

# Rich lizards: How affluence and land cover influence the diversity and abundance of desert reptiles persisting in an urban landscape



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## ABSTRACT

Fourteen native lizard species inhabit the desert surrounding Phoenix, AZ, USA, but only two occur within heavily developed areas. This pattern is best explained by a combination of socioeconomic status, land-cover, and location. Lizard diversity is highest in affluent areas and lizard abundance is greatest near large patches of open desert. The percentage of building cover had a strong negative impact on both diversity and abundance. Despite Phoenix's intense urban heat island effect, which strongly constrains the potential activity and microhabitat use of lizards in summer, thermal patterns have not yet impacted their distribution and relative abundance at larger scales. As Phoenix emerges from an economic recession, efforts to restrict urban sprawl and encourage higher density development could lower water and energy use while benefiting lizards in undisturbed habitats. However, this would likely exacerbate the urban heat island effect, and pose a threat to native species within the urban landscape.

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## 1. Introduction

Socioeconomic variables such as household income are correlated with ecosystem productivity (Buyantuyev and Wu, 2009) and urban biodiversity patterns of plants (Hope et al., 2003; Walker et al., 2009), birds (Kinzig et al., 2005; Lerman and Warren, 2011), and bats (Li and Wilkins, 2014). In some cases, these “top-down” controls have even more predictive power than the biophysical variables that regulate species distributions and relative abundance from the “bottom-up” (Luck et al., 2009). A ubiquitous “luxury effect” emerged from these studies, in which more affluent areas have higher biodiversity through ecosystem engineering, whereby homeowners introduce exotic plants and supplement natural sources of food and water for animals (Fuller et al., 2008). These changes in the structure and composition of

habitats alter the diversity and abundance of arthropods (Bang and Faeth, 2011), which could also influence the habitat selection of highly mobile species such as bats.

Less mobile ground species, such as lizards, risk road mortality when moving in an urban environment and have less choice of which neighborhood they inhabit. However, their persistence in Phoenix, AZ, USA, may still be correlated with affluence because a \$10,000 increase in median household income is associated with a 0.3 °C decrease in mean surface temperature (Jenerette et al., 2007). High summer temperatures can reduce the potential activity of lizards in Phoenix to one hour per day (Ackley et al., in press), and cooler temperatures in affluent areas could mitigate a heterogeneous urban heat island effect, which makes the city 3 °C warmer (on average) than the surrounding desert (Brazel et al., 2007). Since management efforts to reduce road mortality and heat stress would differ from efforts to enlarge and connect patches of suitable habitat, determining the relative importance of these variables at different scales will be crucial for managing native species in urban areas. Land-cover maps with a 1 m<sup>2</sup> resolution have recently become available for Phoenix (Li et al., 2014), enabling studies that integrate biophysical and socioeconomic variables with historical changes in the composition and configuration of landscapes. Many of these variables are correlated with each other,

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and may have complex relationships with lizard diversity (e.g., road density could impact dispersal, but may also influence lizards through increased surface temperatures). However, the proliferation of studies that only consider one or two threats to urban reptiles has resulted in uncertainty on how to best concentrate management efforts (Mitchell et al., 2008). Thus, the primary goal of our study is to determine which urban variables have the largest impacts on the diversity and abundance of native lizards.

## 2. Methods

### 2.1. Site selection

The Central Arizona-Phoenix Long-Term Ecological Research (CAP-LTER) project has established over 200 field sites within the city and surrounding desert (Grimm and Redman, 2004). We chose a subset of 28 sites along a gradient of urbanization, stratified by land-use type. Following a protocol similar to Germaine and Wakeling (2001), four sites were located in each of the following categories: desert, urban recreation/open space, agricultural, institutional/commercial, low density residential ( $>0$  and  $\leq 2$  dwelling units per acre), medium density residential ( $>2$  and  $\leq 5$  dwelling units per acre) and high density residential ( $>5$  dwelling units per acre). These land-use categories are roughly equal in relative abundance within Phoenix. Selected plots could not be alongside a  $\geq 4$  lane road, within 0.5 km of an interstate highway, within heavy industrial/commercial areas without open space/landscaping, within 3 km of a previously selected plot, above 600 m elevation, or inaccessible to private citizens by car or foot.

### 2.2. Response variables

Lizard diversity (number of species per site) and abundance data (lizards per site) were collected by the same person (JWA), using 20 min visual transect surveys at each site. This person scanned the area within 10 m on each side of a 200 m transect for lizards. Time spent identifying species with binoculars was not counted. The orientation and shape of transects were often dictated by roads, in which case it was walked once on each side. As this approach resulted in non-linear transects at many urban sites and some desert sites, the circular buffers mentioned below were drawn as close as possible to the center of the area surveyed. Each site was surveyed twice during fall 2012 (September–October), and four times during spring 2013 (March–May). Surveys were varied to accommodate the range of conditions in which different species were active (25–39 °C air temperature and 08:00–18:00 h on days with low wind and cloud cover). Unidentified lizards were only included in abundance estimates. A site at which only one unidentified lizard was observed was treated as having one species present.

### 2.3. Explanatory variables

We collected a preliminary data set comprising nearly 50 variables from three functional groups. (1) Site-scale characteristics included measures of habitat area, isolation, land-use history, temperature, traffic, and affluence. (2) Percent abundance of land-cover types within circular buffers of 200-m, 500-m, and 2-km diameter. (3) Landscape-scale metrics of all land-cover types (patch diversity, density, shape, size, spatial configuration, etc.) measured within the same buffers. As expected, Spearman's Rank correlation and a test of variance inflation factors (VIFs) (O'Brien, 2007) identified many of these variables as highly correlated; therefore, we began a process of reducing this collinearity to acceptable levels. Data reduction approaches such as principal

component analysis (PCA) were not applicable as the preliminary set of explanatory variables was larger than the number of sites we surveyed for lizards.

Extremely high correlations were found between different buffer sizes of the same land-cover types and landscape metrics. Redefining the 500 m and 200 m extents as the difference between their values and the extent they were nested within (500 m<sub>new</sub> = 500 m–2 km, 200 m<sub>new</sub> = 200 m–500 m) (Zuur et al., 2009) did not reduce their correlations to acceptable levels, so we eliminated the 500-m and 2-km variables because the 200-m extent directly matched the area we surveyed for lizards. The remaining 25 variables were further reduced to 14 by eliminating one of each pair that produced a rank correlation over 0.7. We retained variables according to their management potential, source quality, distinctiveness within our dataset, and if it had been identified as having a significant effect on lizards in previous studies. The final set of 14 variables had variance inflation factors approaching 30, but those in the most likely statistical models had variance inflation factors and rank correlations well below acceptable limits (less than 5 and 0.5, respectively) (Graham, 2003; O'Brien, 2007).

We calculated the final set of site variables (see Fig. 2 below) as follows. Straight-line distance to a large desert patch ( $>5$  km<sup>2</sup>) was measured in ArcGIS. Median household income was determined from data collected during the 2010 US census (block group data from Maricopa County). Years since a  $>25\%$  land-cover change was calculated from historical aerial imagery, which are available for Phoenix in  $\sim 15$  year intervals from 1937 to 1990, and  $\sim 2$  year intervals from 1990 to 2013. The spatial standard deviation of surface temperatures within circular buffers 200 m in diameter was calculated using the Geospatial Modelling Environment and ArcGIS from one of the final images taken by NASA's Landsat 5 Thematic Mapper (Landsat TM) satellite during a day in September 2011 before it was decommissioned. While this was a year before we began collecting lizard data, development (and changes in relative surface temperature differences between sites) had largely stalled following the economic recession. Previous surface temperature images taken in summers of 2010 and 2011 had a correlation of 0.8, despite differences in average temperature between years. We used the standard deviation instead of mean or maximum temperatures for three reasons. First, areas with slightly lower mean temperatures have much greater temperature variance. Second, thermal variation actually impacts potential activity of lizards in Phoenix much more strongly than mean temperatures does (Ackley et al., in press). Third, if future warming in Phoenix imperils the potential for lizards to survive, thermal variation will likely dictate local extinctions rather than maximum temperatures (Ackley et al., in press). Traffic density was calculated within a circular buffer 2 km in diameter, using the Geospatial Modelling Environment and ArcGIS. We used a larger buffer because the data were much coarser in resolution than those for land-cover and temperature. Traffic data were based on a validated model obtained from the Maricopa Association of Government's Transportation Division. Unlike observed traffic counts, modeled traffic data are available for all major road segments within the Phoenix Metropolitan Area. The most recent traffic counts were from 2008. As with temperatures, while average traffic density might have changed since then, relative differences between sites likely remained similar.

We calculated percent abundance of land-cover types using the Geospatial Modelling Environment and ArcGIS from a map with a resolution of 1 m<sup>2</sup> (Li et al., 2014). The classification included trees, grass, shrubs, pavement (roads, sidewalks, and parking lots), buildings, agriculture, and bare soil (including rock). Permanent water was not included in our analysis as it almost never occurred within 200 m of our sites; swimming pools were also removed due to their low relative abundance and a high correlation with grass

cover. The accuracy of this ground-truthed map was 92%; it was produced from multi-spectrum aerial photography and cadastral data from summer and fall 2010 (Li et al., 2014). Our site visits and a visual comparison with the most recently available imagery confirmed only minor changes in land-cover (and no major changes in land-use) had occurred within 1 km of our sites.

We calculated landscape metrics for each site from the complete land-cover map (not from individual cover classes) using FRAGSTATS (McGarigal et al., 2002) and ArcGIS. All but one of these metrics were highly correlated with another metric, a specific land-cover type, or a site variable. We only included the most distinctive metric (mean patch size, an indicator of landscape homogeneity), because site and cover data are more widely available and generally easier to calculate, communicate, and manage from an urban planning perspective.

#### 2.4. Statistical analysis

To account for the remaining collinearity between explanatory variables, we constructed a set of possible generalized linear models for lizard abundance, and another set for lizard diversity, following the procedure described in Zuur et al. (2009) using the R software program (R, 2005). Firstly, the explanatory variables were each standardized to have a mean of zero and a standard deviation of one. Then we constructed a set of potential models using an iterative backwards selection procedure that included every possible combination of the explanatory variables this method produces.

We ranked the resulting 90 models (and a null model with no explanatory variables) according to their AIC values, and calculated their AIC weights (the probability that a single model was better than the best model). As no one model stood out as being vastly superior to the others, summing the highest AIC weights until they exceeded 0.95 gave us a reduced set of the most likely models, which we were 95% certain contained the best model (Zuur et al., 2009). We calculated the relative impact of each explanatory variable from this final set by summing the AIC weights of each model it appeared in (its sign  $[\pm]$  was determined by model coefficients). Plotting the normal quantile–quantile or residuals against the expected values derived from the most likely models did not reveal strong violations of the models' assumptions. We found no evidence of spatial auto correlation using spline correlograms of Pearson model residuals for all explanatory variables with either diversity or abundance (Zuur et al., 2009).

### 3. Results

During surveys, we observed more than 300 lizards representing seven native species. Hardly any lizards were seen in the heavily developed area of downtown Phoenix, but similar numbers of lizards were observed in urban parks and sites in open desert. Location did not strongly correlate with diversity; however, a different set of species was present in the city than in the desert (Fig. 1). The most common lizard in developed areas—the ornate tree lizard (*Urosaurus ornatus*)—was never observed in desert areas. The most common lizard in desert areas—the side-blotched lizard (*Uta stansburiana*)—was rarely observed in developed areas. Of the seven species that we encountered, five were rarely observed outside their natural habitats, and only the tiger whiptail (*Aspidoscelis tigris*) was commonly observed across all land uses and cover types.

Our analysis of land-cover types, site variables, and landscape metrics revealed that the proportion of building cover within a 200-m diameter buffer had a relatively large negative impact ( $<-0.7$ ) on both lizard diversity and abundance (Fig. 2). The proportion of grass, pavement, and agriculture had small

( $-0.1$ ;  $-0.3$ ) to moderate ( $-0.3$ ;  $-0.7$ ) negative impacts on diversity and abundance. The proportion of bare soil had a moderate negative impact on abundance alone. The proportion of trees and the proportion of shrubs had a negligible ( $<|0.1|$ ) or statistically insignificant ( $p > 0.05$ ) impact on diversity and abundance.

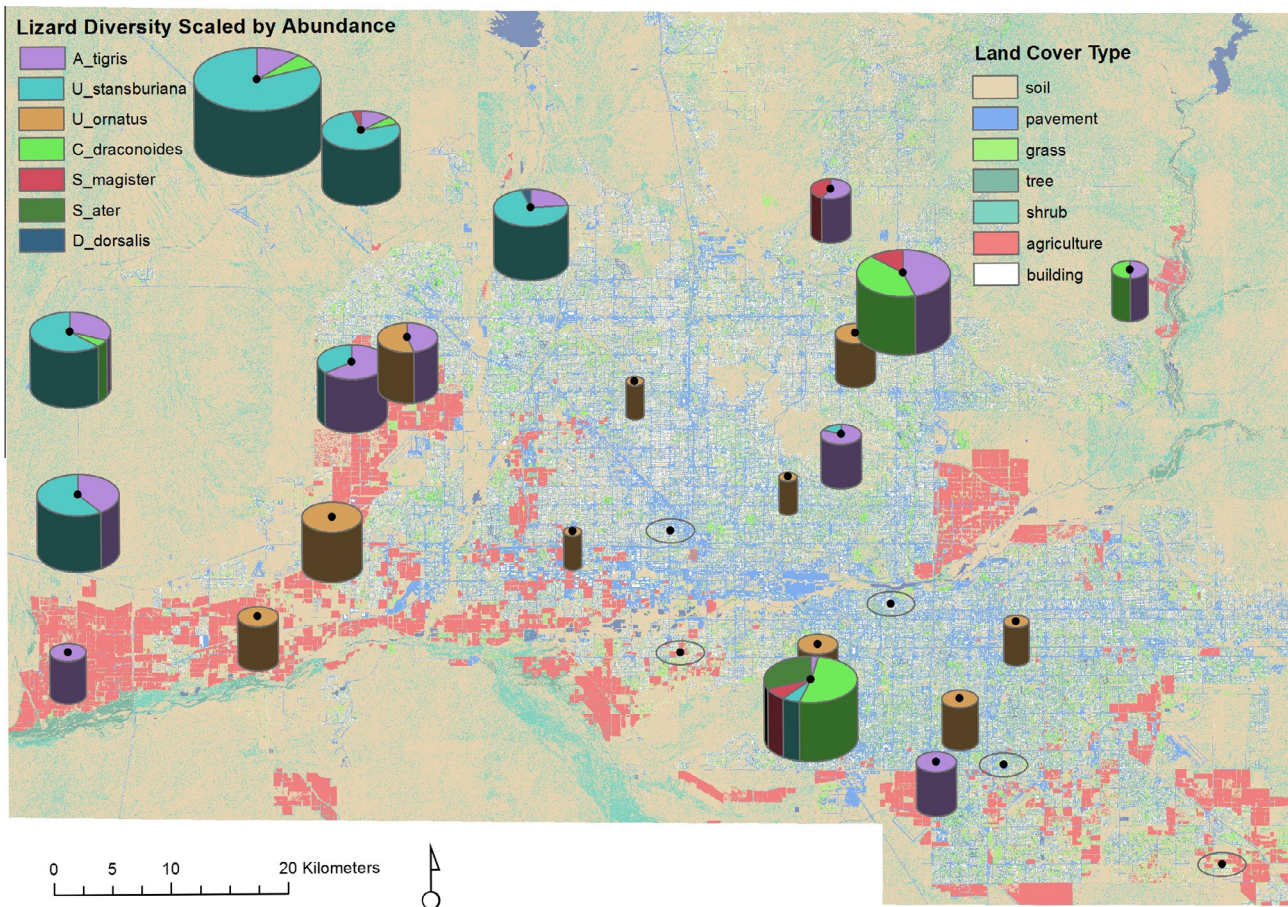
Sites with high median household income had a large increase in lizard diversity, and a small increase in abundance. Sites located more than 5 km<sup>2</sup> from a desert patch had fewer lizards. The number of years since a  $>25\%$  change in land-cover moderately decreased abundance and slightly decreased diversity. Traffic density and standard deviation of surface temperature within a 200-m diameter did not significantly impact diversity or abundance ( $p > 0.05$ ). Mean patch size of all land-cover types (the only landscape metric included in our analysis) had a moderate positive impact on diversity.

### 4. Discussion

A weak ( $r^2 \approx 0.1$ ) “luxury effect” of increasing plant richness with increasing average household income has been repeatedly observed in Phoenix, where substantial affluence is required to plant and maintain exotic vegetation in a desert environment (Hope et al., 2003; Walker et al., 2009). We observed a much stronger luxury effect on lizards ( $r^2 = 0.26$ ); in fact, median household income predicted lizard diversity better than any biophysical variable except for building cover. However, all the lizard species we observed were native and homeowners have limited control over them. Since affluence cannot directly enhance lizard diversity, an indirect mechanism must operate. We accounted for correlations between explanatory variables, so the high relative importance of income is not simply a matter of affluent sites having less agricultural cover or being more recently disturbed by land-use change. Income was one of the most distinct variables we considered; all of its other possible regression coefficients with significant diversity variables were very weak or in the direction that would make income less likely to explain diversity.

The positive relationship between affluence and lizard diversity was likely driven by a variable correlated with affluence that we were unable to include in the model, possibly a measure of habitat quality such as the relative abundance of insects or specific plant species. Alternatively, affluence enables one to not only engineer an idealized environment but also to choose where one lives. In Phoenix, high income homeowners prefer more xeric landscaping (Larsen and Harlan, 2006; Larson et al., 2009), and less urban and more natural environments are highly valued regardless of income (Larson et al., 2009). Phoenix residents also prefer (and can correctly estimate) high native bird diversity, but again, low income neighborhoods have fewer species of birds (Lerman and Warren, 2011). If affluent residents are choosing to live in more xeric, less urban, and more biologically diverse areas, they may be indirectly choosing to live in areas with high lizard diversity.

Surface temperatures are substantially lower in affluent areas of Phoenix (Jenerette et al., 2007). This could also explain the luxury effect that we observed, because small differences in temperature may cause global extinctions of lizard populations under climate change (Sinervo et al., 2010). However, our analysis indicated that temperature did not influence the diversity or abundance of lizards during spring or fall surveys. Thermal variation strictly determines the use of microhabitats and the potential duration of activity by lizards in Phoenix during summer (Ackley et al., in press), but this period of potentially lethal heat stress does not yet seem to be having a year-round impact on lizards at larger spatial scales in our study. Future studies will be more likely find an effect, as the loss of foraging opportunities may reduce the population size of future generations, precipitating extinction if individual plasticity and



**Fig. 1.** Lizard abundance declined sharply in Phoenix's urban core. The volume of the cylinders and colored slices indicates relative abundance of different species (the five clear ovals indicate an abundance of zero, the three smallest cylinders indicate a single lizard observation). Sites near the urban fringe and in mostly natural urban parks had similar abundances to desert sites, though a different set of species was present in natural and developed areas. The most species-rich site (bottom center,  $N = 5$  species) lies within the largest urban park in the USA. It is the only site with mountainous terrain and had the highest median household income ( $>200,000$  \$US per year). The common names of the species listed on the figure are (from top to bottom), tiger whiptail, side-blotched lizard, ornate tree lizard, zebra-tailed lizard, desert spiny lizard, chuckwalla, and desert iguana. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

genetic adaptation cannot track climate changes (Urban et al., 2014).

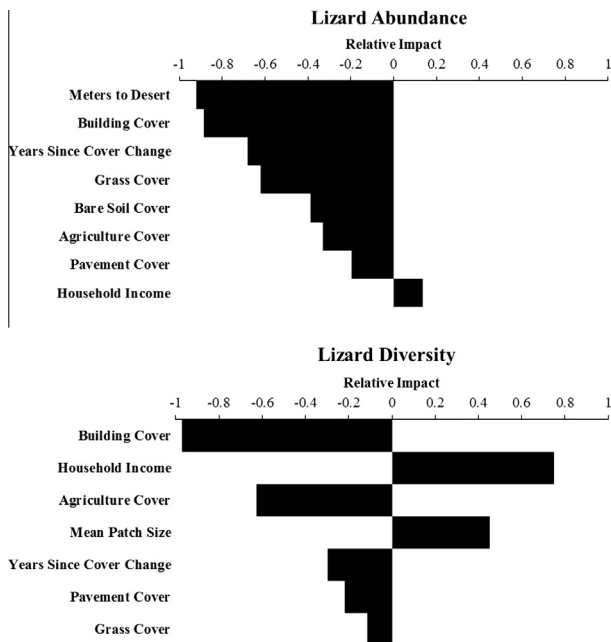
Instead of using a diversity index that combines the number of species (richness) and their relative abundance (evenness), we decided to consider lizard diversity and abundance separately as they were not strongly correlated and different processes appeared to influence these variables. Diversity and abundance are respectively driven by rare and common species; and management efforts are usually targeted at one or the other. For example, urban habitats could be designed to support rare species and exclude “urban exploiters” that are already thriving (Rosenzweig, 2003). Another issue rarely considered in ecology is the suitability of diversity indices for statistical modeling. Common indices such as the Shannon–Wiener index take on values of either zero, one, or any continuous number greater than one. We are not aware of a probability distribution that works for small numbers of species, because the data cannot include negative values (precluding bell curved distributions) and include discrete counts (precluding the gamma distribution) and continuous numbers (precluding the Poisson and Negative Binomial distributions).

Ecological processes related to habitat size and isolation likely underlie the relationships between land-cover and lizard diversity that we observed. The distance from a large desert patch—a proxy for isolation from a source population—strongly impacted abundance but not diversity. Defining habitat size and fragmentation is challenging in urban environments, because lizards use many

built structures and exotic plants. The complete lack of tree lizards at desert sites, and their unparalleled ability to survive in Phoenix's urban core was likely due to their extensive use of concrete walls and introduced shade trees. The desert sites we surveyed were predominantly flat, bare soil, dappled with 10–30% shrub cover (most native tree species have shrub-like morphology, and were usually identified as such by the land-cover classification).

With increasing urbanization, the addition of land-cover types, and fragmentation of large contiguous patches of bare soil patches common to open desert, we observed a reduction in the mean patch area of all land cover types. Although previous studies have used mean patch area as a measure of habitat fragmentation (Fahrig, 2003), this is more appropriate when it is applied to a few types of natural land-cover. When used with highly detailed maps of urban cover such as our map of Phoenix, mean patch area better reflects overall landscape homogeneity. In our case, this variable had a positive impact on lizard diversity.

We found that the years since a land-cover change ( $>25\%$  conversion) negatively impacted diversity and abundance, suggesting that some changes in land-cover might actually be beneficial on intermediate time scales as undisturbed sites generally had lower diversity. This coincides with previous reports of increased lizard abundance and diversity in lightly developed areas (Ackley et al., 2009; Germaine and Wakeling, 2001). It is important to note that the most recent major land-cover change at any of our sites was 6 years prior to lizard data collection (the oldest available imagery



**Fig. 2.** Lizard diversity was only moderately correlated with abundance ( $r^2 = 0.49$ ), and the relative impact of these response variables was best explained by different factors (relative impact was the variables cumulative AIC weight in the 95% confidence interval of most likely models). Building cover and other consequences of urbanization generally had a negative impact on diversity and abundance, but median household income had a strong positive impact on lizard diversity and a small positive impact on lizard abundance. Variables which were included in our analysis but did not appear to have a significant impact on lizard populations included: traffic density, surface temperatures, and the relative proportional land covers of trees, shrubs, and bare soil (all measured within a 200 m diameter circular buffer).

was taken 76 years ago, this was the value given to undisturbed sites). Thus, we cannot directly attribute this as an example of the bell-curved intermediate disturbance hypothesis where diversity is highest at moderate disturbance frequencies (Grime, 1973). Lizard diversity and abundance might not have declined during or immediately following cover changes, however it seems likely that lizards could get driven out of an area during construction activities, and return as the landscape stabilizes.

Building and agricultural cover had the most consistently negative impacts on lizards in our study. More than half of the land-use changes in Phoenix between 1970 and 2000 involved the urbanization of outlying agricultural fields (Keys et al., 2007), which increased the urban heat island effect while holding overall water use relatively constant during a period of rapid population growth (Chow et al., 2012; Gober and Kirkwood, 2010). More recently, Phoenix's urban fringe had been expanding into the Sonoran Desert at a rate of 1 km per year (MIPP, 2000) prior to the housing-market crash of 2008. An important choice for Phoenix's future ecology is whether to restrict urban sprawl and encourage high density developments that cover smaller areas (Collins et al., 2000), although this would likely have negative consequences for native species currently persisting within the city. As we emerge from the great recession, an opportunity exists to re-imagine what forms of urbanization and economic growth get to count as ecologically sustainable on specific scales—and what elements of nature are desirable to have in a desert city.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.11.009>.

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