Effects of urbanization on plant species diversity in central Arizona

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Modern urban development provides an excellent laboratory for examining the interplay among socioecological relationships. We analyzed how the rapidly urbanizing Phoenix, Arizona metropolis has affected plant species diversity and community composition at a regional scale. Species diversity and plant density probably result from abiotic sorting in undeveloped desert sites, but not in urban sites. We found that species richness at the plot scale was higher for desert as opposed to urban sites; however, the estimated total species pool in the urban ecosystem is higher than that in the desert, as a result of the increased importation of introduced species through the nursery trade. Ordination of plant communities suggests three unique groupings of species based on land-use type of the site (desert, urban, and agriculture) and two unique groupings of urban sites based on landscaping aesthetics (mesic or xeric). We therefore recognize both bottom-up and top-down controls of plant biodiversity within the urban ecosystem.

Edgar Anderson proclaimed that "man carries whole floras about the globe, that he now lives surrounded by transported landscapes" (Anderson 1952). With this acknowledgement of one of our global impacts, it has become apparent that ecological theory must incorporate human action (McDonnell and Pickett 1993; Vitousek *et al.* 1997; Kareiva *et al.* 2007), and nowhere is the effect of humans greater than in and around cities (Pickett *et al.* 1997; Grimm *et al.* 2000, 2008). In this paper, we present and test a set of hypotheses regarding the effects of urbanization on plant diversity in the Phoenix metropolitan area in the Sonoran Desert of central Arizona (Panel 1). Controls on plant community assembly and productivity in deserts include soil properties (Shreve 1951), especially soil moisture (Went 1949; Beatley 1969) and nitrogen (Schlesinger *et al.* 1990). Soil moisture is a function of both the amount of precipitation and the water-holding capacity of the soil. Species richness (Boeken and Shachak 1994) and community composition (McAuliffe 1999) in desert systems are positively associated with productivity. In the Sonoran Desert, productivity is strongly correlated with annual precipitation (Shen *et al.* 2005), which in turn is positively correlated with elevation (Sheppard *et al.* 2002). Although Sonoran Desert plant ecology is well-studied, our understanding of the effects of humans on this ecosystem is much less developed.

Anthropogenic drivers of ecosystem change via urbanization operate as both top-down and bottom-up controls (Figure 1). In an urbanizing system, top-down, anthropogenic regulation of vegetation dynamics is initiated by land-use change, which is constrained by governmental regulation through zoning. During urbanization, development usually involves wholesale removal of vegetation (Rebele 1994). Once the urban infrastructure (eg roads, buildings, and so forth) becomes established, plant communities are reconstructed by landscape architects and assembled by landscaping installation companies. These companies acquire vegetation stock from the nursery trade, which is driven by the public's horticultural aesthetic, as reflected in the market for nursery plants. Nurseries diversify their investments by filling their greenhouses with many varieties of "showy" plants, most of which are exotic species. As a result, we predict that this addition of exotic species will elevate the species pool of the urban ecosystem above that of its desert counterpart. Another form of top-down regulation of plant diversity occurs through neighborhood homeowners' associations, which can limit the species pool within the confines of their governance (Martin *et al.* 2003). Together, these interactions comprise the primary top-down anthropogenic forces that determine patterns in urban plant diversity and abundance.

Bottom-up anthropogenic forces also affect diversity and abundance patterns at a household scale. In an earlier study on plant diversity in Phoenix, Hope *et al.* (2003) suggested a so-called "luxury effect", in which wealthier neighborhoods tended to have increased numbers of perennial genera, afforded by homeowners' additional disposable income. We build upon this earlier work using a richer dataset of plant diversity (ie including both perennial and annual species) and propose a mechanism based on a combination of socioeconomics and landscape aesthetics that can better explain patterns of plant diversity and community composition within the Phoenix metropolitan area. Phoenix's urban ecosystem differs from that of many other American cities, in that three disparate landscaping aesthetics have developed (Martin 2001; Martin *et al.* 2003). Before the

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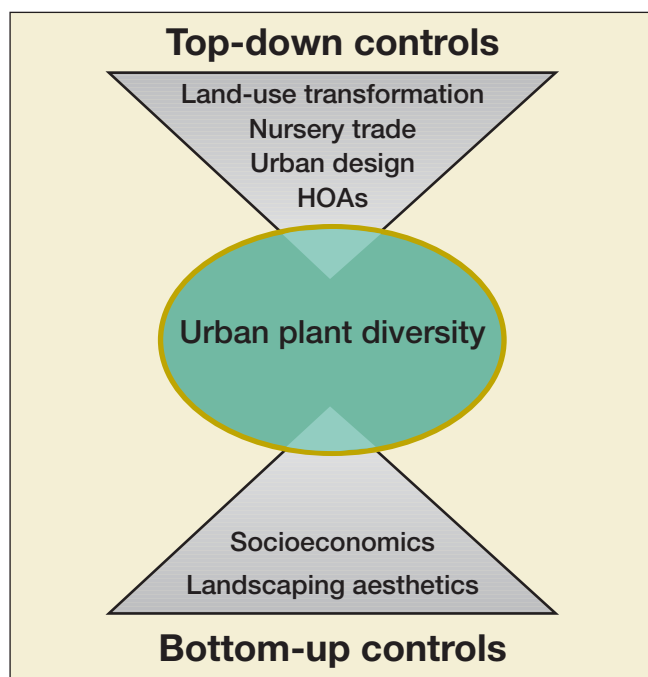
Figure 1. *Conceptual model of the top-down versus bottom-up effects of urbanization on plant diversity and community composition within the city. HOAs = homeowners' associations.*

advent of the air conditioner, the most common home landscape was mesic. This landscaping type was originally supported by flood irrigation and featured shade trees and flowering shrubs planted in lawns for the purpose of reducing heat around living spaces (Folkner 1958). These mesic landscapes emulated the landscape aesthetic – but not necessarily the species pool – common to the eastern US. Once air conditioners became common, Phoenix residents were afforded the climatic luxury of xeric landscaping, characterized by low water-use plants planted in inorganic mulch, such as crushed rock (Martin 2001). Martin *et al.* (2003) recognize a third common landscaping type, oasis, which merges elements of the xeric and mesic palette and is typified by ground cover, including both inorganic mulch and lawn within the same landscape. We anticipate that this differentiation in landscaping aesthetic, which is largely a result of homeowner choice, will produce distinct differences in patterns of both plant diversity and community composition within the urban ecosystem.

Our general hypothesis is that plant diversity and community composition in an urbanizing area are controlled at different scales by top-down and bottom-up factors. Regionally, land-use change during urbanization is a top-down anthropogenic effect, directly altering plant diversity. Within the desert, diversity is typically explained by bottom-up, biophysical factors – mainly precipitation, soil texture, and nutrient content. In contrast, plant diversity within urban areas is affected by household factors, such as income and landscaping aesthetic.

■ Methods

As part of the Central Arizona–Phoenix Long Term Ecological Research (CAP LTER) program, ecological surveys were conducted between February and May 2005, at 204 sites across 6400 km^2, encompassing the entire Phoenix metropolitan area, including agricultural lands and undeveloped upland in the Sonoran Desert (Figure 2a). The sampling unit at each site was a 30-m x 30-m (900 m^2) plot, in which all plants in all taxa were identified, collected, and archived at Arizona State University's herbarium. All perennial plants were counted within the plot, in order to obtain density (perennials per 900 m^2). Density of annual plants was estimated as the linear proportion along two 60-m perpendicular lines that dissected the plot exactly into quarters.

Analysis of variance was conducted (Figure 2d) for two complementary metrics of diversity (richness and evenness) and density (perennial and annual species) based on regional land use (urban, desert, and agriculture). Differences in plant richness were also analyzed for urban land use (commercial, vacant, transportation, and residential) and landscaping (xeric, mesic, and oasis) categories. Sample-based rarefaction was conducted to interpolate species accumulation curves for each of the regional land-use classes (Figure 2f), estimated as S_{exp} (the expected species richness for a given sample; Colwell *et al.* 2004; Colwell 2005). Ordination via non-metric, multidimensional scaling (NMS) was used to suggest patterns in community structure (Clarke 1993; McCune and Grace 2002). We adopted this approach to address whether plant communities formed assemblages based on the abovementioned land-use and landscaping categories (Figure 3). For a detailed explanation of the methodology and analyses used throughout this study, refer to WebPanel 1.

Panel 1. Hypotheses

Within this paper, we test the following hypotheses:

H$_1$: Biodiversity within desert sites will be significantly correlated with abiotic factors, such as soil texture, as well as geomorphic and geochemical variables, whereas biodiversity in urban sites will not be related to these variables.

H$_2$: The urban ecosystem is a "transported landscape", characterized by the removal of native species and promotion of introduced species.

H$_3$: In an urbanizing ecosystem, plant density is positively correlated with the proportion of impervious surface.

H$_4$: Within the urban ecosystem, variations in plant diversity and community composition are a function of bottom-up forces involving human action. We predict plant species richness will be positively correlated with income, and plant community composition will differ among landscaping regimes (eg xeric versus mesic).
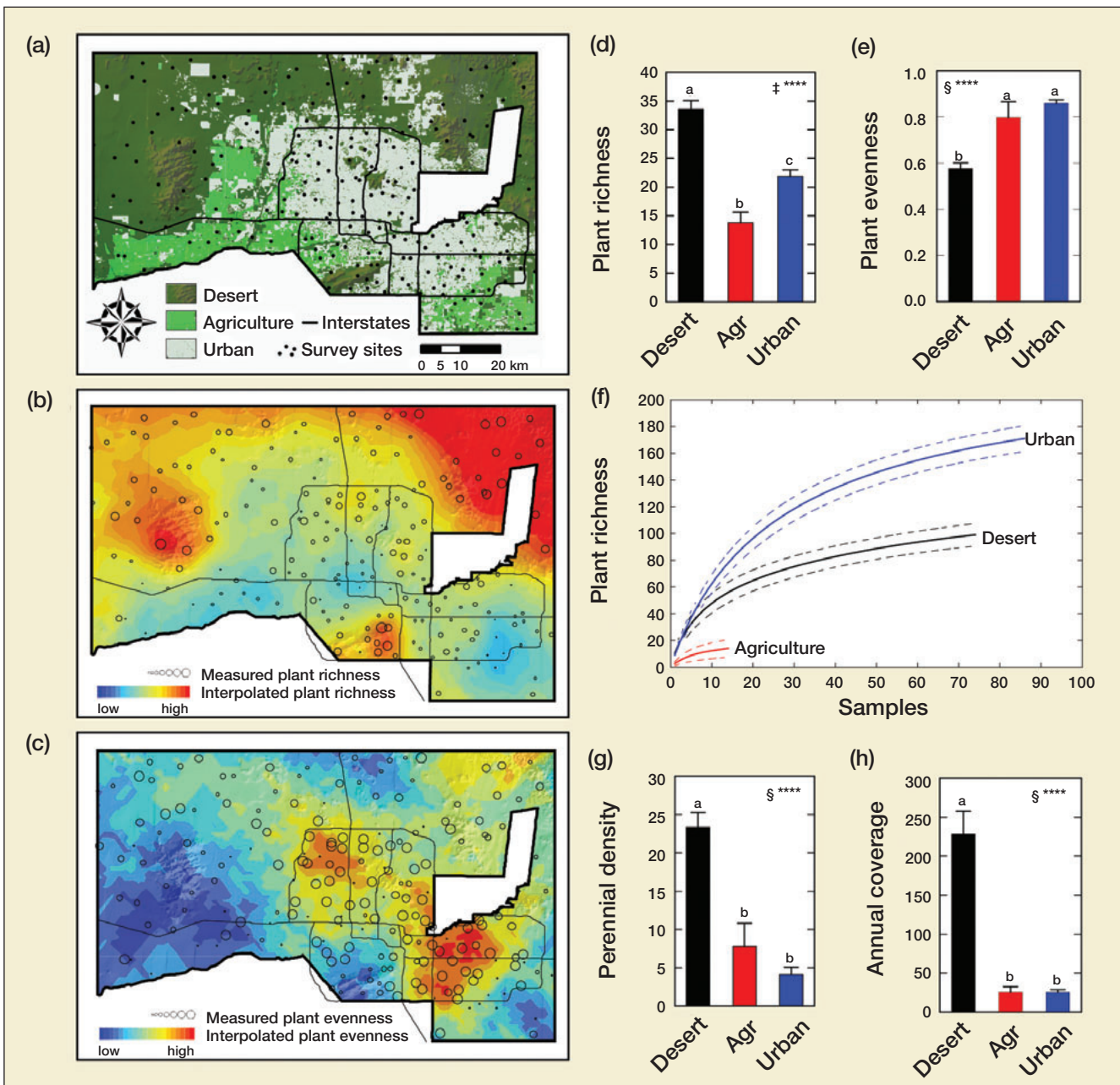
Figure 2. *(a) Regional land-use map of Central Arizona–Phoenix Long Term Ecological Research and survey site locations. Measured and interpolated plant (b) richness and (c) evenness. Interpolations were conducted via ordinary kriging. Multiple pairwise comparisons were conducted on plant diversity and density across three regional land-use types: desert, agriculture, and urban. Diversity was measured as (d) richness (taxa per 900 m^2) and (e) evenness. (f) Species pools were estimated for each of the land uses with EstimateS (Colwell 2005). Dashed lines represent 95% confidence intervals. Density was measured as (g) perennial density (individuals per 900 m^2) and (h) annual coverage (m/60 m). Analysis of variance (ANOVA) was conducted by the F test[‡] if assumptions of that test were met. Otherwise, ANOVA was conducted by the Kruskal-Wallis test[§] (Kruskal and Wallis 1951). Letters in panels (d), (e), (f), (g), and (h) refer to groups that were different according to either Tukey-Kramer's test[‡] (Kramer 1956) or Dunn's test[§] (Dunn 1964), respectively; error bars represent standard deviation. $\alpha = 0.05$ for all tests.[****] indicates $P < 0.0001$. Agr = agriculture.*

■ Results

Abiotic controls of desert plant diversity

We predicted that variability in biodiversity within the desert would be explained by abiotic factors (eg soil texture, as well as geomorphic and biogeochemical variables), whereas biodiversity in urban sites would not. To analyze the

effect of these variables on plant diversity, we conducted forward stepwise regression, with $\alpha_{in} = 0.05$, separately on diversity measurements from two subsets of the dataset – desert only and urban only – on the eigenvectors from the factor analysis from the following abiotic variables: elevation, slope, aspect, nitrogen (N), inorganic carbon (C_{inorg}), organic carbon (C_{org}), phosphorus (P), and the proportions
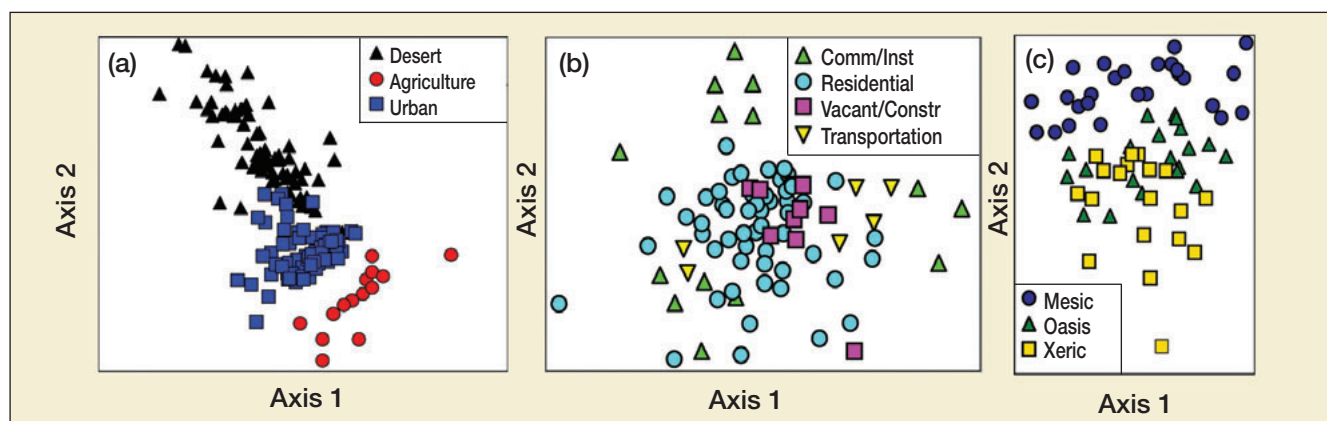
Figure 3. *Plant community ordination via non-metric multidimensional scaling. (a) Regional land use; (b) urban land use; (c) landscaping. Comm = commercial; Inst = institutional; Constr = under construction.*

of sand, silt, and clay. As predicted, none of the variables explained the variance in taxa richness or evenness in the urban ecosystem. However, in the desert sites, 20% of the variability in plant richness and 6% of the variability in evenness were explained by a factor with a high loading for elevation. Within desert sites, the positive influence of elevation on plant richness may be attributed to increases in rockiness with increasing elevation. Plant-available water is increased as a result of condensation and reduced evaporation between rocks and within rock fissures. This increases productivity and density, factors that in arid regions also tend to be positively correlated with species richness (Rosenzweig 2002). In addition, increasing substrate heterogeneity at higher elevations may promote coexistence by creating independent microsites, thereby minimizing competitive exclusion by dominants (Levins 1969; Tilman 1994). This supports the hypothesis (H_1) that abiotic variables traditionally used to explain plant diversity in the Sonoran Desert are still valid when applied to the desert near a large metropolis. However, these variables are not significant predictors of plant diversity within the urban ecosystem.

Urbanization as a transported landscape: top-down effects

At a regional scale, urbanization has a dramatic effect on plant abundance and biodiversity patterns and is affected by a combination of top-down and bottom-up anthropogenic factors. At the largest scale, land-use transformation is the most obvious determinant of plant community dynamics, and has resulted in dramatically altered patterns of biodiversity. At the plot scale, urbanization has decreased species richness while increasing plant community evenness (Figure 2d, e). These results suggest that at local scales urbanization homogenizes the plant community, creating a community that consists of fewer species and a greater proportion of individuals per species relative to those of desert plant communities. Analysis of species-accumulation curves provides a different insight for the largest scale (Figure 2f). The total plant species pool is higher in the urban area than the desert, as was predicted (H_2).

Conversely, desert sites have higher species richness than urban sites at the plot scale (Figure 2d). This enhancement of the urban species pool can largely be attributed to introductions of plant species, purposefully and incidentally, into agricultural and urban areas, which show elevated incidence of exotic species and lower incidence of native species (Figure 4a). Thus, local-scale species richness is highest for desert sites; however, the cumulative species richness, or species pool, is highest for urban sites as a result of the promotion of introduced species.

Land-use change not only affects patterns of plant diversity, but also plant community composition. Ordination, or multidimensional data clustering, of species' occurrence coded by regional land-use type yields three unique plant communities (Figure 3a). This suggests that at a regional scale, there is a dominant, top-down effect of land-use change, which clearly alters both plant diversity and plant community composition, with profound consequences. A subset of the urban sites overlaps the desert sites within this ordination. Further examination of these sites reveals that they occur at the urban "fringe". This might be indicative of an urban-to-rural ecotone of plant community composition, or it could be spurious. Unfortunately, we lack the statistical power to analyze the results appropriately at this level of detail. However, many of the urban fringe sites developed into previous desert locations without complete removal of the extant vegetation, which may have produced an overlap in plant community composition, such that plots contain both residential and desert remnant species.

In contrast to the regional land-use analysis, ordination on different land uses within the urban system (eg residential, commercial) suggests no clear plant assemblages at this finer scale (Figure 3b). Thus, land-use change appears to be a dominant top-down factor affecting vegetation composition of an urbanizing region only at its coarsest scale. The effects of land-use transformation on modern plant communities are visible through coarse, but not fine, scales. The effect on plant community composition from the initial transformation to an urban land use far exceeds the effect on plant community composition from the specific type of urban land use.

The most dramatic effect of urbanization is a reduction in plant density (Figure 2g, h). One factor that may be driving this pattern is lower availability of growing space in the city. To evaluate this, we conducted a regression using the proportion of impervious surface coverage, which we predicted to be inversely related to available growing space for plants, as a possible predictor of plant density. Within urban sites, we did not find any relationship between plant richness ($P = 0.46$) or the density of perennial plants ($P = 0.43$) and impervious surface coverage. We did find a significant positive, though weak, correlation between annual plant density and impervious coverage ($P = 0.005$, $r^2 = 0.10$). Although urbanization results in a decrease in diversity and density of plants, this decrease cannot be explained by lack of growing space, contrary to our hypothesis (H_3), except in the case of annual plants. Water is a strong controlling factor for desert plant productivity, but given the abundance of irrigation water in the urban environment (Martin 2001), we would expect plant density to *increase*, in a sort of "oasis effect". However, we found plant density to be lower in the city than in the desert, despite the added water, suggesting that other human factors play a primary role in determining plant density. Perhaps humans limit density by favoring fewer, larger specimens – an idea that is supported by the higher woody vegetation coverage in the city relative to that in the desert (Walker and Briggs 2007).

Household-level effects on the urban plant community

Although there is evidence that the process of land transformation from desert to agricultural to urban can produce distinct changes in patterns of plant diversity and community composition, variation within the urban ecosystem probably results from individual action at the household level. To explore household-level effects, we analyzed plant species richness as a function of average household income for the surrounding neighborhood. We evaluated the effects of landscaping aesthetics on plant community composition. Based on their analysis of data from the 2000 survey, Hope *et al.* (2003, 2006) suggested the presence of a "luxury effect", in which wealthier neighborhoods tended to have greater richness of perennial plant genera (partial $r^2 = 0.17$ for a multiple regression model, $P = 0.0003$). In this study, we enhanced the earlier analysis by including annual taxa and identifying individuals to the species level, where possible. Furthermore, we omitted desert and agricultural samples. We found that although plant richness did vary significantly with income ($P = 0.01$), income explained an even lower proportion of the variance than in the 2000 studies ($r^2 = 0.09$, compared with 0.17 for the latter). The relationship between income and species richness was weaker with the inclusion of annual species, which was not incorporated in the earlier studies. Analysis of the income–species richness relationship using only perennial species in the 2005 survey gave nearly identical results to those of the 2000 survey ($P = 0.0006$, $r^2 = 0.17$). Thus, evidence of a luxury effect remains, even with finer taxonomic resolution. The luxury
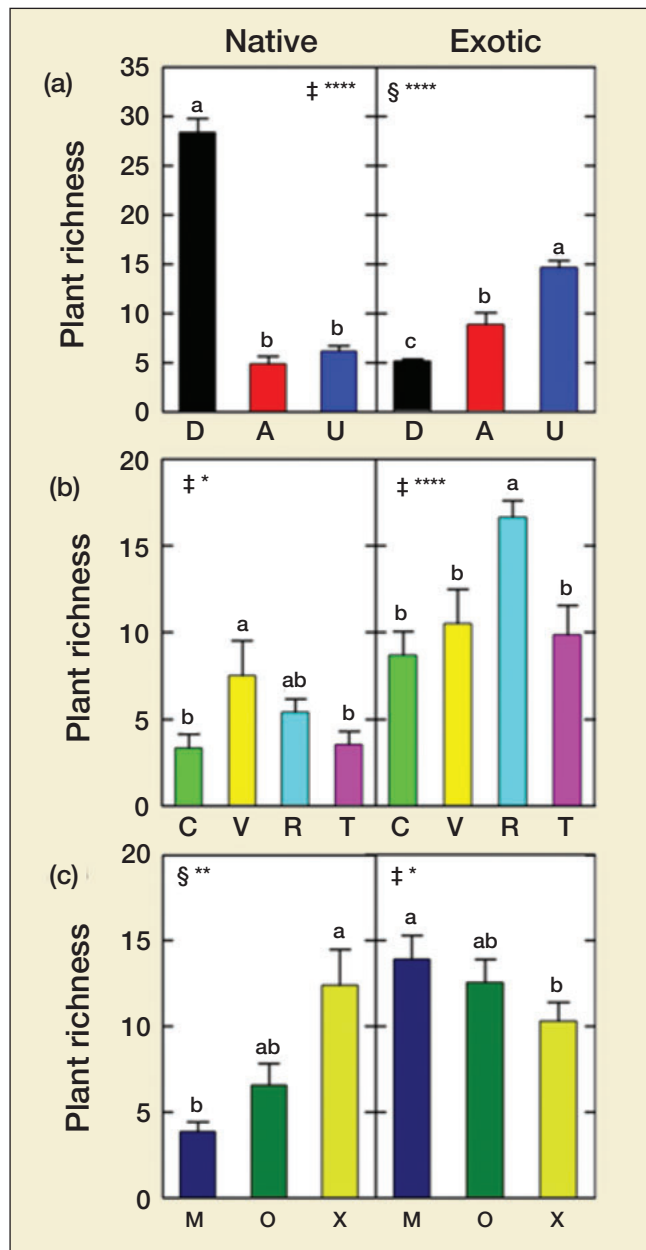
Figure 4. *Multiple pairwise comparisons of native and exotic plant richness across land-use types: (a) regional and (b) urban, and (c) landscaping aesthetics within urban areas. Regional land-use types: desert (D), agriculture (A), and urban (U). Urban land-use types: commercial/institutional (C), vacant/under construction (V), residential (R), and transportation (T). Landscaping aesthetics: mesic (M), oasis (O), and xeric (X). Statistical tests and symbols follow those described in Figure 2. Of all the taxa sampled, 15% were uniquely within the urban ecosystem and 58% were uniquely within the desert ecosystem.*

effect appears to be stronger for perennial species alone, as compared with that for all species of plants.

We anticipated that the different landscaping aesthetics (mesic, oasis, and xeric) would produce unique plant assemblages within one land-use category (residential) of the urban ecosystem, owing to household-level controls. Ordination based on landscaping aesthetics suggests two

unique groupings (Figure 3c), with mesic landscapes forming an assemblage of plant taxa distinct from that of xeric and oasis landscapes. Plant assemblages of oasis landscapes were indistinguishable from those of xeric landscapes, probably because the xeric portions of the oasis landscapes are more important than small patches of lawn to overall diversity and community structure in these landscapes. Relative to the mesic sites, xeric sites have higher numbers of native species and fewer exotic species (Figure 4). Collectively, these household-level factors (income and landscaping aesthetics) appear to be more robust predictors of plant diversity, density, and composition than the specific type of urban land use. Therefore, *within* the urban ecosystem, household controls on vegetation deriving from human action appear to be influential determinants of urban biodiversity and community composition.

At a regional scale, plant diversity and community composition within the city are driven by the process of land-use transformation during urbanization and corresponding importation and promotion of introduced species, primarily through the nursery trade. At more local scales, diversity within desert sites is largely a product of biophysical controls by abiotic variables. However, at local scales within the urban ecosystem, variations in diversity and density of plant species are driven by two bottom-up anthropogenic forces: landscaping aesthetics and household economics.

Understanding the effects of humans on their ecosystems is becoming increasingly necessary. Deconstructing this complexity is challenging and will require the synthesis of data and methods from both the social and natural sciences. It also requires an evolution of blended theories that can account for both ecological processes and human effects.

◾ Conclusions

Urbanization causes a dramatic shift in biodiversity and plant community composition. Relative to the surrounding Sonoran Desert, the Phoenix metropolitan area has lower species richness but a much larger species pool. This is explained by increased use of exotic species within the urban core. While community composition shifted dramatically during the process of land-use transformation during urbanization, the effects of specific urban land use on plant diversity or community composition were unclear. Rather, landscaping aesthetic was a better predictor of plant community composition within the urban ecosystem.

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