Changes in spider community composition are associated with urban temperature, not herbivore abundance

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Abstract

Urban forests provide many ecosystem services. The urban heat island effect can alter these services, in part by increasing arthropod herbivore abundance. Natural enemies, such as predators and parasitoid wasps, play a crucial role in controlling street tree herbivores, but their responses to urban warming are almost completely unknown. In this 2-year study, we investigated how urban warming and herbivore abundance affected arthropod natural enemies in street trees using an urban warming gradient and herbivore removal treatments. Spiders were by far the most abundant natural enemy group, but spider abundance did not increase with urban warming as herbivore abundance often does. In addition, spider and herbivore abundances were not related, either when herbivore abundance increased with warming or decreased with horticultural oil applications. Instead, urban warming was associated with altered spider community structure. This was due in part to loss of Anyphaenids—ghost spiders, which are known to control herbivorous arthropods in other systems—at the hottest urban sites in a relatively hot year. Together, the decline of this important spider group and the lack of increase in spider abundance with urban warming or prey abundance may contribute to abundant street tree herbivores in the hottest areas within cities. Our study is the first to manipulate a combination of biotic and abiotic factors to understand the forces driving natural enemy composition, abundance, and diversity in cities.

Key words: urban heat island effect, spider, biological control, urban forest

Introduction

Urbanization is a force of habitat change worldwide (UN 2014). Plants that remain in cities or are added as green infrastructure provide important services to people, such as shade and carbon sequestration (Nowak et al. 2013), but are often exposed to stressful conditions, such as heat and drought. In addition, urban landscape plants often have greater herbivore abundance and damage than plants in rural or natural areas (Raupp et al. 2010). One reason for this is that biological control is sometimes reduced in urban areas, because food resources, reproductive and overwintering sites, or both decline (Hanks and Denno 1993; Shrewsbury and Raupp 2006; Tooker and Hanks 2000). However, effects of urbanization on specific natural enemy groups remain largely unexplored.

The urban natural enemy taxa that have been studied thus far, notably carabid beetles and spiders, have distinct responses to urbanization. For example, urbanization favors small herbivorous carabid beetles with affinities for open habitats (Martinson and

Raupp 2013). Similarly, the abundance of certain spider taxa increases in response to urbanization. For example, ground-dwelling wolf spiders (Lycosidae) were more abundant in urban yards than in surrounding desert habitats in the arid southwestern USA (Shochat et al. 2004). This was attributed to higher primary productivity in urban yards, though multiple factors including prey availability, disturbance and temperature could have driven this pattern. Similarly, two web-building spiders *Nephila plumipes* (Nephilidae) and *Latrodectus hesperus* (Theridiidae) were more abundant in more urbanized areas due, in part, to more abundant prey (Johnson et al. 2012; Lowe et al. 2014, 2015). In most cases, the specific abiotic and biotic factors driving such patterns remain correlative or unexplored, which limits our ability to manage urban areas for conservation of natural enemies and, thus, urban plants.

The urban heat island effect warms cities up to 12 °C compared to rural areas and is driven by impervious surfaces and vegetation removal (Oke 1973). Interestingly, the urban heat island effect also varies in intensity within cities, and trees that live in hotter areas within cities have higher insect herbivore abundances (Meineke et al. 2013, 2014, 2016; Dale and Frank 2014a,b). In part, this is because insect herbivores survive better (Meineke et al. 2013) and are more fecund (Dale et al. 2014b) at hotter urban sites. However, the extent to which urban warming reduces biological control and, thus, contributes to higher herbivore abundance is not well studied.

Reductions of biological control by urban warming are plausible, as warming can change natural enemy abundance, behavior and community structure in natural and agricultural systems (Hance et al. 2007; Romo and Tylianakis 2013; Evans et al. 2013). For example, in natural grasslands, warming caused intraguild predation, which led to local extinction of a spider species (Barton and Schmitz 2009). It is also possible that community composition of spiders shifts across temperatures, such that species that are not heat tolerant flee or do not survive (Kingsolver et al. 2013), leading to losses of important species for biological control. Across a variety of landscape types, warming has been associated with lower spider abundance (Shochat et al. 2004). In urban areas, one study found that warming decoupled interactions between a parasitoid wasp and its scale insect host (Meineke et al. 2014), but other studies found little effect of warming on parasitoid composition or parasitism rate (Meineke et al. 2013; Dale and Frank 2014b). In contrast, it is plausible that the high abundance of small, soft-bodied herbivores at hotter urban sites could benefit some natural enemies, particularly spiders, which frequently increase in abundance with prey abundance (Johnson et al. 2012; Lowe et al. 2014, 2015). Therefore, the net effects of urban warming on natural enemy communities are difficult to predict.

Here, we used a novel experimental system to dissociate warming and prey abundance, providing one of the first assessments of how urban abiotic and biotic factors affect natural enemies. We chose trees living in a range of urban temperatures and sprayed half of them with horticultural oil to kill small, soft-bodied herbivores—including those that become more abundant with urban warming (Meineke et al. 2016)—without negatively affecting natural enemies (Baxendale and Johnson 1988; Raupp et al. 2001; Frank 2012). We predicted that warming would be a dominant factor influencing natural enemy community structure. Specifically, because herbivorous arthropods are more abundant in warmer trees, and because prey availability is a predictor of natural enemy abundance (Wise 1979; Chen and Wise 1999; Halaj and Wise 2002), our first hypothesis was that certain natural enemies would be more abundant at warmer urban sites, though not on trees treated with oil to reduce prey abundance. Our second hypothesis was that natural enemy diversity would be lower and, thus, community composition would be different in hotter compared to cooler urban trees, because warming could alter community composition by reducing the abundance of less heat-tolerant species.

Methods

Study area

Raleigh, North Carolina, located at 35.77°N, 78.64°W, is the second-largest municipality in the state, covering 37,900 hectares (Raleigh Department of City Planning 2015) and home to 451,066 people according to the US Census 2015 (www.census.gov). The city has shown rapid total growth over the past 5 years (6.99% increase from 2010 to 2014; North Carolina Office of State Budget and Management 2015) and is estimated to be one of the fastest-growing cities in the USA in the next 15 years (Chesser 2014; UN 2014). The city has a humid subtropical climate with an average long-term winter temperature of 5.8 °C and an average long-term summer temperature of 25.6 °C. Climate data were retrieved from the NOAA National Climatic Data Center (www.ncdc.noaa.gov) from the North Carolina State University weather station as 1981–2010 station normals.

Study sites

To investigate natural enemy communities living in street trees, we sampled arthropods from willow oaks (*Quercus phellos*). This species is a common shade tree found throughout the eastern USA and across the urban warming gradient in Raleigh, NC. Twenty sites were selected using a map of Raleigh street trees overlaid with a Landsat infrared layer of surface temperature from April 7, 2011. Ten of the relatively hot sites and 10 of the relatively cold sites (above or below median surface temperature of all street trees) found within the city of Raleigh were chosen, each with two willow oak trees <30 m apart from one another. Therefore, we chose 40 trees in total. The mean (±SEM) study tree diameter at breast height (DBH) was 20.9 ± 1.2 cm. To reduce spatial autocorrelation, we selected sites that were at least 200 m apart and spread throughout the city (Fig. 1).

One willow oak tree per site was sprayed with horticultural oil (SuffOil-X; BioWorks, Victor, NY) using a mist blower (model: 451, Solo, Newport News, VA) to remove small, soft-bodied herbivores that often increase with warming and may be prey for natural enemies. This treatment was repeated six times. A concentration of 2 l per 100 l of water was used in March 2013, September 2013, February 2014 and March 2014. A concentration of 1 l per 100 l of water was used in July 2013, April 2014 and May 2014. Therefore, each site had two trees, one of which was sprayed and one of which remained unsprayed. A thermocron iButton data logger (model: DS1921G, precision: 0.5 °C, accuracy: ±1.0 °C; Dallas Semiconductor, Dallas, TX), housed in wall mounts (Dallas Semiconductor of Dallas) and 2.54-cm deep plastic cups to protect from direct sunlight and precipitation, was installed on the northern, bottommost branch of one tree per site to record air temperatures every hour.

Data collection

Samples were collected from each tree once per year in August 2013 and August 2014 using a funnel beat sampler (Sperry et al. 2001). This sampler is a 30.5-cm diameter funnel attached to a 2.5-m pole, with a hinged lid. The lid is attached to a rope that allows the user to beat the tree branches, causing arthropods to fall into the funnel and down into a sampling jar fixed to the
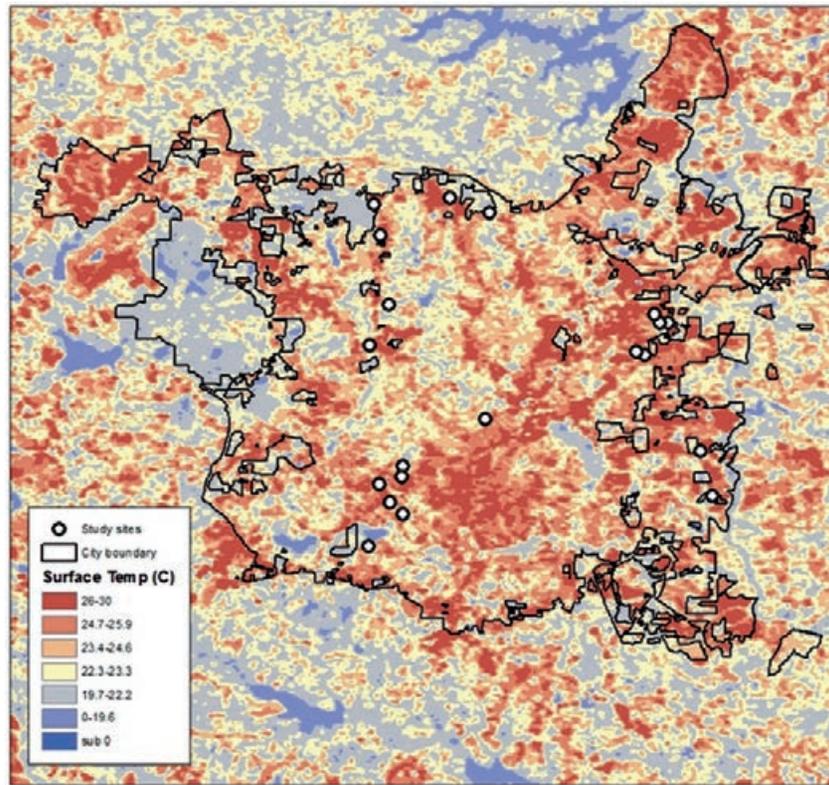
Figure 1. Map of study sites. We sampled a total of 40 trees at 20 sites across a gradient of urban temperatures within the Raleigh, NC, USA urban heat island.

bottom of the funnel, filled with ethanol. To standardize sampling, we beat leaves into the funnel to dislodge arthropods at 12 locations around the perimeter of the lower canopy. We beat each set of leaves four times. Samples were collected from the lowest part of the crowns and stored in 95% ethanol. Herbivores were identified to the lowest taxonomic level possible without dissection under a dissection microscope. Spiders (Order Araneae) were removed from the samples, sorted into separate vials per tree, counted, and identified to family under a dissection microscope. We think it likely that our sampling method is more likely to capture roving and sit and wait spiders and is less effective for web builders.

Statistical analyses

All analyses were performed in RStudio (R Core Team 2015). The ibuttons recorded inaccurate midday temperatures ($+45\,°C$). We thought this was due to solar radiation that heated ibuttons directly, such that readings were inaccurate (Hubbart et al. 2005). To avoid using these biased readings, we extracted readings between 1800 and 2000 hours and used these in analyses. These data capture the urban heat island effect, which becomes more intense steadily after 1500 and levels off around 2000 hours (Gaffin et al. 2008), without capturing biases introduced by solar radiation. We calculated all average temperatures used in analyses in the *plyr* package (Wickham 2011). In 2013, ibuttons failed at two sites, and, in 2014, an ibutton failed at one site. These sites were discarded from analyses. An additional site was removed from the study due to a dissatisfied homeowner. In addition, we conducted a simple linear regression between average temperatures in 2013 and in 2014 to confirm that sites that were hotter in 2013 were also hotter in 2014.

We examined the effects of August 1–15 average temperature and oil treatment on spider and herbivore abundance ($\log + 1$ transformed) using a linear mixed-effects model (LME) in the *nlme* package (Pinheiro et al. 2013). We used August 1–15 temperatures because these were the dates just before spiders were collected during which we had thermal data from both years. In all LMEs, R^2 values were derived from formulae for marginal and conditional R^2. We used these same methods to analyse spider family diversity, richness, and evenness. To calculate diversity, we used the Shannon diversity index in the *vegan* package. We calculated Pielou Evenness as Shannon diversity/log(family richness) (Pielou 1966).

We used NMDS in the *vegan* package (Oksanen et al. 2016) to examine differences in spider family composition among trees. NMDS is a robust ordination method for community analysis because it does not make distributional assumptions about the data (Minchin 1987). NMDS was used to create a dissimilarity matrix among all study trees using the Bray-Curtis dissimilarity coefficient (Faith et al. 1987). We visualized the NMDS matrix using *ggplot2* (Wickham 2009) and then fitted spider family and environmental vectors using the 'envfit' function in the *vegan* package. The only environmental variable we included was August 1–15 average temperatures. This allowed us to determine what spider families' abundances were significantly correlated with the matrix, i.e. which spider families drove spider community structure, using temperatures that were comparable across years. Similarly, this allowed us to test whether urban temperatures were associated with changes in spider community structure.

Having found that spider community structure correlated with temperature in 2013, we then examined the effect of August 1–15 temperatures and oil treatment on spider

presence/absence across both years of study. To do this, we used logistic regressions in the *lme4* package (Bates et al. 2014). Temperature and oil treatment (yes/no) were specified as fixed effects and site was specified as a random effect. Having found nearly significant effects of August 1–15 temperatures on Anyphaenid occurrence, we then ran these same models with summer average temperatures from July to August in each year to more thoroughly test spider family responses to the urban heat island effect.

Results

'Hot' sites were consistently hot in 2013 and 2014, as expected because urban temperatures are driven by impervious surface and coarse vegetation (Dale and Frank 2014b), characteristics that are structural and should drive consistent relative air temperatures across sites ($F_{1,14}$= 13.85, R^2=0.46, P=0.002). In both years, spiders were by far the most abundant natural enemies (Fig. 2). In total, we collected 328 spiders from 17 families (Supplementary Fig. S1). As expected from previous studies, herbivorous arthropods were more abundant at hotter urban sites, but only in 2013 ($F_{1,15}$=8.19, P=0.011; Fig. 3a) and not in 2014 (P > 0.05; Fig 3b) when conditions were cooler and wetter. Similarly, oil treatments significantly reduced herbivorous arthropod abundance in 2013 ($F_{1,16}$=4.69, P = 0.046; Fig. 3a) but not in 2014 (P > 0.05; Fig 3b). Spider abundance (Fig. 3c, d), diversity, richness and evenness were not correlated with site air temperatures in either year (P > 0.05; Supplementary Fig. S2). Spider community composition was significantly correlated with site air temperature in 2013 (R^2=0.165, P=0.035, Fig. 4a) but not 2014 (P > 0.05, Fig. 4b). In 2013, Anyphaenids were significantly less likely to be found at sites with hotter summer average air temperatures (Z = -1.962, P=0.048; Fig. 5).

Discussion

Spiders were by far the most abundant natural enemy group in our study and, thus, were the focus of our analyses. Experimental reduction of arboreal herbivores did not measurably affect spiders. However, spider community composition was associated with urban warming in 2013 and was driven by lower abundance of Anyphaenidae ('ghost spiders'), a family known to eat aphids and other soft-bodied insect herbivores (Patt and Pfannenstiel 2009; Ximenez-Embun et al. 2014). In contrast, urban heat did not affect spider community composition

in 2014, nor were ghost spiders absent from the hottest sites in that year. We suggest that urban heat affected ghost spider abundance in 2013 and not in 2014 because 2013 was a warmer, drier year during which spiders were exposed to more extreme urban conditions. Specifically, 2013 temperatures in our focal city of Raleigh, NC, were substantially warmer than those in 2014 (mean= 26.4±0.7 °C vs. 24.0±0.5 °C in August when samples were collected); similarly, Raleigh got 12 cm less rain in August 2013 than in August 2014. Together, we find that, while prey availability did not affect spiders, urban warming in a relatively warm, dry year was associated with reduced ghost spider prevalence.

As climate fluctuates, sensitive species capable of rapid dispersal, such as spiders, which balloon to new habitats across far distances (Bell et al. 2005), may cycle in and out of urban arboreal communities. Our results suggest that ghost spiders cannot withstand temperatures at the hottest urban sites in hot, dry years but can recolonize these sites when conditions are milder. This is consistent with another study that shows ghost spiders were less abundant at sites in Maryland, USA, that had more sun exposure (Shrewsbury and Raupp 2006). Interestingly, ghost spiders in this study were important predators of lace bug pests. Likewise, a 2-year study in Arizona showed that spider abundance was greater in a cool, wet El Niño year than a subsequent hot, dry year (Shochat et al. 2004). As the climate warms globally, and urban warming intensifies locally, sensitive organisms may be eradicated from hot areas within cities. However, as the differences between 2013 and 2014 demonstrate in our study, effects of urban warming will depend on background climate, yearly temperature fluctuations, and extreme heat events, all of which may increase with climate change; for a thorough discussion of this topic, see Diamond et al. (2015). If spiders are important biological control agents in urban trees, as they are in other systems (Riechert and Bishop 1990; Riechert and Lockley 1984), lower abundances of certain spider species within the hottest parts of cities may release herbivores in trees from predation, allowing them to become pests.

Spider abundance is correlated with spider prey abundance in other studies (Wise 1979; Chen and Wise 1999; Halaj and Wise 2002). Therefore, we predicted that the removal of soft-bodied arthropods with horticultural oil would change spider community composition. However, we did not find that treating trees affected overall spider abundance, community composition, or diversity. One explanation for this could be that spiders do not feed on the prey removed by the oil treatment, such as
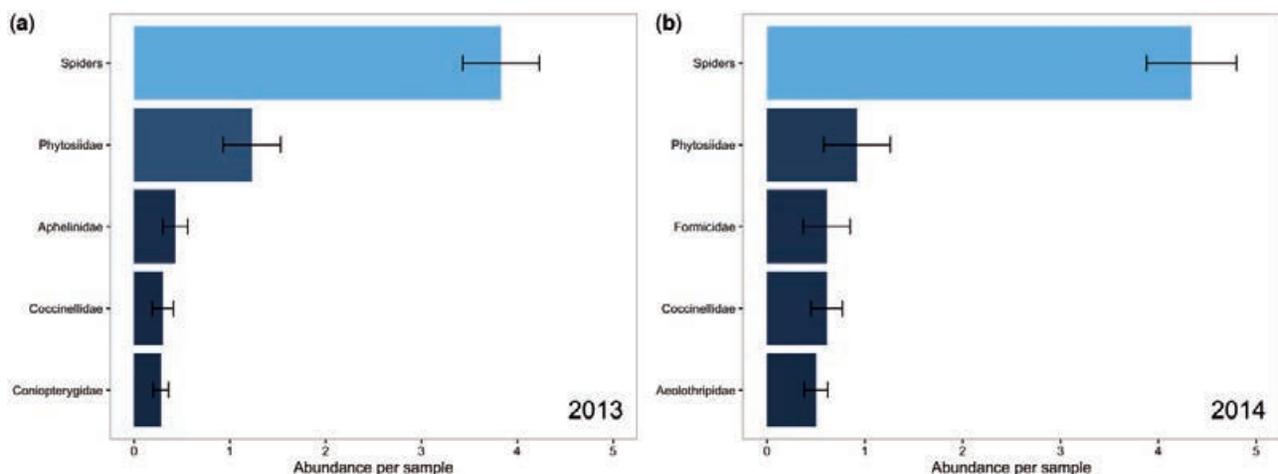

Figure 2. Most abundant 5 natural enemy families. Spiders were the most abundant natural enemies captured in (a) 2013 and (b) 2014.
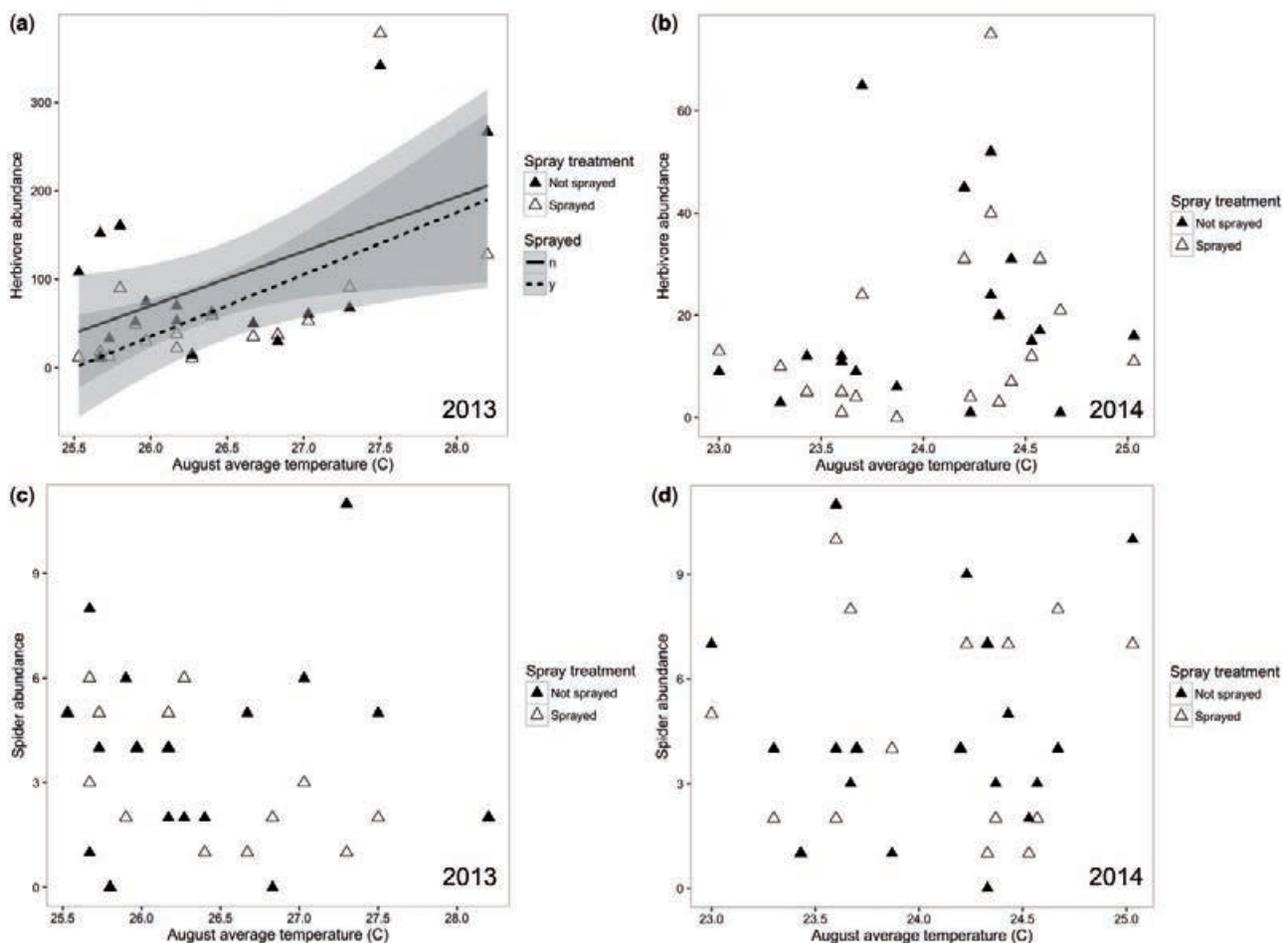
Figure 3. Effects of urban warming on herbivore and spider abundances. Herbivore abundance was significantly higher at hotter sites in (a) 2013 but not (b) 2014. (c, d) Spider abundance did not respond to temperature in either year. Lines represent means and shaded areas represent 95% confidence intervals in cases wherein response was significant.
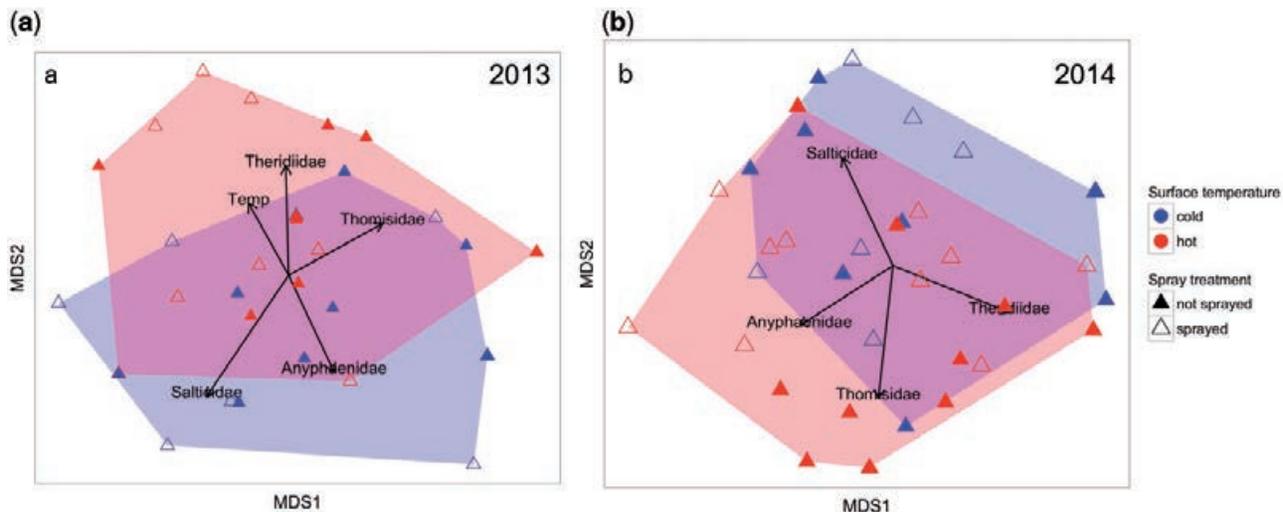

Figure 4. Effects of urban warming on spider community composition. Spider community composition was significantly correlated with site temperature in (a) 2013 but not in (b) 2014. Colors represent surface temperatures from a thermal map used to choose study sites. Hot sites had surface temperatures above the median experienced by all Raleigh city street trees, and cold sites had temperatures that were cooler than this median.
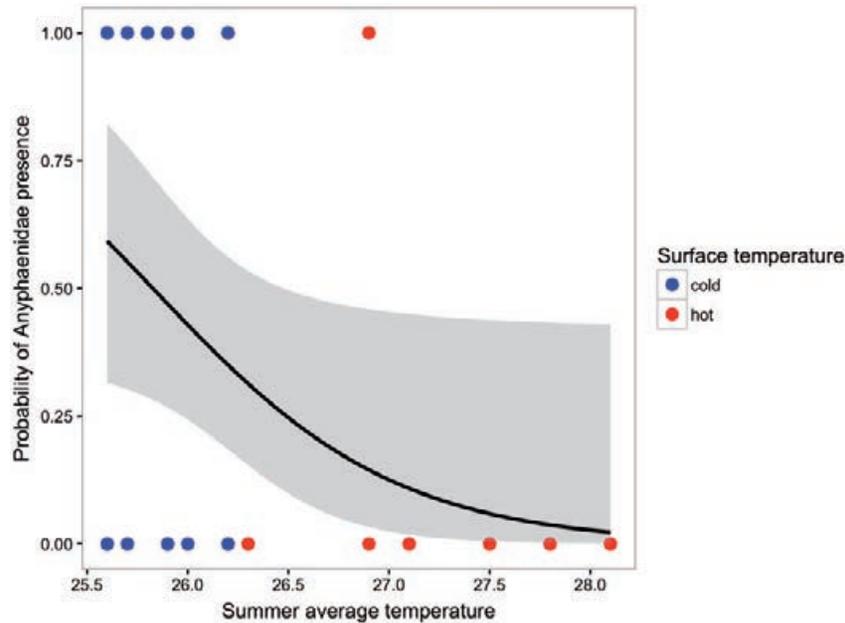
Figure 5. Effects of urban warming on incidence of ghost spiders. Anyphaenidae ("ghost spiders") were significantly less likely to occur at urban sites with higher air temperatures in 2013. The line represents predicted probability of Anyphaenid presence and shaded areas represent the 95% confidence interval.

spider mites. However, we think it more likely that certain spider groups were able to supplement their diets with remaining prey, including other spiders (Wise 2006). Our results suggest that spiders' generalist diets are convenient for maintaining biological control, as horticultural oil is a common tactic to manage arboreal herbivores but has low toxicity to natural enemies (Fondren and McCullough 2005; Hubbard and Potter 2006; Raupp et al. 2001; Frank 2012).

Few studies address the community ecology of species that live in urban trees. Our paper is a starting point for understanding how arboreal natural enemy communities are structured in relation to specific biotic and abiotic factors. Our study units were individual urban trees, which helped control for local plant species diversity and plant structure that can affect prey abundance and natural enemy communities (Hanks and Denno 1993; Tooker and Hanks 2000; Shrewsbury and Raupp 2006;). Our oil treatment further allowed us to disentangle warming from prey abundance, which tend to be positively correlated in urban trees (Meineke et al. 2016). We also controlled for habitat factors at a landscape scale, as we compared urban trees that differed in temperature rather than comparing urban to rural trees, as is common in urban ecology research. Family level taxonomic resolution in studies such as ours can be sufficient to document effects of warming and urbanization on spiders and arthropods, generally (Shochat et al. 2004; Youngsteadt et al. 2016). However, future studies could use our study design to reveal how individual species and their unique life histories and physiological responses drive this pattern and biological control.

Data availability

Data will be submitted to the Dryad repository upon publication.

Supplementary data

Supplementary data are available at *JUECOL* online.

Ethics statement

This project was approved by the City of Raleigh Parks, Recreation, and Cultural Resources Department.

Author contributions

E.K.M. and S.D.F. conceived of the study. E.K.M. collected arthropods and identified all non-spider arthropods. A.J.H. identified spiders. E.K.M. carried out statistical analyses. G.M.W. consulted on community analyses. All authors wrote the paper and gave final approval for publication.

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