss. Thus, urbanization of mesic regions may lead to greater likelihood of desiccation, with consequences for food webs. We tested the effects of animal water balance on a mesic urban food web by supplementing animal-available water (but not plant) within trees in a parking lot in Raleigh, NC, a mesic city with previously documented urban warming. We found that during dry periods, arthropods in control trees were desiccated (lower water content), with higher water demand behavior. This coincided with shifts in community composition during dry periods. Continuous experimental supplementation of animal-available water mostly reduced or erased these patterns. Thus, animal water balance may play a role in mediating food web dynamics in mesic cities.

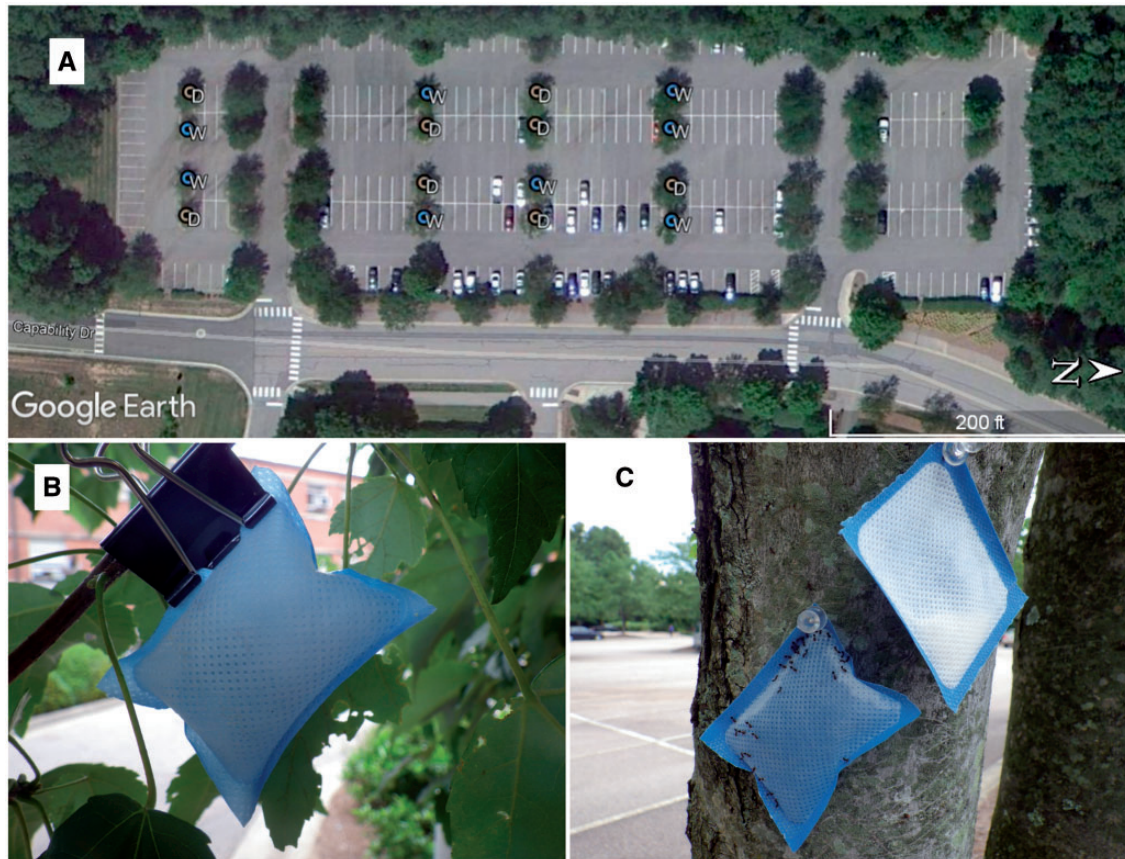
**Key words:** heat, soil moisture, food web, ants, spiders

## Introduction

Preventing desiccation represents a significant challenge for terrestrial organisms—dehydration can lead to slower growth (McCluney and Date 2008), reduced reproduction (Lorenzon, Clobert, and Massot 2001; Benoit et al. 2010) and greater mortality (Hood and Tschinkel 1990; Bujan, Yanoviak, and Kaspari 2016). Considerable attention has focused on physical characteristics and physiological mechanisms for minimizing water losses (e.g. the influence of cuticular hydrocarbons or excretory systems) (Hadley 1994; Chown, Sørensen, and Terblanche 2011). But behavioral responses to desiccation are also possible, and these changes may have implications for food webs (McCluney 2017). For instance, crickets and spiders with low availability of drinking water can increase consumption of moist food to meet water demands, leading to strong top-down effects and trophic cascades (McCluney and Sabo 2009; McCluney and

Sabo 2016). Alternatively, mobile animals may recruit to areas with greater water availability (Valeix et al. 2008; Allen et al. 2014), which could have relatively unexplored indirect effects on food webs.

Much of the existing research on the influence of water balance (gains vs losses) on food webs comes from dryland ecosystems [defined by Middleton and Thomas (1997) as areas with an aridity index <0.65] (McCluney et al. 2012). But a recent study shows that in mesic regions, arthropods in urbanized areas can have lower mean water content, likely representing desiccation (McCluney, Burdine, and Frank 2017). Impervious surfaces can increase temperatures in cities (Yuan and Bauer 2007) and might also restrict access to moist soils. Thus, within mesic regions, one might expect animal water balance to have a greater impact on terrestrial food webs within highly urbanized locations.



**Figure 1:** (A) Map of experimental design. Trees with water added are blue ('W') and control trees are brown ('D'). (B) A water pillow attached to a tree to supplement water. (C) Wet and dry water pillows attached to a tree to measure drinking behavior, a proxy for increased water demand. The wet pillow, but not the dry, has a large number of acrobat ants (*Crematogaster* sp.) drinking water.

Here we test the hypothesis that desiccation of urban insects (both predators and herbivores), alters mesic food webs. To test this hypothesis, we continuously added animal-available water (via 21 water pillows per tree—water pillows are pouches containing a polymer that absorbs water and provides it to arthropods) to a subset of landscape trees in a parking lot in Raleigh, NC, USA, without altering plant-available water. Thus, we isolated the effects of animal water balance from plant water balance or other soil moisture effects. We expected that during dry periods arthropods on ambient control trees would display (i) desiccation (lower water content), (ii) higher water demand behavior (attraction to temporarily added water sources), (iii) greater herbivory and predation and (iv) shifts in community composition. We expected supplementation of animal-available water to reduce or erase these patterns.

## Methods

### Study site

The experiment occurred in a rectangular parking lot (~180 × 50 m) on the centennial campus of North Carolina State University in Raleigh, NC, containing 18 islands, with 2 red-maple trees (*Acer rubrum*) per island (Fig. 1A). The surface of each island was covered in a layer of wood chips and islands were >5 m apart. The parking lot was embedded in a residential landscape matrix, but was immediately surrounded on three sides by forested areas with some connectivity to a larger remnant forest.

### Design

We continuously supplemented animal-available water to eight randomly selected trees, from 10 July 2013 to 14 August 2013, with eight other trees serving as ambient controls. Water was supplemented via cricket water pillows, 5.5 × 6.5 cm pouches filled with a polymer that holds up to 30 ml of water, allowing access to arthropods via a cloth surface that is moistened by the underlying polymer (R-Zilla Cricket Water Pillows, Central Garden and Pet Company, Walnut Creek, CA, USA). These pillows have been used to supplement water to a variety of arthropods in other experiments (McCluney and Sabo 2009; Allen et al. 2014; McCluney and Sabo 2016). A total of 21 water pillows were added to each water addition tree (replaced every 1–4 days depending on observed dryness of pillows), to provide a continuous water source. Fifteen pillows were added to the branches, six to the trunk and three on the ground at the base of each tree. Pillows were attached to trees with binder clips, which were either clipped directly to a branch or were hung on a pushpin (Fig. 1B). Care was taken to place each pillow so that nonflying arthropods would be able to access the pillow.

We measured arthropod drinking behavior (water demand) once a week (excluding week 1), on all trees, by temporarily placing one wet and one dry pillow on the trunk or in the branches of each tree for 8–9 h and making observations of arthropods present on the pillows (Fig. 1C). Pillows were added at approximately 2 pm and checked at approximately 5 pm (day) and 10 pm (night) during each trial, and then removed.

Observed invertebrates were counted and photographed, for later identification.

Prior to water pillow observations, we collected one sweep net sample from each tree. Captured arthropods were asphyxiated with CO<sub>2</sub> gas and sorted into pre-weighed, air-tight vials (Pelco Mini-vials). The hydration of arthropods in these vials was measured gravimetrically using a Sartorius Cubis MSA balance, recording wet and dry weights (dried for 48 h at 50°C), following McCluney, Burdine, and Frank (2017). Individuals collected in these samples were later identified to family and used to examine shifts in community composition.

Rates of herbivory were measured through repeated photography of three marked leaves on each tree. Relatively undamaged leaves were selected at the beginning of the experiment and weekly photographs were taken on a white background with a ruler. At the end of the experiment, each leaf was collected and scanned. The number of new marks each week was counted. We used the frequency of leaf consumption rather than total leaf consumption because there were likely multiple unknown consumer species of various, but unknown size, so a single large consumption event would not necessarily equal greater demand for vegetation, but could reflect individual differences in consumer traits.

We also counted the consumption of corn earworm (*Helicoverpa zea*) eggs, following Gardiner et al. (2013). Eggs were laid on 2 × 2 cm cheesecloth, with each covered in 10–72 eggs. All eggs were frozen for at least 24 h prior to addition. Once each week, prior to water pillow observations, one egg cloth was pinned to the trunk and one to a leaf of each tree, and left out from ~5 pm to 10 am the next day. The number of eggs on each sheet was counted before and after to get an index of egg consumption and we calculated average egg consumption per hour.

We recorded soil moisture measurements every 2–3 days using a delta-T SM150 with an ML3 ThetaProbe (Dynamax, Inc., Houston, TX, USA). Soil moisture was recorded in three locations near the base (within 1 m) of each tree, across variation in microtopography.

## Data processing and statistics

For observations of arthropods on water pillows, arthropod hydration and consumption of eggs, we divided the dates of measurement into periods of wet and dry soil moisture (Fig. 2A) and took either the total (abundance on water pillows) or the mean (hydration, egg consumption) for each tree across those dates. For leaf consumption, we similarly divided into periods of wet and dry soil moisture, but then calculated the number of observations where some leaf consumption was observed, out of the total number of observations, per period (frequency of leaf consumption, over time). Our hydration metric was calculated by first determining the dry-mass-weighted mean hydration, per tree (*sensu* McCluney, Burdine, and Frank 2017) and then taking the mean over time within each soil moisture period. This metric was necessary because multiple vials were collected per tree, with a variable number of individuals per vial. For egg predation, we calculated eggs eaten per hour prior to taking the mean per period.

We tested most hypotheses using generalized linear models. Statistical analyses were performed in R v. 3.4 and assumptions were assessed via examination of plots of residuals. For total abundance on water pillows, we fit a model with an interaction between water pillow wetness and soil moisture period, with a block for tree (since wet and dry pillows were present on each tree), with natural log transformed data and a Gaussian

distribution. For hydration, leaf consumption, and egg predation, we fit a model with an interaction between experimental treatment (continuous addition of water pillows) and soil moisture period. However, for leaf consumption, we used a mixed model (in the *lme4* package in R) with a random effect for tree to control for having observations from three leaves per tree and two soil moisture periods. Additionally, for hydration and egg predation we used a Gaussian distribution while using a binomial distribution for leaf consumption. For all generalized linear models, we tested treatment effects using a type II analysis of deviance table, using the *car* package. For mixed effect models, we tested fixed effects by iteratively dropping terms from the model and comparing effects via likelihood ratio tests, following recommendations of Bolker et al. (2009).

We examined treatment effects on community composition of sweep net samples, at the family level, using the *mvabund* package in R, which fits generalized linear models with multivariate counts (Wang et al. 2012), simultaneously allowing examination of changes in community composition and abundance of individual taxa. Moreover, using restricted permutations, we were able to appropriately account for repeated measurements from the same trees. Thus, we fit a Poisson distributed *mvabund* model with a time by treatment interaction and restricted permutations based on each tree to account for repeated sampling.

Finally, we examined the relationship between soil moisture and arthropod presence on water pillows explicitly, using generalized linear mixed models in the *lme4* package in R. We fit a model with an interaction between water pillow wetness and max soil moisture as fixed effects and survey date and location as nested random factors, with a presence/absence response and a binomial distribution (logistic mixed model regression). We then tested fixed effects by iteratively dropping terms from the model and comparing effects via likelihood ratio tests, following recommendations of Bolker et al. (2009).

## Results

### Environmental conditions

Soil moisture was high near the beginning of the study period, prior to experimental treatment initiation, fell prior to beginning treatments, increased again immediately after treatments began, fell for an extended period in the middle of the treatment period, and then rose again near the end of the experiment (Fig. 2A). This resulted in a prolonged dry period in the middle of the treatment period with wetter periods at the beginning and end.

### Water demand observations

The abundance of arthropods was higher on temporarily added wet water pillows than dry pillows during both soil moisture periods, but the response was much stronger when the soil was dry (Table 1 and Fig. 2B). Moreover, soil moisture was a significant continuous predictor of the frequency with which arthropods were observed on pillows, with frequency on wet pillows declining substantially with max soil moisture above about 15%, but frequency on dry pillows showing a weakly opposite pattern (Table 1 and Fig. 3). Ants (predominantly acrobat ants, *Crematogaster* sp.) responded strongly to water pillows (Fig. 5), making up 68% of the observations on wet pillows. However, we also recorded 25 other morphospecies on wet water pillows during nonsystematic photographic observations, including

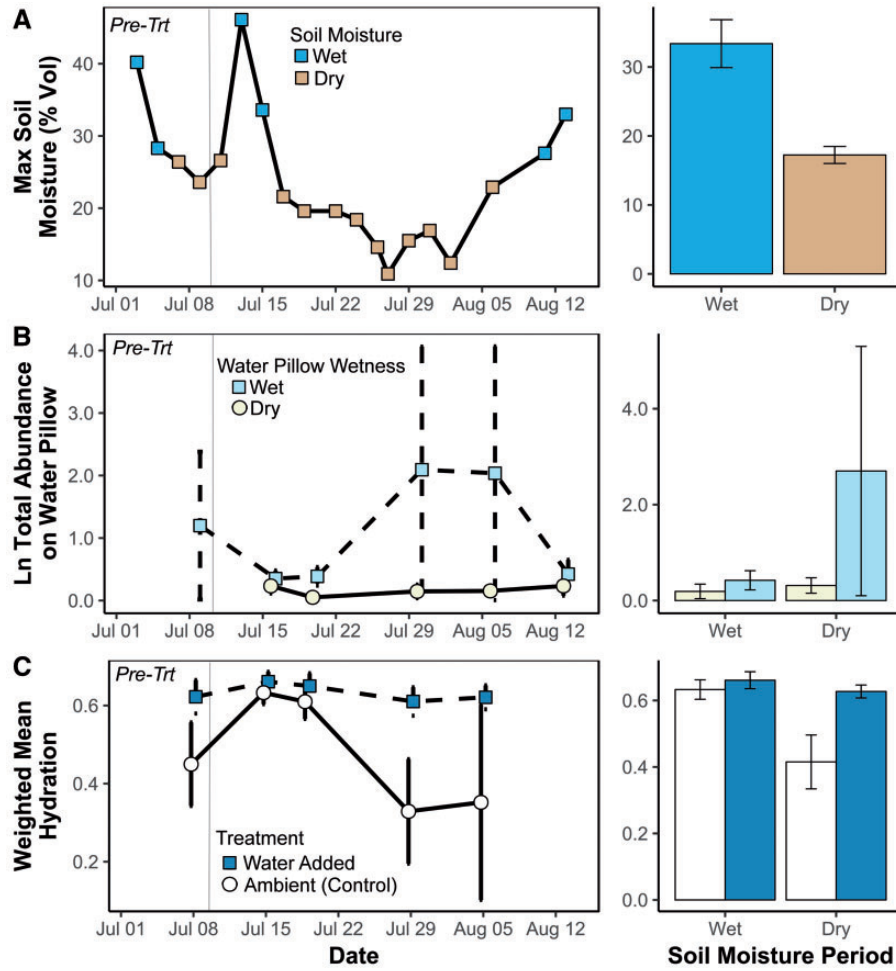


Figure 2: Soil moisture (A), arthropod water demand behavior (B) and arthropod water content (C) during the experimental period. The panels on the left display responses over time, including the period before water addition ('Pre-Trt'), while the panels on the right show responses within periods of wet and dry soil moisture, matching the approach used in statistical tests (Table 1). Note that panel B compares attraction to a single pair of wet and dry water pillows placed for approximately 8 h on a single day on all trees, ignoring treatment, whereas panel C examines the response to the treatment—the addition of 21 wet water pillows to certain trees for the entire experimental period.

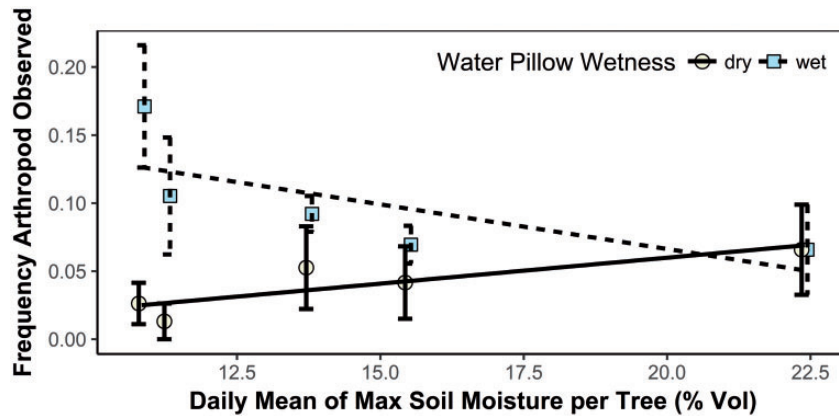


Figure 3: The relationship between measurements of soil moisture on each survey date and the frequency of arthropod water demand behavior across all trees on that survey date (points have been offset by 0.2 units to improve readability). Repeated sampling was accounted for statistically using mixed effects modeling.

**Table 1:** Results of statistical tests

Factor	df	LRT $\chi^2$	P-value
Analysis of total abundance on water pillows			
Water pillow wetness × Soil moisture period	1	2.68	0.102
Water pillow wetness	1	8.35	<b>0.004</b>
Soil moisture period	1	5.49	<b>0.019</b>
Tree (Block)	18	29.61	<b>0.041</b>
Analysis of frequency arthropod observed on water pillows <sup>a</sup>			
Water pillow wetness × Mean of max soil moisture	1	5.29	<b>0.021</b>
Analysis of weighted mean hydration			
Treatment × Soil moisture period	1	3.62	0.057
Treatment	1	6.86	<b>0.009</b>
Soil moisture period	1	6.79	<b>0.009</b>
Analysis of frequency of leaf consumption <sup>b</sup>			
Treatment × Soil moisture period	1	4.44	0.035
Treatment	1	0.83	0.361
Soil moisture period	1	0.00	1.000
Analysis of egg predation			
Treatment × Soil moisture period	1	0.18	0.674
Treatment	1	0.99	0.319
Soil moisture period	1	4.16	<b>0.041</b>
Analysis of community composition <sup>c</sup>			
Time × Treatment	4	65.99	<b>0.039</b>

<sup>a</sup>Logistic mixed model regression including nested random effects for survey date and location of pillow on the tree to control for repeated sampling.

<sup>b</sup>Logistic mixed model regression including a random effect for tree to control for having observations from three leaves per tree and two soil moisture periods.

<sup>c</sup>Modeled using the *many glm* approach in the *mvabund* package in R, with restricted permutations accounting for repeated sampling over time.

Note: Bold values indicate significance at  $\alpha = 0.05$ .

beetles, lepidopterans, crickets, other genera of ants, flies, hemipterans, isopods, millipedes, spiders, and yellow jackets.

### Treatment effects

Trees with continuous water supplementation had significantly higher weighted mean arthropod water content, especially during periods of dry soil moisture (Table 1 and Fig. 2C). Frequency of leaf consumption showed a suggestive declining trend with water supplementation but this effect was only significant at  $\alpha = 0.1$  (Table 1). We did not detect an effect of water supplementation or soil moisture period on predation of caterpillar eggs (Table 1).

Community composition of sweep net samples shifted over time and varied with water supplementation (Fig. 4). This was driven by a larger effect on one date, 29 July, during the dry experimental period (assessed via deviance as a proxy for effect size, Fig. 4). Moreover, ghost spiders (family Anyphaenidae) were the most strongly affected taxonomic group (based on deviance as a proxy for effect size, Fig. 4), with lower abundance on water supplemented trees on that date (Fig. 5).

### Discussion

Overall we found changes in urban food webs with variation in animal water availability. Diverse groups of arthropods, but especially ants, showed greater demand for water during periods of low soil moisture. Water content of arthropods on ambient control trees declined during these dry periods, but water supplementation prevented this desiccation. Moreover, water addition altered community composition on particular dates with

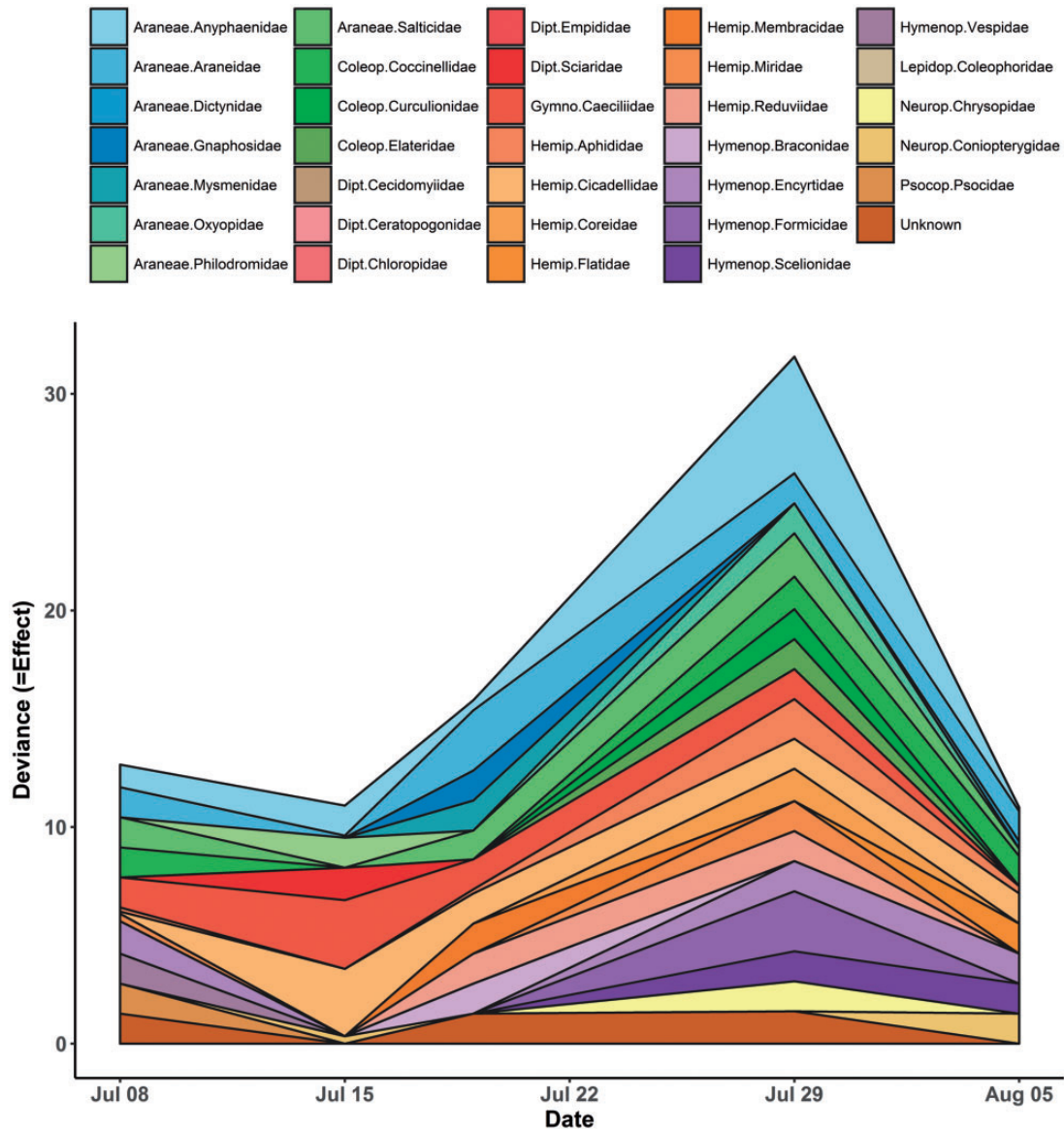
low soil moisture. The pattern in the data suggests that greater herbivory may have occurred on ambient control trees, but we had insufficient observations of herbivory to conduct a strong test of this hypothesis. Overall, we found that arthropod communities on urban trees were influenced by changes in animal water balance.

Although results often matched predictions, several results were somewhat unexpected. First, we did not expect the exceptionally strong response of ants to water addition nor fewer ghost spiders with water addition. We hypothesize these two observations might be related. We regularly observed acrobat ants recruiting to our wet water pillows (Figs 1C and 5), as well as consuming caterpillar eggs placed on trees. Moreover, these ants are venomous and can be aggressive and predatory. Thus, if acrobat ants were more active in trees with added water pillows, they may have also reduced the abundance of other taxa like ghost spiders (Styrsky and Eubanks 2007).

The fact that ants and ghost spiders were two taxa with strong responses to changes in water availability in this urban system is noteworthy because others have found these taxa to show important responses in urban systems. Ants are important parts of the food web in urban systems (McIntyre et al. 2001; Bang and Faeth 2011; Menke et al. 2011), where they can play large roles in removing food waste (Penick, Savage, and Dunn 2015; Youngsteadt et al. 2015). Additionally, ghost spiders were also found to respond strongly to habitat complexity (Shrewsbury and Raupp 2006) and urban warming (Meineke et al. 2017) in other studies [although Meineke et al. (2017) found spiders were lost from warmer locations, while here we find greater abundance on drier trees]. This study contributes to evidence that ants and ghost spiders may be key to understanding responses of tree food webs to changes in temperature and water associated with urbanization of mesic cities.

Another unexpected finding was the lack of effect of water supplementation on either herbivory or consumption of lepidopteran eggs (note: a mean of  $50.2\% \pm 3.5\%$  SE of eggs were consumed across treatments, trees and dates). One possible explanation for this lack of an effect could have to do with the proximity of trees within each island in the parking lot and the potential for arthropods, especially ants, to forage among multiple trees. Ants were a key consumer of eggs (~80% of photographic observations of consumption). Although we cannot say for certain if ants foraged among trees, it is certainly a reasonable possibility that ants moved between a pair of trees on an 'island' (less likely to have regularly moved between islands separated by >5 m of asphalt). This idea seems to have some support within the data, as there is a correlation between egg consumption on trees that share the same islands—a stronger correlation when one of the pair received water supplementation, but the other did not (weaker when the two trees either both received water or both did not). This suggests that when adjacent trees differed in water supplementation, it may have promoted foraging by ants on both trees (although we are uncertain if ants on the ambient dry tree were more likely to forage on the water supplemented tree or vice versa). If ants did forage between trees within an island, it could have hidden a potential treatment effect on egg consumption or herbivory or weakened other treatment effects. However, it should not negate the observed significant responses.

Based on previous work from drylands (McCluney and Sabo 2009; McCluney and Sabo 2016), we had expected both herbivory and predation to decrease with water supplementation. However, this previous research focused on consumption of crickets by wolf spiders, and consumption of picked leaves by



**Figure 4:** Effect size of animal water supplementation on abundance in sweep net samples, over time, partitioned by arthropod family and sorted by order (listed as abbreviated order.family). Larger effects occur on 29 July, which is a period of dry soil moisture (see Fig. 3), with ghost spiders (Anyphaenidae) and ants (Formicidae) showing some of the strongest responses (see Fig. 5).

crickets, while here we recorded consumption of immobile caterpillar eggs by varied predators (frequent photographic observation of ants, but also wasps, spiders, and isopods) and consumption of attached leaves, likely by varied, but unknown herbivores. Complex food web responses involving many species may have moderated potential effects of predator water balance on egg consumption or herbivore water balance on leaf consumption. Thus, further testing is needed to better understand how animal water balance might influence rates of predation or herbivory in speciose food webs, including in urban systems.

Overall, our finding that animal water balance influences urban food webs, altering behavior and community composition has important implications. Urbanization may be making mesic cities hotter and drier, which may have consequences for the biology of herbivores and predators, which may, in turn, influence plant health. More research is needed to disentangle direct effects of urbanization on landscape trees from indirect

mechanisms mediated through the food web. But here we find that animal water balance may partly underlie food web responses to urbanization.

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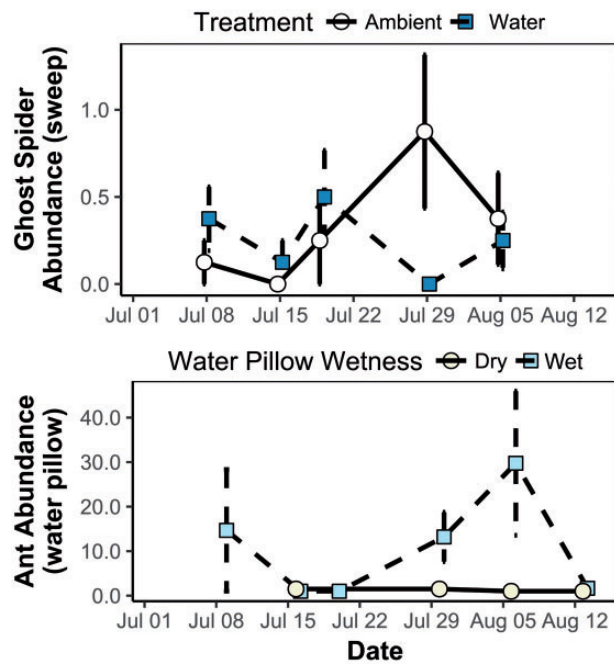


Figure 5: Abundances of ghost spiders in sweep net samples from animal water supplemented and ambient trees (top) and ants on wet and dry water pillows (bottom), over time.

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## Author contributions

K.E.M. designed, conducted, and analyzed the study and wrote the manuscript. T.G. helped conduct the study and helped analyze leaf consumption patterns. S.D.F. helped with the design, analysis, and interpretation of the study and edited the manuscript.

**Conflict of interest statement.** None declared.

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