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Top-down vs. bottom-up regulation of herbaceous primary production and composition in an arid, urbanizing ecosystem

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ABSTRACT

Plant growth and composition are regulated by top-down (e.g., herbivory) and bottom-up factors (e.g., resource availability). The relative importance of consumers and multiple resources for net primary production (NPP) and community structure have rarely been studied in drylands, which cover about one third of Earth's land surface, or with respect to increasingly common environmental changes such as urbanization. Urban expansion in drylands is likely to alter both nutrient availability and consumer populations. We explored the relative roles of herbivory, precipitation, and soil nitrogen (N) availability as drivers of aboveground NPP and composition of herbaceous communities in protected native ecosystems in the Sonoran Desert within and surrounding Phoenix, Arizona. Precipitation was the primary driver of production, while soil N availability had little effect on growth. Herbivory was secondarily important relative to precipitation, reducing aboveground biomass by ~33% regardless of proximity to the city. Protected desert open space supported distinct plant communities within and surrounding the city, but these patterns were more strongly related to bottom-up resources than consumers. Together, our results suggest that urbanization does not significantly affect the relative drivers of plant growth and structure in this arid ecosystem.

1. Introduction

Decades of research have explored the factors regulating primary production in ecosystems, including the distribution and abundance of consumers and resources (e.g., Hairston et al., 1960; Oksanen et al., 1981; Polis, 1999). "Bottom-up" models predict that resources such as water and nutrient availability regulate primary production, and "top-down" models focus on the effects of consumers on lower trophic levels and plant growth. Current research on consumer–resource theory emphasizes the relative importance and interactions between bottom-up and top-down factors to determine the conditions under which one is more important than the other (e.g., Borer et al., 2014; Ernest et al., 2000; Meserve et al., 2003). However, these relationships are not well studied in terrestrial ecosystems – particularly in drylands, even though water-limited systems cover over a third of the Earth's land area and are expanding rapidly from desertification (Gruner et al., 2008; Hillebrand et al., 2007; MEA, 2005). Furthermore, consumer–resource interactions may be altered in ecosystems that are influenced by human activity, as people can simultaneously modify both consumer populations and soil resource availability through direct and indirect mechanisms (Faeth et al., 2005; Hall et al., 2009). To date, few studies have examined the relationship between urbanization and resource vs. consumer control over primary production and plant composition. To address these gaps, we examined the independent and combined effects of herbivory, climate, and soil nitrogen (N) availability on aboveground biomass and composition of winter herbaceous plant communities along a precipitation gradient in native Sonoran Desert ecosystems within and surrounding Phoenix, Arizona (USA).

Desert herbivores alter plant composition and growth by

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consuming plant material, dispersing seeds, recycling nutrients, and creating opportunities for competition, yet the overall influence of consumers on aridland aboveground production and composition is uncertain (Báez et al., 2006; Belsky, 1986; Chase et al., 2000). The effect size of herbivory on plant biomass has been shown to vary along precipitation gradients, where consumer effects on plant biomass appear to be larger in low productivity ecosystems (Chase et al., 2000). However, theory predicts herbivores will have a relatively small effect on plant biomass in low productivity ecosystems where herbivore abundance is low (Oksanen and Oksanen, 2000), and results are mixed across the dryland literature (Báez et al., 2006; Brown and Ernest, 2002; Ernest et al., 2000; Gutiérrez and Meserve, 2000). Similarly, some research suggests that herbivores have small impacts on plant species composition in low productivity systems (Báez et al., 2006; Chase et al., 2000; Gutiérrez and Meserve, 2000), while other studies find plant species richness and evenness increase with herbivory (Guo et al., 1995; Inouye et al., 1980). The diversity of findings suggest that the consumer–resource–primary producer relationship is nuanced in arid and semi-arid ecosystems, thus requiring consideration of interactions between herbivory and other abiotic factors, such as soil resources and light availability (Borer et al., 2014).

Mean annual precipitation controls aridland primary production at large scales (Muldavin et al., 2008), but rainfall variability and landscape properties can lead to complex interactions between producer and consumer populations (Collins et al., 2014; McCluney et al., 2012). For example, as in other systems, both desert plant biomass and herbivore abundance increase with precipitation, but consumer population sizes lag behind primary producers as they are more closely related to the previous years' production (Báez et al., 2006; Brown and Ernest, 2002; Chase et al., 2000; Ernest et al., 2000). In addition to quantity, the timing of precipitation affects plant water use efficiency, reproductive allocation, and germination strategies, which in turn influence inter- and intra-annual variability of plant communities as a food resource (Adondakis and Venable, 2004; Warne et al., 2010). Once rainfall occurs, the interaction of water with soil also affects the availability of other belowground resources that are important to primary producers (Austin et al., 2004; Collins et al., 2008). For example, soil inorganic N rather than water appears to limit plant growth during wet years, wet times of the year, or in low-lying areas of the landscape where water accumulates (Gutierrez and Whitford, 1987; Hall et al., 2011; Hooper and Johnson, 1999). This heterogeneity of resource limitation across space and time leads to complex ecological patterns that are difficult to interpret with single-factor experiments. For example, elevated N availability results in a decline of native annual plant species relative to non-native species abundance in the Mojave Desert (Brooks, 2003; Rao and Allen, 2010) but has no effect in other aridland locations and years (e.g., Ladwig et al., 2012). Soil nutrient availability and consumers can have important and contrasting roles in controlling primary production and composition (e.g., Borer et al., 2014), but few dryland studies have examined the nuanced consumer–resource relationships on ecosystem structure relative to precipitation variability.

The direct and indirect impacts of humans on ecological properties and processes add further complexity to our understanding of the relative role of bottom-up and top-down influence on primary producers. Cities are characterized by land fragmentation, urban heating, and altered biogeochemical cycles, which affect resources, consumers, and their relative importance in controlling primary production (Grimm et al., 2008). In addition, human activity alters landscapes far beyond urban boundaries (Seitzinger et al., 2012). For example, atmospheric N deposition from human activities increases primary production and leaf tissue quality for herbivore consumption, as well as changes plant species composition (Pardo et al., 2011; Rao and Allen, 2010). Additionally, bird and small mammal herbivore populations are often more abundant and less diverse in urbanized regions than in surrounding wild lands due to greater resource availability and reduced predation (Chace and Walsh, 2006; Rodewald and Shustack, 2008; Shochat et al., 2006). Even small changes in resource availability or herbivore populations may have cascading effects on ecosystem structure and function in low productivity ecosystems, but little is known about how urbanization changes the relative importance of these regulating factors.

To address these gaps, we examined the combined effect of limiting resources (water and soil inorganic N availability) and herbivore consumption on winter herbaceous aboveground biomass and community structure in protected native Sonoran Desert areas within and surrounding Phoenix, Arizona. Using a natural precipitation gradient across urban and rural desert parks, we hypothesized that – as in other low productivity ecosystems – water availability would be more strongly related to aboveground biomass and community composition than either soil nutrient availability or herbivores. However, we expected that herbivory would exert stronger control over plant production and composition in urban relative to outlying regions. Rates of herbivory may be higher in urban open space areas compared to undeveloped outlying land due to the exclusion of higher-order predators or higher quality plant material resulting from elevated atmospheric N deposition.

2. Methods

2.1. Study site and experimental design

We addressed our research question in the Central Arizona–-Phoenix Long-Term Ecological Research (CAP LTER) site, a 6400 km^2 area that encompasses urban lands and surrounding northern Sonoran Desert. The Phoenix metropolitan area currently supports more than 4 million people, and human population has increased by 47% since 1990 (US Census Bureau, 2010). Rainfall in the Sonoran Desert is bimodal: ~65% of annual rainfall occurs in the winter from November through April and supports diverse annual herbaceous plant communities that account for up to 50% of aboveground net primary production (ANPP) during wet seasons (Shen et al., 2008). The remaining ~35% of precipitation occurs as monsoonal thunderstorms from June through August. Average annual rainfall in Phoenix is 193 mm, and mean daily high and low temperatures are 30 °C and 15 °C, respectively (NCDC, 2013). A slight elevation gradient across Phoenix from west to east results in higher winter–spring rainfall in the outlying desert east of Phoenix (Oct–Mar; 181 mm rainfall; ~600 m above sea level) compared to the urban core (118 mm rainfall; ~350 m elevation; NCDC, 2013).

We compared ANPP and composition of winter–spring annual plant communities in desert patches that were accessible to herbivores ('Control') and patches where small mammal and avian herbivores were excluded ('Exclosure'). Plots were located within areas of native, protected Sonoran Desert both within the city boundaries ('Urban') and outside of the city ('Outlying'; N = 5 sites per location, Fig. 1 and Table 1). Ecological properties and processes in these sites have been studied since 2005 as a part of the CAP LTER project (Hall et al., 2009, 2011). The remnant desert ('Urban') sites are undeveloped but are exposed to a host of urban factors such as elevated gaseous N concentrations and deposition, land fragmentation, and altered biodiversity (Lohse et al., 2008; Shochat et al., 2010; Wu et al., 2011). At each site, we established six 1-m^2 replicate sub-plots in flat areas at least 0.5 m away from woody vegetation and large boulders. Around three of the sub-plots