

Articles

Drivers of Spatial Variation in Plant Diversity Across the Central Arizona–Phoenix Ecosystem

DIANE HOPE, CORINNA GRIES,
DAVID CASAGRANDE, AND CHARLES L. REDMAN

International Institute for Sustainability, Arizona State University,
Tempe, Arizona, USA

NANCY B. GRIMM

School of Life Sciences, Arizona State University, Tempe, Arizona, USA

CHRIS MARTIN

Department of Applied Biological Sciences,
Arizona State University East, Mesa, Arizona, USA

We examined how growth of the Phoenix urban landscape has changed spatial patterns in native Sonoran desert plant diversity. Combining data from the U.S. Census with a probability-based field inventory, we used spatial and multivariate statistics to show how plant diversity across the region is influenced by human actions. Spatial variations in plant diversity among sites were best explained by current and former land use, income, housing age, and elevation. Despite similar average diversity in perennial plant genera between desert and urban sites, numerous imported exotics have significantly increased variation in plant generic composition among urban sites, with a “luxury effect” of higher plant diversity at sites in wealthier neighborhoods. We conclude that controls on natural spatially autocorrelated desert plant diversity are replaced by a variable suite of site-specific human factors and legacy effects, which require an integration of ecology and social science to be fully understood.

Keywords desert, geomorphic template, integrated field survey, perennial plant genera, socioeconomic factors, spatial statistics, urban ecosystem

Received 13 April 2004; accepted 29 April 2005.

We thank Steven S. Carroll for sampling design and statistical assistance, Amy Nelson for U.S. Census data work and input, and Ann Kinzig for comments on the manuscript; M. Myers, A. Budet, S. Paine, M. Clary, A. Stiles, L. Stabler, and S. Holland for field and lab assistance; Salt River Project for the donation of helicopter time; and the cities of Phoenix, Scottsdale, and Tempe, Maricopa County Parks, Tonto National Forest, Arizona State Lands Department, Sky Harbor Airport, and all the private property owners involved for giving us permission to access their land. This work was funded by National Science Foundation grants DEB-9714833 and DEB-0423704 (the Central Arizona–Phoenix Long-Term Ecological Research Project).

Address correspondence to Diane Hope, International Institute for Sustainability, Arizona State University, PO Box 873211, Tempe AZ 85287, USA. E-mail: di.hope@asu.edu

Cities represent extreme cases of human influence on ecosystem function (McDonnell et al. 1993; Pickett et al. 1997) and provide unique opportunities for researchers to integrate humans into ecology (Collins et al. 2000; Grimm et al. 2004). In urbanized landscapes, humans are the primary agent in creating new plant communities (Anderson 1956; Whitney and Adams 1980). Yet many published studies on urban vegetation have largely focused on invasive weed species (e.g., Franceschi 1996; Dana et al. 2002), or on remnant fragments of native vegetation (e.g., Bastin and Thomas 1999), and have ignored the abundant “human-created floras” occurring in urban landscapes (Savard et al. 2000).

Why should people care about plant diversity in urban areas and how the plants differ from the natural environments they replace? Plant diversity is an important determinant of overall ecosystem biodiversity, influencing the composition and abundance of associated biota (Matson et al. 1997). Plant diversity (and species composition) in metropolitan areas can potentially impact water use and conservation, groundwater quality and recharge, and may ameliorate the urban heat island (Baker et al. 2002). Moreover, as the proportion of people living in cities increases worldwide every year, urban ecosystems become increasingly important in shaping human perceptions about the natural environment (Savard et al. 2000). There is also some indirect evidence that biodiversity can significantly affect people’s quality of life (Sebba 1991). In urban environments of the arid southwestern United States this has been manifested as an increasing interest in establishing “xeric” (desertlike, low-water-use) landscapes that simulate the visual appearance of native desert vegetation communities, reflecting the social ethos of water conservation and preservation of desert habitat (Martin 2001; McPherson and Haip 1991).

Classic ecological theory correlates plant diversity and abundance with abiotic factors such as irradiance and precipitation, with total plant diversity generally being lowest in arid ecosystems. Conventional wisdom also holds that humans reduce diversity (e.g., Liu et al. 2003), yet in arid environments urban plant diversity and abundance may actually be higher than in the surrounding deserts (Williams et al. 2005). This may be because of direct human-mediated drivers such as irrigation, as well as the indirect effect of the value placed on urban landscapes as a manifestation of social wealth. Hence, desert cities like Phoenix are an excellent arena for testing the existence of linkages between socioeconomic variables and urban biodiversity and ultimately for exploring the mechanisms producing those linkages.

As a first step toward understanding the complex interplay between biodiversity and human perceptions and activities across the rapidly urbanizing region of Central Arizona-Phoenix, we wanted to determine to what extent plant diversity differs between urban and undeveloped desert parts of the region. Next our aim was to identify the human drivers that might control that change. Typically, ecologists approach such a problem by examining factors such as water availability, soil type, elevation, slope, and aspect. However, in human-dominated ecosystems it is also necessary to consider the dynamic effects of land-use history and social, economic, technological, and cultural aspects of human behavior (Grove and Burch 1997; Dow 2000; Grimm et al. 2004; Hope et al. 2003). For example, the advent of drip irrigation and air conditioning in the mid 20th century catalyzed a change in the balance between landscape function and form in cities such as Phoenix. As a result, large broad-leaf shade trees and expansive areas of turf grass once valued for their

Table 1. Summary statistics for plant diversity (number of perennial genera per site)

	All genera			Native genera		Exotic genera	
	All sites (<i>n</i> = 204)	Urban (<i>n</i> = 91)	Desert (<i>n</i> = 73)	Urban (<i>n</i> = 91)	Desert (<i>n</i> = 73)	Urban (<i>n</i> = 91)	Desert (<i>n</i> = 73)
Total	188	156	63	50	55	116	8
Mean	6.8	8.0	8.4	4.2	9	8	1.5
SD	6.5	7.1	5.5	3.6	6.2	5.9	0.7

Note. Plant diversity is usually reported at the species rather than at the genus level. Individual plant genera often contain species that occupy entirely different habitats or niches that can render diversity at the generic level of little ecological meaning. However, across the Central Arizona–Phoenix (CAP) ecosystem perennial plant diversity on the genus level corresponds closely to diversity at the species level, except in the case of two desert genera (*Ambrosia* and *Cylindropuntia*), of which there were two or three species present in approximately 30 plots. Moreover, in this study we discuss only total plant diversity at the generic level, with no distinction being made between native and exotic genera.

evapotranspirational cooling are now considered to be water wasters. Hence, we asked the question, “To what extent are the spatial variations in plant diversity across the urban area and surrounding desert related to biophysical factors versus variations in conditions brought about by human decisions, actions, and social structure?”

Studying an extensive metropolitan area such as Central Arizona–Phoenix represents a unique challenge, both due to the sheer size of the developed region and because of very rapid, radical changes in land cover (Jenerette and Wu 2001). In order to address these challenges, we used a probability-based sampling approach, which has been used previously at national and regional scales (Stevens 1994; Stapanian et al. 1998), although our application of this approach to an urban area is unique. Our aim was to disaggregate spatial variation in plant diversity caused by nonhuman landscape characteristics from that caused by human actions. To do this, we used a set of geophysical and social independent variables that minimized colinearity (Table 1) to model variations in plant diversity from site to site across our study area. Although some potentially interesting variables (e.g., potential evapotranspiration and real estate values) were unavailable for all or many of the sites, the 13 variables selected for inclusion encompass a range of abiotic, geographic, and human-related features of the study area.

Selection of Biophysical and Human Social Variables

In an undeveloped desert ecosystem, variations in plant diversity from place to place are typically caused by factors such as elevation, slope, aspect, water availability, and soil type (Whittaker and Niering 1975; McAuliffe 1994; Wondzell et al. 1996). Therefore, to represent the main geographic characteristics of the study site we used elevation (slope and aspect were zero for the majority of sites and so were not included), site latitude, site longitude, distance from urban center, population density, distance to the nearest major freeway, and soil nitrate concentration. To represent land use and land cover we used an indicator variable to denote land-use type, percentage impervious surface on the plot, and an indicator variable to show whether the site

had ever been in agriculture. Three additional human social variables, justified later in this report, were also included.

The biophysical variables expected to affect biological diversity are well documented in the ecological literature. Our challenge was to choose variables that would reflect human systemic drivers of biodiversity at an analytical scale comparable to the nonhuman variables.

Identity and Socionormative Behavior

Using items from nature to construct individual and social identity has an evolutionary basis, and young children across cultures having innate and specific capacities for learning and reasoning about plants and animals (Casagrande 2004a). Every culture has a complex, shared system for recognizing, naming, and attributing symbolic meaning to plants and animals (Berlin 1992); for example, three of the four professional sports teams in the Phoenix area are named after animals: the Cardinals, Diamondbacks, and Coyotes. Financial investment in housing development in metropolitan Phoenix over the last 30 years has fueled large-scale mass production of homogenous neighborhoods. The result is an increasing need for individualism and a tendency toward greater socionormative constraint. Homebuyers with greater financial resources may have a better capacity to choose which landscapes to live in or may find ways to symbolically manipulate an existing landscape, given social and climatic constraints. Any effect of this on plant diversity might be more pronounced in newer developments, where social controls are tighter. Hence to capture the social variables most likely to be important for documenting this trend, we included individual financial resources, housing age, and legacy effects.

Individual Financial Resources and Plant Diversity

Most social science research on direct and/or cognizant manipulation of landscape biodiversity pertains to subsistence-based indigenous populations (e.g., Wilshusen et al. 2002). Such studies strongly suggest that human-enhanced biological diversity is a result of shaping landscapes to provide ecosystem services, or conserving specific habitats for spiritual reasons (Casagrande 2004b). The valuing of diversity necessitates the ability to make trade-offs between potentially exclusive goals. In metropolitan Phoenix, an individual's relationship with the local landscape represents goal-based compromises among ecosystem services and economic benefits—for example, providing shade to reduce the cost of air conditioning or a more comfortable area for outdoor recreation, versus keeping water bills low. The ability to substitute money for one or another ecosystem service suggests that higher financial resources will confer greater flexibility in these trade-offs.

Median housing value, total individual assets, and median income are all indicators of wealth. We wanted to use the measure of financial capacity most closely related to landscape alterations. Therefore we chose median family income as the most appropriate variable of analysis because it is income that best represents available financial resources that may affect plant diversity and structure (Whitney and Adams 1980). Developers, real estate salespeople, and lenders all structure their marketing, sales, or development strategies around specific income groups. We chose not to use median housing value as a variable of analysis, because housing value is likely to covary with income.

History, Legacy Effects and Macro-Scale Decisions

We refer to inherited present day conditions arising from past events as “legacy effects.” The landscape, as transformed by past biophysical and human action, provides the template on which individual pursuits are played out. Decisions of policy-makers and developers, environmental constraints, fashionable trends in ornamental plants, and developing technologies interact to set this stage, in ways that change over time. Of the variables that best link these large-scale processes with the individual, we believe that land use is the most important (Dow 2000). To capture historical effects, we decided to include past and current land use at each of our sample points.

Another important legacy component of large-scale historical events in the southwestern United States has been policy on water distribution. Agricultural water rights are often transferred to residential developers, leading to residential landscapes quite different from those on nonagricultural land. However, concern among policymakers over the amount of water available to sustain growth has led many municipalities in the Phoenix area to restrict the amount and types of vegetation in new residential developments (Jacobs and Holway 2004; Martin 2001). Municipal water conservation efforts also include incentives for individual homeowners to convert water-intensive landscapes to xeriscapes. Thus, we might expect different vegetation around houses built after the 1980s. Correlation of plant diversity with median housing age may also reflect changes in vegetation as landscapes mature, or the divergence in between individual lots over time. Hence the third human variable we chose to include in our model of spatial variations in plant diversity was median housing age.

Study Area and Survey Design

Our study area consisted of a large, geometrically defined, roughly rectangular area of 6400 km² (Figure 1), encompassing the entire Phoenix metropolitan area, surrounding agricultural and desert land. This large area was chosen well beyond current incorporated municipal boundaries, to ensure that our sampling frame will continue to contain nonurban, open space well into the future. The study boundaries approximate the northern, eastern, and western borders of Maricopa County, truncated by mountains and Indian Reservation land to the south (Figure 1). This largely sociopolitical boundary was chosen in preference to the watershed unit more typically used in ecology, because many natural watershed functions in this region have been superceded by human management and the built environment. Hence our sampling universe is more effective for understanding an urban ecosystem.

Sampling was designed to ensure a representative and unbiased characterization of ecological resources (Peterson et al. 1999a; Stevens 1997), as well as to ensure a spatially dispersed sample that would retain maximum flexibility for a variety of subsequent uses, within the bounds of what was practical to carry out within a one-season synoptic survey period (i.e., 3 months). We superimposed a 4 km × 4 km grid across the survey area of 6400 km², then surveyed one randomly placed 30 m × 30 m quadrat in each of the squares within the developed urban area and within every third square outside that area (Hope et al. 2003). This gave a total sample size of 206 survey plots (Figure 1). For our survey, we defined “urban” using land cover type (McIntyre et al. 2000), that is, developed land that was not native desert or agricultural.

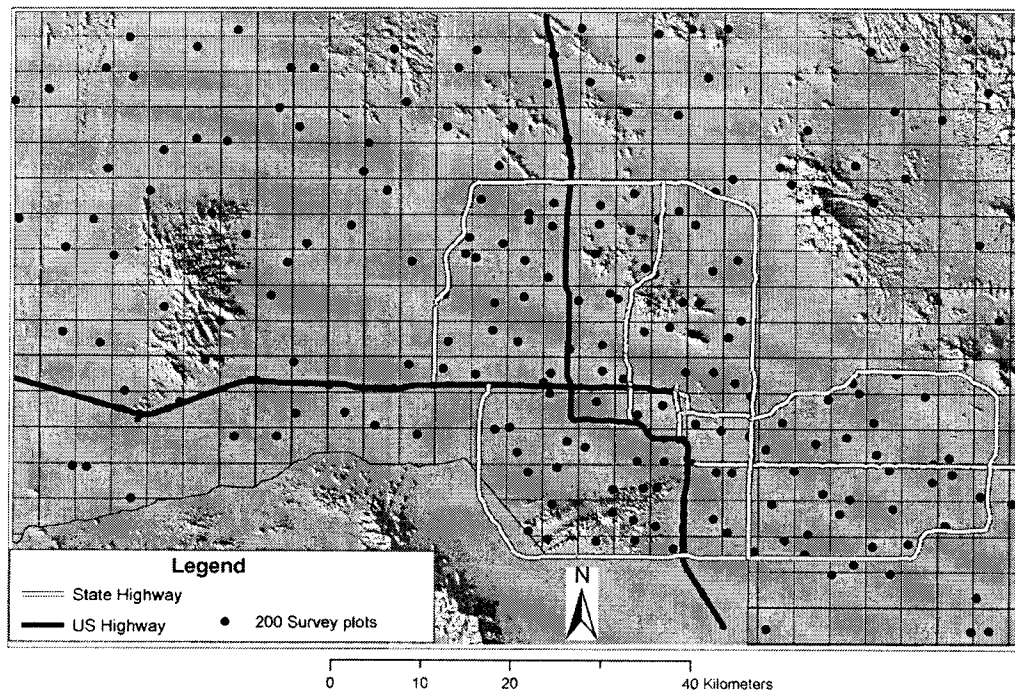


Figure 1. The Central Arizona–Phoenix study area and dual-density tessellation stratified sampling design.

Field Protocol and Data Acquisition

In each 30 m × 30 m survey plot we carried out a synoptic (one-time) field inventory of key biotic and physical variables during spring 2000 (Hope et al. 2003). At each site, all perennial plants were identified, along with the position and extent of all surface cover types (from which the percentage of impervious surface cover on each plot was determined), and soil core samples (top 10 cm) were taken and analyzed for nitrate concentration (Hope et al. in press). Land use at each of the sites was classified into five main categories (Hope et al. 2003): urban ($n = 91$ sites), desert ($n = 73$), agriculture ($n = 23$); transportation ($n = 6$), and a “mixed” class ($n = 11$). Elevation was obtained from the USGS Digital Elevation Model (30 m × 30 m resolution), and the distance of each site from the urban center and distance from nearest major freeway were calculated using ARCVIEW GIS (geographic information system). Population density, along with the socioeconomic variables of median family income, and median age of the housing stock, were obtained from the U.S. Census of Population and Housing for the appropriate block group within which each survey point was located (Hope et al. 2003). Land use history (specifically whether the site had ever been in agriculture) was taken from an analysis by Knowles-Yáñez et al. (1999).

Hypothesis and Statistical Analyses

Our hypothesis was that the underlying geomorphic template (e.g., elevation, slope, aspect) would be a primary control on spatial patterns in plant diversity in undeveloped desert (Whittaker and Niering 1975; McAuliffe 1994; Parker and Bendix

1996), and that our chosen human variables, along with those often used to define the “urban–rural gradient” (i.e., distance from urban center, population density, percentage impervious surface), would become more important at urban sites.

Spatial variations in plant diversity were modeled using the 13 independent variables (latitude, longitude, elevation, land use, distance from urban center, distance from nearest major freeway, impervious surface cover, population density, soil nitrate-N concentration, number of years in agriculture, whether ever in agriculture, median housing age, median family income) and a suite of spatial statistical techniques. Urban ecology has typically used the concept of an urban-to-rural gradient (McDonnell et al. 1993), although with an increasing recognition that such gradients are also complex (Alberti et al. 2001; McDonnell et al. 1997). We chose not to prescribe any spatial constraints, but instead allowed the main drivers to emerge from the analysis; in other words, our approach was inductive.

Since model variables were chosen to minimize covariance, none of the variance inflation factors (a measure of collinearity) between the independent variables used exceeded seven and most were substantially less, so collinearity was not a significant problem in our analyses (Gujarati 1995). The data were tested for spatial autocorrelation (i.e., whether diversity at one point was a function of diversity in adjacent sites), and then multivariate models of variation in total perennial plant diversity from site to site were constructed, varying all possible combinations of the independent variables until the bestfit models were found (see Hope et al. 2003). Statistical modeling was performed using PROC MIXED of SAS/STAT software, Version 9 of the SAS System for Windows (SAS Institute, Inc., 2004) which allows for spatially correlated error structures. Where spatial dependence was found, a semivariogram was used to determine how differences in concentrations change with increasing separation between sites, using the geoR package in R (Ribeiro and Diggle 2001). In order to investigate how spatial patterns might have been changed by urbanization, we performed the modeling for the desert and urban sites separately, as well as for the region as a whole. We then compared the findings from the models to see which variables best predicted any spatial variations in plant diversity between desert and urban parts of the region (see Hope et al. 2003; Hope et al. in press).

When making inferences about the parameters, we used a significance level of $\alpha = .05$ unless otherwise noted. We do not report r^2 values for the resultant models, since in the linear mixed models used there is no statistic that is the counterpart of the r^2 value in regression. This means that it is not possible to ascribe how much of the variation in biodiversity is explained by the individual variables. Instead, the marginal t -test, chi-square, or F value and their corresponding significance (p) levels are given (Table 2). These test statistics and their significance levels give the order of importance of the variables (a smaller value representing a more important variable) and indicate the marginal effect, that is, the contribution of each variable above and beyond the information supplied by the other variables already in the model.

Results

In total, 188 perennial plant genera were identified across the entire study area (Table 1). Urbanization has apparently greatly increased this whole-system diversity (termed “ γ diversity” by ecologists), with a total of 156 plant genera in the urban

Table 2. Best-fit models of plant diversity (number of perennial genera per site), with test statistics and the sign of the effect shown in parentheses

Parameter	All sites ($n = 204$)	Urban sites only ($n = 91$)	Desert sites only ($n = 73$)
Model type	Spherical semivariogram	GLM	GLM
Data transformation	Log link	Log link	Square root
Predictor variables	Land use: Urban (+27.35)*** Agriculture (-10.21)* Elevation (+24.88)*** Family income (+12.72)** Ever farmed (-6.04)	Family income (+8.08)* Median housing age (-6.65)* Ever farmed (-4.34)	Elevation (+7.59)*** Distance from urban center (-2.89)* Median housing age (+2.50)

Note. Perennial plant diversity is represented by number of woody plant genera per plot. Significant variables are listed in order of importance as judged by the level of significance denoted by asterisks (*** $p < .0001$; ** $p < .001$; * $p < .01$; no asterisk, $p < .05$). Test statistics are either t value, chi-square, or F value. In the case of plant diversity for the whole site, all of the F statistics are approximations and have degrees of freedom 1 and 196.

plots compared to 63 at desert sites (some native genera were also found at urban sites). Although the average number of genera per plot (α diversity) for urban and desert sites was similar, urban plots had on average twice as many exotic as native genera (Table 1). This pattern exists because the plant communities in urban landscapes are composed of a much expanded suite of genera, many of them imported from other regions (Table 2). Exactly which plants are present at any given urban site is highly variable; hence, there is considerably greater compositional “turnover” (β diversity) in the city compared to the desert sites (Table 1).

The modeling results suggest what determines the spatial variation of plant diversity from site to site (Table 2). At desert sites, plant diversity was spatially auto-correlated—in other words, dependent on diversity at adjacent sites up to 10 km apart, as well as being predicted by elevation (higher diversity with increasing elevation), distance from urban center (higher plant diversity occurred closer to the urban center), and median age of housing (plant diversity adjacent to newer housing tended to be lower than at sites with older houses). For the urban sites and across the region as a whole, plant diversity was found to be spatially independent. The multivariate modeling showed that spatial variations in plant diversity across the entire study region were best explained by elevation and three variables related to human actions: land use, median family income, and whether the plot had ever been in agriculture (Table 2). Of these, urban and agricultural land uses were particularly influential (“urban” $F = 27.35$, $p < .0001$, and agriculture $F = 10.21$, $p < .0014$). Elevation was also a strong predictor, with diversity increasing at higher sites ($F = 24.88$, $p < .0001$). Plant diversity increased with income level in the surrounding U.S. Census block group (Figure 2) up to \$50,750 per year (the median value for all the sites). Although the bivariate relationship appears weak (Figure 2), median family income was also a significant predictor of plant diversity in the multivariate model ($F = 12.72$, $p = .0004$), highlighting the importance of considering variables in combination, rather than attempting to explain the patterns using only a bivariate approach. Plant diversity at sites in neighborhoods with incomes above this amount was on average twice that found in the landscapes of less wealthy areas (11 genera per plot, compared to 5 in less wealthy neighborhoods). Whether a site had ever been

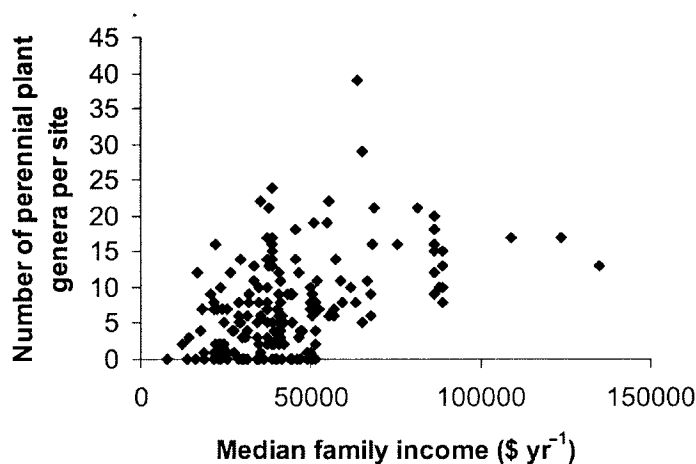


Figure 2. Variation in plant diversity with median family income in dollars per year for all sites.

used for agriculture was the fourth significant predictor ($F = 6.04$, $p = .014$); sites that had been farmed had on average four genera, compared to nine genera at sites not previously cultivated.

The model results for only urban sites differed from those for the region as a whole (Table 2). Within the developed urban area, variation in plant diversity depends on a combination of median family income ($F = 8.08$, $p = .0045$), housing age ($F = 6.65$, $p = .0099$), and whether the plot was ever in agriculture ($F = 4.34$, $p = .0371$). In addition to a positive relationship between plant diversity and medium family income, there was a negative relationship between urban plant diversity and age of housing—in other words, sites in neighborhoods with younger housing had higher diversity. Impervious surface cover did not help to predict plant diversity within the urban area, despite the reduction in growing surface area that increased impervious surface cover represents. However, the legacy effect of agricultural land use was a significant factor, with urban sites that were formerly farmed having 57% fewer perennial plant genera than locations that have never been cultivated.

Discussion

The planting of urban vegetation across the greater Phoenix area has occurred in the presence of a low-cost, abundant water supply, with the native vegetation having been essentially replaced by a diverse “oasis” landscape comprising many imported trees and shrubs (Peterson et al. 1999b; Martin et al. 2003; Martin et al. 2004). Despite this transformation in appearance, humans have apparently created urban landscapes with similar average generic (α) plant diversity to the native desert vegetation they have removed (Table 1). This may reflect a practical upper limit on how many different plants can grow on the area of the survey plot (900 m²), however much water and nutrients are applied. Yet humans have changed the plant diversity of the former Sonoran Desert on which they have developed their city in many other ways. In particular, the breakdown of spatial dependence between neighboring sites within the city suggests that human activities rearrange plant diversity at a finer scale than the grain of our sampling scheme. What is likely to be driving this change?

Role of Geographic Versus Human Variables

Our findings on desert plant diversity (Table 2) reflect the close correlation of plant communities to topography and landform, which govern resource availability. In particular, water and nutrient supply have been shown to be important in predicting native desert plant diversity at the regional scale in arid environments (Shreve 1951; Whittaker and Niering 1975; Parker and Bendix 1996; Wondzell et al. 1996). However, human decisions appear to have had both direct and inadvertent effects on plant diversity of undeveloped desert around metro Phoenix. Diversity at desert sites increased with proximity to the metro center, we suggest due to the deliberate preservation of floristically diverse upland Sonoran Desert habitats on mountain preserves, of which there are several close to the urban core. Meanwhile, the finding that floristic diversity was lower at desert sites located in Census block groups with more recent housing developments is likely to be an inadvertent consequence of many housing developments occurring preferentially on flat, low-elevation sites (Fagan et al. 2001).

Urban Plant Diversity and the “Luxury Effect”

Urbanization fragments natural landscapes and increases overall heterogeneity (Clark et al. 1997; Luck and Wu 2002). In the arid urban environment of metro Phoenix this is enhanced by personal and institutional landscaping choices, with the composition and longevity of woody perennials being largely determined by human choices and landscape maintenance, rather than by natural reproduction and mortality, especially in residential landscapes (Martin et al. 2003). Human choices about what kinds of vegetated landscapes to preserve or create in Phoenix are both personal and institutional (Larsen et al. 2004). These choices, along with the availability of a broad palette of landscape plant materials, modern irrigation technology, and a cheap, abundant supply of water, have significantly impacted plant diversity. The replacement of Sonoran desert vegetation with largely exotic species has resulted in a much greater variation in plant genera from site to site (β diversity), as well as higher total diversity (γ diversity) across the whole city and region (Hope et al. 2003).

Human actions across metro Phoenix (e.g., addition of nonnative plants, water, and fertilizer) thus have modified traditional ecological resource availability–diversity relationships (Tilman 1977). Rather than natural (water and nutrient) resources supply, plant diversity is positively related to economic resources (family income in our analysis). There is instead a “luxury effect” (Hope et al. 2003), whereby as their economic wherewithal increases, humans inhabit landscapes with higher plant diversity, either or by creating them or preferentially settling into locations with naturally high diversity. This apparently mirrors the well-established link between socioeconomic status and quality of the social environment (e.g., Smith et al. 1997; Nelson et al. 1998; Bolin et al. 2002), and vegetation structure (Talarchek 1990; Iverson and Cook 2000). Across the region as a whole there was an apparent threshold of \$50,750 per year (Figure 2), above which diversity did not increase—possibly indicating a perceived “ideal” diversity corresponding to innate or culturally derived ideas about desirable landscapes (e.g., Cronon 1996). We suggest that the “luxury effect” may be a general characteristic of urban ecosystems, whereby access to sufficient financial resources per se is a mechanism of empowerment to manifest human preference.

Our models suggest that the luxury effect, interacts with land use, legacy effects and other sociocultural factors. For example, some of the highest plant diversity at CAP was found in high-income neighborhoods of higher elevation desert foothills, where yards tended to contain relatively undisturbed, native foothills desert vegetation. As in many American cities (Meyer 1994), wealthier neighborhoods are often located at higher elevations. Since there was some colinearity between elevation and income in metropolitan Phoenix (variance inflation factor = 0.506 for the urban sites), our analysis cannot quantify unequivocally the extent to which wealthier people create more diverse landscapes, as opposed to simply acquiring them.

Legacy Effects and Techno-Cultural Controls

The history of a region can be crucial in explaining patterns in vegetation associations. Legacy effects related to the duration and type of land use might also be expected to influence plant diversity (e.g., Kendle and Forbes 1997), and indeed our results showed a clear legacy effect of former agricultural land use. Removal

of native vegetation followed by cultivation apparently depletes the local flora, creating a legacy effect that persists despite the subsequent creation of a vegetated urban landscape over many former agricultural fields. Plant diversity was also higher at sites with younger housing. We suspect that this finding reflects the way in which technological innovation has also changed the ecosystem services people attempt to derive from their landscape. The advent of widespread air conditioning and an increasing public interest in the conservation of water drove the switch from broad, shady, well-watered landscapes to more water-conservative, drip-irrigated, xeric landscapes. This shift began in the mid 1980s, when municipalities stopped allowing flood irrigation of residential areas and provided incentives to convert yards to drip-irrigated landscapes. Changes in popularity of ornamental species can also influence the landscape well after original plantings. The tendency in our study is for yards with urban facsimiles of xeric, desertlike vegetation (termed “xeriscapes”) to have less area devoted to turf grass, coupled with the tendency for drought-adapted plants to be smaller, presumably allows for more individual plants per yard. Also, in order to obtain immediate aesthetic gratification, landscapes in newly established housing developments tend to be created with initially high plant diversity, in an attempt to create a premature appearance of maturity (Conzen 1990). It may also be that wealthy people prefer newer housing, as indicated by weak colinearity between housing age and median family income (variance inflation factor = -0.379 for the urban sites), and that this also affects plant diversity in the urban landscape. These factors combined seem to explain the trend in our models for younger houses to have more diverse plantings.

Future Work

We propose that along with possession of sufficient economic resources, a varying suite of correlated variables may contribute to the form of wealth–diversity relationships in urban landscapes at a finer scale of analysis than we present here. Future research should focus on individual decisions that affect plant diversity—in particular, strategies by which residents create identity and adapt to legacy effects. Identities based on ethnicity, class, or place of origin may contribute to biological diversity, especially in socially heterogeneous neighborhoods, yet personal histories within such groups can be highly diverse (Phoenix Area Social Survey 2003; St. Hilaire et al. 2003) and expressed environmental concerns may not correlate with landscaping preferences (Phoenix Area Social Survey 2003; Kennedy and Zube 1991). Hence it may not be possible to predict which plants people would desire for their yards based on variables like ethnicity, class, or place of origin (Martin et al. 2003).

The tendencies to use plants to express individual identity are also likely to be constrained by socially shared norms, such as availability of nursery stock, advice from landscapers, the ability of homeowners to grow their plants of choice, and the effects of their decisions on the market value of their homes. Ideally, we would like to quantify how much money, time, or energy is actually devoted by individuals to altering plant communities, and how people reconcile these choices with the socio-normative constraints of maintaining the value of homes and environmental concerns (particularly regarding water conservation). In our study area, homeowner associations often decide what landscaping is best for maintaining housing values,

and penalize members who do not comply (Martin et al. 2003); the effect of such associations should be included in future studies conducted at a finer grain.

Conclusions

Traditional approaches used by ecologists may be inadequate and potentially misleading when applied to human-dominated landscapes, because they do not explicitly include the myriad of human behaviors and actions that have produced that landscape. Here, while not suggesting a new paradigm, we have demonstrated the likelihood that variables related to human activities and social organization do play a significant role in establishing floristic diversity patterns. We recognize that our conclusions are necessarily limited to the scale at which the study was carried out. Moreover, some of the independent variables we tested are probably surrogates for more specific human processes, for example, aesthetic thresholds (Ulrich 1993), institutionalized rules such as municipal landscape ordinances and covenants, codes and restrictions (Martin et al. 2003), and changing social demographics. Nevertheless, our study has clearly shown that human management modifies traditional resource availability–diversity relationships, by removing natural resource limitations while simultaneously maintaining high plant diversity. We suggest that this may be related to preferences for particular landscapes, along with the availability of financial resources to realize those landscapes. Since human decisions change abruptly across property boundaries, key drivers can also change at very local scales, generating extreme spatial heterogeneity in urban ecosystems. Our results suggest that this heterogeneity is attenuated by capital resources and shaped by social forces. Future studies should more closely examine the effects of changing human attitudes and behavior, as well as societal institutions, on the resilience and spatial variation of plant diversity throughout the region.

References

- Alberti, M., E. Botsford, and A. Cohen. 2001. Quantifying the urban gradient: Linking urban planning and ecology. In *Avian ecology and conservation in an urbanizing world*, eds. J. M. Marzluff, R. Bowman, and R. Donnelly, 89–115. Boston: Kluwer.
- Anderson, E. 1956. Man as a maker of new plants and new plant communities. In *Man's role in changing the face of the earth*, ed. W. L. Thomas, Jr., 763–777. Chicago: University of Chicago Press.
- Baker, L. A., A. J. Brazel, N. Selover, C. Martin, N. McIntyre, F. R. Steiner, A. Nelson, and L. Musacchio. 2002. Urbanization and warming of Phoenix (Arizona, USA): Impacts, feedbacks and mitigation. *Urban Ecosys.* 6:183–203.
- Bastin, L. and C. D. Thomas. 1999. The distribution of plant species in urban vegetation fragments. *Landscape Ecol.* 14:493–507.
- Berlin, B. 1992. *Ethnobiological classification: Principles of categorization of plants and animals in traditional societies*. Princeton, NJ: Princeton University Press.
- Bolin, R., A. L. Nelson, E. Hackett, D. Pijawka, E. Sadalla, E. Matranga, D. Brewer, and D. Sicotte. 2002. The ecology of risk in a sunbelt city: A multi-hazard spatial analysis. *Environ. Plan. A* 34:317–339.
- Casagrande, D. G. 2004a. Ethnobiology lives! Theory, collaboration, and possibilities for the study of folk biologies. *Rev. Anthropol.* 33:351–370.
- Casagrande, D. G. 2004b. Conceptions of primary forest in a Tzeltal Maya community: Implications for conservation. *Hum. Organ.* 63:189–202.

- Clark, K. C., S. Hoppen, and L. Gaydos. 1997. A self-modifying cellular automaton model of historical urbanization in the San Francisco Bay area. *Environ. Plan. B Plan. Design* 24:247–261.
- Collins, J. P., A. P. Kinzig, N. B. Grimm, W. B. Fagan, D. Hope, J. Wu, and E. T. Borer. 2000. A new urban ecology. *Am. Sci.* 88:416–425.
- Conzen, M. P., ed. 1990. *The making of the American landscape*. Boston: Unwin Hyman.
- Cronon, W. 1996. In search of nature. In *Uncommon ground. Rethinking the human place in nature*, ed. W. Cronon, 23–68. New York: W. W. Norton.
- Dana, E. D., S. Vivas, and J. F. Mota. 2002. Urban vegetation of Almeria City—A contribution to urban ecology in Spain. *Landscape Urban Plan.* 59:203–216.
- Dow, K. 2000. Social dimensions of gradients in urban ecosystems. *Urban Ecosyst.* 4:255–275.
- Fagan, W. F., E. Meir, S. S. Carroll, and J. Wu. 2001. The ecology of urban landscapes: Modeling housing starts as a density-dependent colonization process. *Landscape Ecol.* 16:33–39.
- Franceschi, E. A. 1996. The ruderal vegetation of Rosario City, Argentina. *Landscape Urban Plan.* 34:11–18.
- Grimm, N. B., R. J. Arrowsmith, C. Eisinger, J. Heffernan, D. B. Lewis, A. MacLeod, L. Prashad, W. J. Roach, T. Rychener, and R. W. Sheibley. 2004. Effects of urbanization on nutrient biogeochemistry of aridland streams. In *Ecosystem interactions with land use change*, eds. R. DeFries, G. Asner, and R. Houghton, pp. 129–146. Geophysical Monograph Series, 153. Washington, DC: American Geophysical Union.
- Grove, J. M. and W. R. Burch, Jr. 1997. A social ecology approach and applications of urban ecosystem and landscape analyses: A case study of Baltimore, Maryland. *Urban Ecosyst* 1:259–275.
- Gujarati, D. N. 1995. *Basic econometrics*, 3rd ed. New York: McGraw Hill.
- Hope, D., C. Gries, W. Zhu, W. F. Fagan, C. L. Redman, N. B. Grimm, A. L. Nelson, C. Martin, and A. Kinzig. 2003. Socioeconomics drive urban plant diversity. *Proc. Nat. Acad. Sci. USA* 100:8788–8792.
- Hope, D., W. Zhu, C. Gries, J. Oleson, J. Kaye, N. B. Grimm, and L. A. Baker. In press. Spatial variation in soil nitrate concentrations across an urban ecosystem. *Urban Ecosyst.*
- Iverson, L. R. and E. A. Cook. 2000. Urban forest cover of the Chicago region and its relation to household density and income. *Urban Ecosyst.* 4:105–124.
- Jacobs, K. L. and J. M. Holway. 2004. Managing for sustainability in an arid climate: Lessons learned from 20 years of groundwater management in Arizona, USA. *Hydrogeol. J.* 12:52–65.
- Jenerette, G. D. and J. G. Wu. 2001. Analysis and simulation of land-use change in the central Arizona–Phoenix region, USA. *Landscape Ecology* 16:611–626.
- Kendle, T. and S. Forbes. 1997. *Urban nature conservation*. London: E & FN Spon.
- Kennedy, C. B. and E. H. Zube. 1991. Attitudes towards vegetation in a desert urban forest: Creating a sense of place. *J. Arboriculture* 17:159–166.
- Knowles-Yáñez, K., C. Moritz, J. Fry, M. Bucchin, C. L. Redman, and P. McCartney. 1999. *Historic land use team: Phase I report on generalized land use*. Phoenix, AZ: Central Arizona–Phoenix LTER.
- Larsen, L., S. Harlan, R. Bolin, E. Hackett, D. Hope, A. Kirby, A. L. Nelson, R. T. Rex, and S. Wolf. 2004. Bonding and bridging: Understanding the relationship between social capital and civic action. *J. Plan. Educ. Res.* 24:64–77.
- Liu, J., G. C. Daily, P. R. Ehrlich, and G. W. Luck. 2003. Effects of household dynamics on resource consumption and biodiversity. *Nature* 421:530–533.
- Luck, M. A. and J. Wu. 2002. A gradient analysis of the landscape pattern of urbanization in the Phoenix metropolitan area of USA. *Landscape Ecol.* 17:327–339.
- Martin, C. A. 2001. Landscape water use in Phoenix, Arizona. *Desert Plants* 17:26–31.

- Martin, C. A., K. A. Peterson, and L. B. Stabler. 2003. Residential landscaping in Phoenix, Arizona, U.S.: Practices and preferences relative to covenants, codes and restrictions. *J. Arboriculture* 29:9–17.
- Martin, C. A., P. S. Warren, and A. P. Kinzig. 2004. Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in small parks and surrounding residential neighborhoods in Phoenix, Arizona. *Landscape Urban Plan.* 69:355–368.
- Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. *Science* 277:504–509.
- McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. *Ecol. Monogr.* 64:111–148.
- McDonnell, M. J., S. T. A. Pickett, and R. V. Pouyat. 1993. The application of the ecological gradient paradigm to the study of urban effects. In *Humans as components of ecosystems: Subtle human effects and the ecology of human populated areas*, eds. M. J. McDonnell, and S. T. A. Pickett, 175–189. New York: Springer-Verlag.
- McDonnell, M. J., S. T. A. Pickett, P. Groffman, P. Bohlen, R. V. Pouyat, W. C. Zipperer, R. W. Parmelee, M. M. Carreiro, and K. Medley. 1997. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosyst.* 1:21–36.
- McIntyre, N. E., K. Knowles-Yáñez, and D. Hope. 2000. Urban ecology as an interdisciplinary field: Differences in the use of “urban” between the social and natural sciences. *Urban Ecosyst.* 4:5–24.
- McPherson, G. and R. A. Haip. 1991. Emerging desert landscape in Tucson. *Geogr. Rev.* 79:435–449.
- Meyer, W. B. 1994. Bringing hypsography back in—altitude and residence in American cities. *Urban Geogr.* 15:505–513.
- Nelson, A. L., K. P. Schwirian, and P. Schwirian. 1998. Social and economic distress in large cities, 1970–1990: A test of the urban crisis thesis. *Soc. Sci. Res.* 27:410–431.
- Parker, K. C. and J. Bendix. 1996. Landscape-scale geomorphic influence on vegetation patterns in four environments. *Phys. Geogr.* 17:113–141.
- Peterson, S. A., N. S. Urquhart, and E. B. Welch. 1999a. Sample representativeness: A must for reliable regional lake condition estimates. *Environ. Sci. Technol.* 33:1559–1565.
- Peterson, K. A., L. B. McDowell, and C. B. Martin. 1999b. Plant life form frequency, diversity, and irrigation application in urban residential landscapes. *HortScience* 34:491.
- Phoenix Area Social Survey. 2003. *Community and environment in a desert metropolis: Summary results of the pilot study*. Central Arizona–Phoenix Long-Term Ecological Research Contribution No. 2: Tempe: Arizona State University, Department of Sociology.
- Pickett, S. T. A., W. R. Burch, Jr., S. Dalton, T. Foresman, J. M. Grove, and R. Rowntree. 1997. A conceptual framework for the study of human ecosystems in urban areas. *Urban Ecosystems* 1:185–199.
- Ribeiro, P. J., Jr. and P. J. Diggle. 2001. geoR: A package for geostatistical analysis. *R-NEWS*, 1(2):15–18.
- SAS Institute, Inc. 2004. *SAS/STAT 9.1 User's Guide*. Cary, NC: SAS Institute, Inc.
- Savard, J.-P. L., P. Clergeau, and G. Mennechez. 2000. Biodiversity concepts and urban ecosystems. *Landscape Urban Plan.* 48:131–142.
- Sebba, R. 1991. The landscapes of childhood—the reflection of childhood's environment in adult memories and in children's attitudes. *Environ Behav.* 23:395–422.
- Shreve, F. 1951. Vegetation and flora of the Sonoran Desert, vol. I. *Vegetation* 591:1–192. Washington, DC: Carnegie Institute.
- Smith, T., M. Nelischer, and N. Perkins. 1997. Quality of an urban community: A framework for understanding the relationship between quality and physical form. *Landscape Urban Plan.* 39:229–241.
- Stapanian, M. A., S. D. Sundberg, G. A. Baumgardner, and A. Liston. 1998. Alien plant species composition and associations with anthropogenic disturbance in North American forests. *Plant Ecol.* 139:49–62.

- St. Hilaire, R., J. E. Spinti, D. VanLeeuwen, and C. Smith. 2003. *Landscape preferences and attitudes toward water conservation: A public opinion survey of homeowners in Las Cruces, New Mexico*. Las Cruces, NM: New Mexico State University, Agricultural Experiment Station.
- Stevens, D. L., Jr. 1994. Implementation of a national monitoring program. *J. Environ. Manage.* 42:1–29.
- Stevens, D. L., Jr. 1997. Variable density grid-based sampling designs for continuous spatial populations. *Environmetrics* 8:167–195.
- Talarchek, G. M. 1990. The urban forest of New Orleans—An exploratory analysis of relationships. *Urban Geogr.* 11:65–86.
- Tilman, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58:338–48.
- Ulrich, R. S. 1993. Biophilia, biophobia, and natural landscapes. In *The biophilia hypothesis*, eds. S. R. Kellert and E. O. Wilson, 73–137. Washington, DC: Island Press.
- Whitney, G. G. and S. D. Adams. 1980. Man as a maker of new plant communities. *J. Appl. Ecol.* 17:431–448.
- Whittaker, R. H. and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. 5. Biomass, production, and diversity along an elevation gradient. *Ecology* 56:771–790.
- Williams, J. W., E. W. Seabloom, D. Slayback, D. M. Stoms, and J. H. Viers. 2005. Anthropogenic impacts upon plant species richness and net primary productivity in California. *Ecol. Lett.* 8:127–137.
- Wilshusen, P. R., S. R. Brechin, C. L. Fortwangler, and P. C. West. 2002. Reinventing a square wheel: Critique of a resurgent “protection paradigm” in international biodiversity conservation. *Society Nat. Resources* 15:17–40.
- Wondzell, S. M., G. L. Cunningham, and D. Bachelet. 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. *Landscape Ecol.* 11:351–362.