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

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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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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)

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