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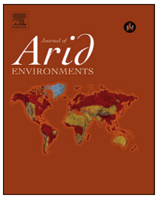

Seasonality and land cover characteristics drive aphid dynamics in an arid city

Riley Andrade [a], [b], [*], Heather L. Bateman [c], Yun Kang [c]

[a] School of Geographical Sciences and Urban Planning, Arizona State University, 975 S Myrtle Ave, Tempe, AZ 85281, United States
[b] College of Integrative Science and Arts, Arizona State University at the Polytechnic Campus, 6073 S. Backus Mall, Mesa, AZ 85212, United States
[c] College of Integrative Sciences and Arts, Arizona State University at the Polytechnic Campus, United States

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ABSTRACT

Urbanization of arid environments results in biotic communities that differ from the surrounding desert. The growth of cities has lowered biodiversity and increased abundance of generalist species, known as urbanophiles. However, the mechanisms by which specific organisms can dominate urban ecosystems remain unclear. Using an 11-year data set from the Central Arizona-Phoenix Long-Term Ecological Research program, we evaluated how aphids, an arthropod urbanophile, were affected by habitat type and seasonality in Phoenix, Arizona, USA. Twenty-five sites were selected in habitat types varying in land use and land cover characteristics. Aphids varied along a gradient of water availability and vegetation, rather than level of urbanization. Seasonal aphid abundance was the highest in the spring and lowest in the summer, a pattern that did not differ between habitat types. We developed a mathematical model parallel to our empirical study to explain how temperature may affect the temporal patterns. The analysis of our model demonstrated that although seasonal patterns were similar across habitats, slight shifts in microclimate can result in dramatic variation of population dynamics. We conclude that both land cover and climate have huge impacts on aphids and that urbanophiles are able to take advantage of favorable environmental conditions caused by urbanization.

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1. Introduction

Urbanization can shift patterns of species composition, whereby environmental filtering caused by human influence creates novel ecological communities (Swan et al., 2011). Cities in arid environments often provide an abundance of resources that are limiting in desert habitats, such as water availability (Martin and Stabler, 2002; Grimm et al., 2008). Rivers are diverted for anthropogenic purposes, redistributing water across the landscape for municipal, residential, and agriculture use (Grimm and Redman, 2004). Human development also causes distinct habitat variation along similar land use types, fragmenting the landscape into pronounced patches of habitat. Overall, urbanization creates a variety of altered environmental characteristics, which provides an interesting and complex contrast with natural habitats (Carreiro and Tripler, 2005; Banville and Bateman, 2012).

Biotic communities in urban environments have been shown to increase in abundance, but decrease in evenness and richness (McKinney, 2008). Shochat et al. (2010) proposed a conceptual model explaining how urban environments can lead to the success of a few select species, commonly referred to as urbanophiles. Urbanophiles are tolerant of urban constraints and are able to maintain stable, if not higher, populations in cities (Blair, 1996). Urbanophiles are able to achieve higher abundances by competitively excluding other species and can often establish enormous population densities when compared to their wildland counterparts (Marzluff et al., 2001; Faeth et al., 2011).

Aphids (Aphididae) are an example of an arthropod urbanophile, as well as a common agricultural pest, which exhibit extreme population variation between urban and non-urban areas. Aphids are able to sustain higher annual population levels and thrive in arid cities (Bang and Faeth, 2011). Part of their ability to succeed is due to cyclical parthenogenesis, an alternation of sexual and asexual reproduction (Simon et al., 2002). During asexual reproduction cycles, which typically occur in the spring or summer months, offspring start developing inside their unborn mother, leading to short generation times and continuous reproduction

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[*] Corresponding author. School of Geographical Sciences and Urban Planning, Arizona State University, 975 S Myrtle Ave, Tempe, AZ 85281, United States.
E-mail address: rkburnet@asu.edu (R. Andrade).

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cycles. Due to their reproduction strategy, aphid populations are able to grow exponentially under ideal temperature and environmental conditions (Logan et al., 1976), but urbanization can potentially alter these controls due to the urban heat island (Brazel et al., 2007) and the increase of limiting resources.

Quantifying the temporal patterns of aphids under different levels of urbanization and land cover is an important step to understand the potential mechanisms responsible for urbanophile success in human dominated landscapes. Despite the number of observational studies of biodiversity in cities, the mechanisms behind these trends remain unclear (Shochat et al., 2006). Theoretical models developed in parallel with empirical studies have increased understanding of mechanisms behind ecological patterns (e.g., MacArthur, 1955; Oksanen et al., 1981; Chase, 1996). Statistical modeling of long-term data combined with theoretical modeling of seasonal aphid dynamics across different habitat types will allow us to better understand the success of urban adapters within coupled human and natural systems.

Our research objectives are to use long-term data to: (1) compare aphid abundance across aridland habitat types (varying in land cover and land use), (2) observe how temporal aphid dynamics are affected by seasonal controls, and (3) develop a theoretical model of aphid dynamics and apply the model to help explain the potential effects of urbanization and microclimate on the population dynamics of aphids.

2. Methods

2.1. Study area and sites

As part of the Central Arizona-Phoenix Long-Term Ecological Research (CAP LTER) program, ground dwelling arthropods have been monitored in Phoenix, Arizona, USA (33° 30′ N, 112° 11’ W) since 1998 (Grimm and Childers, 2017). Phoenix, an urban ecosystem in an arid environment, offers a unique perspective by providing an extreme example of habitat contrast compared to the outlying desert (Faeth et al., 2005). Phoenix is located in the Sonoran Desert, a biome characterized by high temperatures that can exceed 49 °C and minimal precipitation (76–400 mm annually) occurring during two seasonal periods. The urban mosaic is highly heterogeneous in both land use and land cover characteristics. Variation of environmental characteristics can also occur within similar land uses. For example, arthropod habitat in residential yards can vary between factors such as social economy (Hope et al., 2003), plant diversity (Kinzig et al., 2005), water use (Breyer et al., 2012), and microclimate (Jenerette et al., 2007; Middel et al., 2014).

2.2. Habitat characteristics and classification

Previous research on arthropod biodiversity has separated urban habitats in Phoenix into discrete categories in terms of land use and habitat characteristics (McIntyre et al., 2001; Shochat et al., 2004; Bang et al., 2012). Following the established methodology, this study focuses on aphids sampled in across 25 sites categorized into one of five major habitat types: desert, xeric (urban residential), mesic (urban residential), remnant desert, and agricultural (Fig. 1). The five habitat types that were surveyed vary in land use and vegetation density. Distinct vegetation characteristics, irrigation regimes, and microclimates between the different habitat types creates patches characterized by a large amount of environmental dissimilarity within the urban landscape.

Agricultural habitat (n = 6 sample sites) comprises 22% of the study area. Agricultural areas in Phoenix are primarily a mixture of cultivated vegetation and moist bare soil; heavy irrigation regimes are required year round for vegetation watering purposes. A measure of live vegetation cover, determined by the NDVI (Normalized Difference Vegetation Index) indicates higher vegetation cover than other habitat types (Buyantuyev and Wu, 2009). During the summer, when the maximum temperature threshold of many arthropods is reached, agricultural areas in Phoenix have the lowest day and night-time temperatures (Grossman-Clarke et al., 2010).

Mesic habitat (n = 4 sample sites) is defined as urban residential land use with high density vegetation cover that comprises 12% of study area. Mesic habitat is similar to agriculture in terms of heavy irrigation to support vegetation, but consists of smaller, fragmented patches. The NDVI of mesic yards and lawns is similar to agriculture land use, and greater than xeriscaped yards or the surrounding desert. Likewise, irrigation contributes to the cooling effect of residential areas with extensive mesic landscaping (Grossman-Clarke et al., 2010).

Xeric habitat (n = 5 sample sites) comprises 21% of study area. Similar to mesic habitat, xeric habitat is defined as urban residential land use. However, the difference between the two habitat patch types are land cover characteristics and water regimes. Xeric habitat is characterized by low density, native vegetation. Due to drought tolerant plants and sparser vegetation cover, xeric yards often require less irrigation than their mesic counterparts (Richard, 1993), but can be highly variable in their irrigation patterns (Martin, 2001). The NDVI of xeric habitats is decoupled from the precipitation and seasonal patterns that control the surrounding desert landscape. Vegetation indices are often intermediate of desert and mesic habitats (Buyantuyev and Wu, 2009), xeric habitats do not offer the same cooling benefit as mesic habitats. Daytime temperatures in xeric habitats are higher than either mesic or agricultural patches (Grossman-Clarke et al., 2010).

Desert remnant habitat patches (n = 3 sample sites) are a very small portion of the total study area (about 1%). The habitat type is fragmented and surrounded by the urban matrix. Desert remnant patches are often municipal parks and are typically not actively planted or irrigated, unless they are part of a conservation effort. This creates a habitat type that looks similar to the Sonoran Desert, but differs in terms of patch size, ecological functioning, and microclimate.

Desert habitat (n = 7 sample sites) is defined as undeveloped Sonoran Desert and comprises 8% of study area. Patch size is large and continuous, especially compared to the small, discrete habitat patches found in the city. The effects of the urban heat island often cause desert temperatures to be comparable to the urban core during the day, but much lower at night (Brazel et al., 2007). Vegetation productivity is tied to seasonal precipitation and temperature cycles, and is often more variable than the city (Buyantuyev and Wu, 2009).

The approximate distribution of habitat area was derived from a land cover classification of the Phoenix metro area produced in 2005 using the expert system model (Stefanov et al., 2001), the land cover classification has an overall accuracy of 83% with 12 classes (Buyantuyev, 2007). Overall, our five habitat types comprised 64% of the total Phoenix study area (Fig. 1), other habitat types that were not sampled as part of the long-term study would include river gravel, compacted soil, fluvial and lacustrine sediments (canals), and asphalt.

2.3. Sampling and statistical analysis

Ground arthropods were sampled according to Central Arizona-Phoenix Long-Term Ecological Research protocol (available: http://caplter.asu.edu/data/protocols?id=22) from 1998 to 2013. Ground-dwelling arthropods were collected at each site using 10–21 dry, unbaited pitfalls (500-mL plastic cup flush with the ground surface)

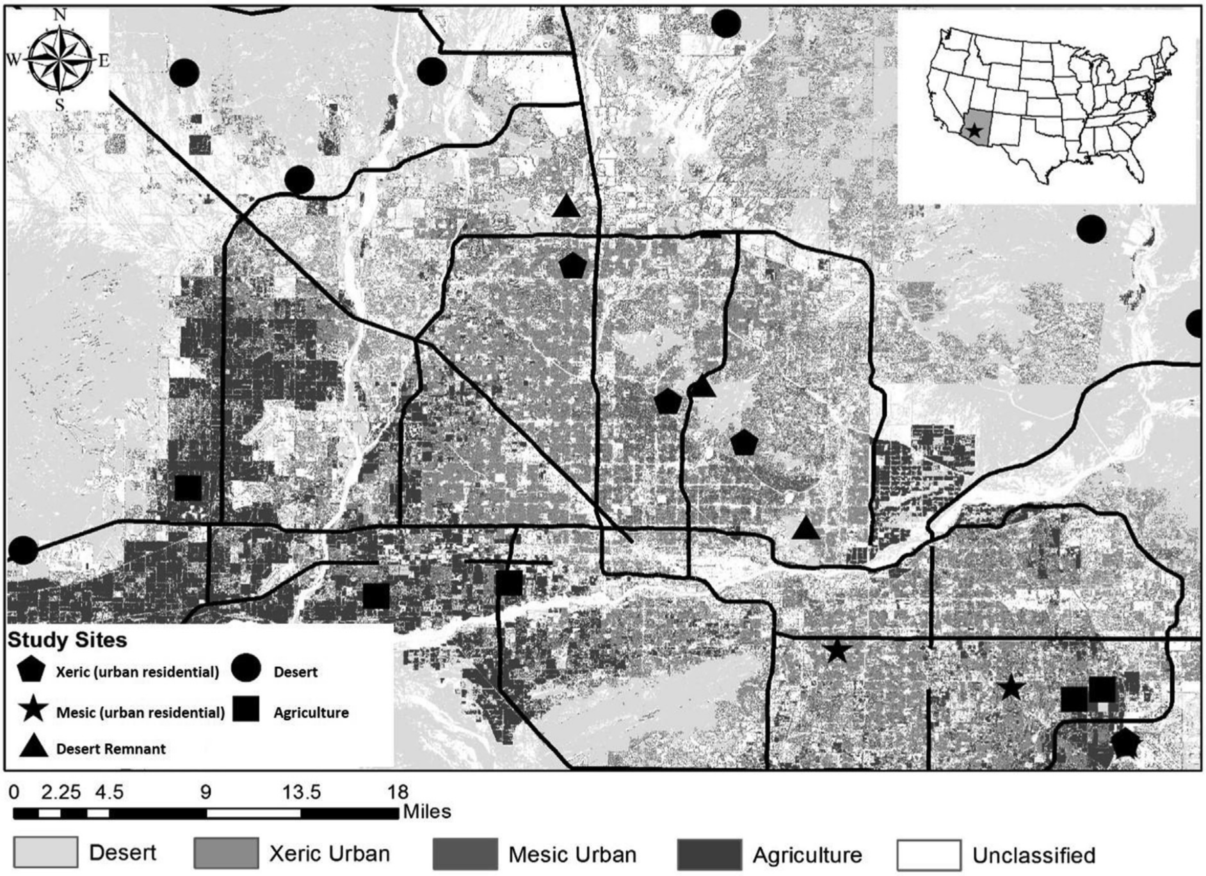

Fig. 1. Study area testing the effect of habitat type and seasonality on aphid abundance in Phoenix, Arizona, USA from 2002 to 2013. Sites differ by land cover classification, shown by a greyscale gradient, where darker colors represent habitat with high moisture availability and productivity, whereas lighter colors represent low amounts of water and vegetation. Sites are defined as: agriculture (square, n = 6), mesic urban (star, n = 4), xeric urban (trapezoid, n = 5), remnant desert (triangle, n = 3), and desert (circle, n = 7).

spaced 5 m apart along a line transect. Traps were set for 72 consecutive hours quarterly. Because a majority of the sites were relocated and traps reduced in 2002, we used data collected from 2002 to 2013. To reduce any potential bias from year effects, we included only sites sampled during each season for at least 2 years during the period of study and did not change in land use during the 11-year time period. Quarterly sampling was defined by a four season calendar cycle: winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November). Since we were interested in seasonal effects, data were averaged across years. Relative aphid abundance at each site was calculated by dividing the amount of aphids collected by number of traps and then standardizing by the average number of traps: ($\sum$aphids/number of traps)*10. Prior to analyses, aphid distribution was determined to be non-normal via a Shapiro test and Normal Probability Plot. We employed the Box-Cox method (Sakia, 1992) and normalized data using an inverse square root. We tested the effect of habitat on temporal controls using a General Linear Model repeated measures within seasons and between habitat types. If a significant difference was detected we employed a Tukey HSD post hoc test to determine between which habitats and seasonal abundance differed. All statistical tests were performed using SPSS (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp).

2.4. Model derivation

Mathematical models have been an important tool in understanding population dynamics of aphids (Dixon, 1977; Carter et al., 1982; Sentis et al., 2012). However, there is limited work on models that incorporate both the mechanisms of change and biological constraints that regulate aphid population dynamics with varied temperature. For this reason, we derived a simple mathematical model with the temperature-dependent growth rate to explore the effects of habitat type and seasonality on the population dynamics of aphids.

Let $A(t)$ be the population density of aphid at time t. We assumed the population dynamics of aphid in a season followed a traditional logistic growth function in the absence of predation that can be described by the following equation:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) \tag{1}$$

Where r is the intrinsic growth rate which can be a function of temperature and K is the carrying capacity of aphids in their environment. Habitat type plays a key role in determining both the intrinsic growth rate and the carrying capacity; factors such as resource availability, space of the patch size, and fragmentation of the habitat can change drastically throughout an urban land use mosaic. For example, we expected a larger value of K, carrying capacity, for aphids in agriculture habitats due to available resources, higher productivity, and increased water availability.

According to Hassel and May (1973), Holling's type II function response was the most common type of response among arthropod predators. More specifically, based on the work of Morales and

Burandt (1985) and Harmon et al. (2009), the number of aphids captured per day by predators corresponded to the functional response of Holling's type II. Thus, we assumed that the functional response for our study system is Holling's Type II, which gave the following formulation of the population dynamics of aphids in the presence of predation:

$$\frac{dA}{dt} = rA\left(1-\frac{A}{K}\right) - \frac{\alpha A}{1+\beta A} = rA\left(1-\frac{A}{K}-\frac{\alpha}{1+\beta A}\right) \tag{2}$$

Where parameter α measures the predation rate from generalist predators; $\alpha = a/r$; and $\beta = a$ * handling time of predators.

Temperature is a key abiotic factor that regulates insect population dynamics, developmental rates, and seasonal occurrence (Campbell et al., 1974; Logan et al., 1976). Intrinsic rate of increase, upper and lower developmental thresholds, fecundity, and survivorship schedules are essential for describing temperature effects on aphid population dynamics (Walgenbach et al., 1988; Aldyhim and Khalil, 1993; Asin and Pons, 2001; McCornack et al., 2004). In urban ecosystems temperature patterns have been shown to vary on a microhabitat scale along urbanization gradients (Stabler et al., 2005). Thus, we expected that aphids will have different growth rates across the urban landscape due to varying local temperatures. For simplicity, we hypothesized that the differences in aphid abundance across seasons is primarily driven and can be proxied by climatic controls; therefore, we assumed that seasonal growth rates in our model are being controlled by biological constraints interacting with temperature fluctuations whereas other parameters such as K, α, β in Model (2) are fixed.

Briere et al. (1999) proposed a temperature-dependent growth rate model with a nonlinear part at low and high temperatures and a linear portion at intermediate temperatures. Let T be the average seasonal temperature, the Briere model is defined as follows:

$$r(T) = r_0 T\left(T - T^A_{min}\right)\left(T^A_{max} - T\right)^{\delta} \tag{3}$$

Where r_0 can be considered as the baseline growth rate of aphid; $\delta > 0$ is a parameter that can be fitted from data; and T_{Amin}, T_{Amax} is the respective minimum, maximum temperature that aphids can tolerate. The formulation (3) implies that aphids have an optimum temperature for their growth rate. Model (3) has been successfully applied in evaluating the intrinsic growth rate of a coccinellid (*Stethorus punctillum*) by Roy et al. (2003) and has also been applied in evaluating the intrinsic growth rate of an aphid species, (*Hyalopterus pruni*), with $\delta = 0.76$ in Latham and Mills (2011), we adopted the value of $\delta = 0.76$ for our analysis. According to the empirical work of Hirano et al. (1996) and McCornack et al. (2004), the minimum temperature that aphids can survive is $T_{Amin} = 8.6$ °C, whereas the maximum temperature that aphids can survive is $T_{Amax} = 35$ °C. Minimum and maximum temperature values were fixed for all simulations and parameter estimations of our model.

We defined quarterly sampling by the four season cycle used for statistical analysis to make our model comparable with our field collected data. We modeled the temperature T as the following sine function with four periods to indicate the average temperature of each season:

$$T(t) = b\sin\left(\frac{\pi t}{2} - c\right) + e \tag{4}$$

Where parameter b, c, e are estimated from historical temperature data. We expected that different habitat types have different values of b, c, and e. Specifically, we used temperature data collected at Sky Harbor airport to fit a sine equation to the average seasonal temperature fluctuations for the last 12 years in metro Phoenix as follows:

$$T(t) = 10.4\sin\left(\frac{\pi t}{2} - 0.1\right) + 24.3 \tag{5}$$

The temperature function (5) has four periods to approximate our defined lunar seasons; where $T(1) = 34.65$, $T(2) = 25.34$, $T(3) = 13.95$, $T(4) = 23.26$ is the average temperature (°C) of summer, autumn, winter, and spring respectively in Phoenix (Fig. 2). To model the temperature variation from the predicted values due to the different degrees of urbanization, we incorporated a parameter d, measuring the average temperature difference between the study area and the Sky Harbor airport, into Model (5):

$$T(t) = 10.4\sin\left(\frac{\pi t}{2} - 0.1\right) + 24.3 + d \tag{6}$$

We then combined Model (6) with the temperature-dependent growth rate function $r(T(t))$ Model (3), to conclude that $r(T(t))$ is a function of temperature which has four periods. This allowed us to define $r(t) = r(T(t))$ as the average intrinsic growth rate of aphid over the season $[t-1, t]$. Model (2) is a continuous time model; thus we modified Model (2) in a way such that each of its output is the average population density of aphids in a season. To do this, we let each time interval $[t, t+1]$ represent one of the four seasons.We assumed that aphid population growth rate in this interval is constant:

$$\frac{dA}{Ad\tau} = \bar{r}\left(1 - \frac{A(t)}{K} - \frac{\alpha}{1+\beta A(t)}\right), \quad \tau\,\varepsilon[t, t+1]$$

Where r is the average intrinsic growth rate over the season [t, t + 1]:

$$\begin{aligned}\bar{r} &= r(T(t+1))\\ &= r_0 T(t+1)\left(T(t+1) - T^A_{\min}\right)\left(T^A_{max} - T(t+1)\right)^{0.76}\end{aligned}$$

Therefore, we have as follows:

$$\begin{aligned}\int_t^{t+1}\frac{dA}{Ad}d\tau &= \ln\left(\frac{A(t+1)}{A(t)}\right)\\ &= \int_t^{t+1}\bar{r}\left(1 - \frac{A(t)}{K} - \frac{\alpha}{1+\beta A(t)}\right)d\tau, \tau\,\varepsilon[t, t+1]\end{aligned}$$

This gives our final population model of Aphid with seasonal changes in temperature:

$$A(t+1) = A(t)e^{\bar{r}\left(1 - \frac{A(t)}{K} - \frac{\alpha}{1+\beta A(t)}\right)}$$

$$\begin{aligned}\bar{r} &= r(T(t+1))\\ &= r_0 T(t+1)\left(T(t+1) - T^A_{min}\right)\left(T^A_{max} - T(t+1)\right)^{0.76}\end{aligned}$$

$$T(t+1) = 10.4\sin\left(\frac{\pi(t+1)}{2} - 0.1\right) + 23.95 + d \tag{7}$$

Where $A(t+1)$ is the average population density of aphids over season $[t, t+1]$ which is a nonlinear function of the average population density of aphids over season $[t-1, t]$ (i.e., $A(t)$), and the average intrinsic growth rate over the season $[t, t+1]$

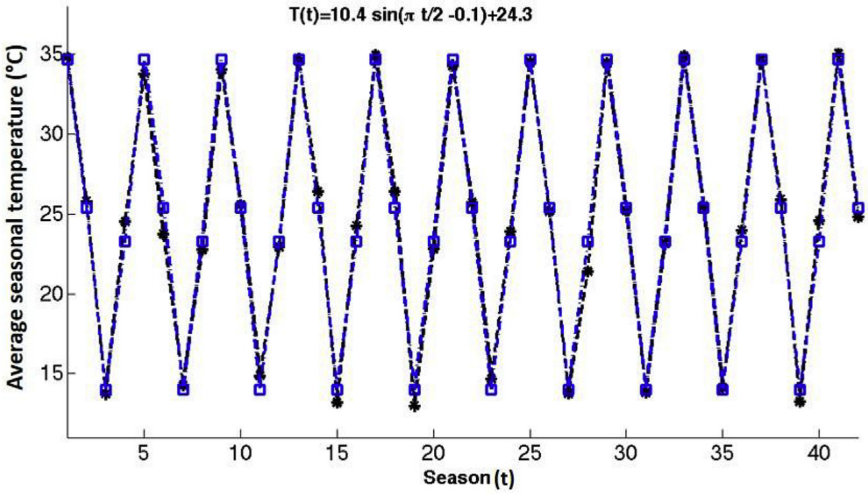

Fig. 2. The fitted temperature function of high seasonal temperature using the sine equation T(t) = 10.4*sin (π*t/2−0.1)+24.3 compared to actual observed temperature data collected at Sky Harbor Airport in Phoenix, Arizona, USA from 2003 to 2013. Time t represents seasonal time segments defined by the lunar calendar cycle: winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November).

(i.e., $r(T(t+1))$). Similar to Model (2), we expected that different habitat types to have different values of r_0, K, α, β, d for Model (7). Due to the limitation of microclimate temperature data for each habitat type, we used the temperature function (6) as a base line temperature function to reflect the average temperature changes over all habitat types in a year. Corresponding to the temperature function (6), we used the data from the average population density of aphids over all habitat types to validate our model (7) and parameterized the values of r_0, K, α, β, d to establish baseline values via Nonlinear Grey-Box Model Estimation in MATLAB (MATLAB and Statistics Toolbox Release, 2012b, The MathWorks, Inc., Natick, Massachusetts, United States). The average density of aphids over all considered habitat types was calculated as follows:

$$A = D_{agriculture}{*}\frac{22}{64} + D_{mesic\ urban}{*}\frac{12}{64} + D_{xeric\ urban}{*}\frac{21}{64} + D_{remnant\ desert}{*}\frac{1}{64} + D_{desert}{*}\frac{8}{64}$$

Where D is the average aphid abundance found at each habitat type and the habitat percentage is standardized to be out of 100%. We then performed a bifurcation diagram on the parameter value d in order to explore the effects of temperature variation on aphid population dynamics.

3. Results

3.1. Statistical analysis of long-term abundance patterns

Aphid abundance was more affected by land cover characteristics than land use (urban versus nonurban, Table 1). Abundance varied amongst habitat types ($F_4 = 8.40$, $p < 0.0001$, Table 2), distinctly separated along a gradient of water availability. Agricultural habitats had the greatest average abundance, followed by mesic (urban residential), xeric (urban residential), desert, and desert remnant (Fig. 3). Agricultural and mesic habitats were able to support abundances at least twice as large as their drier counterparts. Mesic and agricultural habitats, which both had the highest mean abundance, were also the most similar in terms of defined habitat characteristics. Both habitat types are classified by high vegetation, or resource levels, as well as moisture availability due to an input of water (via irrigation) into the system. Agriculture significantly differed from both remnant ($p = 0.003$) and desert ($p=0.004$) habitat types. Mesic habitats, which are comparable to agriculture in terms of productivity levels, but are smaller patches within a fragmented urban matrix, also significantly differed from desert ($p = 0.008$) and remnant ($p = 0.006$) habitats. Aphid abundance in xeric sites was intermediate and similar to all habitat types. Desert habitats did not differ significantly from desert remnant or xeric habitats.

Aphid abundance was the highest in the spring and lowest in the summer across all five habitat types (Fig. 3). Seasonal effects had a stronger influence on aphid abundance than habitat type (Table 2). All habitat types, despite either habitat characteristics or degree of urbanization, followed similar seasonal patterns (Fig. 3). Spring abundance across habitats was 10 times as large as all the other seasons combined and accounted for the majority of aphid abundance. Spring aphid abundance significantly differed from all other seasons-winter ($p < 0.0001$), summer ($p < 0.0001$) and fall ($p < 0.0001$). Summer abundance also differed significantly from winter ($p < 0.0001$) and fall ($p < 0.0001$). Fall and winter did not differ statistically, there was an interaction between season and habitat type due to the fall and winter abundance levels.

3.2. Mathematical model

We validated our model and parameterized the values of r_0, K, α, β, d using the calculated average density of aphids over all habitat types from 2003 summer to 2013 (2002 was omitted due to a lack of sampling in the winter and spring months). We found the best-fit parameter values to be: $r_0 = 0.2545$; $\alpha = 0.995$; $\beta = 0.01669$; $K = 59$; $d = -0.45$. By using these parameters, we compared the simulation output to the average aphid abundance over all habitat types from summer 2003 to fall of 2013 (see Fig. 2). We found that the model simulation with our parameterized values to be a good fit when compared to the mensurative aphid abundance ($r^2 = 0.52$, $p<0.0001$, Fig. 4). Thus, we concluded that our comparison between the data and the simulation output by using: $r_0 = 0.2545$; $\alpha = 0.995$; $\beta = 0.01669$; $K = 59$; $d = -0.45$ was a good indicator of actual aphid patterns. The estimated $r_0 = 0.2545$ proved to be a reasonable value, and fell into the range of the intrinsic rate of *Hyalopterus pruni* studied by Latham and Mills (2011).

Table 1
Descriptive statistics of seasonal abundance of aphids per season per sites across habitat types in Phoenix, Arizona, USA. Abundance is reported as mean number of aphids per season per site averaged between 2002 and 2013.

Habitat Type	n	Abundance	Median	Standard Error
Agriculture	6	26.97	1.00	14.55
Desert	7	9.90	0.29	8.11
Mesic Urban	4	12.51	0.68	5.22
Desert Remnant	3	3.95	0.00	2.11
Xeric Urban	5	4.72	0.50	0.51

Our estimation was also close to the estimation of aphids by similar studies (Ozgokce and Athhan, 2005; Wang and Tsai, 2001). One major difference in our model was that our estimation for growth rate was for all types of aphids within the family Aphididae found in Phoenix, and was not species-specific. The estimated value of $\alpha/\beta = 59.62$ was an approximation of the average predator population density handling time of a generalist predator for one aphid. This provided information on the maximum population of aphids that the average predator can consume per unit of time per trap. The estimated carrying capacity is $K = 59$. The estimated $d =$ -0.45 suggested that the average temperature of all types of landscape in Phoenix was about 0.45 °C less than the average temperature at Sky Harbor airport.

The parameter estimations of our Model (7) based on the historical data on temperature patterns observed at Sky Harbor airport and the average aphid dynamics over different habitat types and seasons provided us a baseline of work to explore how the temperature differences driven by the different degree of urbanization can affect the population dynamics of aphids. To address this, we performed the bifurcation diagram on d of Model (7) by varying the value of d from -5 to 2 and fixing $r_0 = 0.2545$, $K = 59$, $\alpha = 0.995$, and $\beta = 0.01669$ where d = 0 is the average temperature at Sky Harbor airport. Our bifurcation diagram (Fig. 5) showed that temperature has dramatic and complex effects on aphid dynamics. $d = 0$ is the baseline temperature at Sky Harbor airport, a commercialized area with a large amount of pavement, urban habitats with less pavement can be expected to have slightly different microclimates and lower temperatures. We expect the population to be fairly stable period two dynamics around $d = 0$ for habitats with similar temperature ranges as Sky Harbor airport. We can see that for d between -0.3 and 0.4, population dynamics of aphids show low and high oscillations. Higher temperature can drive aphid dynamics towards being chaotic, see the values of d between 0.5 and 0.7 or also drive aphid dynamics extinct: e.g., if $d > 0.7$. Lower temperatures have more complex dynamics and can drive the population towards being chaotic or to stabilize, see d between -0.8 and -1.35 and -1.4 to -1.75. Subtle differences in temperature that occur across habitat types would fall into this range, where urban residential habitat would be slightly warmer and tend towards chaos, whereas desert and agricultural temperatures can be expected to be below $d = -0.8$ and tend towards stabilization. This explains why habitat types with similar land cover characteristics and seasonal abundance patterns; e.g. mesic compared to agriculture or xeric compared to desert, differed in overall abundance (Table 1). In addition, our bifurcation diagram (Fig. 5) also showed the aphid population will go extinct if d is larger than 1.8; suggesting that increased local temperature due to global warming and the urban heat island can have profound impacts on the persistence and population size of aphids, thus affecting local ecological communities and ecosystems.

4. Discussion

Our study highlights several important mechanisms that allow arthropod urbanophiles to thrive in arid cities. We found that seasonal patterns have a strong effect on aphid population density, but the magnitude of this effect changes due to variation in microclimate and resource availability across a heterogeneous mosaic caused by urbanization. The direction of seasonal patterns is not influenced by habitat type; however, dampened seasonal effects have the potential to drastically change arthropod population dynamics. Activate management of water and vegetation in arid cities provides plant resources that are decoupled from precipitation and the creation of discrete microclimates in habitat patches that can extend arthropod life cycle events and increase activity time.

4.1. Resource availability and seasonal fluctuations

One major conclusion of our study is that aphids respond to altered hydrological conditions in urban areas that increase resource availability. One of the main drivers behind patterns observed in urban biota, especially in arid urban environments, is the availability of water to a habitat (Bateman et al., 2015). Urbanization of arid cities diverts and relocates historic water supply, causing urban vegetation to be less associated with annual precipitation and more associated with the amount of irrigation needed for a specific land use (Hilaire et al., 2008). This is particularly pronounced in arid environments, where water is often a limiting resource. Urbanization in arid climates can significantly increase primary production because plants are subsidized by the addition of water in an otherwise dry environment (Buyantuyev and Wu, 2009). Irrigated patches of habitat are able to sustain higher vegetation levels, with reduced seasonal fluctuations in productivity.

The increase of primary productivity due to water usage directly relates to resource availability for arthropod herbivores. Similar to other studies in aridland systems (Báez et al., 2006), precipitation shapes vegetation communities that cascade through to consumers. Increased abundance and consistency of available resources in mesic habitat patches has the potential to support higher abundances of arthropod herbivores when compared to drier desert habitats. Aphids are able to thrive in urban areas based on their ability to exploit an increase in resource availability in urban and disturbed habitats, despite fragmentation within the

Table 2
The effect of habitat and seasonal controls on aphid abundance in Phoenix, Arizona, USA between 2002 and 2013. Between Subjects Design: Intercept + Habitat. Within Subjects Design: Season.

Effect	Type III sum of squares	df	Mean square	F	Sig.	Partial eta squared
Habitat	0.33	4	0.08	8.40	p < 0.0001	0.63
Season	1.44	3	0.48	88.33	p < 0.0001	0.82
Season*Habitat	0.24	12	0.02	3.59	p < 0.0001	0.42
Error (Season)	0.327	60	0.005			
Error (Habitat)	0.198	20	0.010			

$\alpha = 0.05$. The F test is significant at the p < 0.05 level. Sphericity is assumed $p > 0.53$.

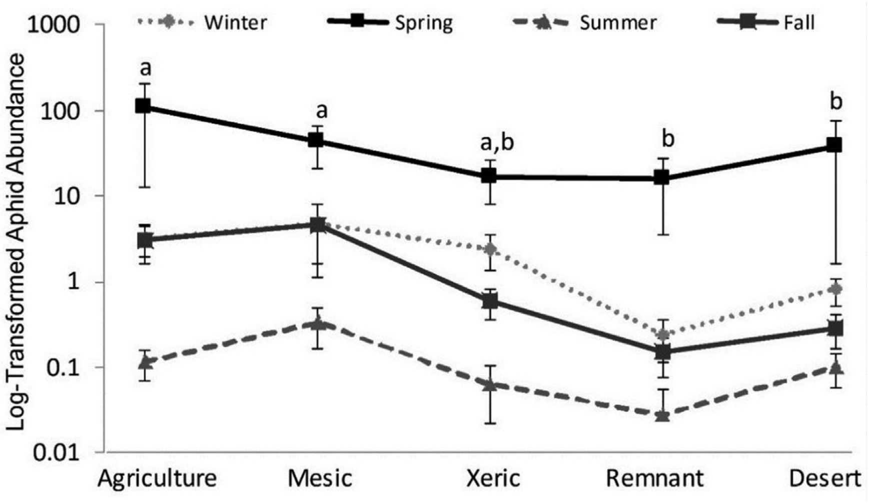

Fig. 3. Seasonal abundance of aphids per season per sites across habitat types in Phoenix, Arizona, USA. Abundance is reported as mean number of aphids per season averaged between 2002 and 2013. Habitat groups with different letter subsets are significantly different at a $p < 0.05$ level.

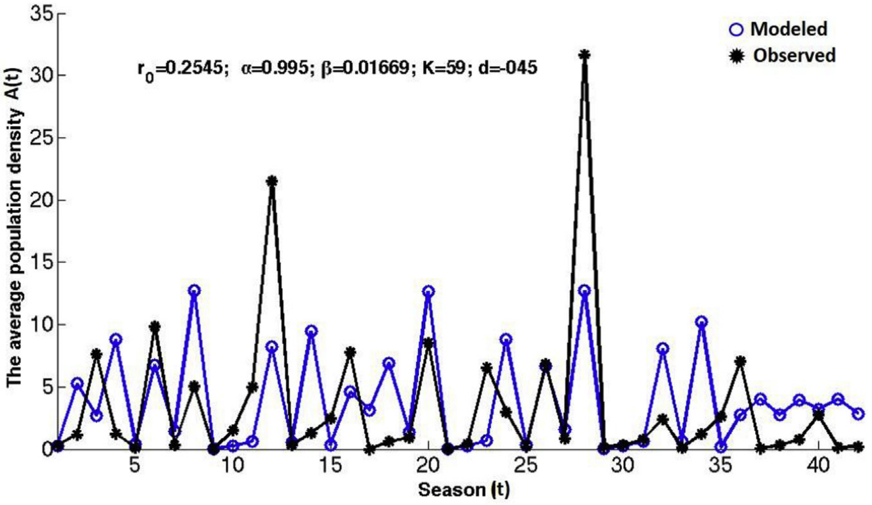

Fig. 4. The model validation and parameterization based on the average of population density of aphid over all types of landscape from summer 2003 to autumn 2013 in Phoenix, Arizona, USA. The x axis is broken across four seasons. Time 0 on the x axis indicates the summer of 2003 and oscillates through aphid population dynamics for seasonal time points from 2003 to 2013 as follows: 5-summer, 10- fall, 15- winter, 20-spring, 25- summer, 30-fall, 35-winter, 40- spring. The black star * represents the data while the blue circle is the simulation output from Model (7) by using $r_0 = 0.2545$; $\alpha = 0.99499$; $\beta = 0.016695$; K = 59; d=-0.45. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surrounding matrix. Similarly, Shochat et al. (2004) found wolf spiders (Lycosidae), a predatory urbanophile, were able to achieve high levels of abundance due to irrigation regimes and variation in patch size.

4.2. Microclimate variation in cities

Microclimate across discrete habitat patches in cities influences activity time of wildlife (Ackley et al., 2015) and can ultimately impact biodiversity outcomes in an urban environment. Our model offers insight on the effects of microclimate variation in arid cities on arthropod populations. Although seasonal patterns of aphids are similar across varying levels of urbanization and comparable to other studies on aphid populations (Wellings et al., 1980), changes in local temperatures based on abiotic and biotic characteristics of the environment can result in the different magnitudes of abundance between habitat types. This is due to factors such as shade provisioning that prevent solar radiation from reaching surfaces and reduce ambient temperature during the day (Konarska et al., 2014). Land surface temperature in arid cities is often directly related to vegetation cover (Jenerette et al., 2011) and vegetation in mesic habitats provides cooler temperatures through evapotranspiration by reducing the overall heat gain (Shashua-Bar et al., 2009). Therefore, mesic and agricultural habitat patches offer a dual benefit to arthropods by providing food resources decoupled from seasonal fluctuations, but also provide a buffer against extreme maximum temperatures. Because arthropod reproduction and activity is tightly associated with temperature, variation in microclimate between habitat patches by just a few degrees can result in dramatic differences in population success. Ultimately, our study shows that changes in microclimate, resource, and water availability caused by land cover characteristics allow certain species to thrive in arid cities.

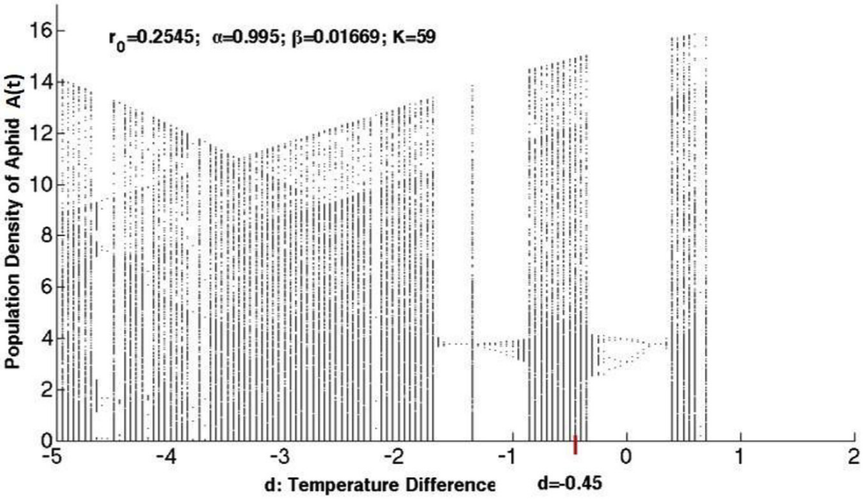

Fig. 5. Bifurcation diagram of d versus aphid dynamics for Model (7) when r0 = 0.25; $\alpha = 0.99499$; $\beta = 0.016695$; K = 59. As the temperature varies the y axis shows all possible values of final aphid density. The D 0 is the temperature at Sky Harbor airport and represents maximum urban temperatures due to the large amount of asphalt. The red dashed vertical line is the value of $d = -0.45$ for the best fit parameter of the temperature difference across all habitat types in comparison to Sky Harbor airport used in the mathematical model output of aphid density. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

Our study determined that a number of factors contribute to the ability of aphids to thrive in arid cities. Aphids were able to take advantage of higher water availability and vegetation in fragmented habitats provided in small patches of preferred habitat that may not be found in the surrounding desert or drier environmental conditions. Despite overall differences in abundance, seasonal patterns were consistent in direction but varied in magnitude under different land cover characteristics. Subtle shifts in temperature that are known to occur across habitat types can have dramatic effects on aphid dynamics. Our model illustrates the importance of bottom up, abiotic controls on urban arthropod populations. These findings are highlighted by cities that are located in arid climates, which offers an opportunity for future research to compare urbanophile patterns across environments in different geographical and climatic regions.

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