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.

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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
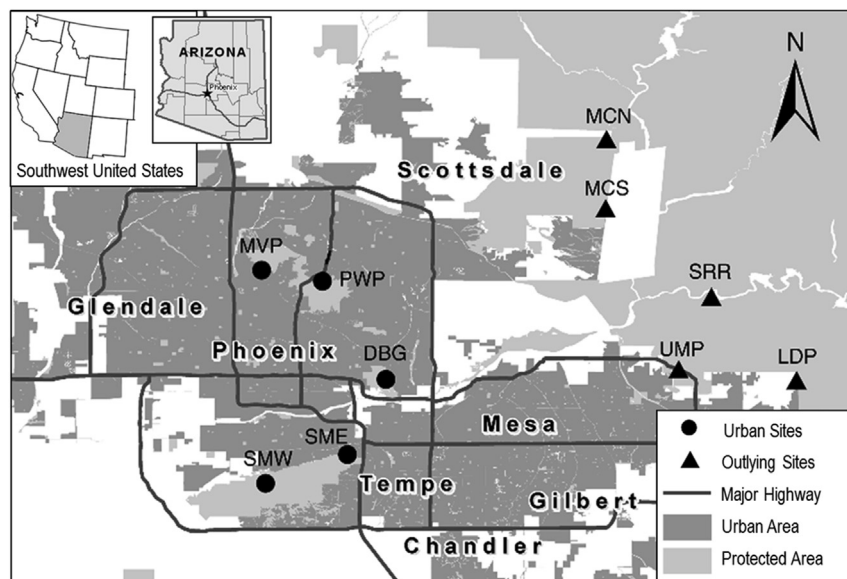
Fig. 1. Map of study sites both within the Phoenix metropolitan area (central AZ; 'Urban') and surrounding the city ('Outlying') Urban sites located within the metropolitan area of Phoenix: Mountain View Park (MVP); Piestewa Peak (PWP); Desert Botanical Garden (DBG); South Mountain Park, east side (SME); South Mountain Park, west side (SMW). Outlying desert sites located to the east of the urban boundary: McDowell Mountain Regional Park, north side (MCN); McDowell Mountain Park, south side (MCS); Salt River Recreation Area (SRR); Usery Mountain Regional Park (UMP); Lost Dutchman State Park (LDP).

('Exclosure'), we placed 0.9 m high metal mesh (0.6 cm × 0.6 cm square holes) with bird netting on top to form a 1.3 m × 1.3 m × 0.9 m structure that excluded small mammal and avian herbivores (Appendix A). Additionally, 30 cm of hardware mesh was secured to the ground around the plot with galvanized spikes as a dig-guard to prevent underground mammal access. The three remaining sub-plots ('Control') were designed similarly to the exclosures to control for microclimate and light availability but allowed access for birds and small mammals (no bird netting; fences were truncated 0.3 m from the ground).

2.2. Plot watering, plant/soil sampling and analysis

Growing season rainfall data were compiled from meteorological stations located close to each of the ten study sites (station location listed in Appendix B, Hall et al., 2011). Both 2011 and 2012 received below-average winter precipitation for this region. Average precipitation from October to March in 2011 and 2012 in outlying locations was 112 mm and 77 mm, respectively, and in urban locations was 82 mm and 53 mm, respectively, compared to the long-term winter average of 181 mm in outlying sites and 118 mm in the urban sites (FCDMC, 2012; NCDC, 2013). To ensure germination and growth of annual plants in our plots during the course of this study, all plots were amended with an additional 4.4 mm of deionized water every 1−2 weeks during spring growing seasons. In total, 31 mm of water was added to plots in 2011 (32% of the average precipitation from October−March 2011), and 22 mm (outlying) − 27 mm (urban) of water was added in 2012 (38% of average precipitation from October−March 2012). Care was taken to add water at a slow enough rate to avoid run-off. We use total precipitation (natural precipitation + water additions at each site) in all analyses.

At the end of each spring growing season (March 2011 and 2012), we assessed community composition of the annual plants within each 1-m^2 sub-plot and harvested aboveground biomass from one of four plot quadrants (0.25 m^2). The harvest quadrant was rotated in 2011 and 2012 to avoid sampling from the same area.

Harvested biomass was dried at 60 °C for at least 24 h and weighed for each sub-plot per location and treatment. Biomass data were then averaged across sub-plot types (exclosure and control) in each site. To measure species composition, we placed a grid of one hundred 10 cm × 10 cm squares over each 1-m^2 plot and counted the number of squares in which each species was present (Muldavin et al., 2008; Xia et al., 2010). To account for possible abundance overestimation using the method above, we also estimated percent cover for each species using bins of <1%, 1%, 2−5%, 6−10%, 11−20%, 21−30%, 31−40%, 41−50%, 51−60%, 61−70%, 71−80%, 81−90%, and 91−100%. Unknown species were found in 1 out of 60 plots in 2011 and in 2 of 60 plots in 2012; the percent cover of each unknown species was <1% of the plot in which it was found. These species were not identified and were excluded from the analyses.

Soil inorganic nitrogen (NO_3^- and NH_4^+) availability (henceforth referred to as soil iN) was quantified over the course of the winter growing season using ion-exchange membranes (Drohan et al., 2005; Plant Root Simulator (PRS) probes; Western Ag Innovations, Saskatchewan, Canada). PRS probes were inserted vertically into the top 15 cm of soil in mid-December and remained there until collection in mid-March. Western Ag Innovations Inc. analyzed the PRS probes by shaking them in 0.5 N HCl solution for an hour and analyzing the eluate colormetrically with an automated flow injection analysis system (Western Ag Innovations). In 2011, two sets of anion/cation exchange probes were located outside of our study plots (between shrubs) but within 20−40 m of the control or exclosure fencing at each site. The two sets of anion/cation probes per site were analyzed together, resulting in one set of anion/cation data per site (N = 10 sets of anion/cation data across all sites; N = 5 each for urban and outlying locations). In 2012, one set of anion/cation probes was placed within two of three randomly chosen exclosure and control plots at each site (avoiding the quadrant to be harvested). Replicate probes were again analyzed together: probes from the two exclosure plots within a site were analyzed together and those from the two control plots within a site were analyzed together (N = 20 sets of anion/cation probes

Table 1
Characteristics of 10 Sonoran Desert study sites in and around metropolitan Phoenix, Arizona. Mean and standard error (SE) reported for urban and outlying sites.

Location	Site[a]	Elevation (m)	MAT (°C)[b]	MAP (mm)[b]	2010—2011 Total precipitation (mm)[c]	2011—2012 Total precipitation (mm)[c]
Urban	SME	372	23	194	101	76
	SMW	458	22	180	145	104
	DBG	396	24	172	94	75
	MVP	397	21	190	116	71
	PWP	456	21	177	107	74
Urban mean (SE)		**416 (17)**	**22 (<1)**	**183 (4)**	**113 (9)**	**80 (6)**
Outlying	LDP	620	22	203	132	93
	UMP	592	23	205	123	77
	SRR	434	22	197	141	96
	MCS	539	23	241	152	100
	MCN	476	23	281	171	127
Outlying mean (SE)		**532 (35)**	**23 (<1)**	**225 (16)**	**144 (8)**	**99 (8)**

[a] Site name abbreviations as in Fig. 1.
[b] Mean annual precipitation (MAP) and mean annual temperature (MAT) originally reported in Hall et al. (2011) for the same sites.
[c] Total precipitation includes natural annual precipitation and water additions. Rainfall at each site estimated from the nearest Flood Control District of Maricopa County meteorological tower (FCDMC, 2012). For tower locations, see Appendix B.

across all sites; N = 10 each for urban and outlying locations).

2.3. Data analyses

Measurements of biomass (ANPP), species diversity and composition, and soil iN were averaged across all sub-plots per location (urban vs. outlying), herbivory treatment (control vs. exclosure), and year (2011 and 2012). Total water inputs were calculated as the sum of the natural winter rainfall and the water additions that were applied in the field. Biomass data were natural log transformed for all analyses to achieve linearity, normality and homoscedasticity.

We determined the effects of landscape region, herbivory treatment (control or exclosure), and year (each as categorical independent variables) on ANPP, precipitation and available soil inorganic N using multi-factor ANOVAs. We also used a three-way ANOVA to explore relationships between our independent variables and species diversity metrics such as density, diversity, and evenness (see below). In addition, we conducted one-way ANCOVA tests separately for each year of data with ANPP as the dependent variable, treatment as the categorical independent variable and precipitation and soil iN as covariates. Precipitation and soil iN were significantly related to site location and year, violating ANCOVA assumptions, so we used these as the covariates rather than independent variables. The covariates (precipitation or soil iN) and the dependent variable (ANPP) were not significantly related across all levels of the independent variable (exclosure vs. control herbivory treatment) and thus met the assumption of homogeneity of regression slopes. We also used one-way ANCOVA to test the relative importance of the independent variables on species diversity metrics. We used omega squared effect size (ω^2) to compare the relative strength of each independent variable on the dependent variables, as this statistic is more conservative than other estimates of effect size (such as eta square or partial eta square; Levine and Hullett, 2002) and is recommended for small sample sizes such as ours. All ANOVA and ANCOVA analyses were conducted in SPSS 20.0.0 (IBM SPSS Statistics, 2011).

Species diversity metrics were determined on untransformed abundance data with all species represented. Individual-based species accumulation curves (Gotelli and Colwell, 2001) were graphed using data from all separate sub-plots in EstimateS 8.2.0 for Mac (Colwell, 2011). Richness was estimated based on the ACE and Chao 2 estimators after 50 randomization runs without replacement. Differences in richness between locations and treatments were estimated based on overlap of 95% confidence intervals on the species accumulation curves (Barlow et al., 2007). Species density (# species per sampling unit), diversity (Shannon—Weiner's H′) and Shannon—Weiner evenness ($H'/\ln[S]$) were determined using PC-ORD (McCune and Grace, 2002) for each location and treatment using averages of all sub-plots.

We also explored differences in community composition across our study design using non-metric multidimensional scaling (NMDS) ordination and two-way, non-parametric perMANOVA tests on species abundance data with all sub-plots averaged for each treatment and location. NMDS and perMANOVA analyses were conducted in PC-ORD using the Sorensen (Bray—Curtis) distance metric on arcsine square root-transformed counts following removal of rare species from the dataset (species with <5% occurrence in all sample plots within a year). The removal of rare species, which resulted in omission of 2 species with 1 occurrence each in 2011 and 3 species with 1 occurrence each in 2012 out of a total of 24 species in both years, is used to reduce the noise (stress levels) in multivariate analyses (McCune and Grace, 2002). All ordination methods are subjected to potential biases by including rare species given that all start with a resemblance matrix that is based on species abundances. Keeping or removing rare species remains an unresolved debate in vegetation science. Poos and Jackson (2012) is perhaps the most thorough recent analysis of the impact of removing rare species. They find that removing rare species can have a big impact on results that can influence interpretations relevant to conservation or bioassessments if doing so results in deleting a species of conservation concern or a particular indicator species. Neither is true in our case. The few species that were removed occurred once and had very low relative abundance values. So, we chose to follow the advice of McCune and Grace (2002) in this case and remove these species from our analyses. For the NMDS analyses, we first used a random starting configuration with a maximum of 6 axes, 250 runs with real data, and the same number of runs with randomized data followed by a Monte Carlo test of significance (autopilot mode in PC-ORD). We chose a 2 dimensional solution for both the 2011 and 2012 datasets based on evaluation of stress values by dimension after three simulations. We then ran the procedure with the 2 dimensions three additional times (250 runs of real data followed by 249 runs of randomized data) with orthogonal axis rotation and ended with a stable final run of 70 iterations and stress value of 9.8 for 2011 and 11.1 for

2012. After the analysis, we determined the fraction of variation represented by each axis by calculating a coefficient of determination (r^2) from the relationship between the distances in the original, unreduced matrix to distances among the points in ordination space (McCune and Grace, 2002).

3. Results

3.1. Climate, soil iN, and annual plant growth across study years and by proximity to the city

Aboveground production of herbaceous annual plants was similar across years, despite significant differences in inter-annual precipitation (2011 > 2012) and soil iN availability (2011 > 2012; Table 2). However, aboveground biomass was significantly greater in outlying compared to urban plots, similar to patterns in winter rainfall (outlying > urban) and the inverse patterns in soil iN (urban > outlying).

3.2. The effect of herbivory on biomass and community composition

Across all locations and years, aboveground herbaceous biomass was higher in exclosure plots compared to control plots (p = 0.003; Table 2, Fig. 2). In both study years, rates of herbivory were highly variable across plots and sites, ranging from 0 to 78% difference between exclosure and control plots. On average, herbivory reduced herbaceous biomass by ~33% across all sites, regardless of
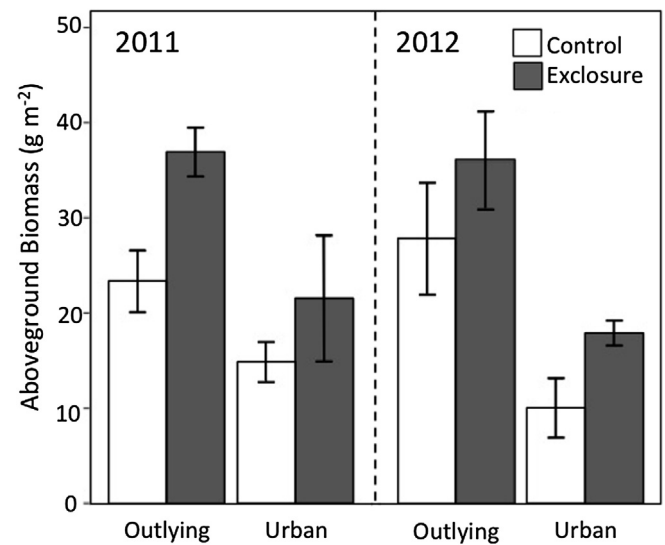

Fig. 2. Average aboveground herbaceous annual biomass (g m^{-2}; ±1 standard error, N = 5) in urban and outlying treatments (control and exclosure) in 2011 and 2012.

proximity to the city (Table 2, Fig. 2; location × treatment interaction, p = 0.83).

Twenty-four species of winter annuals were encountered across both treatments and sites in 2011 and 2012 (Appendix C). Three species composed ≥80% of the total plot cover across both years in all sites: the exotic invasive grass, *Schismus arabicus*, and two native forbs, *Pectocarya recurvata* and *Plantago ovata*. Although plots exposed to herbivores (control plots) contained lower amounts of herbaceous biomass overall, herbivore exclosures did not

Table 2
Aboveground biomass, precipitation and available soil inorganic N in control and exclosure plots located within urban and outlying desert locations in 2011 and 2012. Values reported are means with standard error in parentheses (N = 5 averaged plots per treatment, location and year). Multi-factor ANOVA results shown for each dependent variable by year, location and treatment (exclosure vs. control). Significant ANOVA results are bolded.

Year, location, Tmt	Aboveground biomass (g m^{-2})	Total precipitation (mm)[a]	Soil inorganic N (μg 10 cm^{-2} 3 months^{-1})[b]
	Mean (SE)	Mean (SE)	Mean (SE)
2011			
Urban, control	15 (2)	113 (9)	141 (43)
Urban, exclosure	22 (7)		ND
Outlying, control	23 (3)	144 (8)	98 (15)
Outlying, exclosure	37 (3)		ND
2012			
Urban, control	10 (3)	80 (6)	43 (10)
Urban, exclosure	18 (1)		34 (10)
Outlying, control	28 (5)	99 (8)	18 (5)
Outlying, exclosure	36 (5)		16 (3)
Multi-factor ANOVA results			
Year	0.4	**<0.001**	**<0.001**
Location	**<0.001**	**<0.001**	**0.01**
Treatment	**0.003**	NA	NA
Y × L	0.3	0.3	0.2
Y × T	0.6	NA	NA
L × T	0.8	NA	NA
Y × L × T	0.3	NA	NA

[a] Total precipitation includes natural precipitation and water additions. Precipitation was the same for control and exclosure plots at each site, thus precipitation was compared between year and location in two-way ANOVA. Rainfall at each site estimated from the nearest Flood Control District of Maricopa County meteorological tower (FCDMC, 2012). For tower locations, see Appendix B.
[b] Soil inorganic N is averaged N flux from ion-exchange resin probes from December–March during each study year. In 2011, soil inorganic N was only measured in control plots, thus soil inorganic N was compared between year and location in two-way ANOVA (treatment excluded from analysis). In analysis of 2012 data only, soil inorganic N was not significantly different between treatments (exclosure vs. control, p = 0.5). ND = No data.

Table 3
Plant species diversity metrics in control and exclosure plots located within urban and outlying desert locations in 2011 and 2012. Species richness estimated using all three subplots within each treatment and location (N = 15 plots). Species density, diversity, and evenness estimated after averaging species abundance counts across the 3 subplots per treatment at each site (N = 5 averaged plots per treatment, location, and year). Multi-factor ANOVA results shown for dependent variables by year, location and treatment (exclosure vs. control); significant ANOVA results are bolded.

Year, location, Tmt	Species richness		Species density (# spp quadrat^{-1})	Species diversity (H′)	Evenness (J)
	ACE	Chao 2	Mean (SE)	Mean (SE)	Mean (SE)
2011					
Urban, control	9.0	9.0	4.2 (1.0)	0.6 (0.2)	0.4 (0.1)
Urban, exclosure	9.0	9.0	5.0 (1.1)	0.7 (0.2)	0.4 (0.04)
Outlying, control	17.0	17.0	9.0 (1.2)	1.4 (0.1)	0.7 (0.04)
Outlying, exclosure	20.8	22.7[a]	11.0 (1.1)	1.5 (0.1)	0.6 (0.03)
2012					
Urban, control	10.0	10.0	5.4 (0.9)	0.9 (0.2)	0.5 (0.1)
Urban, exclosure	15.0	17.5[a]	6.4 (0.7)	1.0 (0.2)	0.5 (0.1)
Outlying, control	21.9	20.0[a]	11.8 (0.2)	1.7 (0.04)	0.7 (0.01)
Outlying, exclosure	19.0	18.9	12.4 (0.5)	1.7 (0.1)	0.7 (0.02)
Multi-factor ANOVA results					
Year		**0.01**	**0.004**		**0.03**
Location		**<0.001**	**<0.001**		**<0.001**
Treatment		0.1	0.4		0.8
Y × L		0.5	1.0		0.8
Y × T		0.6	0.9		0.8
L × T		0.8	0.8		0.7
Y × L × T		0.5	0.8		0.9

[a] Chao 2 based on classic (not bias-corrected) option in EstimateS.

significantly alter the relative percent cover of these three species in either year, in part due to the high variance in species composition and cover between plots and sites. In contrast, cover of *S. arabicus*, *P. recurvata*, and *P. ovata* combined was higher in the wetter, outlying desert sites compared to urban locations (Appendix C).

On average, species richness in outlying desert sites was nearly double that of remnant desert sites within the city, although this pattern was statistically significant only in 2011 (Appendix C). Species density, diversity, and evenness were significantly higher in outlying compared to urban remnant desert sites across both years, and they were highest in 2012 (Table 3).

Diversity and composition of winter annual plants were significantly related to location and year, but not herbivory (Table 3, Fig. 3, Appendix D). NMDS plots revealed distinct plant communities between outlying and urban desert sites, but similar communities between exclosure and control plots (Fig. 3). Site location was significantly related to plant community composition (perMANOVA, p < 0.001 in both years) but herbivory was not (p > 0.86 in both years).

Table 4
Relative importance of bottom-up and top-down factors for aboveground biomass and species diversity metrics. P-values are for one-way ANCOVA analyses for each study year; significant results are bolded. The relative importance of precipitation, available soil inorganic N, and herbivory is indicated by omega squared (ω^2), which estimates the effect size and proportion of total variance explained by each independent variable. Biomass was natural log transformed for all analyses.

	Biomass (g m^{-2})		Species density (# spp quadrat^{-1})		Species diversity (H′)		Evenness (J)	
	p value	ω^2	p value	ω^2	p value	ω^2	p value	ω^2
2011								
Corrected model	**0.01**		**0.01**		**0.02**		**0.03**	
Precipitation	**0.02**	0.18	**<0.01**	0.35	**0.01**	0.24	0.08	0.09
Soil inorganic N	0.10	0.06	0.33	0.00	0.14	0.05	**0.03**	0.16
Herbivory	**0.04**	0.11	0.50	0.00	0.70	0.00	0.72	0.00
2012								
Corrected model	**<0.01**		**0.02**		**0.01**		**0.01**	
Precipitation	**<0.01**	0.33	0.35	0.00	0.52	0.00	0.93	0.00
Soil inorganic N	0.22	0.01	**0.01**	0.25	**<0.01**	0.33	**<0.01**	0.36
Herbivory	**0.02**	0.11	0.72	0.00	0.85	0.00	0.94	0.00

3.3. The relative importance of soil resources and herbivory for annual plant growth and composition

In a comparison of all factors (one-way ANCOVA), herbivory significantly reduced ANPP in both study years after controlling for the independent effects of precipitation and soil iN (Table 4). In both years, precipitation was positively related to ANPP, while soil iN availability had no effect (Table 4, Fig. 4). Using omega squared values to compare the relative importance of precipitation, soil inorganic N and herbivory, we found that precipitation accounted for the most variation in biomass (18% in 2011, 33% in 2012), followed by herbivory (11% in both years).

Species density, diversity and evenness were not significantly related to herbivory in either year, but were significantly related to precipitation and soil iN (Table 4). In the wetter winter of 2011, precipitation explained the most variation in species density and diversity, while available soil iN explained the most variation in species evenness (although the total contribution is small). In the drier 2012, soil iN was the most strongly related (inversely) to all three species composition metrics.

4. Discussion

We tested the relationship among bottom-up and top-town controls on desert herbaceous aboveground biomass and community composition along a precipitation and urban-rural gradient. We hypothesized that limiting resources of water and soil inorganic N (bottom-up factors) would be strongly related to the growth and composition of desert annual plants, but that urbanization would have an important influence on the relative role of top-down factors, such as herbivory. Thus, we predicted that herbivory would have a greater relative influence on desert herbaceous biomass and community composition in the urban desert parks than in the outlying desert. Overall, we found bottom-up factors were significantly related to ANPP and were also the primary drivers of community composition. While herbivory was secondarily important in controlling plant growth, contrary to our predictions, urbanization did not alter the relative influence of herbivory or soil resources on annual plant growth or composition.

4.1. Regulation of aboveground net primary productivity (ANPP)

Across our two relatively dry study years, precipitation was the strongest regulating factor of herbaceous annual plant production,
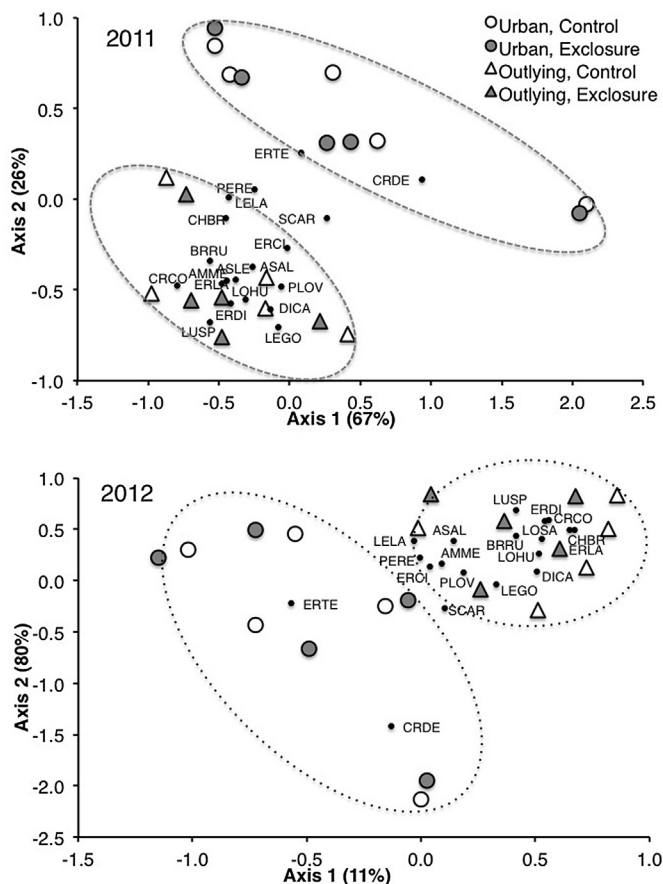

Fig. 3. Nonmetric multidimensional scaling analyses of species abundance data, showing winter annual species and their relation to desert location (urban, outlying) and treatment (control, exclosure). AMME = *Amsinckia menziesii*; ASAL = *Astragalus allochrous*; ASLE = *Astragalus lentiginosus*; BRRU = *Bromus rubens*; CHAL = *Chamaesyce albomarginata*; CHBR = *Chorizanthe brevicornu*; CRCO = *Crassula connata*; CRDE = *Cryptantha decipiens*; DICA = *Dichelostemma capitatum*; ERDI = *Eriastrum diffusum*; ERLA = *Eriophyllum lanosum*; ERCI = *Erodium cicutarium*; ERTE = *Erodium texanum*; ESCA = *Eschscholzia californica*; LELA = *Lepidium lasiocarpum*; LEGO = *Lesquerella gordonii*; LOHU = *Lotus humistratus*; LOSA = *Lotus salsuginosus*; LUSP = *Lupinus sparsifolus*; PERE = *Pectocarya recurvata*; PHDI = *Phacelia distans*; PLAR = *Plagiobothrys arizonicus*; PLOV = *Plantago ovata*; SCAR = *Schismus arabicus*.
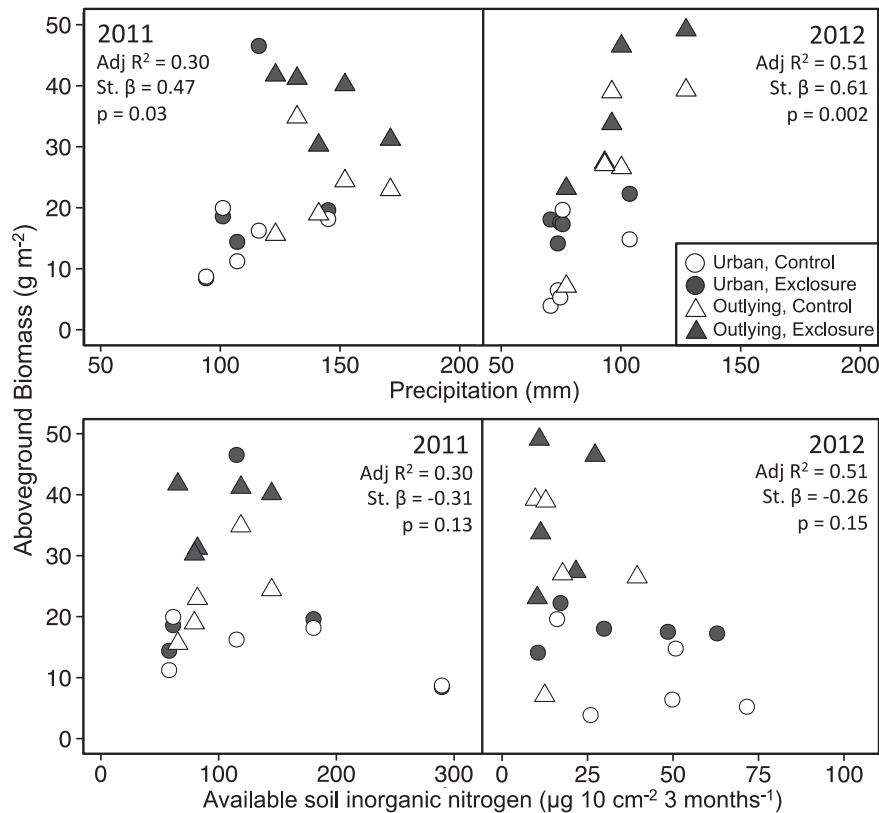
Fig. 4. Relationships between precipitation, soil inorganic N, location, and primary production of desert annuals for each study year. In both study years, precipitation (top) is a significant predictor of annual biomass, while soil inorganic N availability (bottom) is not. Note the different x-axis scales between 2011 and 2012 for soil inorganic N.

and available soil inorganic N had no significant influence on production. Precipitation explained more biomass variation (33%) in the drier 2012 year than in 2011 (18%; Table 4). Typically, as water availability increases, production becomes limited by other ecological factors (Austin et al., 2004; Hall et al., 2011). Despite water additions, our sites received an average of 13% (2011) and 39% (2012) less water than the long-term average winter precipitation (FCDMC, 2012), and water remained the limiting factor in these study years. As a result, soil inorganic N availability was not significantly related to primary production during either year in urban or outlying areas, despite greater available soil inorganic N at the urban locations compared to outlying locations (Table 2, Fig. 4).

On the other hand, herbivory significantly reduced biomass across years regardless of precipitation and location relative to the city. Herbivory in our Sonoran Desert sites reduced total herbaceous biomass by a third across locations (Fig. 2) and was the second most important factor related to aboveground plant growth (Table 4). Despite the greater overall production in outlying sites as a result of more precipitation, herbivores consumed a similar proportion of annual plant material, on average, at both urban and outlying locations. Average rates of herbivory in this study (ranging from 23 to 44%) were comparable to rates in other arid and terrestrial systems (18—27%, Cyr and Pace, 1993; Roth et al., 2009).

4.2. Regulation of desert plant communities

Annual plant community composition was primarily driven by bottom-up factors and was not affected significantly by herbivory.

Sonoran Desert plant communities in urban open space parks were distinct, less diverse, and contained a lower density of species than desert parks located outside the city. Diversity, density, and evenness were highest in the outlying sites where there was greater rainfall, lower available soil inorganic N, and greater ANPP.

Across locations, the variability in community diversity metrics can be explained mainly by water availability in the wetter 2011 and, surprisingly, by available soil inorganic N in the drier 2012 (Table 4). We expected higher N availability to be associated with a reduction in species diversity (e.g., Clark and Tilman, 2008; Gough et al., 2000), as we saw in the urban sites compared to less N rich outlying sites. However, we did not expect soil inorganic N to explain the most variability in diversity during a particularly dry year. One possible explanation is that the variability in diversity metrics is driven by distinct urban and outlying winter annual plant communities that persist across years as a result of long-term patterns of higher atmospheric N deposition and soil N within the city (Hall et al., 2011; Cook et al. in prep). Thus, regardless of precipitation, we would expect to see differences in plant communities driven mainly by soil N that in turn affect site-specific germination patterns.

Similarly, species density, diversity, and evenness were significantly higher in 2012 than 2011, despite the lower total winter precipitation in 2012. Differences in diversity metrics may reflect the timing of rainfall each year, where early season rainfall is an important determinant of bet-hedging and germination strategies of desert winter annuals (Adondakis and Venable, 2004). In 2012, almost all winter precipitation occurred during the main

germination period for Sonoran Desert winter annuals, between early November and mid-December (sites received only three small (<5 mm) rain events after Dec 20, 2012 in addition to our water additions). In 2011, however, the majority of the precipitation fell after mid-December. The number of individuals (Appendix D) as well as the diversity (Table 3) was likely higher in 2012 as a result of the early pulses of rain, leading to ephemeral pulses in soil resources such as soil inorganic N. Finally, some herbaceous Sonoran Desert species have long-lived seeds that can survive multiple years of drought, ensuring their survival while water is scarce or until favorable conditions exist (Adondakis and Venable, 2004; Pake and Venable, 1995). Community composition in 2012 also may be related to the specific plant species present in 2012 as a result of the low water and N availability. For example, species with increased presence in outlying (low soil inorganic N) sites in 2012 included several N-fixers, including *Astragalus allochrous*, *Lotus salusiginosa*, and *Lupinus sparsifolia* (Appendix C).

During the relatively dry study years, herbivory did not affect community composition in our study system, supporting similar findings in other arid and semi-arid systems (Báez et al., 2006; Chase et al., 2000; Gutiérrez and Meserve, 2000). Herbivores control plant communities not only by foraging on plant biomass, but also by consuming and dispersing seeds. Thus, given the variability in particular species germination rates (Adondakis and Venable, 2004), we might expect herbivory to impact plant communities over longer periods of time. Guo et al. (1995) reported minimal effects of bird and rodent removal on Chihuahuan Desert winter annual composition until the third year of study when herbivores decreased the density of plant species. Over a longer study period, we would expect changes in plant community structure as a result of small mammal herbivory, such as decreased density of large seeded winter annual species and increased plant community evenness (Inouye et al., 1980). However, our two year findings support previous studies in arid systems that found rodent removal had no effect on cover, species richness, or community structure over longer time periods (Báez et al., 2006).

4.3. Relative role of bottom up and top down regulation

Current consumer—resource theory highlights the relative importance and interactions between bottom-up and top-down factors and seeks to identify consistent mechanisms or drivers of consumer—resource relationships that hold across multiple systems and scales (Chase et al., 2000; Gruner et al., 2008; Hillebrand et al., 2007). Examining the relative role of bottom-up and top-down factors along gradients of productivity has been an important area of study (Chase et al., 2000; Hillebrand et al., 2007; Borer et al., 2014). However, few studies have examined the relationship in low productivity arid systems while also considering the effects of both water and soil nutrient availability as bottom-up resources (Báez et al., 2006; Brown and Ernest, 2002; Meserve et al., 2003). In our study in the northern Sonoran Desert, bottom-up factors were the primary control of desert plant production and composition, although herbivory had a significant and important impact on plant production in this system. While the availability of bottom-up resources differed between years and between urban and outlying locations, water availability was the primary driver of production, while herbivory was the secondary driver. We would expect, however, soil inorganic N availability to become a more important regulating factor for production in years with above average precipitation (Hall et al., 2011; Ladwig et al., 2012). Plant community composition in this two-year study, on the other hand, was explained primarily by bottom-up factors, including both water and soil inorganic N.

The relative role of factors may fluctuate in arid systems over seasons and longer time scales based on resource availability and external environmental factors that affect both herbivore and primary producer populations (Meserve et al., 2003). In this highly water-limited system, we expected precipitation to have a strong relationship to plant community structure. However, our study covered only two below-average precipitation seasons and thus did not capture longer-term controls on plant and herbivore populations. Primary production and composition may also be related to other abiotic factors that vary temporally, such as temperature and elevated atmospheric ozone and carbon dioxide concentrations, and spatially, such as rock cover and light availability. For example, herbivory increases light availability that in turn positively influences species richness regardless of soil N availability or production (Borer et al., 2014). Feedbacks that influence plant—herbivore interactions are also dynamic over time. For example, resource availability can affect the tolerance of plant responses to herbivore damage (Wise and Abrahamson, 2006). The timing, frequency and amount of rainfall also impacts predator—prey interactions and herbivore specialization (Brown and Ernest, 2002; McCluney et al., 2012). It may take several seasons for herbivore populations to respond to elevated annual production from high rainfall years (Brown and Ernest, 2002).

In addition to examining the influence of consumers and resources in low productivity systems, we examined whether urbanization would be an important mechanism that alters consumer—resource relationships. As urbanization in arid systems increases worldwide, human activities can simultaneously modify both consumer populations and soil resource availability through direct and indirect mechanisms, with cascading impacts on consumer—resource relationships and ecosystem structure and function (Faeth et al., 2005; Hall et al., 2011). We expected large predators would be less common in the urban remnant desert sites, and in turn lead to more abundant small mammal and avian populations and higher rates of urban herbivory (Chace and Walsh, 2006; Faeth et al., 2005; Shochat et al., 2010). Contrary to our hypothesis, the relative role of top-down regulation on herbaceous plant production and composition did not vary relative to urbanization (i.e., herbivory rates were the same between urban and outlying locations regardless of variation in precipitation). Former studies have recorded higher abundance of herbivores in highly modified urban landscapes of Phoenix (residential landscapes, agricultural fields) than the outlying desert (Faeth et al., 2005), but the abundance and composition of herbivores within protected remnant desert parks may be more similar to our outlying sites than other landscape types. We did not monitor herbivore populations in this study, but further research comparing consumer populations between urban and outlying open space locations is an important next step.

5. Conclusion

Results of this study help to clarify the relative and dynamic role of resources and consumers in regulating aboveground production and community composition of herbaceous annual plants in dryland systems. We found herbivores had modest impacts on annual plant communities in native desert locations across the city of Phoenix, reducing winter primary productivity by an average of 33% with no effect on species composition. Across all locations, bottom-up factors had the greatest influence on desert annual plant growth and composition, but the importance of soil inorganic N availability for annual plant communities was dynamic, changing from year to year depending on precipitation. Finally, urbanization did not appear to change the relative importance of

the major arid ecosystem regulating factors for annual plant production or composition in the below average precipitation study years. However, human-induced environmental changes in climate and atmospheric N deposition have been shown to significantly impact winter herbaceous annual plant growth and diversity (e.g., Rao and Allen, 2010; Xia et al., 2010). Moreover, land degradation and urbanization are occurring more rapidly in drylands than other ecosystems and continued human impacts are predicted to significantly modify ecosystem structure and function (MEA, 2005; Reynolds et al., 2007). In order to implement effective management and conservations strategies for protected native ecosystems both near and far from human activities, it is essential to understand how human activities affect resources and consumer populations and their relative influence on consumer-—resource dynamics.

Author contributions

MKD, EMC, SLC, and SJH conceived of and designed the project. MKD and SJH secured funding for the project. MKD conducted the field work and initial analyses as her undergraduate honors thesis with guidance from EMC, SLC, and SJH. EMC and SJH analyzed the final data, MKD and EMC wrote the manuscript, and SLC and SJH edited the manuscript and provided guidance and feedback throughout the project.

Acknowledgments

Appendix A. An herbivore exclosure plot (top) and a control plot (bottom) at the McDowell Mountain North site before the winter rainfall season. Three exclosure plots and three control plots served as sub-plots that were averaged within each of ten sites (5 sites each within urban and non-urban locations).
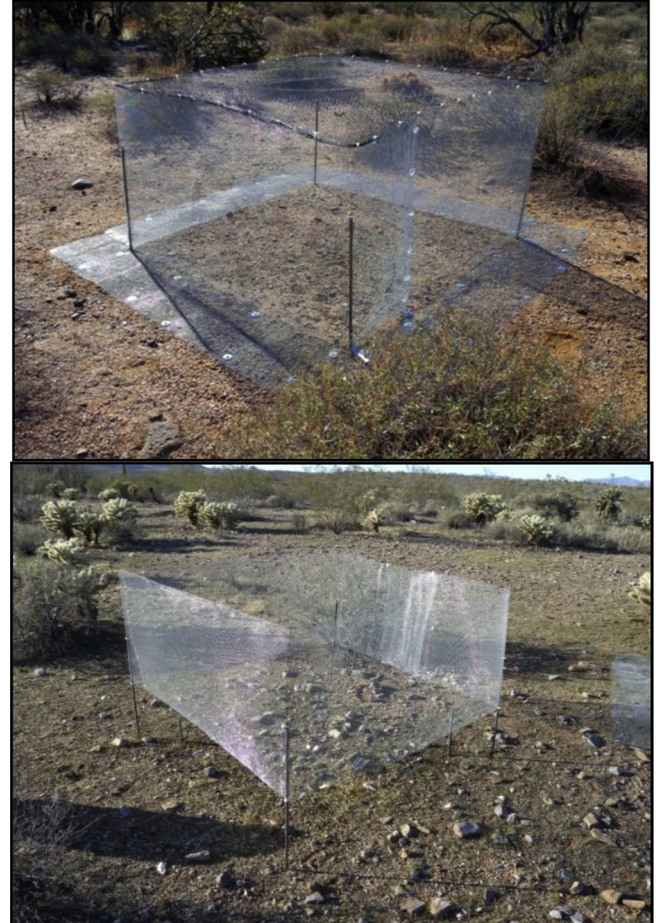
Appendix B. The identification numbers and locations of the meteorological stations used in this study to obtain precipitation data (FCDMC, 2012). At DBG, MVP, and MCS precipitation data from 2 to 3 nearby weather stations were averaged. For a map of sites, see Fig. 1.

Landscape region	Site name	ID number	Rainfall station name, *Station Location*
Urban	SME	6510	South Mountain Park, *Alignments of Elliot Rd. and 24th St.*
	SMW	6525	South Mountain Park, Headquarters, *In South Mtn. Park, alignments of Elliot and 7th Ave.*
	DBG	4520	Salt River at Priest, *West side of Salt River bridge at Priest Drive*
		4740	Papago Park, *1/4 mi. N of McDowell Rd. and 52 nd St.*
		4815	10th Street Wash Basin#1,*1/4 mi. SW of Peoria Ave. and Cave Creek Rd.*
	MVP	4825	Phoenix Basin#3, *Near Peoria Ave. and 16th St.*
		4800	Dreamy Draw Dam, *1/4 mi. SSW of the 24th St. and Dunlap Ave. alignments*
	PWP	4635	Tatum Basin Inflow, *Near Shea Blvd. and 44th St.*
Non-urban	LDP	6675	Apache Trail, *1/3 mi. NE of Broadway Rd. and Idaho Rd.*
	UMP	6650	Usery Park WS, *1/4 mi. WNW of the Crismon Rd. and Thomas Rd. alignments*
	SRR	4565	Granite Reef, *Bush Highway at Granite Reef Dam*
	MCS	4660	Lost Dog Wash, *1/2 mi. NNW of Shea Blvd. and 128th St.*
		5975	Cloudburst Wash, *2 mi. NW of SunRidge Golf Course, Fountain Hills*
	MCN	5995	Hesperus Wash, *NW 1/4 ofT4N-R6E-Section 31 near Dixie Mine*

Appendix C. Average percent cover and constancy (% of plots sampled) of species in control and herbivore exclosure plots in urban remnant desert and outlying desert plots. Species sorted by average % constancy across years, regions, and treatments. N = 3 plots per treatment, region, and year.

Species	Cover (% of plot) 2011 Urban Control Mean	SE	Exclosure Mean	SE	Outlying Control Mean	SE	Exclosure Mean	SE	Two-way ANOVA Dist	Tmt	Dist × Tmt	2012 Urban Control Mean	SE	Exclosure Mean	SE	Outlying Control Mean	SE	Exclosure Mean	SE	Two-way ANOVA Dist	Tmt	Dist × Tmt	Constancy 2011 Urban Cntl	Excl	Outlying Cntl	Excl	2012 Urban Cntl	Excl	Outlying Cntl	Excl
Schismus arabicus	6.1	2.0	12.3	4.1	14.1	2.2	15.4	2.1	**0.05**	0.18	0.38	3.6	1.7	10.5	3.7	9.5	3.2	11.6	4.1	0.18	0.27	0.44	93.3	93.3	100.0	100.0	93.3	100.0	100.0	93.3
Pectocarya recurvata	36.8	9.0	34.4	7.9	28.0	5.1	38.7	4.8	0.43	0.43	0.53	7.5	2.6	11.3	3.9	21.4	4.2	27.7	4.8	**<0.001**	0.24	0.94	86.7	93.3	100.0	100.0	93.3	100.0	100.0	93.3
Plantago ovata	0.1	0.1	0.2	0.1	10.5	6.8	6.7	3.7	**0.01**	0.91	0.55	0.4	0.2	0.5	0.2	3.0	2.3	5.2	2.7	**0.01**[*]	0.79[*]	na[*]	20.0	40.0	53.3	60.0	53.3	53.3	86.7	73.3
Erodium cicutarium	0.3	0.2	0.4	0.2	2.2	1.1	2.7	1.3				0.4	0.2	0.4	0.2	1.9	0.6	1.8	0.7				33.3	20.0	46.7	53.3	46.7	53.3	66.7	60.0
Bromus rubens	0.0	0.0	0.0	0.0	1.7	1.1	1.5	0.7				0.1	0.1	0.5	0.5	1.3	0.5	1.1	0.3				6.7	0.0	40.0	60.0	20.0	13.3	93.3	93.3
Lepidium lasiocarpum	0.2	0.2	0.1	0.1	0.1	0.0	0.2	0.1				0.2	0.1	0.2	0.1	0.4	0.1	0.6	0.2				13.3	20.0	13.3	46.7	40.0	46.7	73.3	66.7
Eriophyllum lanosum	0.0	0.0	0.0	0.0	2.4	1.0	2.7	1.3				0.0	0.0	0.0	0.0	1.2	0.3	1.4	0.5				0.0	0.0	80.0	73.3	0.0	0.0	73.3	73.3
Astragalus allochrous	0.0	0.0	0.1	0.1	0.2	0.1	0.3	0.2				0.1	0.1	0.2	0.1	0.7	0.3	0.8	0.2				0.0	6.7	26.7	33.3	26.7	46.7	53.3	73.3
Amsinckia menziesii	0.0	0.0	0.0	0.0	0.2	0.1	0.3	0.2				0.1	0.1	0.2	0.1	0.5	0.2	0.2	0.1				0.0	0.0	33.3	40.0	20.0	33.3	73.3	40.0
Erodium texanum	0.3	0.1	1.0	0.5	0.1	0.0	0.0	0.0				0.2	0.1	0.7	0.3	0.0	0.0	0.0	0.0				46.7	46.7	13.3	6.7	46.7	53.3	0.0	0.0
Lotus humistratus	0.0	0.0	0.0	0.0	0.2	0.1	0.8	0.3				0.0	0.0	0.0	0.0	0.5	0.2	0.5	0.2				0.0	40.0	53.3	0.0	0.0	0.0	53.3	53.3
Chorizanthe brevicornu	0.0	0.0	0.1	0.0	0.2	0.2	0.2	0.1				0.0	0.0	0.0	0.0	0.5	0.2	0.8	0.5				6.7	13.3	20.0	33.3	0.0	6.7	46.7	46.7
Eriastrum diffusum	0.0	0.0	0.0	0.0	0.2	0.1	2.4	2.3				0.0	0.0	0.0	0.0	0.4	0.2	0.2	0.1				0.0	0.0	40.0	13.3	0.0	6.7	46.7	33.3
Crassula connata	0.0	0.0	0.0	0.0	0.4	0.2	0.1	0.1				0.0	0.0	0.0	0.0	0.2	0.1	0.2	0.1				0.0	0.0	20.0	26.7	0.0	0.0	40.0	46.7
Cryptantha decipiens	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0				0.2	0.1	0.3	0.2	0.0	0.0	0.0	0.0				20.0	26.7	0.0	6.7	40.0	26.7	6.7	0.0
Lotus salsuginosus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.3	0.1	0.4	0.2				0.0	0.0	0.0	0.0	0.0	0.0	60.0	60.0
Lupinus sparsifolus	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2				0.0	0.0	0.0	0.0	0.1	0.1	0.6	0.3				0.0	0.0	0.0	20.0	0.0	0.0	20.0	40.0
Dichelostemma capitatum	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1				0.0	0.0	0.0	13.3	0.0	0.0	6.7	26.7
Astragalus lentiginosus	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1				0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	26.7	13.3	0.0	0.0	0.0	0.0
Lesquerella gordonii	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0				0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0				0.0	0.0	13.3	6.7	0.0	0.0	13.3	6.7
Chamaesyce albomarginata	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2				0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0				0.0	0.0	0.0	6.7	0.0	6.7	0.0	0.0
Phacelia distans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.0	0.0	13.3	0.0
Eschscholzia californica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7
Plagiobothrys arizonicus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0

Two way ANOVA tests (or two Kruskal Wallis tests [*]) conducted on percent cover of the three most dominant species (fixed factors: distance from city and treatment). Significant results highlighted in bold.

Appendix D. Individual-based species accumulation curves on winter annual species abundance data from 2011 to 2012.

Number of Individuals
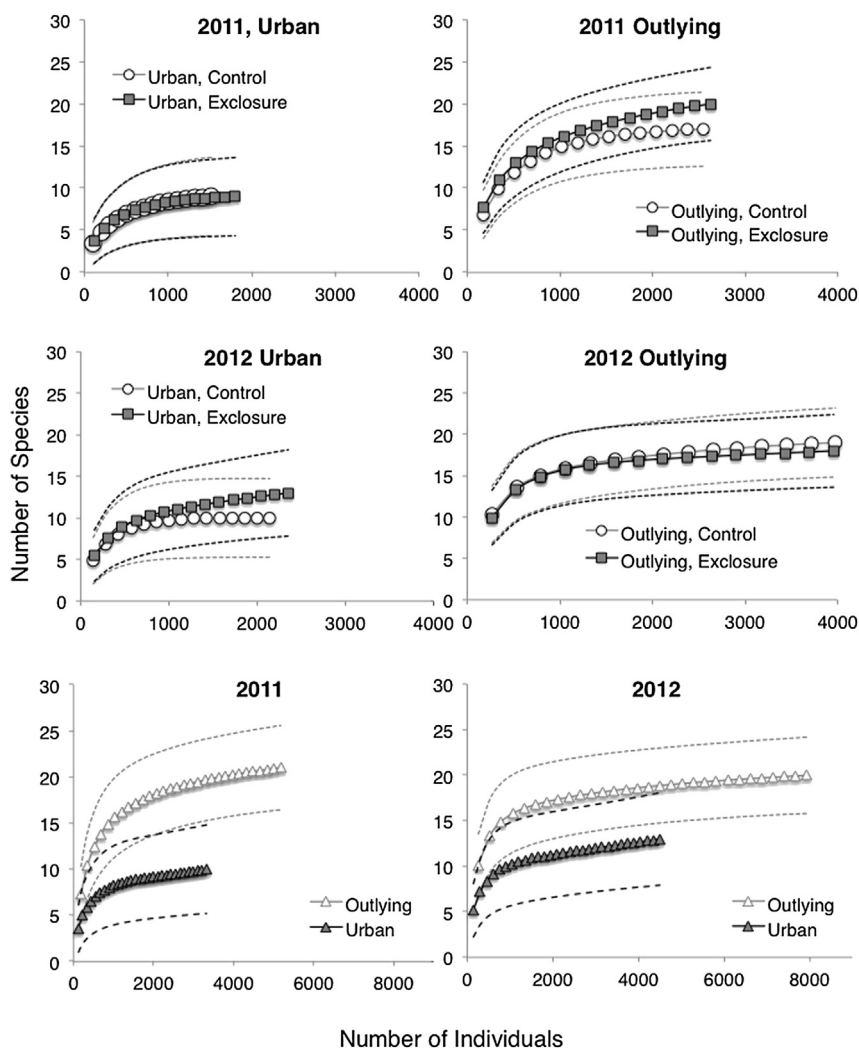
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