

Effects of exurban development on trophic interactions in a desert landscape

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Abstract

Context Mechanisms of ecosystem change in urbanizing landscapes are poorly understood, especially in exurban areas featuring residential or commercial development set in a matrix of modified and natural vegetation. We asked how development altered trophic interactions and ecosystem processes in the matrix.

Objectives We examined the effect of varying degrees of exurban development (housing density) on a trophic system that included an apex mammalian predator (coyote, *Canis latrans*), mammalian herbivores (lagomorphs and rodents), and herbaceous plants. We tested the hypothesis that plant recruitment

would be negatively affected by exurban development due either to increases in herbivores associated with increased resource availability (a bottom–up effect) or to a reduction in predators that avoid humans (a top–down effect).

Methods In Las Cruces, New Mexico, USA, four replicate sites were located in each of three urbanization levels: high density exurban, low density exurban, and wildland dominated by Chihuahuan Desert vegetation. Seedling trays measured herbivory rates, live trapping estimated abundance of pocket mice and kangaroo rats, and remotely-triggered wildlife cameras estimated the activity of lagomorphs and coyotes.

Results Increased herbivory on seedlings and decreased herbaceous plant recruitment were observed in high density exurban areas. Overall rodent abundance, seed consumption rates, and activity of the lagomorph *Lepus californicus* did not vary with urbanization level. Activity by another lagomorph, *Sylvilagus audubonii*, and coyotes was highest in dense exurban areas, consistent with a bottom–up effect.

Conclusions Exurban development can have important indirect effects on trophic interactions occurring in adjacent, untransformed ecosystems. Similar to earlier studies, such effects in the Chihuahuan Desert may be mediated by bottom–up processes associated with anthropogenic inputs.

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Introduction

Urban growth and its impacts on ecosystems are increasing globally, yet little is known about the patterns and processes of ecosystem change associated with urbanization (Fischer et al. 2012; Magle et al. 2012; Pejchar et al. 2015). Our understanding of exurban ecosystems—low density developments outside of urban areas—is especially limited (Magle et al. 2012). Nonetheless, most built-up areas are exurban or rural, now covering 9.1 % of the United States (Theobald 2014), and exurban development is rapidly expanding into remaining wildlands (Hansen et al. 2005). In particular, arid landscapes across the western United States are experiencing high rates of exurban development (York et al. 2011; Theobald et al. 2013; Bestelmeyer et al. 2015). Such rapidly urbanizing ecosystems merit greater attention from ecologists (Pejchar et al. 2015), and changes caused by urbanization can create ideal opportunities to test ecological theory (Grimm et al. 2000).

Exurban ecosystems feature residential or commercial structures set in a matrix of modified and natural vegetation (Odell and Knight 2001). Research on exurban effects often focuses on how development and associated human impacts alter trophic interactions and ecosystem processes in the matrix (Fischer et al. 2012). Top-down effects or trophic cascades may be initiated by a reduction in the activity or abundance of predators that leads to increased activity of herbivorous prey species (Kitchen et al. 2000; Waser et al. 2014). In arid ecosystems of the southwestern USA, reduced predation pressure can lead to increases in abundance and expanded foraging activity by rodents and lagomorphs (Henke and Bryant 1999; Brown and Kotler 2004; Laundré et al. 2014). Changes in small mammal abundance and activity can, in turn, have important effects on vegetation. In the Chihuahuan Desert, exclusion of lagomorphs can increase cover of shrubs, such as creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) (Havstad et al. 1999). Grass cover can be limited by kangaroo rats (*Dipodomys* spp.) that consume vegetative parts of perennial grasses. By feeding on both seeds and seedlings, kangaroo rats can also limit vegetation biomass and recruitment (Kerley et al. 1997; Curtin et al. 2000).

Urbanization can have profound effects on animal communities via bottom-up pathways as well.

Urbanized areas in arid ecosystems can have elevated productivity throughout the year, including during periods that would otherwise have low productivity (Imhoff et al. 2000). Increases in water inputs from irrigation for agriculture and green spaces, and a desire for mesic vegetation in residential areas, can increase the amount and stability of plant productivity (Faeth et al. 2005; Shochat et al. 2006). Increased production can affect trophic structure by supporting greater abundances of animals, especially those that have learned to coexist with humans (Cook and Faeth 2006; Manley et al. 2006; Glennon and Porter 2007; Šálek et al. 2015). Furthermore, the effects of productivity, competition, and predation can vary and interact such that the signal of bottom-up versus top-down effects can vary over space and time (Hunter and Price 1992; Meserve et al. 2003; Faeth et al. 2012).

We examined how varying degrees of exurban development affected trophic interactions among an apex mammalian predator, mammalian herbivores, and herbaceous plants within an area undergoing rapid urbanization in the arid Southwest USA. Las Cruces, New Mexico is typical of cities in the arid southwest experiencing increasing growth, with varying housing densities associated with peri-urban (urban fringe) and exurban development (York et al. 2011) occurring in desert shrublands around the city. We compared primary production, natural plant recruitment, rates of herbivory and granivory, and distribution and activity of herbivores and a key carnivore across an urbanization gradient, providing an unusually comprehensive perspective on trophic interactions. Our gradient included undeveloped wildlands, low density exurban development, and high density exurban development. We focused on the matrix of natural desert vegetation occurring within developed areas, thereby evaluating processes occurring in the same vegetation type but with varying urban context.

We hypothesized that urbanization would have a negative effect on recruitment of native herbaceous plants through one of two potential trophic pathways, top-down or bottom-up (Hunter and Price 1992). The top-down model suggests that higher housing density should reduce predator occurrence or activity (Kitchen et al. 2000; Fischer et al. 2012), thereby leading to increased activity of mammalian herbivores (rodents and lagomorphs; Henke and Bryant 1999; Brown and Kotler 2004; Laundré et al. 2014), higher rates of herbivory and granivory, and reduced herbaceous

plant recruitment (Kerley et al. 1997; Havstad et al. 1999; Curtin et al. 2000). Alternatively, the bottom–up model suggests that greater or more constant resource availability (water availability and plant production) associated with higher housing density (Imhoff et al. 2000) would support increased abundance of mammalian herbivores, higher rates of herbivory and granivory, and an increase in predator activity due to increases in prey (Faeth et al. 2005). Both top–down and bottom–up models predict decreased herbaceous plant recruitment and increased herbivore activity with increased urbanization. However, the two models differ in predictions about predator activity. Higher predator activity in wildland areas as compared to exurban areas would support the top–down model. In contrast, higher predator activity in exurban than wildland areas would be consistent with the bottom–up model.

Methods

Site characteristics

We conducted this study during the summers of 2013 and 2014 in and around Las Cruces, NM, USA, a city with a human population size of 101,408 in 2014. We chose sites representing three levels of urbanization and human activity. The high density exurban (ca. 0.40-ha lots) and low density exurban (ca. 1.20-ha lots) sites were located in residential areas. Wildland sites were located adjacent to the city but at least 500 m from structures or paved roads; this distance was assumed to be sufficient to minimize anthropogenic influences on vegetation and wildlife but ensured that wildland sites would occur in similar vegetation and soil types as the exurban sites. Each urbanization level included 4 replicate sites for a total of 12 sites (Supplementary Figure S1). All sites were characterized by similar perennial native vegetation, dominated by creosotebush and mesquite shrubs. We restricted soil types to Torripsamments and Torriorthents bordering the Rio Grande valley, particularly Bluepoint loamy sands. We sampled exurban sites within areas of natural vegetation located outside of developed backyards, in areas accessible to wild animals.

All experiments and observations were centered on a focal plot within each of the 12 sites. At each site, we measured the density of built-up structures around the

0.10-ha focal plot by digitizing houses and related buildings as points and then calculating the density of points within a circle with a radius of 250-m (half the distance from wildland sites to the nearest structure) around the center of each plot, using ArcGIS 10.2 (ESRI 2014). We also measured the Euclidean distance from the plot center to the nearest paved road. To estimate primary production around each plot, we calculated the annual integrated normalized difference vegetation index (I-NDVI) for the 250-m radius buffer centered on the plot (2013: April–December; 2014: January, March–October; months with available data from Landsat 8 satellite). The 250-m buffer distance was assumed to circumscribe habitat elements that would influence the occupancy or abundance of animal species at the focal plots. We assessed differences in the density of houses, distance to roads, and I-NDVI among urbanization levels using Kruskal–Wallis tests followed by post hoc Mann–Whitney tests.

We also characterized perennial vegetation at each plot in 2014 using the line–point intercept method for foliar cover and belt transects to record shrub densities (Herrick et al. 2009). These measurements, gathered before the onset of the monsoon rains in July, focused on long-lived perennial plants rather than the annuals and geophytes that were the focus of other measurements (see below). We placed two 50-m transect lines within each study plot, separated by 10 m. Every 50 cm along each line, we dropped a pin flag and recorded every plant that the pin flag intercepted and the type of ground surface (soil, rock, embedded litter, or duff). We then calculated percent foliar cover, percent bare ground, and percent basal cover. Along the same transect lines, we used belt transects with a 2-m width to estimate shrub density. For shrubs that had at least half of their base within the belt transect, we recorded species and height class (<50, 50–100, and >100 cm in height). ANOVA and post hoc Tukey’s HSD tests were used for comparisons among urbanization levels.

Natural plant recruitment

We measured the fates of wild herbaceous plants that germinated at each study plot following rainfall events during the summer of 2013. These plants are largely annuals or perennial geophytes (*Senna roemariana* and *Pectis* spp.) that develop aboveground structures

following rains, although new perennial grass recruitment also occurs. Variations in plant germination may reflect differences in seed availability due to chronic differences in herbivory, granivory, or dispersal. At each plot, we marked 10 1-m² quadrats in intershrub areas where new plant growth was expected. We placed the quadrats at 5-m increments along a 50-m transect, adjusting quadrat position to be slightly outside the canopies of shrubs ≥ 50 cm in diameter. We tallied germinating plants in each quadrat by condition (undamaged, damage due to herbivory, dead due to herbivory, dead due to other causes; Bestelmeyer et al. 2007) every day for 5 days, then on day 10 and 15. After heavy rainfall and significant growth at the end of August, we examined quadrats once per month until plants started to desiccate and quantified percent cover of all plants. We used repeated measures, linear mixed models (PROC MIXED; SAS Version 9.4, SAS Institute, Cary, NC) to compare the natural recruitment of plants based on either counts of individual plants (day 1–15), or percent cover (September–November). Urbanization level and its interaction with day were fixed effects, site was a random effect, and day was a repeated effect where the subject was quadrat nested within site. We used an unstructured temporal covariance structure based on the minimum Akaike Information Criterion evaluated for a range of possible covariance structures. We applied the Kenward-Roger method to adjust denominator degrees of freedom.

Herbivory rates

We used seedling trays to determine the influence of herbivory on plant recruitment across the urbanization gradient during the summers of 2013 and 2014. Trays were seedling starter trays consisting of 6 cells. We grew sunflower seedlings in a greenhouse until they were approximately 5–7 cm tall, then placed 10 trays of seedlings in 5-m increments along a 50-m transect at every site. Sunflowers were used because they germinate reliably, grow quickly, and therefore served as a practical standard for comparison of herbivory pressure among sites. We placed each tray at least 1 m away from shrubs to simulate new herbaceous growth in shrub interspaces. We monitored the seedlings for damage by counting the number of remaining seedlings each day and assigning the damage to a category (as above). We removed the trays after

10 days, or after all seedlings had died. We calculated seedling survival as the proportion of deployed seedlings that survived until a given day. We then used repeated measures linear mixed models to analyze daily survival. The model structure was the same as for the natural recruitment sub-study, but with seedling tray nested within site as the subject of the repeated measures.

Granivory rates

We used seed trays to determine the influence of granivory by rodents on seedling recruitment during summer 2014. We built foraging trays using clear plastic storage containers (Sterilite, 5.7 L, 35.6 × 20.3 × 12.4 cm) with 4.5-cm diameter holes drilled in the sides to allow rodents to enter while excluding larger animals, and covered the trays with window screening held in place by elastic. The screening prevented access to the seeds from above but did not modify cover or, presumably, the perception of predation risk by rodent seed predators. We mixed 5 ± 0.05 g of millet seed with 1 L of fine sand and added it to each container. At each plot, we placed ten trays along a 50-m transect, at 5-m increments. We conducted this study for three consecutive days and nights during July 2014. We monitored the trays daily for signs of foraging, such as scat, scratches, or excavation. If signs of foraging were present, we removed the sand and sifted out and weighed the remaining millet to determine seed consumption. We then added another 5 g of millet to the foraged tray, so that the amount of seed in each tray was the same at the beginning of each night. We analyzed seed foraging data using a repeated measures linear mixed model, where the model structure was the same as the natural recruitment and seedling sub-studies but with tray nested within site as the subject of the repeated measures.

Rodent abundance

We performed live trapping at every site to estimate rodent abundance during 2013 and 2014. At each site, we established a 3 × 6 trapping grid (total area 0.10 ha), consisting of 18 total Sherman live traps (H.B. Sherman Traps, model XLK, 7.62 × 9.53 × 30.48 cm) with 10-m spacing between grid points. We chose this grid size because it was the

largest that could be accommodated at all high density sites. We baited traps with millet and set them for 4 consecutive nights during the new moon. We checked all traps before sunrise and determined species of captured animals. We assigned each animal a unique identification code, using metal ear tags for kangaroo rats (National Band & Tag Co., style 1005-1) and non-toxic permanent marker (Sharpie) on the ventrum for the smaller rodents, and released the animals at the capture site. We estimated abundance of the two most frequently captured rodent species (Merriam's kangaroo rat, *Dipodomys merriami*; Chihuahuan pocket mouse, *Chaetodipus eremicus*) and determined the influence of urbanization level on rodent abundance using closed population full likelihood models in Program MARK (White and Burnham 1999). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to determine the most parsimonious model. We also determined the influence of urbanization level on another measure of abundance, the minimum number of individuals known alive at each plot, using ANOVA.

Lagomorph and predator activity

We used camera traps to compare occurrence and activity of lagomorphs (black-tailed jackrabbit, *Lepus californicus*; desert cottontail, *Sylvilagus audubonii*) and coyotes (*Canis latrans*) among levels of urbanization (Ordeñana et al. 2010). Other predators (e.g., bobcats, *Lynx rufus*) were detected too infrequently for analysis. We used trail cameras (Bushnell Trophy Cam, Model 119436) at all plots during May and June 2013 (5 weeks) and 2014 (7 weeks). We set the cameras, equipped with a passive-infrared motion sensor, to take a series of 3 photographs once triggered, followed by a 10-s delay. We placed two cameras at every plot, back to back, positioned 30 cm from the ground, and facing an open area. Data from the two cameras were combined for analysis. We did not bait the camera traps, and we hid them under shrubs as much as possible. We checked the cameras weekly, downloading the photographs, storing them according to the protocol by Harris et al. (2010), and categorizing photographs using the protocol by Sanderson and Harris (2013).

We integrated the camera-trap data with occupancy modeling to estimate the probability of species occurrence at sites, while allowing for imperfect detection (MacKenzie et al. 2006; Robinson et al.

2014). Each survey was equal to 1 week of sampling (5 surveys in 2013, 7 surveys in 2014). We used single-season models (MacKenzie et al. 2006) within Program PRESENCE (Hines 2006) and evaluated only simple models due to our moderate sample size. For each species, we used likelihood ratio tests to compare a model with urbanization level as a covariate for occupancy (Psi) with an intercept-only model. We did not include covariates for per-survey detection probability (p). For 2014, occupancy modeling was not possible due to model convergence issues due largely to data sparseness.

For 2013 and 2014, we assayed the activity of coyotes and lagomorphs by using the total number of independent photographs taken at a plot divided by the number of working camera days to obtain a photo-activity rate for each species. Photographs taken ≥ 60 min apart were considered independent. There is debate about using photographic rates as an index for abundances (e.g., Jennelle et al. 2002; Bengsen et al. 2011). We considered our rates only as an index of relative activity of species at a site, not as a measure of abundance. We used repeated measures linear mixed models (PROC MIXED; SAS, Version 9.4; SAS Institute, Cary, NC) to test the effects of urbanization level, year, and an urbanization \times year interaction on photo-activity rates. Site was the subject of the repeated measures, and we used an unstructured covariance structure.

Unless otherwise noted, statistics were conducted in R v.3.1.1 (R Core Team 2014), and all means are reported ± 1 SE.

Results

Site characteristics

As expected, density of houses differed among urbanization levels (Kruskal–Wallis test, $\chi^2_2 = 10.20$, $p = 0.01$). There were more structures in high density exurban sites (0.12 ± 0.02 houses/km²) than in low density exurban sites (0.03 ± 0.01 houses/km²; Mann–Whitney *U*-test; $W = 16$, $p = 0.03$) and wildland sites (0 houses/km²; $W = 16$, $p = 0.02$), and more structures in low density exurban than wildland sites ($W = 16$, $p = 0.02$). Distance to roads also differed by urbanization level ($\chi^2_2 = 8.70$, $p = 0.01$). Both high density

exurban sites (50 ± 10 m; $W = 0$, $p = 0.03$) and low density exurban sites (98 ± 19 m; $W = 0$, $p = 0.03$) were closer to roads than were wildland sites. High and low density exurban sites did not differ in the distance to nearest paved roads ($W = 2$, $p = 0.11$).

I-NDVI varied among urbanization levels in 2013 ($\chi^2_2 = 5.35$, $p = 0.07$). Mean I-NDVI was greater in high density exurban sites (1.10 ± 0.02) than in wildland sites (0.97 ± 0.04 ; $W = 15$, $p = 0.06$). However, there was no difference in mean NDVI between high and low density exurban sites (1.04 ± 0.02 ; $W = 14$, $p = 0.11$), or between low density exurban and wildland sites ($W = 11$, $p = 0.49$). I-NDVI was not related to urbanization during 2014 ($\chi^2_2 = 0.962$, $p = 0.62$; high density = 1.11 ± 0.02 , low density = 1.12 ± 0.02 , wildland = 1.01 ± 0.07).

Urbanization levels had similar shrub ($F_{2,9} = 0.34$, $p = 0.72$) and perennial grass ($F_{2,9} = 2.07$, $p = 0.18$) foliar cover; however, there was a difference in cactus foliar cover ($F_{2,9} = 8.35$, $p = 0.01$). Cactus cover was higher in high density exurban plots (0.02 ± 0.003 %) than in low density exurban plots (0.005 ± 0.005 %; Tukey's HSD; $p = 0.03$) and wildland plots (0.001 ± 0.005 %; Tukey's HSD; $p = 0.01$), but cover was generally very low. Mesquite foliar cover ($F_{2,9} = 1.73$, $p = 0.23$) and foliar cover of other shrubs (mainly creosotebush) did not differ among urbanization levels ($F_{2,9} = 1.63$, $p = 0.25$). Similarly, there was no difference in density of total shrubs ($F_{2,9} = 0.01$, $p = 0.99$) or density of large (>1 m) shrubs ($F_{2,9} = 1.07$, $p = 0.38$).

Natural plant recruitment

Both urbanization level and time affected the total number of wild plants before heavy rainfall (urbanization level, $F_{2,12.32} = 7.42$, $p = 0.007$; time, $F_{6,112} = 9.80$, $p < 0.001$; interaction, $F_{12,171.70} = 3.49$, $p < 0.001$). There were fewer individual plants in the high density exurban plots than in the low density exurban plots ($t_{12.32} = -2.84$, $p = 0.01$, Fig. 1a) or wildland plots ($t_{12.32} = -3.67$, $p = 0.003$, Fig. 1a). Low density exurban plots and wildland plots had similar numbers of individual plants before heavy rainfall ($t_{12.32} = -0.83$, $p = 0.42$, Fig. 1a). After heavy rainfall, there was an effect of urbanization level and time on the percent of

vegetation cover (urbanization level, $F_{2,10.37} = 13.03$, $p = 0.001$; time, $F_{2,116} = 29.67$, $p < 0.001$; interaction, $F_{4,138.39} = 5.06$, $p < 0.001$). There was lower plant cover in the high density exurban plots than in the low density exurban plots ($t_{10.37} = -3.22$, $p = 0.009$, Fig. 1b) or wildland plots ($t_{10.37} = -5.22$, $p < 0.001$, Fig. 1b). Low density exurban plots and wildland plots had similar plant cover ($t_{10.37} = -1.83$, $p = 0.10$, Fig. 1b).

Herbivory rates

Seedling herbivory rates for summer of 2013 differed among urbanization levels and over time (urbanization level, $F_{2,7.38} = 8.98$, $p = 0.01$; time, $F_{9,109} = 82.41$, $p < 0.001$; interaction, $F_{18,178.56} = 8.24$, $p < 0.001$). We observed higher herbivory rates (fewer surviving seedlings) at the high density exurban plots than the low density exurban plots ($t_{7.38} = -3.46$, $p = 0.01$, Fig. 1c).

We also observed a difference in herbivory between the high density exurban and wildland plots ($t_{7.38} = -3.85$, $p = 0.01$, Fig. 1c). We saw no difference between the low density exurban and wildland plots ($t_{7.38} = -0.40$, $p = 0.70$, Fig. 1c). Seedling herbivory rates did not differ between urbanization levels in 2014 because most seedlings were eaten within the first day (urbanization level, $F_{2,119.67} = 0.09$, $p = 0.91$; time, $F_{2,116} = 480.82$, $p < 0.001$; interaction, $F_{4,138.39} = 1.28$, $p = 0.28$; Supplementary Figure S2).

Granivory rates

Granivory rates were affected by time and the interaction between time and level of urbanization (urbanization level, $F_{2,9.05} = 2.92$, $p = 0.11$; day, $F_{2,114.44} = 35.98$, $p < 0.001$; interaction, $F_{4,136.62} = 19.41$, $p < 0.001$; Supplementary Figure S3). The wildland plots had constant high consumption of seeds, whereas the low density exurban plots had constant low rates of seed consumption ($t_{9.05} = -2.41$, $p = 0.04$). However, seed consumption increased through time in high density exurban plots, and was not different from seed consumption in either low density exurban ($t_{9.05} = 1.29$, $p = 0.22$) or wildland plots ($t_{9.05} = -1.12$, $p = 0.29$).

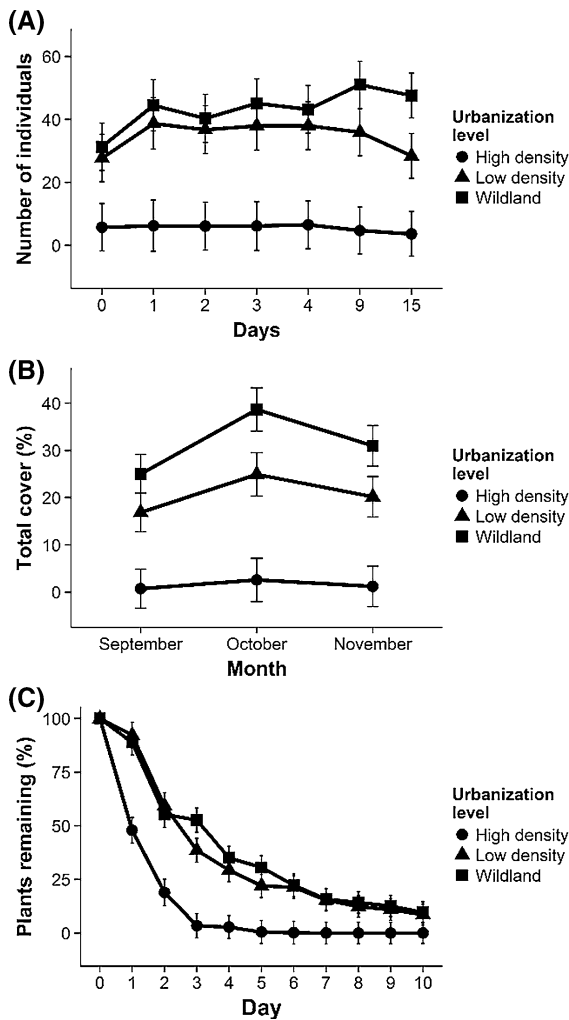


Fig. 1 Herbaceous plant response to urbanization for **a** counts of individual plant seedlings that had emerged before major rain events in summer 2013, **b** percent herbaceous vegetation cover after major rain events in summer 2013, and **c** percent of live plants remaining in seedling trays after each day exposed to herbivory in summer 2013. All points represent the mean \pm 1 SE. For the seedling herbivory study (c), day 0 represents the day the seedlings were placed at the sites

Rodent abundance

MARK models for pocket mouse abundance in 2013 and 2014 did not indicate an overall effect of urbanization (Table 1). Due to high support for multiple models, we used model averaging to estimate pocket mouse abundance (Supplementary Figure S4a). Similarly, analysis of the minimum number known alive showed that time, but not urbanization level, affected

abundance (ANOVA: time, $F_{1,18} = 43.64$, $p < 0.001$; urbanization level, $F_{2,18} = 0.90$, $p = 0.42$).

There was no effect of urbanization level on kangaroo rat abundance during either 2013 or 2014 (Table 1; Supplementary Figure S4b). Again, model averaging was applied and the weighted average population size estimate was used for kangaroo rat abundance. Neither time nor urbanization level had an effect on the minimum number known alive (ANOVA: time, $F_{1,18} = 1.36$, $p = 0.26$; urbanization level, $F_{2,18} = 0.89$, $p = 0.43$).

Lagomorph and predator activity

Jackrabbits occurred at most sites across the urbanization gradient in both years. In 2013, however, there was a tendency for a lower probability of site occupancy for jackrabbits at high density sites (Likelihood ratio test: $\chi^2_2 = 5.27$, $p = 0.072$; Supplementary Figure S5a). The photo-activity rate for jackrabbits did not differ among urbanization levels ($F_{2,9} = 0.36$, $p = 0.71$; Fig. 2a), but did differ between years ($F_{1,9} = 20.95$, $p = 0.001$) and there was no interaction between urbanization level and year ($F_{2,9} = 0.60$, $p = 0.57$). Jackrabbit activity was much higher in 2014 than in 2013 (Fig. 2a).

In 2013, site occupancy for desert cottontails was affected by urbanization levels (Likelihood ratio test: $\chi^2_2 = 6.26$, $p = 0.04$; Supplementary Figure S5b) with highest occupancy in high density urban sites and lowest occupancy in wildland sites. Photo-activity rates for cottontails differed among urbanization levels ($F_{2,9} = 10.34$, $p = 0.005$) but not between years ($F_{1,9} = 0.00$, $p = 0.98$), and there was no interaction between urbanization level and year ($F_{2,9} = 2.27$, $p = 0.16$). Cottontail activity was higher at high density sites than at low density ($t_9 = 3.20$, $p = 0.01$) or wildland sites ($t_9 = 4.40$, $p = 0.002$; Fig. 2b).

In 2013, the probability of site occupancy for coyotes also differed among urbanization levels (Likelihood ratio test: $\chi^2_2 = 6.26$, $p = 0.04$; Supplementary Figure S5c) with coyotes occurring more often at high and low density urban sites as compared to wildlands. Photo-activity rates for coyotes also differed among urbanization levels ($F_{2,9} = 2.91$, $p = 0.10$) and between years ($F_{1,9} = 3.73$, $p = 0.09$), but there was no interaction between

Table 1 Candidate models for the estimation of pocket mouse and kangaroo rat abundance

Model ^a	Δ AICc	AICc weight	No. parameters	Deviance
Pocket mice 2013				
$p = c(\cdot) \cdot N(\cdot)$	0	0.446	2	76.224
$p = c(\text{urban}) \cdot N(\cdot)$	0.334	0.377	4	72.434
$p = c(\text{urban}) \cdot N(\text{urban})$	2.670	0.117	6	70.567
$p = c(\cdot) \cdot N(\text{urban})$	4.010	0.060	4	76.107
Pocket mice 2014				
$p = c(\cdot) \cdot N(\cdot)$	0	0.626	2	131.291
$p = c(\text{urban}) \cdot N(\cdot)$	2.129	0.216	4	129.373
$p = c(\cdot) \cdot N(\text{urban})$	3.836	0.092	4	131.080
$p = c(\text{urban}) \cdot N(\text{urban})$	4.512	0.066	6	127.680
Kangaroo rats 2013				
$p = c(\text{urban}) \cdot N(\cdot)$	0	0.425	4	47.514
$p = c(\cdot) \cdot N(\cdot)$	0.113	0.401	2	51.749
$p = c(\text{urban}) \cdot N(\text{urban})$	2.748	0.108	6	46.068
$p = c(\cdot) \cdot N(\text{urban})$	3.715	0.066	4	51.229
Kangaroo rats 2014				
$p = c(\cdot) \cdot N(\cdot)$	0	0.728	2	58.703
$p = c(\text{urban}) \cdot N(\cdot)$	3.214	0.146	4	57.828
$p = c(\cdot) \cdot N(\text{urban})$	3.820	0.108	4	58.433
$p = c(\text{urban}) \cdot N(\text{urban})$	7.355	0.018	6	57.827

^a Model covariates p capture rate, c recapture rate, N abundance; \cdot does not vary (constant), *urban* varies with urbanization level

urbanization level and year ($F_{2,9} = 1.55$, $p = 0.26$). Activity of coyotes was greater at low-density sites than at wildlands ($t_9 = 2.38$, $p = 0.04$; Fig. 2c).

Discussion

Our results suggest that exurban development around Las Cruces has strong indirect effects on herbaceous plant recruitment, likely mediated by trophic interactions. We found lower herbaceous plant recruitment, higher herbivory rates, and higher cottontail activity in high density exurban areas compared to wildland areas. Greater occurrence and activity of coyotes at exurban sites compared to wildland sites is consistent with a bottom-up model of trophic control.

We confirmed that housing density and distance to roads varied as expected along the urbanization gradient. I-NDVI measurements indicated that primary production was higher in high density exurban areas than in wildlands in 2013, supporting a basic assumption of the bottom-up model. Greater production in high density exurban areas is likely to be caused by irrigation for green spaces, such as yards and parks, and from introduced plants that may be more

productive throughout the year than native plants (Imhoff et al. 2000; Shochat et al. 2006). I-NDVI values did not differ among urbanization levels in 2014, however, possibly due to an overall higher NDVI compared to 2013.

Rodent abundance did not differ among urbanization levels, potentially because desert rodents, especially heteromyids such as kangaroo rats and pocket mice, are seed predators and rely on native seed producing species rather than introduced plants (Heske et al. 1993; Curtin et al. 2000). Similarly, jackrabbit activity did not differ consistently among urbanization levels. Since jackrabbit diets consist mainly of native shrubs, such as creosotebush (Daniel et al. 1993; Roth et al. 2007), anthropogenic resources may be less important to these herbivores. Although jackrabbit activity increased dramatically from 2013 to 2014, this change occurred similarly across the urbanization gradient.

In contrast to the other herbivorous mammals in our study, desert cottontails were more active and had a higher probability of occupancy in high density exurban areas. Thus, herbivory by cottontails in particular is a likely explanation for the high herbivory rates and low herbaceous plant recruitment rates

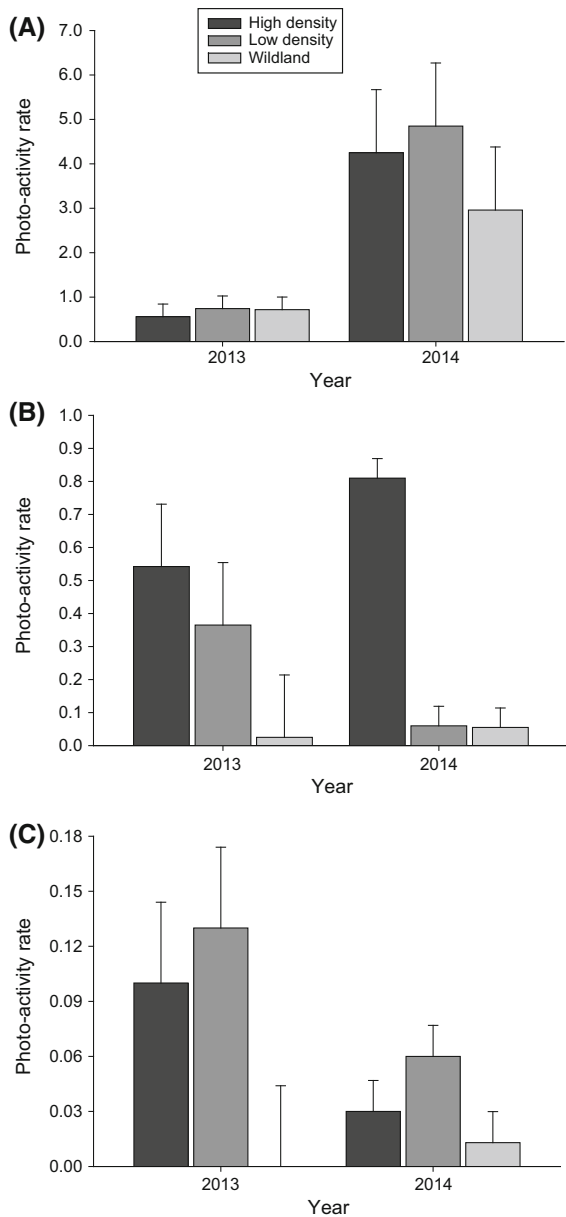


Fig. 2 Photo-activity rates (independent photographs per day) for **a** black-tailed jackrabbits, **b** desert cottontails, and **c** coyotes in summer 2013 and 2014. Bars indicate least-squares mean \pm 1 SE

observed in high density exurban areas. Previous studies demonstrate cottontails can prefer more urbanized areas (Bock et al. 2006; Hunt et al. 2013), and that herbaceous seedlings are targeted by these herbivores (Turkowski 1975).

Differences in the relative abundance or activity of carnivores among urbanization levels is the key

pattern distinguishing the top-down and bottom-up models. We found that coyote occurrence and activity were higher in more urbanized areas, supporting the bottom-up model. Our results are similar to those of some previous studies (Fedriani et al. 2001; Ordeñana et al. 2010), but others have found that coyotes avoid urban areas and human activity (e.g., Randa and Yunger 2006; Magle et al. 2014a). Housing densities in our exurban areas may have been below any threshold that might negatively affect coyotes. Moreover, when coyotes have territories that overlap with developed areas, they may exploit anthropogenic resources but continue to prefer natural prey (Fedriani et al. 2001; Gehrt and Riley 2010; Magle et al. 2014b). In our study, however, anthropogenic subsidies do not appear to have led to decreases in prey activity.

The concurrent increase in activity by both coyotes and cottontails with increasing urbanization is consistent with the notion of the “predation paradox,” in which predator activity increases in urban areas, but effects of predators on prey appear to decline (Fischer et al. 2012). This paradox could occur in our study system either because omnivorous coyotes are subsidized by anthropogenic food, which reduces predation rates on prey species, or because cottontails are hyperabundant relative to predators, due to their own anthropogenic subsidies (Fischer et al. 2012). Untangling these potential mechanisms would require additional research on diets of predator and prey, and predation rates, across our urbanization gradient. Furthermore, the different patterns between 2013 and 2014, including the absence of differences in I-NDVI among urbanization levels, higher herbivory rates, and dramatically higher activity of jackrabbits in 2014 indicates that predator-prey-resource relationships vary temporally and should be observed over longer timeframes than was possible in this study.

Overall, our results are consistent with a three-level, bottom-up trophic cascade (Pace et al. 1999) that is supported by anthropogenic inputs, but is spatially coupled to natural shrubland patches where increased herbivore populations constrain plant recruitment. Anthropogenic inputs within modified patches, such as gardens or lawns, might directly support herbivores whose foraging activities spill over into adjacent shrubland patches. Such spatial subsidies allow for greater numbers of animals than local resources alone could support (Stapp and Polis 2003; Anderson et al. 2008). Spatial spillover of predators or

herbivores from resource-rich to resource-poor patches can have important consequences for trophic interactions (Casini et al. 2012; Liere et al. 2015) and lead to deviations from expected predator-prey relationships based on local habitat characteristics alone (Rodewald et al. 2011). In this way, exurban ecosystems might usefully be viewed as “meta-ecosystems” composed of built-up, modified (e.g. irrigated), and natural patch types among which spatial interactions control trophic dynamics and other ecosystem properties (Loreau et al. 2003).

In spite of the large and increasing extent of exurban developments (York et al. 2011), their effects are incompletely understood (Magle et al. 2012). Our work illustrates that consideration of several trophic levels may be necessary to fully comprehend dynamics of exurban ecosystems. Our results are consistent with previous studies indicating an important role for bottom-up trophic cascades and spatial subsidies in the functioning of urban ecosystems (Faeth et al. 2005; Rodewald et al. 2011; Fischer et al. 2012). Future studies should seek to quantify spatiotemporal variations in potentially limiting resources, including water, food, and safe spaces, and the impact of these variations on the distribution and abundance of key species. In addition, long-term monitoring studies will be needed to test whether the importance of bottom-up and top-down forces varies over time in response to weather-driven variations in resource availability and population dynamics (Hunter and Price 1992, Meserve et al. 2003). Such studies are needed to provide a scientific basis for the management of biodiversity in arid exurban systems.

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References

- Anderson WB, Wait DA, Stapp P (2008) Resources from another place and time: responses to pulses in a spatially subsidized system. *Ecology* 89:660–670
- Bengsen AJ, Leung LK-P, Lapidge SJ, Gordon IJ (2011) Using a general index approach to analyze camera-trap abundance indices. *J Wildl Manag* 75:1222–1227
- Bestelmeyer BT, Khalil NI, Peters DPC (2007) Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland-shrubland ecotones. *J Veg Sci* 18:363–370
- Bestelmeyer BT, Okin GS, Duniway MC, Archer SR, Sayre NF, Williamson JC, Herrick JE (2015) Desertification, land use, and the transformation of global drylands. *Front Ecol Environ* 13:28–36
- Bock CE, Jones ZF, Bock JH (2006) Abundance of cottontails (*Sylvilagus*) in an exurbanizing southwestern savanna. *Southwest Nat* 51:352–357
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014
- Casini M, Blenckner T, Möllmann C, Gårdmark A, Lindgren M, Llope M, Kornilovs G, Plikshs M, Stenseth NC (2012) Predator transitory spillover induces trophic cascades in ecological sinks. *Proc Natl Acad Sci USA* 09:8185–8189
- Cook WM, Faeth SH (2006) Irrigation and land use drive ground arthropod community patterns in an urban desert. *Environ Entomol* 35:1532–1540
- Curtin CG, Kelt DA, Frey TC, Brown JH (2000) On the role of small mammals in mediating climatically driven vegetation change. *Ecol Lett* 2:309–317
- Daniel A, Holecheck JL, Valdez R, Tembo A, Saiwana L, Rusco M, Cardenas M (1993) Range condition influences on Chihuahuan Desert cattle and jackrabbit diets. *J Range Manag* 46:296–301
- ESRI (2014) ArcGIS Desktop: Release 10.2. Environmental Systems Research Institute, Redlands
- Faeth SH, Saari S, Bang C (2012) Urban biodiversity: patterns, processes and implications for conservation. eLS. doi:10.1002/9780470015902.a0023572
- Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. *BioScience* 55:399–407
- Fedriani JM, Fuller TK, Sauvajot RM (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24:325–331
- Fischer JD, Cleeton SH, Lyons TP, Miller JR (2012) Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *BioScience* 62:809–818
- Gehrt SD, Riley SPD (2010) Coyotes (*Canis latrans*). In: Gehrt SD, Riley SPD, Cypher BL (eds) *Urban carnivores: ecology, conflict, and conservation*. Johns Hopkins University Press, Baltimore, pp 79–98
- Glennon MJ, Porter WF (2007) Impacts of land-use management on small mammals in the Adirondack Park, New York. *Northeast Nat* 14:323–342
- Grimm NB, Grove JG, Pickett STA, Redman CL (2000) Integrated approaches to long-term studies of urban ecological systems. *BioScience* 50:571–584
- Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH, Jones K (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecol Appl* 15:1893–1905

- Harris G, Thompson R, Childs JL, Sanderson JG (2010) Automatic storage and analysis of camera trap data. *Bull Ecol Soc Am* 91:352–360
- Havstad KM, Gibbens RP, Knorr CA, Murray LW (1999) Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *J Arid Environ* 42:155–166
- Henke SE, Bryant FC (1999) Effects of coyote removal on the faunal community in western Texas. *J Wildl Manag* 63:1066–1081
- Herrick JE, Van Zee JW, Havstad KM, Burkett LM, Whitford WG (2009) Monitoring manual for grassland, shrubland, and savanna ecosystems. Volume 1: quick start. USDA-ARS Jornada Experimental Range, Las Cruces
- Heske EJ, Brown JH, Guo Q (1993) Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95:520–524
- Hines JE (2006) PRESENCE2- Software to estimate patch occupancy and related parameters. USGS-PWRC. <http://www.mbr-wrc.gov/software/presence.html>
- Hunt VM, Magle SB, Vargas C, Brown AW, Lonsdorf EV, Sacerdote AB, Sorley EJ, Santymire RM (2013) Survival, abundance, and capture rate of eastern cottontail rabbits in an urban park. *Urban Ecosyst* 17:547–560
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732
- Imhoff ML, Tucker CJ, Lawrence WT, Stutzer DC, Rusin RJ (2000) The use of multi-source satellite and geospatial data to study the effect of urbanization on primary productivity in the United States. *IEEE Trans Geosci Remote Sens* 38:2549–2556
- Jennelle CS, Runge MC, MacKenzie DI (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Anim Conserv* 5:119–120
- Kerley GIH, Whitford WG, Kay FR (1997) Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia* 111:422–428
- Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. *Can J Zool* 78:853–857
- Laundré JW, Hernández L, Medina PL, Campanella A, López-Portillo J, González-Romero A, Grajales-Tam KM, Burke AM, Gronemeyer P, Browning DM (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95:1141–1152
- Liere H, Kim TN, Werling BP, Meehan TD, Landis DA, Gratton C (2015) Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield. *Ecol Appl* 25:652–661
- Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol Lett* 6:673–679
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington
- Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: past, present, and future. *Biol Conserv* 155:23–32
- Magle SB, Poessel SA, Crooks KR, Breck SW (2014a) More dogs less bite: the relationship between human-coyote conflict and prairie dog colonies in urban landscape. *Landsc Urban Plan* 127:146–153
- Magle SB, Simoni LS, Lehrer EW, Brown JS (2014b) Urban predator-prey association: coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosyst* 17:875–891
- Manley PN, Murphy DD, Campbell LA, Heckmann KE, Merideth S, Parks SA, Sanford MP, Schlesinger MD (2006) Biotic diversity interfaces with urbanization in the Lake Tahoe Basin. *Calif Agric* 60:59–64
- Meserve PL, Kelt DA, Milstead WB, Gutierrez JR (2003) Thirteen years of shifting top-down and bottom-up control. *BioScience* 53:633–646
- Odell EA, Knight RL (2001) Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conserv Biol* 15:1143–1150
- Ordeñana MA, Crooks KR, Boydston EE, Fisher RN, Lyren LM, Siudyla S, Haas CD, Harris S, Hathaway SA, Turschak GM, Miles AK, Van Vuren DH (2010) Effects of urbanization on carnivore species distribution and richness. *J Mammal* 91:1322–1331
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol* 14:483–488
- Pejchar L, Reed SE, Bixler P, Ex L, Mockrin MH (2015) Consequences of residential development for biodiversity and human well-being. *Front Ecol Environ* 13:146–153
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Randa LA, Yunker JA (2006) Carnivore occurrence along an urban-rural gradient: a landscape-level analysis. *J Mammal* 87:1154–1164
- Robinson QH, Bustos D, Roemer GW (2014) The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology* 95:3112–3123
- Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator-prey relationships. *Ecol Appl* 21:936–943
- Roth GA, Whitford WG, Steinberger Y (2007) Jackrabbit (*Lepus californicus*) herbivory changes dominance in desertified Chihuahuan Desert ecosystems. *J Arid Environ* 70:418–426
- Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mamm Rev* 45:1–14
- Sanderson J, Harris G (2013) Automatic data organization, storage, and analysis of camera trap pictures. *J Indones Nat Hist* 1:6–14
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21:186–191
- Stapp P, Polis GA (2003) Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* 134:496–504
- Theobald DM (2014) Development and applications of a comprehensive land use classification and map for the US. *PLoS One* 9:e94628

- Theobald D, Travis W, Drummond M, Gordon E, Betsill M (2013) The changing southwest. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds) Assessment of climate change in the southwest United States. Island Press/Center for Resource Economics, Washington, DC, pp 37–55
- Turkowski FJ (1975) Dietary adaptability of the desert cottontail. *J Wildl Manag* 39:748–756
- Waser N, Price M, Blumstein D, Arózqueta SR, Escobar BC, Pickens R, Pistoia A (2014) Coyotes, deer, and wildflowers: diverse evidence points to a trophic cascade. *Naturwissenschaften* 101:427–436
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138
- York AM, Shrestha M, Boone CG, Zhang S, Harrington JA Jr, Prebyl TJ, Swann A, Agar M, Antolin MF, Nolen B, Wright JB, Skaggs R (2011) Land fragmentation under rapid urbanization: a cross-site analysis of Southwestern cities. *Urban Ecosyst* 14:429–455