STRUCTURE AND DISTRIBUTION OF SONORAN DESERT PLANT COMMUNITIES IN METROPOLITAN PHOENIX, ARIZONA

by

Arthur Stiles

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

ARIZONA STATE UNIVERSITY

May 2006

STRUCTURE AND DISTRIBUTION OF SONORAN DESERT PLANT
COMMUNITIES IN METROPOLITAN PHOENIX, ARIZONA

by

Arthur Stiles

has been approved

November 2005

APPROVED:

, Co-Chair

, Co-Chair

Supervisory Committee

ACCEPTED:

Director of the School

Dean, Division of Graduate Studies

ABSTRACT

This study investigates Sonoran Desert plant communities in the Central Arizona – Phoenix Long Term Ecological Research (CAP-LTER) site located in and around metropolitan Phoenix, Arizona. There are two main emphases: (1) an examination of vegetation within undeveloped remnant habitat islands with regard to species richness, nestedness, and species accumulation with area, and (2) an effort to generate maps depicting the distribution of natural vegetation types on desert lands using remotely sensed data. Island-level woody species richness is positively related to island area; this relationship arises from larger islands containing both more individuals and higher elevation environments. Local-scale woody species richness is not influenced by island area, but is structured by passive sampling dependent on plant density, productivity associated with elevation, study site identity, and proportional sampling from the island species pool. Nestedness in woody vegetation arises as a consequence of an aggregate response of constituent species involving multiple mechanisms. Nestedness in herbaceous communities arises from an area effect, involving either extinction or passive sampling, and is reinforced by colonization of exotic taxa. In terms of species-area curves, sample curves in both woody and herbaceous vegetation are most often best fit by sigmoid functions, whereas convex functions best describe the relationship between island area and island species richness. Landsat ETM data was used to generate vegetation maps for subsets of the CAP-LTER, with classes determined from field data collected within the study area. Results were varied, with vegetation on clayey soils mapped to an accuracy of 91%. Other subset maps were 70% accurate or less. Mapping of desert vegetation is particularly challenging since bare soil exposure is high and background soil spectra potentially interfere with vegetation signatures. These results demonstrate that image classification of desert vegetation using only Landsat ETM data can be problematic and may not be practical without other supporting data, such as radar imaging, which generally agrees with results of other efforts.

ACKNOWLEDGMENTS

This research was made possible by the assistance of some very capable and gracious people. I wish to thank my doctoral committee members for advice and guidance throughout the years: Samuel Scheiner, John Briggs, Julie Stromberg, Jianguo Wu, and Elaine Joyal. This work would not have been possible without the assistance of Samuel Scheiner, my advisor, who helped to formulate the structure of the research, provided statistical advice, and reviewed early drafts of the dissertation. John Briggs, who served as a co-chair, was also instrumental in this effort by lending laboratory space and necessary technology, varied guidance, and valuable moral support. Kevin Fantozzi and Alejandro Castro provided field assistance in the early years of the project. Assistance with the use of Geographic Information Systems (GIS) was offered by Shea Lamar and Mike Zoldak. Advice about remote sensing was provided by Will Stefanov, Casey Adams, Alex Buyantuyev, and John Briggs. The staff of the CAP-LTER was also helpful with varied aspects of the project, especially the designer of the plant diversity database, Peter McCartney. This research was funded by National Science Foundation Grant DEB-9714833.

TABLE OF CONTENTS

Page

CHAPTER Page

CHAPTER Page

LIST OF TABLES

Table Page

Table Page

Table Page

Table Page

Table Page

LIST OF FIGURES

CHAPTER 1. EFFECTS OF FRAGMENTATION ON WOODY PLANT SPECIES RICHNESS OF REMNANT DESERT HABITAT ISLANDS IN PHOENIX, ARIZONA

ABSTRACT

Land use conversion is a common phenomenon responsible for creating remnant islands out of formerly continuous natural habitat. Attributes of insular environments influence the character of remnant vegetation, including species richness. While much research has been done on plants in terrestrial insular communities, explicit knowledge of how species richness varies at multiple spatial scales remains incomplete. This study examines how woody species richness at the island-level and the local-scale is structured in undeveloped remnant islands embedded within the Phoenix metropolitan area, and how richness is related to ecological mechanisms hypothesized to influence remnant communities. Island-level richness was significantly influenced by area, though not to other variables, such as isolation, habitat heterogeneity, and density of individuals. This species-area effect resulted from larger islands supporting higher numbers of individuals and containing higher elevations, which typically support species rich vegetation. Island area had no significant influence on local richness, which was positively related to island-level richness, density of individuals, and elevation. Local communities were unsaturated with species and increased linearly with island-level richness.

INTRODUCTION

A burgeoning human population has transformed extensive tracts of land into human-dominated systems, fragmenting formerly continuous expanses of natural ecosystems into smaller remnant patches. This change in landscape structure can have drastic effects on biota. Both components of fragmentation, habitat loss and insularization of remnants, tend to reduce the diversity of ecological communities (Wilcox 1980). Reduction in diversity may be very quick or can occur after a considerable time lag (Wilcox and Murphy 1985). These fragments likely experience greater amplitude or frequency in population, community, and ecosystem dynamics compared with continuous habitats (Laurance 2002). Given the ubiquity of fragmentation and its pronounced influence on ecological function, fully comprehending the effects of fragmentation is crucial for ensuring the preservation of biological resources. While a number of studies have investigated fragmentation's impact on the vegetation of varied insular habitats (e.g. Levenson 1981, Scanlan 1981, Simberloff and Gotelli 1984, Dzwonko and Loster 1988, Hobbs 1988, Soule et al. 1992, Drayton and Primack 1996), we still do not have explicit understanding of how multi-scale factors affect species richness at multiple scales. Variables potentially influencing the number of species observed on a habitat island include area, degree of isolation, density of individuals, and elevation. In this chapter, the effects of these factors on woody species richness in Sonoran Desert remnant islands within the Phoenix metropolitan area are examined, and the relationship between richness at both local and island-level scales is assessed.

Fragmentation effects on species richness

The area of a given remnant, operating at the island-level scale, is one of the most important influences on species richness. The relationship between area and species richness, in which the number of species typically increases with area, has been recognized for 150 years (de Candolle 1855, Rosenzweig 1995) and studied for much of modern ecology's history (e.g., Arrhenius 1921, Gleason 1922, 1925, Preston 1962, Coleman 1981, Coleman et al. 1982, Williams 1995, Scheiner et al. 2000). This positive relationship can arise through two mechanisms: an increase with area of either the total number of individuals or the number of types of habitats (Coleman 1981, Coleman et al. 1982, Lack 1976, Scheiner 2003, Scheiner and Willig 2005). The total number of individuals in a habitat island is determined by the density of individuals and the area over which they occupy (Preston 1962). Reduced areas support smaller populations, which provide less insulation from fluctuations and the risk of local species extinction from stochastic events (Preston 1962, MacArthur and Wilson 1967). Larger assemblages of individuals also increase the probability that rare species will be observed along with common taxa through simple sampling effects, a phenomenon often referred to as passive sampling. Greater densities can inflate richness at both the local and island-level scale. Likewise, larger areas are more likely to include a greater variety of habitats. Each new habitat type incorporated into an area potentially increases richness by including species with affinities for a habitat that may be absent in other environments.

Island biogeography was originally proposed to explain diversity patterns on oceanic islands (McArthur and Wilson 1967), but has subsequently been applied to insular terrestrial habitats. Most studies report a positive relationship between area and species richness [e.g. chaparral and sage scrub (Soule et al. 1992), remnant forest patches in metropolitan areas (Hobbs 1988) and agricultural landscapes (Scanlan 1981, Jarvinen 1982, Peterken and Game 1984, Simberloff and Gotelli 1984, Dzwonko and Loster 1988, 1989, 1992, van Ruremonde and Kalkhoven 1991, Grashof-Bokdam 1997, Honnay et al. 1999a)]. Most researchers who found an area effect argued that area is a surrogate for habitat heterogeneity. Measuring a host of abiotic habitat features within English woodlands, Peterken and Game (1984) found that the combined habitat factors explained 45% of the variance, versus 59% for simple area, and they argued that a full accounting of habitat traits would likely explain the entire area effect. Using PCA ordination, Honnay et al. (1999a) found that the first two axes of variation corresponded to habitat characteristics in Belgian forest patches. Dzwonko and Loster (1988) found an area effect in heterogeneous, but not homogeneous, woodlots in Poland, also indicating the effects of habitat heterogeneity.

Isolation is a factor operating at the between-island scale affecting communities according to the position and character of other habitat elements within the landscape (Honnay et al. 1999a). Isolation potentially affects the composition and quantity of propagules moving between patches (McArthur and Wilson 1967). Fragmentation decreases the connectivity and increases isolation of patches on a landscape (Forman 1995). The nature of the surrounding matrix influences how strong a barrier it provides to migration. In a human-dominated area such as an agricultural or urban landscape, the effect of isolation can be substantial (Matlack 1994, Rebele 1994).

There are varied results regarding the effects of isolation in the literature. Several authors (Scanlan 1981, Dzwonko and Loster 1988, Kadmon and Pulliam 1993, Kadmon 1995) found that isolation decreased the species richness of woodlots. Sharpe et al. (1987) concluded that isolation of woodlots prevented colonization by sugar maple (*Acer saccharum*). Kadmon and Pulliam (1993) and Kadmon (1995) observed that species composition of reforested islands, which had been logged and then isolated by the filling of a reservoir, were more dissimilar with increasing distance to the mainland shore. On the other hand, Honnay et al. (1999a) found only very minor isolation effects, while multiple authors (e.g. Jarvinen 1982, Peterken and Game 1984, Bond et al. 1988, Hobbs 1988, van Ruremonde and Kalkhoven 1991, Soule et al. 1992) found no evidence for any influence due to isolation. Failing to find evidence of isolation can imply either ready dispersal between habitats, as with highly vagile plant species, or a lack of significant migration. For example, both Peterken and Game (1984) and Dzwonko and Loster (1992) found little evidence that newer stands were accumulating species endemic to older forests.

Elevation has a strong effect on the composition of Sonoran vegetation whereby greater species richness and more extensive vegetative groundcover tend to be observed at higher elevations (Yang and Lowe 1956, Barbour 1973, Halvorson and Patten 1974, Phillips and MacMahon 1978, Bowers and Lowe 1986, Hope et al. 2003). Increases in elevation within the Sonoran desert are accompanied by higher precipitation, lower temperatures, and an increase in mean particle size in the rockier soils on mountains and hilltops which retard evaporation and promote the deep percolation of rain water, resulting in greater water availability to plants (Shreve and Wiggins 1964). Thus, elevation is a surrogate for productivity. Higher productivity can result in a greater density of individuals which in turn can lead to greater species richness at the local-scale through the passive sampling of more taxa. Also, many woody species that thrive on upper bajadas will not be found on the lower slopes and plains due to moisture limitation. Hence, sites with wider ranges in elevation potentially offer a broader productivity gradient and an increase in richness at the whole-island scale.

Relationship between local and regional diversity

Ecologists had long believed that local processes such as predation, competition, and stochastic variation limit species richness at small spatial scales (Gause 1934, Hutchinson 1959, MacArthur and Levins 1967). It was conventionally held that when a community is at equilibrium, all niches are occupied and further additions to diversity are unattainable, according to notions of limiting similarity (Abrams 1983). Such a locality would be closed to species immigration, making richness at local and regional scales independent. Ricklefs (1987) disputed the idea that local habitats have an absolute maximum richness whereby niches are inflexible and necessarily impede colonization when they are occupied. This view holds that communities are indeed invasible, as demonstrated by many introductions of exotic species. Also, while communities geographically separated are often convergent in structure and function, they do not converge to common diversities, contradicting the hypothesis that species assemblages are structured primarily as a response to vacant niches. Rather, local and regional richness are potentially dependent on each other as a result of the balance between local factors that constrain diversity and regional factors, like speciation and long-distance dispersal, which increase diversity. Terborgh and Faaborg (1980), using a plot of local versus regional diversity, showed that the avian community in Caribbean island habitats was saturated.

While other examples of saturated communities have been identified (e.g., Aho 1990, Aho and Bush 1993), reviews now generally agree that unsaturated communities are more common (Caley and Schluter 1997, Cornell 1999, Lawton 1999, Srivastava 1999). Such communities proportionally sample regional richness, in which local richness is more dependent on the quantity of species observed at the regional scale and is less or not dependent on interactions within a community (Cornell and Lawton 1992). As such, a given species' likelihood of occurring within a localized area is dependent upon a species-specific incidence probability determined at the regional-scale (Fox et al. 2000).

A community containing species that are strongly interactive has been hypothesized to more likely saturate while weakly interactive assemblages are not saturated (Cornell 1985) because all non-interactive community models generate unsaturated patterns (Cornell and Lawton 1992). However, since interactive models are also able to produce unsaturated communities, one cannot assume a linear relationship necessarily indicates a non-interactive community (Caswell and Cohen 1993, Srivastava 1999). Studying a community of strongly interactive desert annuals, Valone and Hoffman (2002) found linear, unsaturating relationships predominant over a range of regional pool sizes. Indeed, when interpreting local-regional relationships, it is useful to remember that patterns do not infer processes (Gering and Crist 2002). Saturation is not all or nothing; the resistance of a locality to colonists can increase as local diversity rises (Ricklefs 2000).

For a variety of taxa occupying different continents, Caley and Shluter (1997) reported finding that unsaturating relationships are common when the locality was defined as 1% or 10% of a region encompassing 250,000 km^2. However, Huston (1999) criticized this study because their designation of the local-scale was an area much too large for local interactions. When defining the local-scale, it is crucial to only delineate that area in which direct organismal interactions are feasible, and could control diversity (Srivastava 1999). In the present study, the local-scale is determined by an area within which direct interactions between plants are possible. The region is here defined as the area contained within an island site rather than the whole archipelago of sites.

Urban ecology

The goal of this investigation is to determine how fragmentation affects woody plant species richness within remnant habitat islands isolated by urbanization in the Phoenix metropolitan area. The biota inhabiting an urban landscape confront environmental pressures that often vary in character, timing, and intensity from natural habitats, including higher disturbance rates or stress levels, higher competitive pressure from abundant exotic species, warmer temperatures from the urban heat island effect, lowered water tables, and alterations in soil chemistry and structure (Rebele 1994). While urban areas were historically compact and limited in extent, cities now cover more global surface area and diffuse over the landscape in irregular geometric patterns (Makse et al. 1995). Consequently, developed and undisturbed land sprawls over the landscape in alternating patches, bringing biota in contact with urbanization (Pickett et al. 2001). Energy and materials readily disperse beyond urban boundaries and affect systems far from the city.

Overview of hypotheses

The effect of variables on species richness of communities depends on the spatial and temporal scale under observation (Scheiner et al. 2000). Data considered here represent the state of remnant vegetation at a single point in time following land use conversion. Patterns of species richness are studied at two spatial scales: the whole, continuous area of remnant islands comprising habitable desert capable of supporting Sonoran vegetation, and the local-scale within the plant community. Examining two spatial scales provides information about how species richness is structured in the remnant communities and which mechanisms influence scale-dependent patterns.

Determinants of species richness at the island-level

Land use conversion leads to habitat fragmentation and increases isolation while decreasing the area of remnants, which in turn potentially affects species richness through multiple mechanisms. Decreases in island area can decrease island species richness through effects on habitat heterogeneity, passive sampling, and / or extinction. Declines in area can decrease habitat heterogeneity by excluding species adapted to lost habitats, leading to species loss at the island-scale. Smaller islands also hold fewer individuals which compose smaller insular populations that are more exposed to extinction resulting from stochastic events, demographic imbalances, or inbreeding depression. Fewer individuals also mean that, through a passive sampling effect reflective of the regional incidence of species, there is a reduced probability of encountering rare or uncommon species, which reduces island richness. While area affects both extinction and passive sampling processes, the current study does not assess how species distribution changed over time and it is not possible to disentangle the two mechanisms.

In this system, remnants may be influenced by colonization, extinction, habitat heterogeneity, passive sampling, and productivity. This study used four measurable variables to test the effects of these potential mechanisms: the likelihood of colonization by new species is gauged by the extent of island isolation, habitat heterogeneity is measured as the diversity of soil and geomorphic types, passive sampling and / or extinction is a function of the density of individuals, and productivity is measured through a surrogate variable, mean elevation. Island richness is predicted to increase with increases in habitat heterogeneity, the density of individuals, and elevation and to decrease with increasing isolation. Figure 1.1 depicts the hypothesized relationships between island-level species richness and the independent variables.

Determinants of species richness at the local-scale

Analysis of local-scale richness was conducted at two grains and two foci in order to assess the effects of scaling (Scheiner et al. 2000). Grain is the standard unit which summarizes the data of the dependent variable, here defined as the two sampling-units: a 100 m^2 quadrat and a transect consisting of five quadrats. These grains are used to test the influence of microhabitat variation and passive sampling. A transect of separated plots should capture greater microhabitat heterogeneity and thus a greater species richness. A larger area will hold more individuals and, thus, more species through the effects of passive sampling.

Focus refers to the scale to which a grain is aggregated (Scheiner et al. 2000). Thus, if the grain is equal to the size of a sample-unit, the focus of an analysis may be the values of individual sample-units, or the mean values of collections of sample-units. In this study, there are two foci: mean richness of samples averaged over whole islands and richness values of individual samples. Averaging samples allows for effects of variables at specific locations to be smoothed out so that the aggregate dynamics of whole islands are considered; the ecological conditions most common on the islands dominate the patterns when the focus is at the island-level.

Island species richness and mean density of individuals are two variables which can affect local-scale richness when the focus is on the island-level. Decreased island species richness lowers the maximum richness possible in a locality. A lower richness also increases the probability that an island will be dominated by common species (Preston 1962). The density of individuals at the local-scale should also affect richness, since fewer individuals per unit area reduces the probability of encountering species through passive sampling. Both factors are hypothesized to have a significant positive relationship on local-scale richness, though the influence should be stronger at the transect level since higher numbers of individuals, scattered over multiple patches of vegetation, should sample more rare species and contain a higher proportion of an island's species pool. Furthermore, the character of the correlation between local and island richness was hypothesized to be a nonsaturating relationship, since nonsaturating relationships are more common in nature (Caley and Schluter 1997, Cornell and Karlson 1997, Cornell 1999, Lawton 1999, Srivastava 1999). Investigating the relationship between local and island richness is most appropriate when the focus is on the whole island since a single local and island richness value is paired, thus avoiding a pseudoreplication problem (Srivastava 1999).

When the analysis involves variable values recorded at specific sample locations, this allows for the effects of factors to be examined using their total variability as they are exhibited in the field. Elevation and density of individuals are two variables capable of affecting the local richness of a specific location. Species density tends to increase up the altitudinal gradient because higher productivity allows for the survival of species unable to endure the higher water stress at lower elevations (Shreve and Wiggins 1964) and because the less stable soils on mountain slopes increase the mortality of *Larrea tridentata*, restricting its ability to competitively exclude other species (McAuliffe 1994, 1999). Higher individual density tends to increase richness through passive sampling. Locality species richness should increase with elevation and with the density of individuals. The effect of these variables on localities should be stronger at the transect-level since higher richness is likely for a larger sample area, potentially allowing a wider range of values and a higher magnitude response to their effects.

The influence of individual island characteristics on local richness is also assessed in the analysis of locality richness. Multiple richness values for localities across individual islands enable one to investigate whether specific island identity has had significant impacts on the local-scale richness of plant communities. The remnants are separated by appreciable distances and have likely been affected by different ecological conditions through time, such as divergent disturbance regimes or adjacent land-uses, which potentially leads to idiosyncratic histories affecting vegetative character. Figure 1.1 depicts relationships hypothesized to influence species richness at the local-scale.

METHODS

Data sampling

Plant diversity data was recorded in 22 remnant desert habitat islands scattered throughout the Salt River Valley in the Phoenix area (Figure 1.2). All islands consisted of Sonoran Desert habitat, possibly disturbed in the past but never developed, surrounded by residential and commercial land. Most patches are mountainous parks dedicated to preserving natural habitat for recreational uses and conservation. Since Phoenix is a relatively new city, becoming urbanized only after World War II, most islands have been isolated for less than fifty years.

The woody community consisted of a wide variety of shrubs, trees, and cacti. All data were recorded from a system of transects. A transect consisted of five quadrats, each a circle 100 m^2 in area, separated from each other by 20 m edge to edge. The number of individuals identified to species was counted within each quadrat. Transects were stratified by geomorphic type, which includes: slopes facing one of the four cardinal directions, flatlands, and ephemeral washes. Within a geomorphic type, the position of the first quadrat and the transect trajectory were determined randomly.

Data analysis

Local species richness, at the quadrat and transect-level, was determined for each island as the weighted average across geomorphic types of the mean number of species per quadrat or transect based on the proportion of each geomorphic type in an island. All geomorphic types were mapped using ArcView 3.3 (2002) by tracing polygons over digitized aerial photographs (Kenney Aerial Mapping 2000) taken at approximately a one-third meter resolution. A contour map with 10 m intervals, generated using ArcGIS (2002) and derived from the Maricopa County Digital Elevation (DEM) model, was used in conjunction with the aerial photos to aid in interpretation. Reliance on two-dimensional GIS layers alone would distort the relationship between polygons by overemphasizing flatter areas at the expense of steeper slopes. To compensate for this distortion, the three-dimensional surface areas of each polygon were estimated by dividing the two-dimensional area by the cosine of the mean slope for that polygon; the Maricopa DEM was converted into a map of slope values, at 30 m resolution, and the mean was calculated for each polygon. An estimate of each island’s total richness was calculated using the first order jackknife method, as recommended by Palmer (1990, 1991), using EstimateS (Colwell 1999).

Independent variables describing island properties were calculated with a variety of methods. Effective surface area for each island was calculated as the sum of all three-dimensional habitat polygons, excluding areas with major disturbances or recreational facilities. Habitat heterogeneity maps for the islands were generated by combining the geomorphic type maps with a layer depicting soil types (Soil Survey Geographic Database 2002). Habitat diversity for each island was then calculated using the Shannon index (Magurran 1988) using the proportion of total surface area covered by each habitat-soil class. Isolation was calculated as $I = \Sigma\ [\mathrm{Ln(Area)} / (\mathrm{Distance}^2)]$, where distance extended from the edge of the focal island to the edge of other islands or the nearest expanse of outlying desert. For this purpose, the area of the outlying desert was assumed to be 9000 hectares, which is approximately equal to the area of the largest island, South Mountain Park. Mean elevation was calculated by averaging all DEM measurements within each island. The density of individuals for a site was calculated as the mean number of plants per quadrat, regardless of species identity. This provides a means by which to examine whether simply increasing numbers of individuals, apart from other factors, increases the number of species.

Relationships between variables were analyzed with multiple linear regression analysis using SYSTAT 6.1. The independent variables of island area, extent of isolation, and mean density were natural-logarithm transformed in order to linearize the distribution of values, reduce the leverage and influence of a few outlying data points on the regression, and equalize the residuals. Determination of whether local-scale richness was saturating or not with island-wide (regional) richness was accomplished by comparing linear and quadratic regressions. A statistically significant second order term indicates a saturating relationship. For the last analysis testing variable effects on specific sample-units, three small islands, together containing five transects, were excluded from this test since they contained no variation in elevation. An expanded regression model was tested, containing interaction terms between density and elevation as well as island identity and density, but these interactions were not significant and subsequently dropped in the final analysis.

RESULTS

Island-level species richness

Islands varied in size, habitat heterogeneity, density of individuals, elevation, isolation, and species richness (Table 1.1A, B). There was a pronounced species-area effect at the island-level (Table 1.2, Figure 1.3). However, there were no other statistically significant correlations between island-level species richness and the other independent variables describing island characteristics, including isolation, habitat heterogeneity, mean density of individuals, and mean elevation (Table 1.3). Habitat heterogeneity was the only one of these factors approaching significance, though this was likely due to its high correlation with area (Table 1.4).

Local-scale species richness

The area of the entire island had no effect on species richness at the scale of either the quadrat or the transect (Table 1.2, Figures 1.4A, B). Local species richness was significantly correlated with the mean density of individuals at both the level of the quadrat and the transect (Table 1.5). Local richness was significantly related to island-level species richness at the quadrat-level while richness was marginally short of significance (p=0.056) at the transect-level. Thus, while island richness and mean density both influence local richness, passive sampling had a greater effect than island-level richness. Local and island-level richness is related in a linear fashion, indicating a nonsaturating relationship (Table 1.6, Figure 1.5).

With the focus at the level of individual sample-units, local-scale richness is significantly affected at both grains by density of individuals, elevation, and the specific island identity from which samples were obtained (Table 1.7). Thus, even though at least some of the islands were sufficiently idiosyncratic to influence the richness of localities, this was not enough to override effects of elevation and density on the results. Thus, species richness of specific localities rises through passive sampling with denser stands of vegetation and increases with higher productivities associated with gains in elevation along mountain slopes; local-scale species richness is also affected by the ecological history of the site.

Analyses indicated that grain size at the local-scale did affect the influence of some mechanisms. The hypothesis that transect species richness, with the focus on the entire island, would be influenced more strongly by island-level richness and passive sampling was rejected (Table 1.5). Quadrat richness was found to be more closely related to island-level richness than transect richness, while the effect of plant density was comparable between the grains. When the focus corresponded to the individual sample-units, both elevation and density were highly significant, though the relative strengths differed between the grains. For quadrats, density had a slightly stronger relationship with richness than elevation, while transect richness was much more highly correlated with elevation than density.

DISCUSSION

Island-level species richness

Island-level species richness increases with area. In fact, area appears to be the only independent variable significantly correlated with island-level richness. Area potentially affects richness through its influence on the variety of habitat types and the number of individuals occupying a site. The area effect operating on the number of individuals should be particularly strong if density does not vary with island area. Indeed, this appears to be the case, since area and mean density are not correlated at all (r = 0.09; Table 1.4). Consequently, effects on the total number of individuals results from the insular desert plant communities having more area over which to spread rather than from density effects. However, it cannot be ascertained in this study whether island-level richness is primarily influenced by passive sampling or extinction of smaller populations since data in this study represent a single point in time. In order to disentangle these influences, we would need to track species richness over time with decreases indicating extinction.

Island-level richness in this study appears to be also influenced by an area effect inherent to this study system: larger islands tend to support higher and more massive mountains. Thus, there is a strong correlation between island area and maximum elevation ($r = 0.85$). However, since maximum elevation is more strongly correlated with habitat heterogeneity ($r = 0.70$), the two factors cannot be included in the same regression. Mean elevation was not significantly related to island richness, likely because the largest islands contain substantial flatland habitat that smaller mountainous patches lack, which serves to depress mean elevation values. Nonetheless, species richness and elevation are positively correlated, which is supported by the local-scale analysis and observations in the field. The two highest islands, South Mountain Park and the Squaw Peak Recreation Area, support dense and diverse vegetation on their heights, which are replete with species rare or absent at lower elevations.

Habitat heterogeneity, in terms of the variety of soil types and geomorphic features present at a site, did not significantly influence species richness. This is not entirely surprising since Sonoran Desert communities lack a strong mosaic pattern dependent on habitat traits such as soil chemistry (Shreve and Wiggins 1964). Within a climatic zone, species are able to grow wherever moisture conditions are favorable for their survival; this is provided that salinity is not excessive, but salts do not accumulate if there is good drainage from a sloping landscape (Turner and Brown 1982). Apart from moisture gradients associated with elevation, species distributions were not observed to strongly segregate according to geomorphic type, though they do vary in frequency and abundance (Tables 1.8A – H). The degree to which habitat heterogeneity did approach significance ($p = 0.093$) is likely due to its correlation with area.

Isolation was not significantly correlated with island richness. This outcome likely results from the long time lag necessary to bring about change in the woody community. Without catastrophic and widespread disturbance that clears out adult plants, individuals can live for decades or centuries. For example, *Carnegia gigantea* individuals can live up to about two centuries (Pierson and Turner 1998), while *Larrea tridentata* adults on soils stable over geological time are capable of surviving for a thousand years or more (McAuliffe 1994, 1999). Common woody species, *Larrea tridentata*, *Ambrosia deltoidea*, *Encelia farinosa*, and *Lycium berlandieri*, typically persist on average for up to 330, 40, 16, and 211 years, respectively (Bowers 2005). This is not to imply that fluctuations in the woody vegetation are absent over long intervals. Goldberg and Turner (1986) reported that over a 72-year period on permanent Sonoran

Desert plots, there were shifts in abundance and vegetative cover. However, there was no evidence of consistent, directional change and the relative cover of dominants was relatively constant over that period.

Seedling survivorship is typically low in the desert and depends on favorable climatic conditions throughout the growing season. First year survival for *Parkinsonia microphylla* seedlings on permanent plots on Tumamoc Hill, Tucson, Arizona was 1.7%, with only 2 of 1008 seedlings enduring beyond the first year (Bowers and Turner 2002). Bowers et al. (2004) reported that, averaged across 15 perennial species, first year survival of seedlings was 3.7% with only 0.1% persisting for four years with first year survival rate increasing with higher rainfall. Wetter conditions generally increase *Carnegia gigantea* recruitment, though long term population fluctuations are also dependent on other factors (Pierson and Turner 1998). Thus, even when a propagule is successfully conveyed between habitat islands, individual survival is unlikely. The immigrant propagule must also compete with more numerous seeds spread proximally from within the island. Immigration is not impossible in the time since the valley has urbanized, though odds of success are long without catastrophic disturbances.

Fire can bring about extensive disturbance and great change in Sonoran Desert woody communities (Cave and Patten 1984, Schmid and Rogers 1988, McAuliffe 1995). Intense wildfires can replace diverse communities with almost monotypic stands of *Encelia farinosa*; where heat intensity is more moderate, resprouting of some woody species is possible, though with higher coverage of exposed soil. Currently, there are limited areas in the remnant islands that have been burned, and unburned areas now are far more extensive than scorched areas. Propagule flow from unburned areas should greatly exceed immigration from more distant sources on other islands. This is not to imply that unburned sites are pristine. Cattle grazing was extensive in 19th century Arizona (Bahre and Shelton 1993), but all sites were presumably affected and this disturbance has ceased in recent decades.

While it is unlikely that migration of species would have significantly impacted vegetation character over the relatively short time that urbanization has fragmented the remnants, higher elevation communities would have functioned to some degree as islands even before settlement. Though these habitats had not extended throughout the Salt River Valley in a continuous expanse, propagule flows between mountain tops would have been possible over millennia. Most plant species occurring in upper Sonoran habitats are dispersed by animal vectors, and wind dispersed species are uncommon where vegetative cover is high (Drezner et al. 2001), as it often is at higher elevations. Some species would have been more affected by isolation than others; certainly those species dispersed by birds or larger mammals would have had a higher migration rate than taxa transported by smaller vectors, such as rodents or ants. Before the plains were developed, numerous washes could have acted as corridors to facilitate vector migration. It is currently unknown how pre-settlement dispersal rates would differ from those of the present day, where people or city dwelling birds may act as vectors.

Local-scale species richness

There was no statistically significant relationship for local-scale richness as island area increased. However, local-scale richness at the quadrat-level is significantly influenced by island-level richness, and the influence at the transect-level is marginally short of significance (p = 0.056; Table 1.5). Thus, while area is significantly correlated with island richness and island richness is correlated with local richness, area does not significantly influence local richness. This result likely arises from an accumulation of stochastic variation across the two relationships.

Local species richness increases through density effects more significantly than through the effects of island richness (Table 1.5). Species-poor islands tend to be dominated by taxa that are more common, either because they are more resilient, their larger populations buffer them from extinction, or their higher abundance and frequency makes them more likely to be observed through passive sampling. This tendency can lead to nestedness, in which the taxa in species poor sites form subsets of the species list observed in progressively richer sites, which was observed in this study system (Chapter 2). The rarer species that augment a richer island are less likely to be captured in a given sample. Increases in density allow for a wider sampling of common species well mixed in the community and an increase in richness, which exceeds the benefit of higher island richness since the probability of observing rare species in a locality is lower than that of common taxa.

An intriguing difference for the species-area effect at the local-scale is the tighter association between species and area for the smaller quadrat samples than for transects. The plot for transects shows a cloud of points, while that for quadrats has a tighter pattern, particularly if it were not for three outlying data points (Figures 1.3A, B). The point in the lower center of the plot is Papago Park, which is a moderately-sized island with ravaged vegetation. The two data points in the upper left corner are Twin Buttes and Falcon Hill, which are particularly diverse parcels for their size; this higher richness likely results from the fact that the two sites sit on plains in the eastern Salt River Valley that are more elevated than most other sites. Without these more unusual cases, quadrat richness would have likely attained significance. These idiosyncratic sites are also responsible for the significant effect of island identity on local-scale richness, as was observed with the focus at specific localities (Table 1.7).

The probable explanation for why the smaller grain would show an area effect the other lacks involves how the woody species and individuals are dispersed throughout their habitats. As the quadrat represents an expanded single point, enumeration of species represents the α (or point) diversity of that locality; since a transect contains five quadrats scattered over the terrain, its enumeration consists of a mixture of α and β diversity, which describes the turnover of species across space. If a community loses individuals in a nonselective and nonlocalized fashion, such as through environmental stress or disturbance, species abundance drops before extinction occurs. This decrease in abundance should lower α diversity, as uncommon species are less likely to be captured in a single quadrat. However, β diversity may rise as a result of the increasing mean distance between individuals. Thus, species lists for each of the five component quadrats composing a transect increasingly diverge. This increase in β diversity can buffer the effect of decreasing α diversity so that transects can retain a constant richness even while component quadrats are losing richness. This effect would be the same if the mechanism was an increase in richness through colonization.

This incorporation of β diversity in transects also likely accounts for differences in the relative magnitude of influence for elevation and density in specific sample locations. Increasing plant density serves to raise richness at the quadrat-level by increasing the propensity of passive sampling to increase α diversity. However, at the transect-level, β diversity is able to compensate somewhat for transects at lower densities by sampling across localized patches of vegetation and subtle changes in habitat, enabling more species to be observed. Also, analogous to the accumulation pattern inherent to the species-area effect, the rate of increase in species richness as more individuals are observed is higher among smaller than larger collections. In other words, the slope decreases along the species-individuals curve, though the location of this decrease depends on the characteristics of the curve and whether it follows a sigmoid or convex function (Tjorve 2003).

Relationship between local and island-level richness

As was found in most other studies (Caley and Schluter 1997, Cornell 1999, Lawton 1999, Srivastava 1999), positive monotonic relationships between local and regional (in this case, island-level) richness predominate in this system. This indicates that woody plant communities in the islands at the local-scale are unsaturated with species.

While it cannot be assumed that desert plant communities are non-interactive on the basis of an unsaturated local-regional relationship, there are other reasons to surmise that communities in these sites are weakly interactive in terms of species-specific interactions. While the Sonoran desert is more productive than other arid lands, the lower productivity of deserts compared to other biomes means that a small amount of litter is deposited on the soil. Most of what is dropped is either consumed by termites or, owing to the low vegetative coverage, transported by surface water flow away from its original site (Shreve and Wiggins 1964). Together with the arid conditions dominating for most of the year, there is limited opportunity for a plant to enrich the soil below it and facilitate the growth of later successional species. Thus, there is much less modification of the soil environment by vegetation than is present in other biomes, and species may grow anywhere where moisture and salinity levels permit their survival.

Nurse plant relationships can increase a plant's survivorship, whereby seedling survivorship is higher under a nurse plant canopy due to reduction of light, heat, and wind and an increase in relative humidity in the summer (Kotzen 2003). For example, shade cast by *Olneya tesota* canopies lowers soil surface and cactus stem temperatures compared with open spaces (Suzan et al. 1996). Larger canopies permit growth of larger perennial species (Tewksbury and Lloyd 2001). Additionally, density of arbuscular-mycorrhizae fungi, which alleviate drought and nutrient stress in plants, tends to be higher under canopies (Carillo-Garcia et al. 1999). However, neither the nurse plant nor the seedling is necessarily species specific. As long as a species provides adequate shade and is sufficiently abundant, it may provide a nurse plant role in the community.

Larrea tridentata is one species that can interact strongly with other species and potentially create a saturated condition by hindering establishment of other plants. However, *Larrea*'s superior competitive ability against other species and its capability to exclude them is dependent on a substrate that is very stable throughout geological time. Eroding or aggrading surfaces disrupt its ability to reduce soil water down to levels that prevent colonization by other species (McAuliffe 1994, 1999). *Larrea* cannot dominate a mountain slope simply through water competition because it has a very slow growth rate and the soil fluctuates too quickly over time. Plains within study sites are proximal to mountains and thus receive too much alluvium compared to plains dominating other regions of the Sonoran desert. It is true that one may observe communities dominated or monotypic with *Larrea* in limited areas at these sites, but this scarcity is likely due to disturbance at some time in the past, either from past cattle grazing or human-caused trampling. While *Larrea* is threatened by root exposure or excessive burial over geological time scales (McAuliffe 1994, 1999), it is at the same time very stress tolerant (Gardner 1951, Reynolds 1986, Whitford et al. 2001).

CAP-LTER Study Area

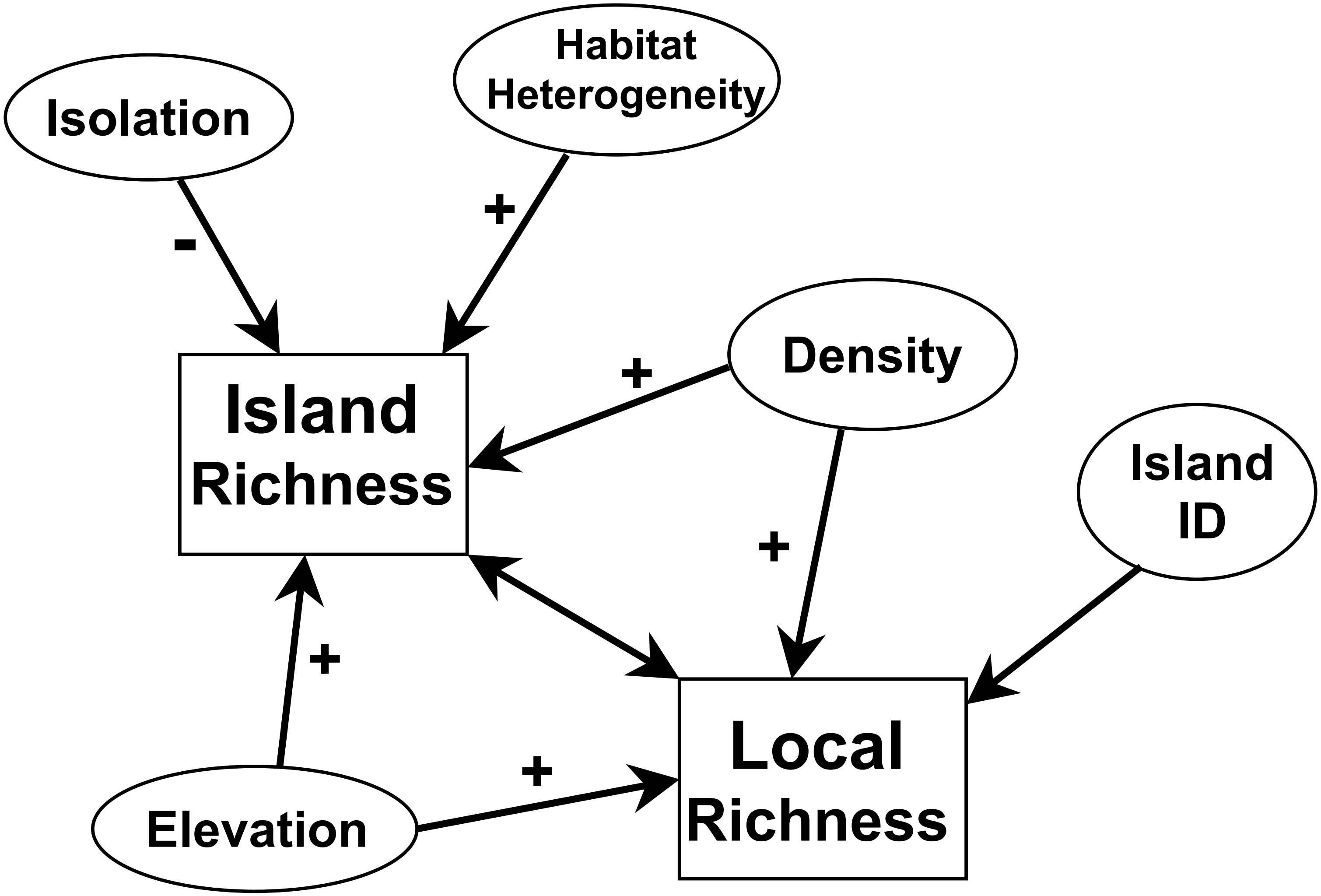
The CAP-LTER study area, centered on metropolitan Phoenix, offers natural vegetation conditions not present, at least in similar degree, to plant communities further from major urban centers. In central Phoenix, the urban heat island effect increases mean daytime temperatures by 3.1 ^{o} C and raises minimum nocturnal temperatures by 5 ^{o} C (Baker et al. 2002). Especially in smaller remnants, this potentially increases heat stress on plants. The city's atmosphere forms a CO^2 dome with levels over the urban center as much as 50% greater than in outlying areas away from the city (Koerner and Klopatek 2002). Since more nitrogen enters than exits the urban system, there is an estimated accumulation of 21 Gg per year (Baker et al. 2001). Studies of lichens collected throughout Maricopa County indicate that elemental concentrations of Zn, Cu, Pb, and Cd have risen in the Phoenix metropolitan area over the last 30 years (Zschau et al. 2003). Additionally, there have been changes in the consumer and predator populations throughout the city (Faeth et al. 2005). Many species of vertebrates have been reduced in abundance on remnant islands and are at risk of local extinction (Sullivan and Flowers 1998). Also, resource subsidies available in the urban matrix have decreased annual and seasonal variations in arthropod species diversity and increased the abundances of some populations (Faeth et al. 2005). The herbivorous arthropod community, which had previously been limited by resource fluctuations, exists in greater abundance and is now primarily controlled by avian predation.

The broad expanse of urban land covers in the Phoenix metropolitan area has created novel vegetative assemblages not present prior to urbanization (Hope et al. 2003, Martin et al. 2004, Kinzig et al. 2005). These plants are usually introduced to an area and maintained by artificial application of water and nutrients. Vegetation characteristics are generally determined by sociological, economic, and cultural factors. For example, species richness of neighborhood assemblages is positively correlated to the socioeconomic status of the neighborhood. Vegetation abundance in neighborhoods also tends to increase along with the median year of neighborhood development so that denser assemblages were found in more recently built residential areas. Furthermore, local generic richness of urban land covers is comparable to desert sites but compositional turnover is greater in the former. Generic richness increases with elevation in the urban matrix, as it does in undeveloped desert, though this is due to higher elevations being occupied by wealthier households.

Conclusion

The species-area relationship is scale-dependent since it is strongly manifested at the island-level but not at the local-scale. Island-level species richness, while positively correlated with area, is not significantly related to the other independent variables. Local richness is influenced by the island-scale variables, island-level richness and island identity, as well as local-scale factors, specific elevation of the locality and density of individuals. Isolation, the only between-island scale variable tested, did not influence species richness of woody vegetation. Thus, local richness is significantly affected by the size of the island species pool, passive sampling, productivity, and the ecological history of the site. Local and island richness were significantly related in a positive monotonic fashion, indicating that woody communities are unsaturated. Figure 1.6 shows significant relationships between variables that were confirmed by this study. A major open question regards how strong extinction is in this system compared to the past. It is possible that islands are still relaxing toward sustainable assemblages, or that most species found in small islands are resistant to stressors and are capable of persisting indefinitely.

Figure 1.1: Flow chart of hypothesized influences on local and island-level species richness.



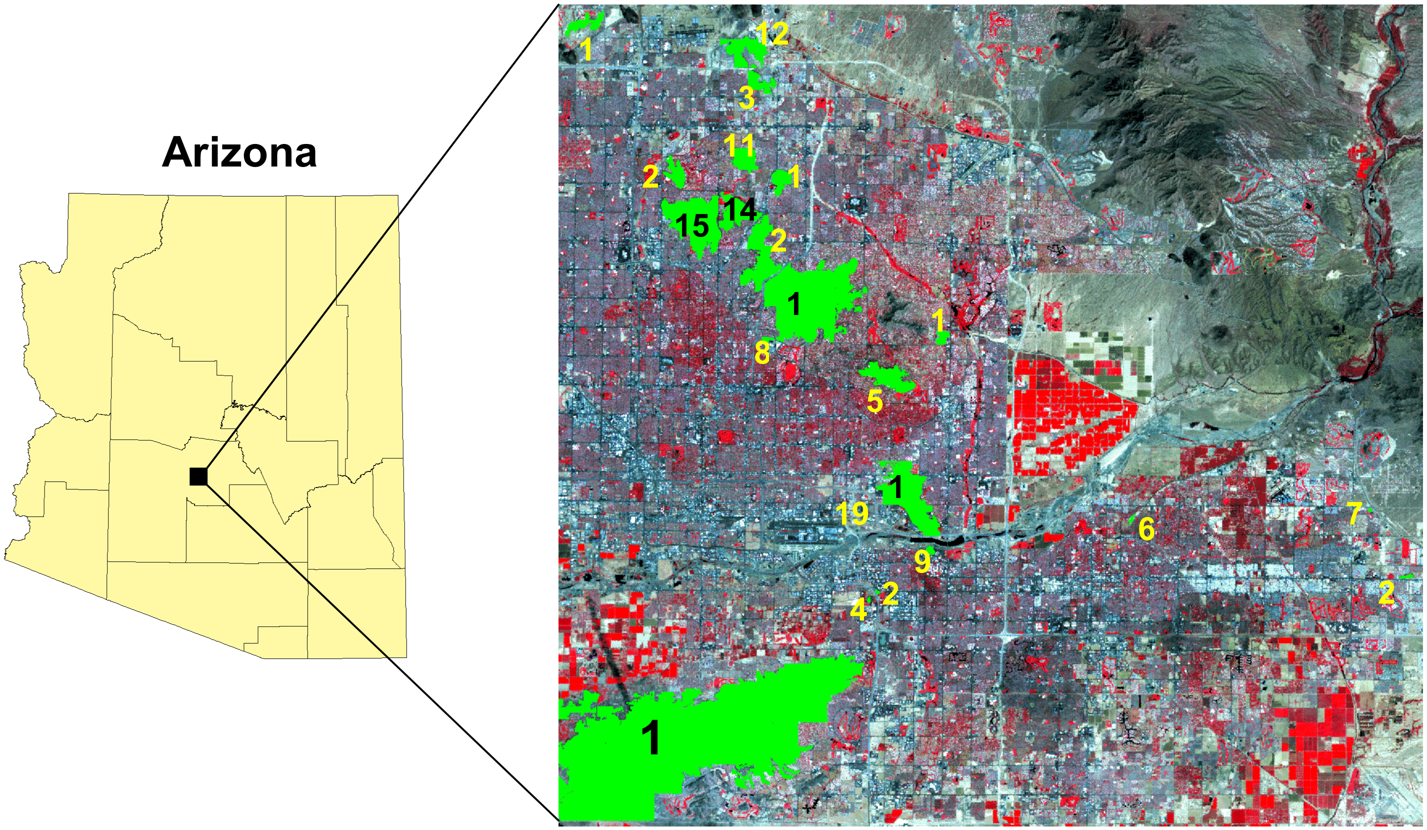


Figure 1. The locations of study sites within the Phoenix metropolitan area. Sites are identified as: 1. Adobe Dam Recreation Area, 2. Broadway Butte, 3. Buffalo Ridge Park, 4. Buttes Resort, 5. Camelback Mountain, 6. Park of Canals, 7. Falcon Hill, 8. Granada Park, 9. Hayden Butte, 10. Lincoln Avenue patch, 11. Lookout Mountain, 12. Outer Union patch, 13. Papago Park, 14. Phoenix Mountain Preserve East, 15. Phoenix Mountain Preserve West, 16. Shadow Mountain, 17. South Mountain Park, 18. Squaw Peak Recreation Area, 19. Tempe Salt Bush patch (currently developed), 20. Thunderbird Avenue Butte, 21. Twin Buttes, and 22. West Squaw patch.

Table 1.1A. Values for dependent variables. Quadrat and transect species richness were calculated as weighted averages based on mean richness per habitat type and proportion of island area covered by each habitat. Island species richness was estimated using the first-order jackknife method.

Site ID	Quadrat Species Richness	Transect Species Richness	Island Species Richness
1	3.7	7.5	25.9
2	2.7	6.1	9.8
3	3.8	7.6	22.0
4	2.8	4.8	8.0
5	4.2	7.5	28.0
6	1.7	3.1	12.7
7	4.7	7.5	13.7
8	3.3	7.5	24.6
9	2.6	5.8	23.8
10	1.2	2.0	7.0
11	2.7	4.5	14.0
12	3.3	5.9	29.9
13	2.0	3.2	25.0
14	3.4	5.7	23.0
15	4.1	6.9	27.9
16	3.5	5.8	27.9
17	4.2	8.3	37.0
18	4.1	7.2	30.0
19	2.4	6.0	8.4
20	3.3	6.4	15.9
21	4.4	8.2	16.0
22	3.7	6.3	30.0

Table 1.1B. Values for independent variables in the study sites.

Site ID	Island Area (hectares)	Isolation	Mean Elevation	Mean Density (quadrat)	Habitat Heterogeneity
1	105.3	1.9	419	114.5	2.0
2	4.7	11.5	369	21.9	0.7
3	94.0	559.3	472	26.8	2.2
4	4.8	11.5	371	19.3	1.6
5	256.5	5.3	553	18.7	1.5
6	8.8	0.5	382	10.5	1.2
7	4.2	1.4	474	37.3	1.3
8	10.5	1170.0	387	17.5	0.02
9	19.2	24.6	384	16.1	1.6
10	42.6	17.6	399	7.4	0.8
11	151.9	17.0	486	22.2	2.8
12	258.2	1878.0	478	26.7	2.6
13	368.7	14.6	385	9.9	2.0
14	255.5	1985.6	461	42.5	2.6
15	710.6	881.0	471	33.6	2.3
16	103.7	20.2	488	35.8	1.9
17	8764.8	2.7	487	21.8	3.4
18	1725.2	1326.9	508	27.8	2.6
19	2.2	10.7	352	21.6	0.9
20	80.0	16.7	441	22.3	1.4
21	12.1	0.5	475	51.9	0.9
22	441.7	2039.8	467	22.1	2.9

Table 1.2. Relationship between Ln(area) and species richness at the local (quadrat and transect) and island-level scales (n = 22).

Variable	Standardized Coefficient	P	R^2
I. Island-Level			
Ln (Area)	0.809	0.00001	0.637
II. Quadrat-level			
Ln (Area)	0.338	0.123	0.070
III. Transect-level			
Ln (Area)	0.190	0.396	0.000

Figure 1.3. The relationship between island area and island-level species richness.

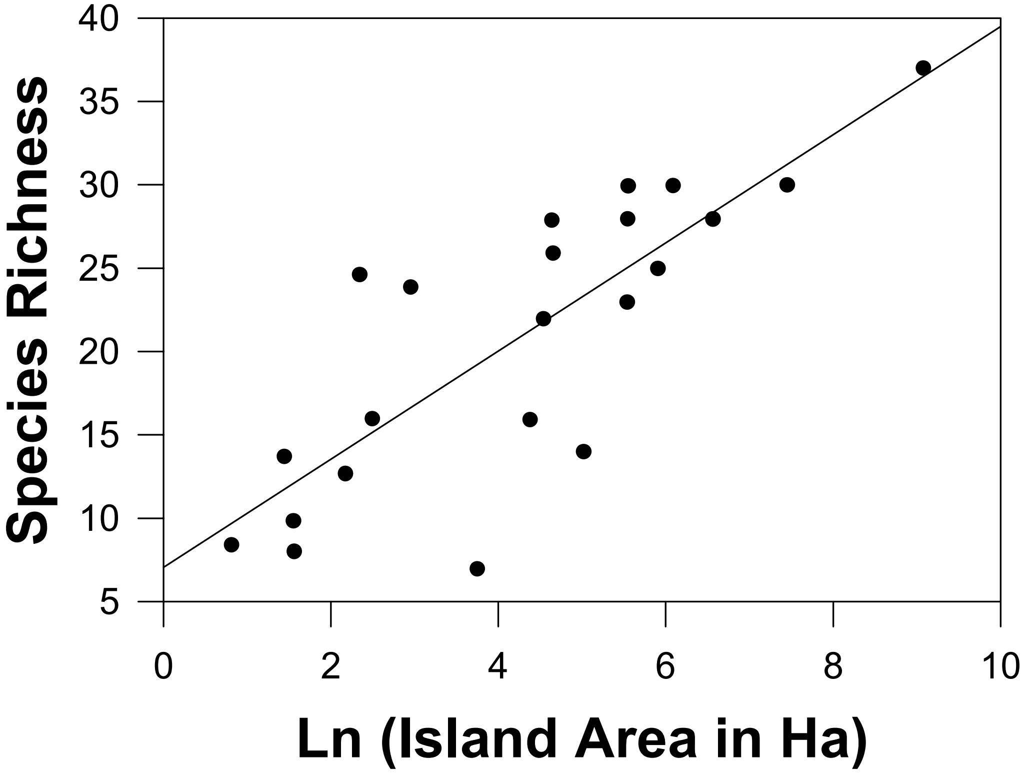


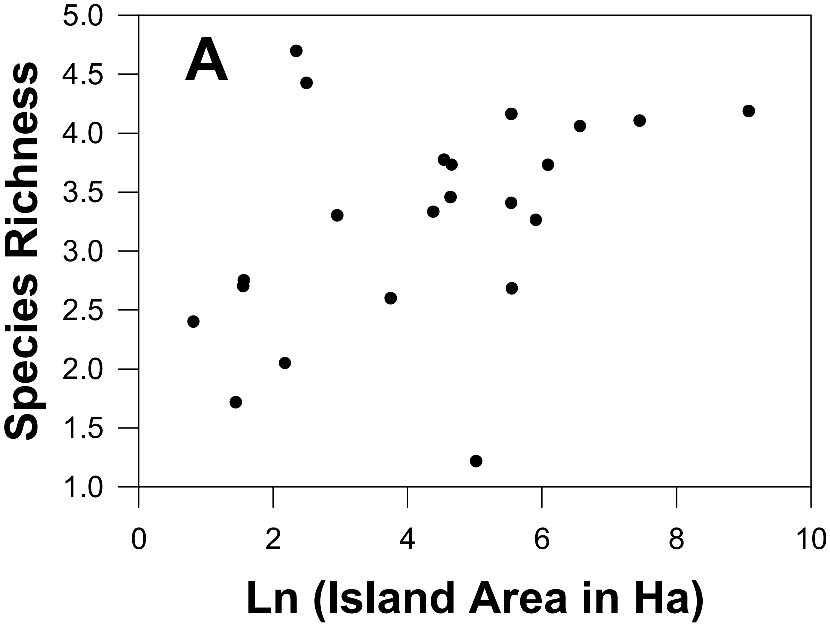
Table 1.3. Analysis of hypothesized contributors to island-level species richness (n = 22). $R^2 = 0.421$.

Variable	Standardized Coefficient	P
Ln(isolation)	0.238	0.196
Ln(mean density)	0.068	0.708
Habitat heterogeneity	0.369	0.093
Mean elevation	0.308	0.156

Table 1.4. Pearson correlation matrix of island characteristics (n = 22).

	Ln (isolation)	Ln (mean density)	Mean elevation	Habitat heterogeneity
Ln (area)	0.386	0.094	0.639	0.812
Ln (isolation)		0.011	0.191	0.335
Ln (mean density)			0.365	0.239
Mean elevation				0.547

Figure 1.4. The relationship between island area and species richness at the scale of quadrats (A) and transects (B).



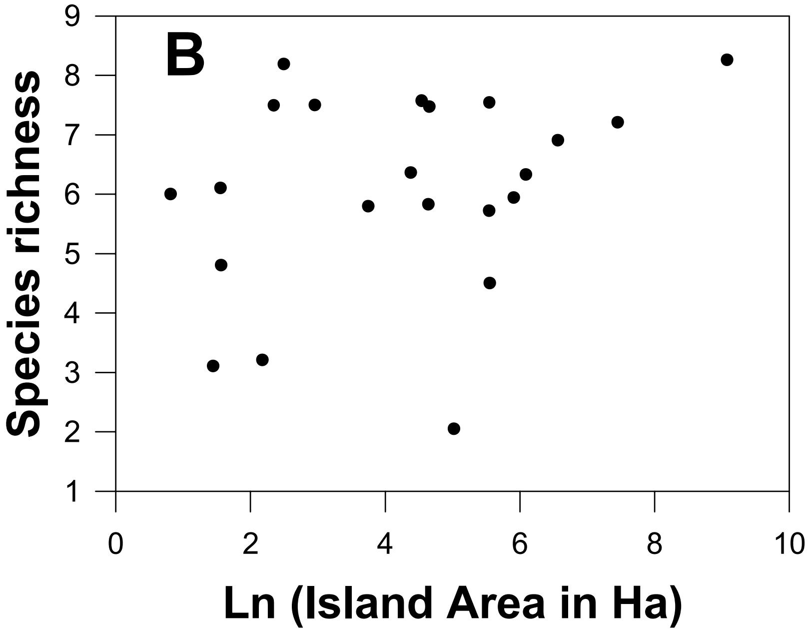


Table 1.5. Analysis of factors affecting local-scale woody species richness, aggregated and averaged across each island (n = 22). $R^2 = 0.585$ and 0.507, respectively.

Variable	Standardized Coefficient	P
I. Quadrat-level		
Island species richness	0.374	0.019
Ln (mean density)	0.602	0.001
II. Transect-level		
Island species richness	0.324	0.056
Ln (mean density)	0.588	0.002

Table 1.6. Significance of the second-order term in quadratic regressions of the relationship between local and island-level species richness (n = 22). R^2 = 0.234 and 0.161, respectively.

Variable	Coefficient	Standard error	P
I. Quadrat-level	-0.002	0.003	0.493
II. Transect-level	-0.002	0.005	0.677

Figure 1.5. Relationship between local and island-level species richness. A. Quadrat-level. B. Transect-level.

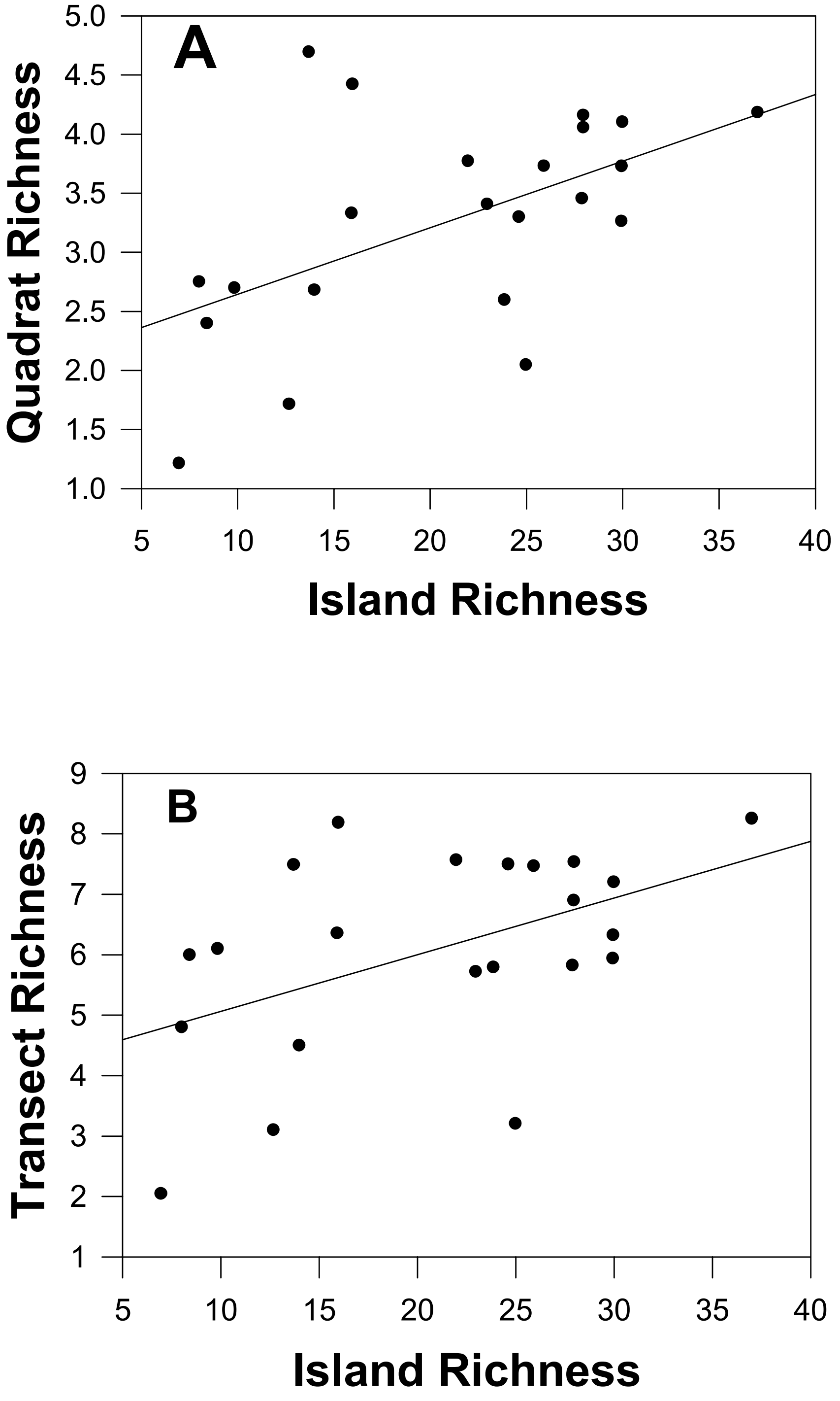


Table 1.7. Regression analysis assessing hypothesized contributors to species richness at the local-scale, at two sample grains (n = 363). Quadrat-level richness was calculated as the mean quadrat richness for each transect. Transect-level richness was the total species observed per transect. The full model was tested, but interaction terms were not significant and were dropped in subsequent analysis. $R^2 = 0.527$ and 0.455, respectively.

Variables	df	F	P
I. Quadrat-level			
Elevation	1	64.961	0.0001
Ln (density)	1	79.769	0.0001
Island ID	18	3.843	0.0001
II. Transect-level			
Elevation	1	71.329	0.0001
Ln (density)	1	15.700	0.0001
Island ID	18	5.660	0.0001

Table 1.8A. Correlations between species abundances occupying different geomorphic types. *Larrea tridentata* correlations are shown in the upper right corner; *Lycium* sp. correlations are shown in the lower left corner.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	0.65	0.76	0.92	0.46	0.11
South facing slope	0.42	--	0.88	0.82	0.62	0.004
East facing slope	0.79	-0.08	--	0.75	0.51	0.33
West facing slope	0.33	0.36	0.33	--	0.54	0.03
Flatland	0.69	0.22	0.77	0.45	--	0.47
Wash	0.60	0.46	0.50	0.94	0.58	--

Table 1.8B. Correlations between species abundances occupying different geomorphic types. *Encelia farinosa* correlations are shown in the upper right corner; *Opuntia acanthocarpa* correlations are shown in the lower left corner.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	0.09	0.32	0.39	-0.23	0.55
South facing slope	0.33	--	0.70	0.71	0.66	0.65
East facing slope	0.45	0.83	--	0.70	0.66	0.37
West facing slope	0.57	0.80	0.83	--	0.57	0.80
Flatland	0.24	0.42	0.60	0.44	--	-0.20
Wash	0.82	0.60	0.36	0.63	0.19	--

Table 1.8C. Correlations between species abundances occupying different geomorphic types. This matrix contains correlations for *Ambrosia deltoidea*.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	0.62	0.35	0.79	0.38	0.78
South facing slope		--	0.48	0.48	0.67	0.64
East facing slope			--	0.54	-0.06	0.23
West facing slope				--	0.74	0.46
Flatland					--	0.40
Wash						--

Table 1.8D. Correlations between species abundances occupying different geomorphic types. *Hyptis emoryi* correlations are shown in the upper right corner; *Bebbia juncea* correlations are shown in the lower left corner. Comparisons indicated by dashes had too few values in common to permit calculation of correlations.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	-0.08	0.95	0.86	0.30	0.14
South facing slope	0.13	--	-0.004	-0.14	-0.22	0.77
East facing slope	-0.02	--	--	0.87	0.3	0.34
West facing slope	--	--	--	--	-0.14	--
Flatland	--	--	--	--	--	0.18
Wash	0.22	--	0.88	--	0.88	--

Table 1.8E. Correlations between species abundances occupying different geomorphic types. *Ephedra fasciculata* correlations are shown in the upper right corner; *Carnegia gigantea* correlations are shown in the lower left corner. Comparisons indicated by dashes had too few values in common to permit calculation of correlations.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	--	-0.13	0.55	0.25	0.09
South facing slope	-0.005	--	--	--	--	--
East facing slope	-0.04	-0.04	--	-0.12	-0.16	0.18
West facing slope	0.71	0.34	-0.09	--	-0.13	0.31
Flatland	0.27	0.39	0.20	0.24	--	-0.14
Wash	-0.01	0.9	-0.10	0.54	--	--

Table 1.8F. Correlations between species abundances occupying different geomorphic types. *Eriogonum fasciculatum* correlations are shown in the upper right corner; *Fouquieria splendens* correlations are shown in the lower left corner. Comparisons indicated by dashes had too few values in common to permit calculation of correlations.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	--	0.26	0.21	--	0.09
South facing slope	0.38	--	--	--	--	--
East facing slope	0.83	0.22	--	0.34	--	-0.14
West facing slope	0.80	0.24	0.82	--	--	-0.10
Flatland	0.85	0.85	0.60	0.73	--	--
Wash	0.91	0.91	0.76	0.91	0.92	--

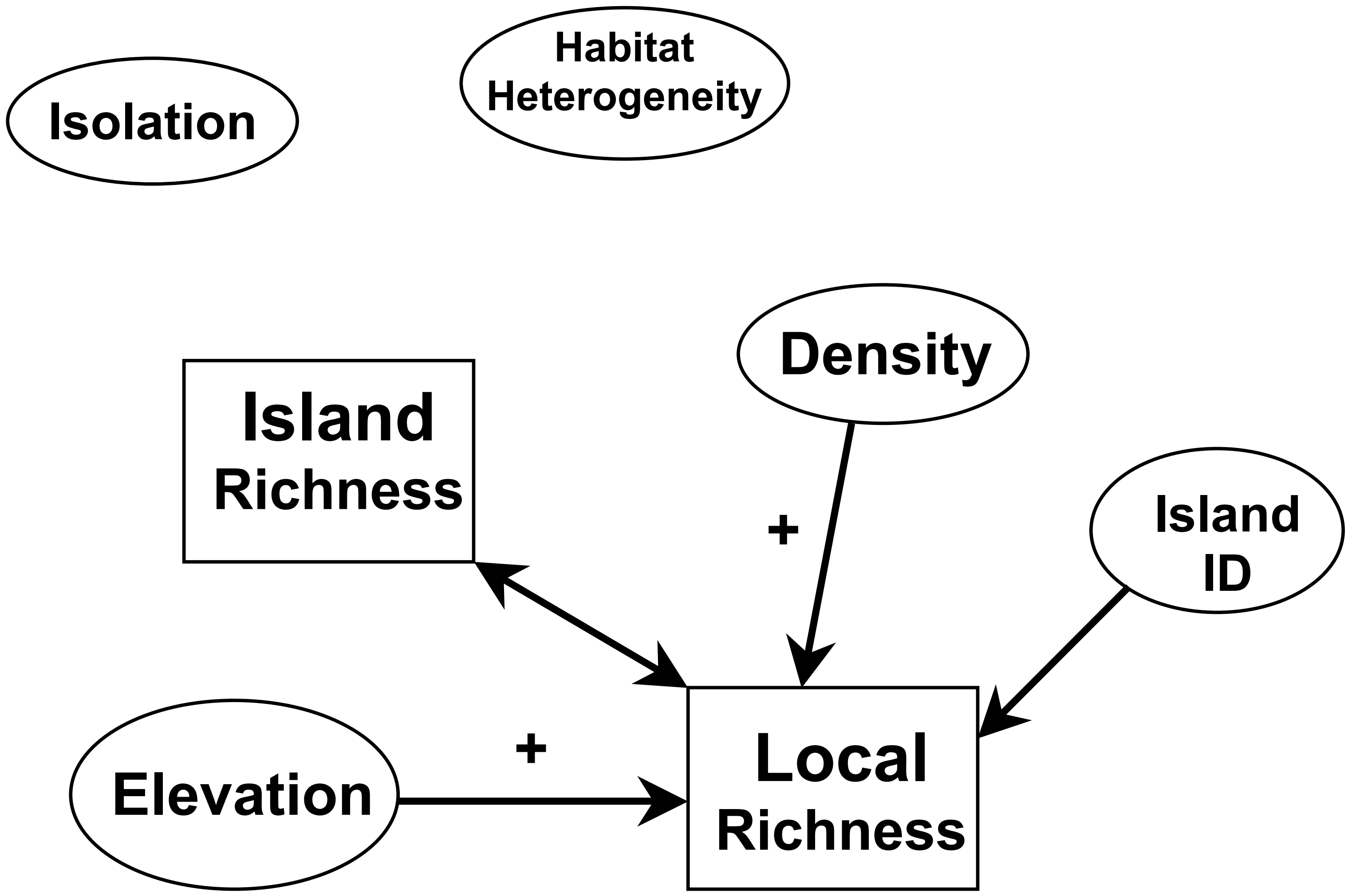
Table 1.8G. Correlations between species abundances occupying different geomorphic types. *Baccharis sarothroides* correlations are shown in the upper right corner; *Olneya tesota* correlations are shown in the lower left corner. Comparisons indicated by dashes had too few values in common to permit calculation of correlations.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	--	--	--	--	0.60
South facing slope	0.18	--	--	--	--	--
East facing slope	--	--	--	--	--	--
West facing slope	--	--	--	--	--	--
Flatland	0.86	0.62	--	--	--	0.10
Wash	0.74	0.61	--	--	0.70	--

Table 1.8H. Correlations between species abundances occupying different geomorphic types. This matrix contains correlations for *Prosopsis velutina*. Comparisons indicated by dashes had too few values in common to permit calculation of correlations.

	North Facing Slope	South F.S.	East F.S.	West F.S.	Flatland	Wash
North facing slope	--	-0.11	0.64	--	--	0.42
South facing slope		--	-0.1	--	--	-0.19
East facing slope			--	--	--	-0.19
West facing slope				--	--	--
Flatland					--	0.59
Wash						--

Figure 1.6. Significant relationships between local and island-level species richness and independent variables.



Chapter 2. NESTEDNESS OF REMNANT SONORAN DESERT PLANT COMMUNITIES IN THE PHOENIX METROPOLITAN AREA

ABSTRACT

A dataset describing species composition for a group of sites exhibits a nested pattern if species composing progressively richer assemblages form a series of subsets. Nestedness can form as a result of the dynamic processes of extinction or colonization; it can also reflect a nested distribution of habitats among the sites or the differential abundance properties of species through passive sampling. This study investigates whether Sonoran Desert vegetation in remnant habitat islands within metropolitan Phoenix is nested, and explores which mechanisms are responsible for the pattern. Both the woody and herbaceous communities were significantly nested. Nestedness in woody vegetation arises as a consequence of an aggregate response of constituent species to multiple mechanisms, and is manifest at the island and habitat-levels. Nestedness in herbaceous communities arises from an area effect, involving either extinction or passive sampling, and is reinforced by colonization of exotic species.

INTRODUCTION

Because of the prevalence of development and landscape change in modern society, natural habitats often consist of discrete, disconnected remnants surrounded by an inhospitable matrix. Owing to their widespread frequency and bounded insularity, understanding how communities in this fragmented landscape are composed is an important goal of resource conservation and ecological theory. Most analyses of landscape fragmentation focus on changes in species richness (e.g. Levenson 1981, Scanlan 1981, Simberloff and Gotelli 1984, Dzwonko and Loster 1988, Hobbs 1988, Soule et al. 1992, Drayton and Primack 1996). However, studying composition, in which attention is paid to species identities rather than their simple numbers, illuminates system features unapparent to analyses of richness alone. Richness data can reveal that species have been lost, but one must examine composition data to know how or why a system loses species. Nestedness analysis can potentially indicate which phenomena structure communities and whether certain species in a fragmented system are susceptible or resistant to colonization or extinction processes. This study considers whether desert habitat islands embedded within the urban matrix of the Phoenix metropolitan area exhibit a nested pattern, and what mechanisms may be primarily responsible for that pattern.

Nestedness theory

A dataset exhibits a nested pattern if species found in progressively richer assemblages form a series of subsets (Patterson 1987, Atmar and Patterson

1993). Perfect nestedness means that all species observed in depauperate sites will be found in all richer locations. While perfect nestedness is very rare in nature, the degree to which nestedness is discernible from random variation in empirical datasets can be measured and significance assessed based on Monte Carlo simulations. Nestedness is present as long as three conditions are satisfied: species possess a shared biogeographical history, habitats are somewhat comparable, and species are hierarchical in distribution and frequency (Patterson and Brown 1991). Since nestedness refers to a condition of ordered composition, any factor that serves to infuse heterogeneity into a dataset will reduce the propensity for nestedness (Mikkelson 1993, Wright et al. 1998). As such, the first two conditions serve as homogeneity constraints on sites and species; the third condition acts as a filter and reflects the factors that lead species to have variable incidences (Wright et al. 1998).

There are several hypotheses regarding the causes of nestedness (Patterson 1987, Cutler 1994, Wright et al. 1998). Darlington (1957) first recognized a nested pattern among oceanic archipelagos and attributed this to the differential colonization of islands by species. Since vagilities differ among species, more isolated islands would only contain those taxa capable of long-distance dispersal over the ocean or an otherwise inhospitable matrix. Extinction of species could also produce nested communities if vulnerability to population collapse differs among species. The area of available habitat acts to constrain population size by dictating an approximate maximum number of individuals capable of being supported on an island (Preston 1962). Small populations are more vulnerable to stochastic extinction events (MacArthur and Wilson 1967).

While colonization and extinction imply the dynamic processes of assembly and disassembly, nestedness can reflect other underlying ecological patterns. Sites differing in habitat heterogeneity can form nested subsets if less common habitats support taxa specific to those habitats (Worthen 1996). Thus, sites containing common and rare habitat types may contain both habitat generalists and specialists, while more homogeneous sites would only contain generalist species. Finally, when species consistently differ in their relative commonness and rarity without regard to habitat (Preston 1962), they can form nested assemblages since common species simply have a higher probability of occupying any given site via passive sampling (Connor and McCoy 1979). These potential mechanisms are probabilistic filters (Wright et al. 1998): habitat nestedness acts to filter habitats, passive sampling is an abundance filter, and isolation and area filters reflect the tendencies for species to differ in their colonization or extinction behavior, respectively. Circumstances over space and time determine whether one or more filters will produce a consistent ordering of species across sites and a nested structure.

The difficulty is how to distinguish which of those filters are primarily responsible for an observed nestedness pattern. The ecological context of an archipelago can be considered as a simple a priori indication of which dynamic process is potentially operating. Archipelagos representing contracted remnants of a formerly continuous environment supporting shared species, such as landbridge islands and fragmented landscapes (Patterson 1987), should develop a nested pattern resulting from differential extinction rates between taxa. On the other hand, oceanic islands formed in isolation from other land masses should exhibit nestedness primarily as a result of colonization. This is not to imply that a process would be completely absent from either type of archipelago, only that the minor mechanism's influence is secondary and likely insignficant. Extinction on oceanic islands would not lead to nestedness because these islands lack a common history and, as a result of endemism, likely contain many unshared species. Colonization would not predominate on remnant islands since communities would likely be oversaturated and moving towards more sustainable, less species rich assemblages, particularly if little time has passed since fragmentation.

Multiple conjectures have been made about how nestedness scores or matrix arrangements can be used to distinguish hypotheses. For example, some have argued that extinction dominated systems should be more nested than those where colonization predominates or where the two processes are equivalent (Patterson and Atmar 1986, Patterson 1987, 1990, Wright and Reeves 1992, Cutler 1994) since an extinction-driven hierarchy is free of the stochasticity of migration. Cutler (1991, 1994) suggested that nested patterns derived from extinction processes would have a hole-rich matrix, containing many unexpected absences, whereas passive sampling would produce an outlier-rich matrix.

However, there is no strong indication, whether through theoretical deduction or empirical demonstration, that different mechanisms would produce fundamentally different nestedness scores (Simberloff and Martin 1991). Comparison of scores may illuminate system properties, but it provides little ability to distinguish between alternative mechanisms. A more promising approach is to analyze the rank-order correlation between the nested order of sites and candidate independent variables (Lomolino 1996). Significant correlations between the nested order of sites and isolation distance or area could indicate the influence of colonization and extinction, respectively, under two fundamental assumptions of island biogeography theory (MacArthur and Wilson 1967): extinction probability declines with increasing area and the likelihood of immigration decreases with greater isolation (Lomolino 1996).

However, since area would affect the total number of individuals present on a remnant island, evidence of an area effect could result from either stochastic extinction of smaller populations or the passive sampling of additional species (Coleman 1981, Coleman et al. 1982, Scheiner 2003). Species differ in relative abundance even within a locality so that smaller collections of individuals will likely be dominated by common species. The probability of including rare species increases as more individuals are included in a sample or community, thus passively sampling more species. Therefore, evidence of an area effect alone cannot disentangle extinction from passive sampling. The most convincing evidence of extinction at the island-level would arise from the demonstration of declines in species richness or the loss of specific taxa over time, which is not available for this study.

Habitat diversity is potentially an important driver of species composition. This relationship is strengthened when at least some species have specific habitat affinities. Therefore, sites containing a plurality of dissimilar habitat types will be more likely to contain rarer habitat types and harbor species specialized to those unique environmental conditions. Sites with low habitat diversity are likely dominated by common habitats containing common species. Thus, significant correlations between habitat heterogeneity and nestedness indicate that having more habitats increases the chance of encountering species not present in more homogeneous sites. If area and habitat heterogeneity are positively correlated, as is often the case, a test for how the total number of individuals affects nestedness, through either extinction or passive sampling effects, would be redundant with habitat heterogeneity. Testing with density of individuals would potentially offer a means by which to gauge the effects of extinction or passive sampling without the area effect.

Elevation has a strong effect on the composition of Sonoran vegetation with greater species richness and vegetative groundcover at higher elevations (Yang and Lowe 1956, Barbour 1973, Halvorson and Patten 1974, Phillips and MacMahon 1978, Bowers and Lowe 1986). Increases in elevation within the

Sonoran Desert are accompanied by higher precipitation, lower temperatures, and an increase in mean particle size in the rockier soils on mountains and hilltops that retards evaporation and promotes deep percolation of rain water (Shreve and Wiggins 1964), resulting in greater water availability to plants. Thus, elevation is a surrogate for productivity. Higher productivity can result in a greater density of individuals which in turn can lead to greater species richness through the passive sampling of more species. Also, many woody species that thrive on upper bajadas will not be found on the lower slopes and plains due to moisture limitation. Hence, sites with wider ranges in elevation potentially offer a broader productivity gradient and an increase in richness at the island-level.

Nestedness in nature

Nestedness is common (Wright et al. 1998, Fleishman et al. 2002). Wright et al. (1998) reviewed the literature and found no strong taxonomic differences in nestedness, though higher-level taxa tended to be more nested than lower-level taxa. They reported that a greater difference between the largest and smallest sites increased the propensity to observe nestedness. Extinction was more commonly indicated than colonization as the primary driver for nested patterns.

Colonization leading to nestedness was the most commonly indicated for immigration experiments. Kadmon (1995) surveyed flora on recently cleared islands created inside a new reservoir and found that nestedness was significantly correlated to the distance from the mainland but not with island area.

Islands with similar isolation supported communities with similar species lists, also supporting isolation as a major contributor. Surveying zooplankton settling on differently sized bricks, Loo et al. (2002) also indicated colonization as the dominant factor.

Habitat heterogeneity has also been identified by some studies as being a chief contributor to nestedness. For example, Honnay et al. (1999b) surveyed plants in Belgian forest patches and found that nestedness was correlated with habitat heterogeneity, but not with area or isolation. Myklestaad and Saetersdal (2004) found similar results for Norwegian meadows; however, they argued that the short time (a few decades) that the traditionally-managed, species-rich meadows had been fragmented and the accompanying time lag to species relaxation prevented area from being a major factor.

Aims of study

This study determined whether nestedness exists among remnant islands in the Phoenix metropolitan area, and what mechanisms may be responsible for the nested pattern. To my knowledge, this is the first investigation of nestedness involving desert vegetation or remnant islands imbedded within an urban matrix. This study also examined whether nestedness is evident within similar habitat types across different remnants. This analysis indicate whether the nested pattern is independent of habitat heterogeneity, thereby implicating other mechanisms, and whether nestedness is a hierarchically-scaled pattern detectable at smaller scales than entire bounded islands. Owing to habitat affinities, there should be smaller assemblages of species in each habitat than are found on entire islands; unknown is how such a limitation will affect nestedness. Since woody sampling was extensive and herbaceous sampling was limited by time and scope, nestedness analysis at the habitat-level was only carried out for the woody species. Finally, recording of woody species abundance allowed for independent tests and potentially greater resolution of mechanisms contributing to nestedness. These mechanisms may act on the abundance characteristics of individual species, apart from the community at large.

METHODS

Data sampling

Plant diversity data was recorded in 22 undeveloped remnant islands scattered throughout the Salt River Valley in the Phoenix metropolitan area (Figure 1.1). All islands consisted of Sonoran Desert habitat, possibly disturbed in the past but never developed, surrounded by residential and commercial land. Most patches are mountainous parks dedicated to preserving natural habitat for recreational uses and conservation. Since Phoenix is a relatively new city, becoming urbanized only after World War II, most islands have been isolated for less than fifty years.

The woody community consisted of a wide variety of shrubs, trees, and cacti. Herbaceous species are generally only present during periods of adequate rainfall, the majority of which occurs during two wet seasons: late winter to early spring and late summer to early autumn. Woody data was collected from all sites, but herbs could only be sampled in half of the sites during the spring of 2001 due to a major drought in other years.

All data was recorded from a system of transects. A transect consisted of five quadrats, each a circle 100 m^2 in area, separated from each other by 20 m edge to edge. The presence of woody and herbaceous species within each quadrat was recorded, as was the number of woody individuals identified to species. Transects were stratified by geomorphic type, which includes: slopes facing one of the four cardinal directions, flatlands, and ephemeral washes. Within a geomorphic type, the position of the first quadrat and the transect trajectory were determined randomly.

Data analysis

Independent variables describing island properties were calculated with a variety of methods. For use in determining both the effective area and habitat heterogeneity of the study sites, all habitat types were mapped using ArcView 3.3 (2002) by tracing polygons over digitized aerial photographs (Kenney Aerial Mapping 2000) taken at approximately a one third meter resolution. A contour map with 10 m intervals, generated using ArcGIS (2002) and derived from the Maricopa County Digital Elevation model, was used in conjunction with the aerial photos to aid in interpretation. Reliance on two-dimensional GIS layers alone would distort the relationship between polygons by overemphasizing flatter areas at the expense of steeper slopes. To compensate for this distortion, the three-dimensional surface areas of each polygon were estimated by dividing the two-dimensional area by the cosine of the mean slope for that polygon; the Maricopa DEM was converted into a map of slope values, at 30 m resolution, and the mean was calculated for each polygon.

Effective surface areas for the 22 islands were calculated as the sum of all three-dimensional polygons, excluding major disturbances and recreational facilities. Habitat heterogeneity maps for the islands were generated by combining the geomorphic type maps with a layer depicting soil types (Soil Survey Geographic Database 2002). Habitat diversity for each island was calculated using the Shannon index (Magurran 1988) which incorporated the proportion of total surface area covered by each habitat-soil class. Isolation was calculated as: $I = \Sigma [\text{Ln(Area)} / (\text{Distance}^2)]$, where distance extended from the edge of the focal island to the edge of other islands or the nearest expanse of outlying desert. For this purpose, the area of the outlying desert was assumed to be 9000 hectares, which is approximately equal to the area of the largest island, South Mountain Park.

The density of individuals for a site was calculated as the mean number of plants per quadrat, regardless of species identity. This provides a means by which to examine whether simply increasing numbers of individuals, apart from other factors, increases species richness so that nestedness is more likely observed. Nestedness is observed when species frequencies are hierarchical; if many species have similar commonness, they will appear as interchangeable in the data, creating a noisier matrix and decreasing the degree of nestedness.

The nestedness of each dataset was analyzed using the Nestedness Temperature Calculator (Atmar and Patterson 1993) which yields a nestedness score ranging from 0 to 100. The score 0 denotes perfect nestedness and 100 describes a completely random array. To test for the influence of potential mechanisms on incidence of nestedness, Spearman rank-order correlations were calculated between the nested rank-order of sites and independent variables. Multiple regression between the nested rank-order of sites and independent variables was utilized to assess the contribution of each factor to the nested pattern.

To investigate whether woody species abundance varies among remnant islands in a manner consistent with nestedness, the relationship between the nested rank-order of sites and individual species abundances was assessed by calculating the Spearman correlation between the variables. A significant positive correlation indicates that species are most abundant in species rich islands with abundance dropping in progressively depauperate sites. Nestedness analysis using the Temperature Calculator is based on presence / absence data; I hypothesized that species will have decreased abundance down the nestedness gradient until they are ultimately lacking in depauperate assemblages. This relationship suggests that individual species are either affected by extinction or by a narrowing of environmental diversity in terms of habitat heterogeneity or productivity. Species prone to extinction would dwindle in numbers until final population collapse, which would contribute to nestedness if different sites were gradually less hospitable for that species' survival. On the other hand, species may be rare or absent in sites lacking higher elevation environments or a multitude of habitat types, leading to nestedness reflective of the availability of growth conditions. Fourteen species were chosen for analysis, each belonging to one of the following categories: five common species (at least 19 sites occupied out of 22), six species intermediate in frequency (8 to 12 sites occupied out of 22) generally following the nested rank-order of sites, and three species intermediate in frequency that did not follow the nested pattern. Spearman rank-order correlations were also calculated between abundances of the fourteen focal species and independent variables.

This study also investigated whether declines in species abundance across sites were evident at the habitat-level. For each focal species, the Spearman rank-order correlation was calculated between species abundance and the nested rank-order of sites determined for that habitat in which the species had the highest mean density of individuals per quadrat. The nested rank-order of sites for habitats was obtained from nestedness analysis conducted for vegetation within each habitat type. A significant positive correlation indicated a decrease in species abundance parallel to the nestedness gradient from species rich to species poor communities at the habitat-level.

RESULTS

Nestedness was ubiquitous in this system. Both woody and herbaceous datasets showed evidence of a nested pattern (scores of 22.6 and 27.5, respectively). Woody species within habitat types were also significantly nested. The flatlands and the north and south facing slopes yielded scores comparable to the entire islands (22.8, 22.4, and 20.9, respectively). The east and west facing slopes were appreciably more nested than the islands as a whole (16.0 and 15.8, respectively), while the washes were less nested (31.2). Thus, nestedness for woody species in this system is a hierarchical pattern present at two scales: the entire island and individual habitat types. The size of the species pool does not appear to affect the ability of nestedness to form in this system. The most frequent woody species were *Ambrosia deltoidea*, *Larrea tridentata*, *Encelia farinosa*, *Lycium* sp., and *Parkinsonia microphylla*.

Several variables were significantly correlated with the nested rank-order of sites. For the woody species, area, habitat heterogeneity, and mean elevation were significantly related to nestedness (Table 2.1A). For the herbaceous species, area and mean elevation were significantly correlated with nestedness (Table 2.1B).

Multiple regression indicated that nestedness in the woody and herbaceous communities are structured by somewhat different mechanisms (Table 2.2). For the woody species, both mean elevation and habitat heterogeneity were significantly related to nestedness. However, since area and habitat heterogeneity are highly correlated (Table 2.3), and cannot be included in the same regression, this also implies a potential area effect contributing to the nested pattern. Herbaceous species were primarily influenced by mean elevation of the remnant. Isolation is almost statistically significant ($p = 0.071$) at the $\alpha = 0.05$ level, which is likely due to the small sample size of 11 sites. This result suggests a possible secondary role for colonization for herbaceous species nestedness.

Some species were less abundant in the species poor sites that occur low on the nested rank-order of sites (Table 2.4). Of the fourteen focal species, seven species had significant positive correlations with the nested rank-order of sites. Of these, two are common species and five are of intermediate frequency that generally follow the nested rank-order of sites. Though insignificant, there are only two species, *Larrea tridentata* and *Prosopsis velutina*, negatively correlated with nested rank-order; these species have higher abundance on the species poor islands toward the bottom of the nestedness gradient. *Fouquieria splendens* and *Larrea tridentata* (Figure 2.1A, B) are examples of species positively and negatively correlated, respectively, to the nested rank-order of sites; note that Spearman correlations depend on rank-order rather than continuous data.

All five independent variables were significantly correlated with between one and seven species' abundance rank-orders (Table 2.4). Only mean elevation was correlated with the same seven species also related to the nested rank-order of sites. The other factors were significantly related to three or fewer species. Species abundance for *Larrea tridentata* was negatively correlated with density of individual plants, meaning that this species was more common in sparse vegetation. *Larrea tridentata* was the only species significantly related to an independent variable but not to the nested rank-order of sites.

Species abundance of four taxa, all intermediate in frequency and following the nested pattern, significantly decreased down the nested rank-order of sites at the habitat-level (Table 2.5). Habitat type containing peak abundance per species varied between the slope aspects and washes; no focal species reached maximum mean abundance in the flatland habitat. *Bebbia juncea* was the only species achieving significance in this analysis but not the previous one. The two species with negative correlations in Table 2.4, *Larrea tridentata* and *Prosopsis velutina*, also had negative relationships in this analysis.

DISCUSSION

Nestedness of woody species

While island area, habitat heterogeneity, and mean elevation are all significantly related to woody species nestedness, Spearman correlations indicate that island area is most highly correlated with nestedness (r = 0.87; Table 2.1). The area effect is indicative of the impact of extinction and / or passive sampling, though exactly how the two mechanisms influence the area effect cannot be disentangled with the data available for this study. Distinguishing between the mechanisms can only be accomplished using information that tracks species data through time. Extinction is demonstrated from evidence of either a change in richness or the loss of specific taxa over a number of years sufficient to allow for community change. For species as long-lived as woody plants in the Sonoran Desert, this would take a number of decades if not centuries. Passive sampling at the island-level is indicated when island richness, remaining constant through time, varies between islands in a manner consistent with differences in area.

Area, in this context, is a surrogate for the total number of individuals present in a continuous patch. Larger islands have more individuals, which allows for larger component populations; these populations are thus buffered from phenomena that may lead to stochastic extinction. With a lower extinction rate, larger islands can support more species. Alternatively, larger assemblages of individuals have a higher probability of containing progressively rarer species along with common ones, so that larger islands passively sample more species. Total number of species is a function of area and density of individuals. Since island area is highly correlated with both habitat heterogeneity and mean elevation, island area cannot be included in the same regression as the other two variables. Thus, density of individuals was used instead, and did not by itself affect nestedness. Consequently, multiple regression indicated a possible role for four of the five tested variables, excepting only isolation in affecting nestedness.

Fortunately, analyses of the abundance of particular species across sites provided an independent means by which to obtain greater resolution on mechanisms contributing to nestedness in woody communities. The analysis of species abundance at the island-level suggests that elevation is an important influence on nestedness. Mean elevation is significantly correlated with each of the seven species also found to be significantly related to nestedness, indicating that sites containing higher elevations also have the highest densities of those species. Three of these species are virtually absent in lower environments, including *Ephedra fasciculata*, *Eriogonum fasciculatum*, and *Fouquieria splendens*. The other species may occur at lower elevations but are more abundant at higher altitudes. On the other hand, abundances for *Opuntia acanthocarpa*, *Carnegia gigantea*, and *Fouquieria splendens* are more highly correlated with area than mean elevation or habitat heterogeneity, which is suggestive of area effects attributable to either extinction or passive sampling.

Analysis of the relationship between species abundance and nestedness within single habitat types shows that abundance for *Bebbia juncea*, *Carnegia gigantea*, *Ephedra fasciculata*, and *Fouquieria splendens* declines down the nestedness gradient from species rich to depauperate sites. Since these data are restricted to a single habitat type, this analysis demonstrates that nestedness at this scale is driven by mechanisms other than habitat heterogeneity. For the three habitats in which these species achieve peak mean abundance, total area of each habitat, within a site, was significantly correlated with nested rank-order:

north facing slope (0.458; n = 17), east facing slope (0.534; n = 14), and wash (0.763; n = 14). Thus, there is an area effect influencing nestedness at the habitat-level. For *Ephedra fasciculata* and *Fouquieria splendens,* this suggests elevation as the operating mechanism since these are higher altitudinal species; this is true to a lesser extent for *Carnegia gigantea,* which may be observed at lower elevations but are more abundant in the upper bajada.

However, for *Bebbia juncea,* which is primarily found in the wash habitat, this result is strongly suggestive of extinction or passive sampling. Washes at lower elevations are necessarily larger than those upslope, since water volume drained per wash increases as smaller tributaries merge. In the Phoenix metropolitan area, washes are more likely than mountain range habitats to experience fragmentation effects since most mountains are preserved intact to their bases, where they transition to the plains. Washes, on the other hand, are usually disturbed or transformed into drainage structures for the urban landscape outside preserves that no longer support intact desert vegetation. Therefore, connectivity between washes is disrupted with fragmentation. While the plains are also vulnerable to fragmentation effects, vegetation in the flatlands is thinner and more dominated by generalists that reach higher abundances on slopes. *Lycium* falls just short of significance; though *Lycium* prospers best in the wash habitat, it is more of a generalist than *Bebbia juncea* and may be found in the other habitats.

Analyses of species abundances have demonstrated that species within a community can respond to fragmentation in varied and potentially contradictory ways. In this study, most species were more abundant in the species rich islands. Two species, *Larrea tridentata* and *Prosopsis velutina*, had negative correlations that were short of significance, either due to subtle responses or small sample sizes (Tables 2.4, 2.5). However, these species were more abundant in smaller, depauperate sites. This is intuitive, since parcels not catastrophically disturbed are able to support stands of woody desert vegetation. As taxa are extirpated from stressed areas, other resilient species will replace them. *Larrea tridentata* is a widespread and resilient shrub that can withstand stressors many other species cannot (Gardner 1951, Reynolds 1986, Whitford et al. 2001) and can live for hundreds or even thousands of years, provided their substrate soils remain intact (McAuliffe 1994, 1999). *Prosopsis velutina* has increased within deserts and rangelands in Arizona, likely resulting from historical cattle grazing and / or fire exclusion (Bahre and Shelton 1993).

As one would expect for an archipelago of remnant patches, there was no evidence for colonization as a mechanism spawning nestedness in woody vegetation. This is not surprising for long-lived woody species in an archipelago of remnant patches that were fragmented in relatively recent times. The independent variable chiefly responsible for generating differential colonization rates, isolation, was not significantly related to nestedness (Tables 2.1A, 2.2). This does not necessarily mean that successful migration and recruitment of propagules has not occurred in this system, but that its cumulative effect would be much weaker than other mechanisms contributing to nestedness.

Further diminishing expectations of colonization from other islands is the fact that under normal circumstances, the probability of successful recruitment in existing stands of long-lived woody species is very low (Went 1948, Niering et al. 1963, Shreve and Wiggins 1964, Barbour 1968, McAuliffe 1986, Bowers and Turner 2002, Bowers et al. 2004). Fire can remove standing vegetation in the Sonoran desert, which is often caused by transmission of flames among patches of exotic grasses, such as *Bromus rubens* (Cave and Patten 1984, Schmid and Rogers 1988, McAuliffe 1995). With sufficient rain in the winter, *B. rubens* can form dense stands of fuel with enough connectivity to carry fire throughout woody vegetation. Intense heat from wildfires can replace diverse communities by almost monotypic stands of *Encelia farinosa*; where heat intensity is more moderate, resprouting of some woody species is possible, though with higher coverage of exposed soil. Nonetheless, unless an island is completely consumed, local sources of seed will usually contribute many more seeds than more distant locations. Fortunately, scorched areas on each island are currently less common than areas that have not been burned. Habitat islands with scorched areas include sections of South Mountain Park, Phoenix Mountain Preserve West, Camelback Mountain, Squaw Peak Recreation Area, Shadow Mountain, and Thunderbird Avenue Butte.

Phenomena that bring about nestedness can have varied effects on species in a community (Patterson 1987, Simberloff and Martin 1991, Kadmon 1995, Wright et al. 1998, Honnay et al. 1999b). Even though species may respond to different mechanisms, cumulative effects can reinforce each other to contribute to an aggregate pattern. This appears to be the case in this study. Some species tend to occupy less common conditions, exemplified in this case by higher elevation environments (e.g. *Eriogonum fasciculatum*, *Ephedra fasciculata*, and *Fouquieria splendens*), so will only be present in mountainous remnants. Other species may be vulnerable to local extinction by directional selection (e.g. palatable species such as *Krameria grayi* are favored by cattle) or generalized disturbance. Smaller islands lack buffer zones so that their limited expanse is exposed to repeated penetration by people from the city. If species are consistent across sites in their extinction vulnerabilities, the nested pattern will emerge (Patterson 1987). It is instructive to conceive of the mechanisms as filters (Wright et al. 1998). Species respond individualistically to patterns and processes in nature, with the collective outcome of nestedness resulting from multiple contributors.

Nestedness in Herbaceous Species

Nestedness in the herbaceous vegetation is highly correlated with area and mean elevation of islands, according to individual Spearman correlations (Table 2.1B). Multiple regression confirms the strong effect of elevation on nestedness (Table 2.2). A major difference between woody and herbaceous species is the lack of influence that habitat heterogeneity has on the herbaceous community, despite a high correlation between habitat heterogeneity and island area (Table 2.3). It is not unexpected that herbs would not respond to the large-scale habitat heterogeneity at the island-level. Woody species are a few to many orders of magnitude larger than the annual and biennial herbs and grasses composing the seasonal groundcover, so woody plants would react to the environment in a coarser grained manner.

Woody and herbaceous species also respond to the environment with very different strategies (Solbrig et al. 1977). The former can either tolerate the extreme heat and aridity of summer or cope with conditions in a deciduous state, dormant until adequate moisture allows a resumption of activity. Herbaceous species escape hot and dry summers by persisting as seeds or inactive taproots in the soil. Thus, woody species must endure successive droughts in order to persist while herbaceous species are more opportunistic, only emerging and completing their life cycle when conditions are favorable. As such, woody plants are sensitive to the structure, depth, and origin of soils, which are much dependent on geology and geomorphology of the landscape, whereas the herbaceous plants respond in a simpler fashion to the ephemeral fluctuations in moisture availability in the surface environment (Shreve and Wiggins 1964).

Isolation was almost statistically significant, falling short likely due to small sample size (Table 2.2). This indicates a secondary role for colonization, which is logically more feasible for plants that complete their life cycles in one to two years. This shorter duration allows for far more rapid population dynamics than is achievable for the woody community in a comparable time scale, since dozens of generations are possible since fragmentation has occurred.

One of the main mechanisms structuring nestedness in the herbaceous flora appears to be the propensity for the flora to retain species. Smaller islands are vulnerable to trophic imbalances whereby herbivores, such as jackrabbits and rodents, are capable of large reductions in the herbaceous biomass since their populations are dense as a result of absent or reduced populations of predators, such as snakes, coyotes, and birds of prey. Larger islands have resident predators capable of limiting the impact of herbivores, so that herbaceous communities are not decimated. This would account for a pronounced area effect, also correlated with mean elevation. Elevation's effect on the herbaceous community is less pronounced than that for the woody species. The herbaceous flora as a whole is more generalist with regard to habitat constraints since their success relies on temporary and localized areas of water availability.

Another major factor promoting the nestedness in the herbaceous flora is the near omnipresence of some exotic species. Unlike the woody vegetation, which is overwhelmingly composed of native species (the exception is *Tamarix ramosissima* occurring in well watered soils near riparian areas and in high magnitude washes), exotic plants are very abundant in the remnant island herbaceous vegetation. In the Sonoran Desert, approximately 8% of all herbaceous species are exotic (McLaughlin 2002). Widespread exotic species present on all or most islands reinforce native taxon losses to produce a strongly nested pattern. Examples of frequent exotic species include *Schismus* sp. (11 sites), *Erodium cicutarium* and *Poa bigelovii* (9 sites), and *Bromus rubens* (8 sites). The Spearman correlation between nested rank-order and exotic species richness is 0.44, which is not statistically significant likely due to small sample size. Thus, it appears that nestedness in the herbaceous community results from colonization of exotic species, as well as extinction and differential recolonization of native species.

Relevance of nestedness to conservation and management

Nestedness analysis can be a powerful tool for land managers and conservationists. There is active debate about the role nestedness analysis can play for guiding land use decisions, most importantly that of refuge design. The issue of whether a single large preserve garners more conservation utility than several small parcels of equal area, termed the SLOSS debate, has been argued since the advent of island biogeography's popularity in the 1970s. Nestedness theory has direct applicability to this matter. If a system is perfectly nested, then policy makers should opt for larger parcels since the smaller tracts, with lower species richness, would be compositionally redundant and contain subsets of the larger area (Worthen 1996).

However, if the archipelago was not perfectly nested, as would be expected, then it is possible that a sum of small island species lists would exceed the larger island richness (Cutler 1994). Wright and Reeves (1992) examined 23 archipelagos, which were all significantly nested, and found that only one case indicated a single large parcel strategy was optimal, demonstrating that nestedness is not necessarily a good indicator for resolving SLOSS questions. Nevertheless, with conservation planning, one is not dealing with a static entity. A consideration that must be made is how vulnerable constituent species are to extinction, particularly in a fragmented, relaxing system. Even if several small patches have a richer assemblage of species at present, these remnants may be exposed to stresses in the future that imperil rare or extinction-prone species (Patterson and Atmar 1986, Patterson 1987, Wright and Reeves 1992). A large parcel with large populations and insulation from surrounding influences may be a better choice to preserve these species. Conservation priorities may favor an approach tailored to protecting several threatened species rather than entire communities, depending on circumstances (Simberloff and Martin 1991).

A related utility of nestedness analysis is to use the approach toward obtaining predictions about specific community types or species. McDonald and Brown (1992) used nestedness information in order to identify specific mammal taxa potentially at risk as a result of global warming related alterations to Great Basin montane environments. While they acknowledge that more individualized attention would be needed to address the species' needs, nestedness analysis provides a useful and cost-effective means by which to assess regional conservation necessities. Nestedness analysis can also be useful for predicting community composition in unsampled habitats that are subjected to stressors or disturbance pressures (Kerr et al. 2000).

Simberloff and Martin (1991) argue that the most useful and important knowledge to arise from nestedness analysis is not whether a system is nested but why it is and which species are responsible. Toward this end, it is beneficial to know which mechanisms are primarily responsible for generating the nested pattern. In the context of conservation, it would be most useful to know whether a system is losing native species or if exotic taxa are supplanting native vegetation. Wilcove et al. (1998) argue that declines in one third of threatened species in the United States are attributable to exotic taxa, though indisputable evidence of ecological perturbation by exotic species is scant (Blossey 1999); there is currently no documented proof of Sonoran Desert plant extinctions caused by exotic species (Wilson et al. 2002). It would also be useful to know whether the nested pattern arises from a dynamic process or simply reflects the distribution of habitat features. If colonization or extinction predominates in a system, then refuge design should serve to minimize extinction of native species and colonization of exotic taxa, while encouraging colonization of natives, if possible. If sites are nested as a result of habitat diversity, then it is likely a persisting pattern, and refuges should be chosen to reflect the greatest variety or the most endangered of habitats.

However, as this study demonstrates, disentangling the mechanisms is obstructed by frequent collinearities in the data. Also complicating matters is the fact that more than one mechanism can be responsible for an archipelago's nestedness (Wright et al. 1998). Trends in individual species abundance revealed that multiple mechanisms appear to play a role in reinforcing the nestedness pattern in desert remnant islands in the Phoenix metropolitan area. Additionally, nestedness is dependent on the mixture of sites and species involved (Patterson and Brown 1991). This heavy dependence on the situation's context potentially limits the ability to discern generalities and explain nestedness outside of a particular situation.

Further questions

There are several open questions spawned by this study. For the woody species especially, it is unclear whether the dynamic or static mechanism is the predominant force structuring nestedness. A multitude of mechanisms appear to contribute to the nested pattern, though the relative degree to which they contribute is unknown. Second, it is not evident how much species distributions were directly affected by fragmentation or existed prior to the separation of the sites. For the herbs, colonization and extinction of native species was likely more important after fragmentation. On the other hand, many exotics were present in Arizona since the late 19th century. However, it is unknown exactly what the temporal dynamics of their spread were pre- and post-fragmentation. Did the exotic species reach their present ubiquity before the rise and spread of metropolitan Phoenix? Some observations indicate that their expansion became widespread in the last half century and that they were rare until the early 1900s

(McLaughlin 2002). For the long-lived woody species, how much of their community structure was determined before and after fragmentation? Cattle grazing no longer occurs on these sites, but disturbance from trampling and herbivores continues. Finally, for the herbs, which recruit every year sufficient rain falls, how constant is the pattern measured in spring of 2001? Do the roles of colonization and extinction vary between years? Only repeated sampling and analysis in the future can answer this question.

Table 2.1A. Nested rank-order of study sites and independent variables for woody species.

Site ID	Area (ha)	Isolation	Habitat Heterogeneity	Mean Elevation (m)	Mean Density
17	8764.9	2.7	3.5	487.1	21.8
18	1725.2	1326.9	2.6	508.3	27.8
12	258.2	1878.1	2.6	478.1	26.7
5	256.5	5.3	1.5	552.9	18.7
15	710.6	881.0	2.3	470.8	33.6
22	441.7	2039.8	2.9	466.9	22.1
13	368.7	14.6	2.0	385.2	9.9
16	103.7	20.2	1.9	488.4	35.8
1	105.3	1.9	2.0	418.9	114.5
3	94.0	559.3	2.2	471.6	26.9
14	255.5	1985.5	2.6	461.0	42.5
9	19.3	24.6	1.6	383.5	16.1
8	10.5	1170.0	0.0	386.5	17.5
21	12.1	0.5	0.9	474.8	51.9
20	80.1	16.7	1.4	441.4	22.3
6	8.8	0.5	1.2	381.7	10.5
11	151.9	17.0	2.8	485.5	22.2
7	4.3	1.4	1.3	474.2	37.3
19	2.3	10.7	0.9	352.0	21.6
4	4.8	11.5	1.6	371.3	19.3
2	4.7	11.5	0.7	369.2	21.9
10	42.6	17.6	0.8	398.7	7.4
Spearman Correlation	0.87*	0.35	0.69*	0.64*	0.23

* Significant at α = 0.05.

Table 2.1B. Nested rank-order of sites and independent variables for herbaceous species.

Site ID	Area (ha)	Isolation	Habitat Heterogeneity	Mean Elevation (m)
1	105.3	1.9	2.0	419
17	8764.9	2.7	3.5	487
16	103.7	20.2	1.9	488
13	368.7	14.6	2.0	385
15	710.6	881.0	2.3	471
11	151.9	17.0	2.8	486
8	10.5	1170.0	0.0	387
14	255.5	1985.5	2.6	461
2	4.7	11.5	0.7	369
9	19.3	24.6	1.6	384
19	2.3	10.7	0.9	352
Spearman Correlation	0.64*	-0.35	0.35	0.70*

* Significant at α = 0.05.

Table 2.2. Multiple regression analysis of the correlation between the nested rank-order of sites and independent variables.

Variable	Standardized Coefficient	P	R^2
I. Woody species (22 sites)			0.508
Isolation	0.088	0.614	
Topographic Heterogeneity	0.455	0.035	
Mean Elevation	0.451	0.032	
Mean Density	-0.127	0.728	
II. Herbaceous Species (11 sites)			0.561
Isolation	-0.47	0.071	
Topographic Heterogeneity	-0.099	0.752	
Mean Elevation	0.833	0.029	

Table 2.3. Spearman rank-order correlation matrix for independent variables. Woody species are listed in the upper right corner; herbaceous species are listed in the lower left corner.

	Area	Isolation	Habitat Heterogeneity	Mean Elevation	Mean Density
Area	--	0.45	0.81	0.62	0.16
Isolation	0.04	--	0.44	0.15	0.06
Habitat Het.	0.86	-0.11	--	0.52	0.32
Mean Elev.	0.66	0.14	0.69	--	0.46

Table 2.4. Spearman rank-order correlations between species abundance, nested rank-order of sites, and independent variables.

Species	Frequency Class	Nested Rank-Order of Sites	Area	Mean Elevation	Habitat Heterogeneity	Mean Density	Isolation
Larrea tridentata	1	-0.34	-0.11	-0.34	-0.06	-0.47 *	0.26
Lycium sp.	1	0.03	-0.002	0.28	-0.02	0.15	-0.18
Encelia farinosa	1	0.21	0.05	0.31	0.10	0.34	-0.003
Opuntia acanthocarpa	1	0.56 *	0.52 *	0.44 *	0.30	0.48 *	0.07
Ambrosia deltoidea	1	0.44 *	0.30	0.53 *	0.38	0.53 *	0.16
Hyptis emoryi	2	0.49 *	0.28	0.50 *	0.14	0.15	-0.04
Bebbia juncea	2	0.39	0.25	0.24	0.16	0.27	-0.11
Ephedra fasciculata	2	0.53 *	0.39	0.50 *	0.36	0.06	0.30
Carnegia gigantea	2	0.63 *	0.66 *	0.45 *	0.52 *	0.22	0.36
Eriogonum fasciculatum	2	0.48 *	0.34	0.46 *	0.29	0.08	-0.10
Foquieria splendens	2	0.76 *	0.75 *	0.56 *	0.66 *	0.18	0.46 *
Baccharis sarothroides	3	0.24	0.19	-0.03	0.19	0.12	0.30
Olneya tesota	3	0.36	0.51	0.06	0.32	-0.39	0.28
Prosopsis velutina	3	-0.24	-0.08	-0.34	-0.16	-0.34	0.08

Notes: Significance is assessed based on $\alpha = 0.05$. Abundance is expressed as the mean number of that species' individuals sampled from a $100 m^2$ quadrat, for each of 22 sites. Frequency class designations are: (1) Common species present in at least 19 out of 22 sites, (2) Intermediate frequency (present in 8 to 12 out of 22 sites) and generally following the nested pattern, and (3) Intermediate frequency in which presence does not follow the nested pattern.

Figures 2.3A, B. Plots depicting the changes in abundance of two selected species along the nested rank-order of sites. *Fouquieria splendens* was significantly and positively correlated with nestedness, indicating a drop in the number of individuals per quadrat as species richness decreases. *Larrea tridentata*, while not significant, is negatively related to nestedness.

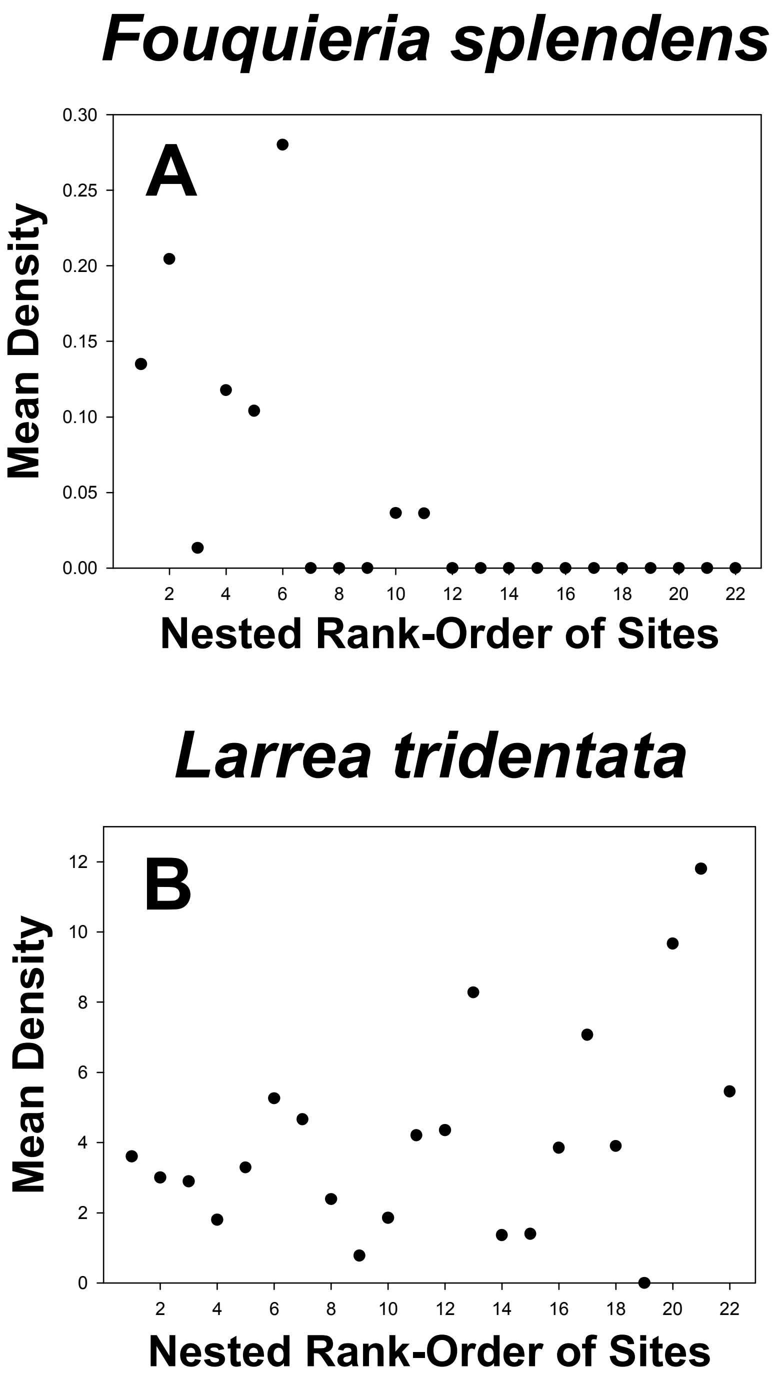


Table 2.5. Spearman correlations between species abundance and the nested rank-order of sites for habitat types.

Species	Frequency Class	North Facing Slope	South Facing Slope	East Facing Slope	West Facing Slope	Wash
Larrea tridentata	1				-0.36	
Lycium sp.	1					0.41
Encelia farinosa	1		-0.05			
Opuntia acanthocarpa	1	0.28				
Ambrosia deltoidea	1	0.32				
Hyptis emoryi	2	0.42				
Bebbia juncea	2					0.49*
Ephedra fasciculata	2	0.47*				
Carnegia gigantea	2			0.53*		
Eriogonum fasciculatum	2	0.20				
Foquieria splendens	2			0.64*		
Baccharis sarothroides	3					-0.10
Olneya tesota	3					0.07
Prosopsis velutina	3					-0.30

Notes: Habitat types indicated for each species are those in which species achieved maximum abundance in terms of mean density of individuals per quadrat. Significance is assessed based on α = 0.05.

Chapter 3. EVALUATION OF SPECIES-AREA FUNCTIONS USING SONORAN DESERT PLANT DATA FROM REMNANT HABITAT ISLANDS IN PHOENIX, ARIZONA

ABSTRACT

Ecologists have been studying the relationship between species richness and area for about a century. As area increases, more species are typically observed. In this time, a multitude of mathematical functions have been proposed that attempt to describe the dynamics of this increase. Many researchers have depended on the power function to describe this relationship despite the fact that there is a range of options. There has been limited work in evaluating which functions are most appropriate for field data. This study presents an effort to test which of the species-area functions best describe how Sonoran Desert plant species richness of remnant habitat islands in the Phoenix metropolitan area vary with sampled area and the area of entire islands. Sample curves were frequently best described by sigmoidal functions for the woody and herbaceous components, whereas convex functions were the optimal choice for curves depicting the relationship between island-level species richness and island area.

INTRODUCTION

Species-area curves describe the propensity for a species list to progressively expand as a greater area is surveyed. The regularity of this phenomenon prompted Schoener (1976) to declare the species-area relationship to be “one of ecology’s few laws”. This relationship exists because sampling more individuals in a larger area increases the probability of observing additional taxa, and incorporating a larger area increases the chance of sampling new habitat types and their associated species (Scheiner 2003). Early in ecology’s history, two equations were proposed to mathematically characterize this accumulation, the power function (Arhennius 1921) and the exponential function (Gleason 1922). Following this introduction, ecologists spent much energy and time researching the power function (Tokeshi 1993), while the exponential function was largely disregarded. Exclusive use of the power function was reinforced by the pioneering work of Preston (1962) and MacArthur and Wilson (1967), which used this function in their theoretical constructs.

The problem with reliance on the power function is that it has not been definitively demonstrated to be the best fit to empirical data for all taxa, at all scales, and in all biogeographic contexts. Based on how the data are organized and describe nature, species-area curves can assume multiple forms, based on sampling scheme, analysis method, and whether the data are spatially explicit or not (Scheiner 2003). There are practical procedures, involving species-area relations, that are instrumental for the study or management of natural communities, including the estimation of species richness, assessment of community structure or degree of disturbance, and guidance for the design of nature reserves (Fisher et al. 1943, Evans et al. 1955, Kilburn 1966, MacArthur and Wilson 1967, May 1975, Soule et al. 1979, Williamson 1981, Hubbell and Foster 1983, Palmer 1990, Lawrey 1991, Baltanas 1992, Grassle and Maciolek 1992). It is clear that the highest accuracy possible in describing the species-area relationship will yield the most reliable estimates and evaluations.

The power function's suitability for describing datasets has not been systematically tested against the many alternative functions (Table 3.1). Indeed, early innovators of the power curve did not argue for its permanence. Arrhenius (1923) and Preston (1962) referred to the power model as an "approximation formula" or a "first approximation" (Williams 1995). There is a need for testing the suitability of the power function and other alternatives using empirical species-area data from a variety of contexts. This research provides an assessment of the effectiveness of various mathematical functions for describing species-area relations of woody and herbaceous taxa surveyed from natural vegetation, in this case from undeveloped Sonoran Desert habitats within and around metropolitan Phoenix, Arizona.

History of species-area functions

Connor and McCoy (1979) concluded that the power function was widely adopted due to its convenience and ability to fit observed data, notwithstanding several objectionable properties. The power function is a convex equation which lacks an asymptote, yielding exceedingly high estimates of species richness at large scales. There have also been questions about whether the power function is suitable for all spatial scales and is capable of fitting more complex species-area patterns, particularly those involving phase shifts within the scale of observation. Thus, inappropriately imposing the power function may misrepresent patterns in the data. This especially applies to the common error of assuming that its logarithmic transformation represents the true relationship between area and species accumulation. These issues will be more fully examined in the Discussion.

Connor and McCoy (1979) demonstrated that the power function does not always provide the best fit to the data. They compared the fit of power, exponential, and linear functions to a compilation of species-area datasets from the literature. They found that 75 out of 100 datasets could be fit by a power function, though only 36 were best fit by this function. Ecologists have been relatively slow in appreciating the implications of these results.

Years passed before alternative models were seriously examined. He and Legendre (1996) concluded that the best choice depends on the spatial scale considered. Analyzing data describing species richness and area for samples as well as islands, they found that the exponential function best described smaller scale data, the power function was most appropriate for the intermediate scale, and the logistic function most suited larger scale data.

Effort has also been spent creating alternative functions. Based on the Random Placement Model of Coleman (1981) and Coleman et al. (1982), Williams (1995) developed the Extreme Value Function (EVF). The Random Placement Model maintains that the increase of species with area is solely a consequence of the sampling of more individuals, which would passively increase the chance of observing novel taxa. Williams (1995) argues that the EVF is effective with species-area data even if the individuals are not distributed randomly in space. Other functions, both convex and sigmoid, have been proposed, and are reviewed by Tjorve (2003).

Scheiner (2003) identified four major classes of species-area curve, based on how the empirical data was collected. Types I, II, and III describe curves generated from successively larger aggregations of samples. Type I refers to curves calculated from a strictly nested sampling scheme. Types II and III refer to curves describing the accumulation of non-nested quadrats that are either contiguous or non-contiguous, respectively. Type IV curves describe species-area relations among bounded areas, including islands or remnant patches.

Tjorve (2003) hypothesized that species–area curves generated from samples (Type I, II, and III) should be convex and Type IV curves should be sigmoid. The most important difference between the two forms is that a sigmoid curve contains a point of inflection, permitting a change in the rate of species accumulation from increasing to decreasing. In contrast, a convex curve can only express a progressive decline in this rate. A sigmoid function necessarily terminates in an asymptote, whereas a convex function may or may not express an asymptote. Tjorve's assertion agrees with the conclusion of He and Legendre (1996) who found that convex functions, specifically the exponential and power functions, were most appropriate at small and intermediate scales, respectively, while the sigmoid logistic function best describes patterns in large-scale data. One surmises that at the smaller spatial scales of sample curves, species will continue to be collected and fail to reach an asymptote for the breadth of the sample, especially since conventional sampling covers only a small fraction of the total study area. On the other hand, island curves would be expected to have collected so many species that at larger areas, most have been observed and an asymptote is approached or attained.

Species-area curves in recent literature

The literature contains no consensus about which curves should be considered. A number of papers only considered the power function (e.g. Chown et al. 1998, Lawesson et al. 1998, McKinney 1998, McKinney and Frederick 1999, Weiher 1999, Hill and Curran 2001, Barrett et al. 2003, Marui et al. 2004). Authors do not always give a reason for why they chose this course. When they do, use of the power function is usually justified by stating that it is the traditional or most commonly used (e.g. Chown et al. 1998). Rosenzweig (1995) goes so far as to state that all species-area curves are power functions, and this claim is frequently cited as the basis for the use of that function. Frequently, authors suggest that other functions are possible but fail to examine them. Ecologists should adequately test the suitability of the power function and other alternatives before proceeding to create and use conclusions from analyses. Some studies using the power function are empirical tests of existing or modified theoretical constructs that mandate this model (e.g. McKinney 1998, McKinney and Frederick 1999, Barrett et al. 2003). Since the power function may not always be appropriate in all circumstances, the wide applicability of theory using only power relationships is questionable.

Some recent studies have examined alternative functions. A number of authors have chosen to evaluate the statistical fit of the power function along with its contemporary, the exponential function. For example, Sagar et al. (2003) found that the exponential function provided more accurate extrapolation estimates at small scales while the power function performed better at intermediate scales (up to 15 hectares), in agreement with He and Legendre (1996). Keely (2003) and Keely and Fotheringham (2003) found that the two functions gave better fits for different plant communities. Ulrich and Buszko (2003) obtained a similar result for butterfly communities in different parts of Europe. Gurd and Nudds (1999) and Rahbek (1997) found that both functions provided comparable fits to Canadian mammal and neotropical bird community data, respectively, but elected to use the power function given its popularity in the literature. Two papers, inspired by Coleman (1981) and Coleman et al. (1982), tested the Random Placement Hypothesis, finding it capable of describing species-area relations for benthic organisms colonizing submerged plates

(Anderson 1998) but not for orthopterans inhabiting small steppe patches (Baldi and Kisbenedek 1999). Using the extreme value function (Williams 1995), Burbidge et al. (1997) reported a successful fit to data describing mammal richness on oceanic islands, though other functions were not considered. Matter et al. (2003) found that the power function, extreme value function, and their own derived metapopulation model yielded comparable fits to data describing animal species richness on islands. He and Legendre (1996) have stimulated some work with the logistic function (Natuhara and Imai 1999, Mulugeta et al. 2001). Nabe-Nielsen (2001) successfully fitted the negative exponential function to Ecuadorian liana data, but gave no indication why this one was chosen to the exclusion of others.

The purpose of this study was to assess which species-area functions provided the best fit for describing species-area relations of woody and herbaceous vegetation in remnant desert habitat islands imbedded within the urban matrix of metropolitan Phoenix, as well as three additional outlying desert areas. The curve forms to be examined are type IIIB and IV (Scheiner 2003). The former refers to a species-area curve generated by aggregating non-contiguous samples in a non-spatially explicit manner. The latter refers to a curve summarizing the richness values of bounded areas, or islands.

METHODS

Data sampling

Plant species richness was recorded in 22 remnant desert habitat islands scattered throughout the Salt River Valley in the Phoenix area (Figure 1.1, Table 3.2). All islands consisted of Sonoran Desert habitat, possibly disturbed in the past but never developed, surrounded by residential and commercial land. Most patches are mountainous city parks dedicated to preserving natural habitat for recreational uses and conservation. Since Phoenix is a relatively new city, becoming urbanized only after World War II, most islands have been isolated for less than fifty years. Three outlying desert areas were also sampled to facilitate comparison between insular and continuous natural habitat. These areas were chosen to represent how the vegetation may have appeared before fragmentation of the habitat islands by urbanization.

The woody community consists of a wide variety of shrubs, trees, and cacti, together contributing to a particularly heterogeneous physiognomy. Herbaceous species are generally only present during periods of adequate rainfall, the majority of which occurs during two wet seasons: late winter - early spring and middle summer - early autumn. Woody data were collected from all sites between 1998 and 2002, but herbaceous data could only be sampled in half of these sites in 2001 due to a major drought in prior and subsequent years.

All data were recorded from a system of transects and quadrats. A transect consisted of five quadrats, each a circle 100 m^2 in area, separated from each other by 20 m edge to edge. The presence of all woody and herbaceous species within each quadrat was recorded. Transects were stratified by geomorphic type including: slopes facing one of the four cardinal directions, flatlands, and ephemeral washes. Within a given geomorphic type, the position of the first quadrat and the transect trajectory were determined randomly.

Data analysis

Type IIIB species-area curves for samples were generated using EstimateS (Colwell 1999). This program calculates how many species are expected in groups of samples based on the means of multiple subsets. The average richness of single quadrats is calculated, followed by average richness for random pairs of quadrats, and so on up to the total number of quadrats. Curve generation was repeated fifteen times and the curves were averaged to generate the empirical curves used in subsequent analyses.

Type IV species-area curves were generated using estimated values of the total species richness of both woody and herbaceous species of each island. The estimates were generated using the first order jackknife (Palmer 1990, 1991). The area for each island was estimated using digitized aerial photos (Kenney 2000) within ArcView (ESRI 2004). The area of interest excluded developed areas and heavily disturbed patches. Reliance on two-dimensional GIS layers alone would distort the relationship between polygons by overemphasizing flatter areas at the expense of steeper slopes. To compensate for this distortion, the three-dimensional surface area of each polygon was estimated by dividing the two-dimensional area by the cosine of the mean slope for that polygon; the Maricopa Digital Elevation Model was converted into a map of slope values, at 30 m resolution, and the mean slope was calculated for each polygon. Because outlying areas are indefinite in size, they were not included in the Type IV curve analyses.

The correspondence between empirical curves and species-area functions (Table 3.1) was assessed using the nonlinear regression function of SYSTAT 6.1. The extreme value function was analyzed as suggested by Williams (1995) and Burbidge et al. (1997): the first constant ‘a’ is replaced with an estimate of the total species richness of each island. The AIC criterion was used to assess which curve model provided the best fit, and is as follows: AIC = Ln(SSE/n)*n + 2k, where SSE is the error sum of squares, n is the number of observations, and k is the number of parameters contained within each model. Smaller AIC values indicate better fits. For these data, because the SSE values were slight and frequently less than 1.0, the smaller values were frequently the more negative.

RESULTS

The analysis revealed that no single species-area function is adequate for describing all empirical data sets, even within a single landscape dominated by similar vegetation (Tables 3.3A, B and 3.4A, B). For the Type IIIB curves, there were strong differences between the woody and herbaceous sample data sets with regard to which functions predominated as the best fitting alternatives. For the woody data set, the three sigmoid functions (logistic, Hill, and Lomolino) usually provided the best fit. The larger samples tended to successfully fit all three functions with equal AIC values while the smaller samples yield more variable results, though still favoring one of these three models. This outcome appears to be the only influence of data set size on function fit. In contrast, the herbaceous data sets were dominated by best fits from either the logistic or the rational function. These functions achieved the best or second best fit for all samples but one. Note that the logistic function is sigmoid and the rational function is convex.

For both the woody and herbaceous data sets, the type IV island curves were best described by convex functions (Tables 3.3A, B and 3.4A, B). The woody island curve was best characterized by the exponential function, with the power function achieving second ranking with an AIC value only about 1.6% higher than that for the exponential function. The herbaceous island curve was best described by the Monod function, with the negative exponential function exceeding the Monod function by less than 1% of the best-fit AIC value. The power function is a less satisfactory choice for describing the herbaceous island curve, though it follows the Monod function by less than 6% of the AIC value. For functions capable of fitting the empirical type IV curves, accuracy was usually not much worse than the best fitting equation. Woody type IV curves had eight other models coming within 7% of the fit of the exponential model; the herbaceous type IV curves had seven functions approaching within 6% of the best fitting AIC value.

DISCUSSION

Determination of the best fitting function is most effectively accomplished by comparing all alternatives. In this study, no function was most appropriate for all data sets. In general, Type IIIB curves most often fit the logistic function. For Type IV curves, the best fit was with convex functions, the exponential and the Monod. The former functions are sigmoid and the latter convex, in contradiction with He and Legendre's (1996) conjecture that convex functions, the power and exponential, are best suited to small and intermediate scale data while the sigmoid logistic function was more appropriate for large scale data. Their data differed in two respects: the Pasoh tropical rain forest tree data was used to generate a Type II sample curve, and their Type IV curve was based on bird data from Pymatuning Lake islands.

For sample curves, a large enough sample in a bounded area should eventually contain all species in the bounded pool (excepting the improbable case that the last individual is a new species), yielding a curve with an asymptote. Yet there is no assurance that, for a Type IV curve, larger islands will always contain the species found in smaller ones. Hence, there is no certainty of an asymptote in this situation. This is particularly the case for stationary versus vagile taxa. Birds can quickly disperse between islands whereas plant propagules have a more restricted migration capability. This reduced capacity to disperse throughout a group of islands should translate into a much longer time between successful island colonization episodes. Potentially more generations will pass between colonization episodes for stationary versus vagile species, contributing more time for population and community dynamics to sort constituent island species and for extinctions to occur. This can result in a higher degree of variation between island communities for stationary species.

Behavior of the alternative logistic functions

The performance of the logistic, Hill, and Lomolino functions is rather interesting, especially given their parity for many of the woody sample data sets. That their error terms are identical is not necessarily surprising, given that the logistic is a simplification of, and the Lomolino an alternative version of, the Hill function (Tjorve 2003). What is perplexing is why this should be true sometimes and not others. As mentioned above, this tendency roughly coincides with the size of the data set. It appears that their capabilities for describing curve behavior tend to converge with larger areas, but that they behave more individualistically with smaller ones. It is unknown why this relationship completely breaks down for the herb samples. One characteristic that the herb samples and smaller woody samples have in common is their magnitude of area coverage. Herb samples were unavoidably small due to the very narrow window of time available to survey them. Larger samples likely have a broader approach to an asymptote and the potential for a more gently shifting inflection point. This may cause them to converge into a common curve form not manifest for smaller areas.

Parameters

Results were unclear about whether increasing the number of parameters in a species-area equation increased the amount of variance that function was capable of explaining. It is true that there were very few woody sample curves best fit by the two-parameter functions (one each for exponential and power), while three-parameter functions completely dominated the herb samples. However, the four-parameter model, the cumulative beta-P function, never worked for a single dataset. Also, the exponential and power models were relatively successful with the island data sets. At this point, it is unknown how much these results may be attributed to the number of parameters compared to the more specific shape and asymptotic characteristics inherent in the mathematical formulations.

Extrapolation of species richness

One of the practical utilities of a fitted species-area function is that it is capable of yielding an estimate of the total species richness for an area. However, one must use caution and pay close attention to the trajectories of the empirical and model curves. Nonlinear regression fits the function based on the totality of the empirical curve, which may not necessarily result in a close fit to its right hand (largest area) terminus. Figures 3.1A and 3.2A illustrate cases in which the model and empirical curves appear to follow similar trajectories at the right hand terminus. However, figures 3.1B and 3.2B contain models that fit the middle of the empirical curve well, but follow divergent trajectories toward the terminus. Tables 3.5A, B contains estimates for the species pool of each island, generated from both curve extrapolation and the first order Jackknife function (Palmer 1990, 1991), as well as the total species actually sampled. Some estimates match closely, but there are some obvious overestimates for the woody datasets for Granada Park, Shadow Mountain Park, and Phoenix Mountain Preserve West.

There was a published flora for South Mountain Park (Daniel and Butterwick 1992) that allowed for a comparison between the jackknife estimate, species-area curve estimate, and an enumeration of species from local herbaria and field visitations. Unfortunately, both predictions (37.0 and 38.7, respectively) underestimated species as listed in the flora (55 species). The flora estimate was derived by lumping four species of *Lycium* as the morphospecies, *Lycium* sp.; *Lycium* species cannot be reliably identified without fruits and flowers, which were usually not available. Table 3.6A includes species sampled in this study also listed in the flora; table 3.6B includes species not sampled in the South Mountain dataset. Ten species not sampled were observed off plot. Most species not sampled were rare to occasional in distribution and abundance, and some were more restricted in habitat affinity. Even with 556 quadrats, some species were too limited in distribution to be sampled, and were likely restricted to the diverse higher altitude habitats. However, Palmer (1990) notes that most richness estimators are highly correlated with true species richness, and so can be used for comparing species richness between sites even if specific estimates are not precise.

The power function

There are disadvantageous qualities of the power function that are inherent to its formulation. The power function lacks an asymptote, increasing without limit (Williams 1995). This unboundedness can produce some unrealistically high estimates of total species richness. While this overestimation may not be a problem at small to intermediate scales, it makes the power function unreliable for estimating species richness in larger areas. There has been debate about whether a curve lacking an upper limit is appropriate for characterizing species-area relations (Lomolino 2000, 2001, 2002; Williamson et al. 2001), but at present this remains unresolved.

Clearly the power function is not suitable for all ecological scales. Studying three curve models, He and Legendre (1996) find that the power function was most successful for fitting intermediate scale data, while the exponential function was best for smaller scale and the logistic function was superior for large scale data. Williams (1995) asserts that some authors (Gilpin and Diamond 1976, Schoener 1976, Connor and McCoy 1979, Martin 1981) have found that the power function's ‘z’ parameter can vary with area even within an archipelago; this ‘z’ parameter corresponds to the ‘b’ parameter as written in Table 3.1. The Small Island Effect (Preston 1962, Lomolino 2000, Lomolino and Weiser 2001) hypothesizes that the species-area relationship holds for islands of sufficient area, but below a threshold area, species richness of small islands is not determined by area but rather by habitat characteristics. The Subsidized Island Biogeography hypothesis (Anderson and Wait 2001) argues that below a threshold size for oceanic islands, estimated to be approximately 3 km^2, resource subsidies are able to penetrate into the interior and either increase or decrease richness, depending on the island's productivity.

The power function may distort or obscure interpretations of the data. The convex quality of the power function makes it unable to detect phase shifts between different patterns apparent at dissimilar scales (Lomolino 2000, 2002). The alternative is to use a sigmoid function which would allow for the Small Island Effect, in which the curve begins roughly horizontal, increases in slope with intermediate islands, and levels off for larger islands.

A common method of fitting data involves taking the logarithmic transformation of the power function. This may have been more appropriate in earlier days when computing power was limited, but with current technology, nonlinear regression procedures on the untransformed function is possible and provides a more suitable analysis of data (Lomolino 2001). In addition, avoiding transformations may prevent ecologists from assuming that the transformed version can be interpreted similarly to the original equation, a mistake common for users of the power function (Rosenzweig 1995). Finally, a limitation of the power function, in which log(0) is undefined, have led some ecologists to exclude very small islands that may lack species, potentially obscuring species-area relations (Williams 1996).

Another issue debated extensively about the power model regards the relevance of its parameters. Ever since Preston (1962) proposed his hypothesis about the lognormal distribution, ecologists have sought the meaning of the ‘z’ parameter. Preston suggested that when ‘z’ equals the canonical value of 0.262, the species curve and individuals curve (describing the number of species and individuals present in different abundance classes) of the lognormal distribution line up, and a variety of community properties can be derived. For many studies, ‘z’ values for islands tend to fall between 0.25 and 0.35, while continental values are likely to range between 0.12 and 0.18 (Rosenzweig 1995). The regularity of this outcome has led many to suspect that ‘z’ holds a fundamental biological relevance. Connor and McCoy (1979) argued that this phenomenon is simply the result of a central tendency. In response to objections by Sugihara (1981), Connor et al. (1983) more rigorously examined the ‘z’ value, concluding that the central tendency results from the distribution of the product of the two independent variables, the correlation coefficient ‘r’ and the ratio ‘sy/sx’. There has been confusion about what exactly ‘z’ controls in the power model. Many have assumed it represents the curve slope, but the slope is actually determined by both ‘C’ and ‘z’ (Gould 1979, Lomolino 1989). ‘C’ has received much less attention. For curve fitting purposes, it may be irrelevant whether the parameters have biological implications or not, but assuming they do when they do not can lead to erroneous conclusions.

Results of this study contradict the frequently encountered assumption that the power function fits all species-area curves (Rosenzweig 1995) or is sufficiently versatile to fit all situations. While it is true that this model provides a good fit to the woody island data, though not best fitting, this was the only case in this study in which it performed particularly well. In fact, the power function may only be best suited for a relatively small number of specific situations.

Conclusion

This study demonstrated that there is no single function that best describes all species–area relations. A widely applicable function must have sufficient versatility to both converge on an estimate and provide an acceptable fit. The much lauded and ubiquitous power function failed to perform in proportion to its reputation. Although it was successful at converging on an estimate, so were other models. A possible reason for its frequent use and adoption may result from ecologists' tendency to fit data to its double logarithmic transformation, which serves to smooth out the distribution. In the past, this was virtually a computational necessity, but technology has freed researchers from this constraint. It is more appropriate to evaluate functions in their untransformed state, as advocated by Lomolino (2001). There is a wealth of theoretical innovation and practical application developed with the power function as its basis (e.g. Preston 1962, MacArthur and Wilson 1967, Rosenzweig 1995).

These advances have helped ecology move forward, but it is unacceptable to apply these constructs to data without ensuring an acceptable fit. These tools should be modified so that other species-area functions can be substituted. The statistical fit need not be the absolute maximum possible, but it must be somewhat comparable to the best fitting function. If a function is negligibly less accurate than the best fitting function, it should be acceptable for use. However, if that difference is too large, the failing model should be jettisoned. Unfortunately, how large a difference violates acceptability is not an objective matter, but one that is best left to the judgment and expertise of the practicing ecologist.

Table 3.1. Species-area functions examined in this study (He and Legendre 1996, Tjorve 2003).

Function Names	Equations	Sources
I. Convex functions		
Exponential	$y = a + b*Ln(x)$	Gleason (1922, 1925), Fisher et al. (1943), He and Legendre (1996)
Power	$y = a*(x^{b})$	Arrhenius (1921), Preston (1962), He and Legendre (1996)
Monod	$y = a*(x / (b + x))$	Monod (1950), de Caprariis et al. (1976), Clench (1979)
Negative exponential	$y = a*(1 - \exp(-b*x))$	Holdridge et al. (1971), Miller and Wiegert (1989), Ratkowsky (1990)
Asymptotic regression	$y = a - (b*c^{-x})$	Ratkowsky (1990)
Rational	$y = (a + b*x) / (1 + c*x)$	Ratkowsky (1990)
II. Sigmoid functions		
Logistic	$y = a / (b + x^{-c})$	He and Legendre (1996)
Tjorve logistic	$y = a / (1 + \exp(-b*x + c))$	Ratkowsky (1990)
Gompertz	$y = a*\exp(-\exp(-b*x + c))$	Ratkowsky (1990)
Extreme value function	$y = a*(1-\exp(-\exp(b*x+c)))$	Williams (1995, 1996), Burbidge et al. (1997)
Morgan-Mercer-Flodin (Hill)	$y = (a*x^{c}) / (b + x^{c})$	Morgan et al. (1975)
Lomolino	$y = a / 1 + (b^{\log(c/x)})$	Lomolino (2000)
Chapman-Richards	$y = a*(1 - \exp(-b*x))^{c}$	Ratkowsky (1990)
Cumulative Weibull distribution	$y = a*(1 - \exp(-b*x^{c}))$	Weibull (1951), Reid (1978), Yang et al. (1978), Brown and Mayer (1988), Rorslett (1991), Flather (1996)
Cumulative beta-P distribution	$y = a*(1-(1+(x/c)^{d})^{-b})$	Mielke and Johnson (1974)

Table 3.2. Area and sampling intensity for study sites.

ID	Study Area	Area in Hectares	Woody Quadrats Sampled	Herb Quadrats Sampled
1	Adobe Dam Recreation Area	105.3	40	40
2	Broadway Butte	4.7	12	5
3	Buffalo Ridge Park	94.0	55	--
4	Buttes Resort	4.8	20	--
5	Camelback Mountain	256.5	85	--
6	Park of Canals	8.8	15	--
7	Falcon Hill	4.3	10	--
8	Granada Park	10.5	20	15
9	Hayden Butte	19.3	40	15
10	Lincoln Avenue lot	42.6	20	--
11	Lookout Mountain Park	151.9	80	20
12	Outer Union patch	258.2	75	--
13	Papago Park	368.7	115	20
14	Phoenix Mountain Reserve East	255.5	83	19
15	Phoenix Mountain Reserve West	710.6	125	17
16	Shadow Mountain Park	103.7	70	20
17	South Mountain Park	8764.9	556	15
18	Squaw Peak Recreation Area	1725.2	230	--
19	Tempe saltbush patch	2.3	5	5
20	Thunderbird Avenue butte	80.1	35	--
21	Twin buttes	12.1	28	--
22	West Squaw patch	441.7	125	--
23	Union Hills	outlying	125	--
24	Usery Mountain Park	outlying	48	10
25	White Tank Regional Park	outlying	150	--

Table 3.3A. AIC values for convex species-area functions fit to woody species quadrat data.

Site ID	Exponential	Power	Monod	Negative Exponential	Asymptotic Regression	Rational
1	-102.8	-4.2	-146.6	-24.7		-170.7
2	-35.0	-48.3	-36.6	-26.0		
3	-109.9	-28.5	-128.6	-33.0		-247.9 **
4	-52.4	-35.7	-84.8	-52.8		
5	-251.5	-61.6	-100.6	29.3		-248.2
6	-18.9	-81.9	-39.7			
7	-37.9	-32.6	-26.1	-13.4		0.5
8	-2.7	-98.2	-27.4	-17.3		-75.8
9	-56.7	-56.6	-108.4	-47.0		-174.1
10	-89.6	-59.6	-106.7			
11	-157.7	-347.5	-105.0	-40.8		-314.0
12	-60.8	-65.2	-99.8	-1.6		-291.0
13	-83.7	-128.9	-216.2	-62.4		-531.2
14	-248.7	-165.6	-135.9	-30.9		-346.9
15	-182.3	-392.2	-2.6	107.4		-194.8
16	-53.0	-264.9 **	-22.9	28.4		-138.9
17	-1033.7	-130.6	-7.1	776.1		-550.4
18	-792.4	-175.5	-128.4			-477.8
19	-16.6	-22.3	1.3	-18.1		-3.2
20	-127.9	-100.3	-58.5	-18.1	-79.4	-103.2
21	-74.1	-30.2	-77.8	-27.7		-124.5 **
22	-101.7	-398.5	-18.6			-259.7
23	-160.4	-5.6	-326.8	-18.0		-658.9 **
24	-88.5	-61.5	-7.4	46.6		-62.1
25	-545.8 **	-44.7	-33.2			-159.8
All Islands	74.6 **	75.8	82.0	85.1	79.3	78.3

Note: Values with asterisks denote best-fit functions. Empty cells did not converge to a solution.

Table 3.3B. AIC values for sigmoidal species-area functions fit to woody species quadrat data.

Site ID	Logistic	Tjorve Logistic	Gompertz	Extreme Value Function	Hill	Lomolino	Chapman-Richards	Cumulative Weibull	Cumulative Beta-P
1	-212.4 **	-13.9	-31.7	56.0	-212.4 **	-212.4 **			
2	-63.1 **	-47.9	-60.3	-16.2	-63.1 **				
3	-202.3	-61.5	-93.2	-93.2	46.4				
4	-83.1	-87.3	-106.5 **	-57.4	-83.1	-83.1			
5	-590.7 **	-30.0	-60.8	105.5	-590.7 **	-590.7 **			
6	-86.3 **	-56.9	-72.1	-22.7					
7	-60.5 **	-32.3	-39.8	-6.7	-60.5 **				
8	-102.1 **	-31.1	-43.6	3.4	-102.1 **				
9	-258.3 **	-35.7		35.1	-258.3 **				
10	-118.3 **	-75.0	-90.4	-28.5	-118.3 **	-118.3 **			
11	-402.8 **	-188.5	-219.3	-62.3	-402.8 **	-402.8 **			
12	-397.0 **	-30.6	-69.9	101.3	-397.0 **	-397.0 **			
13	-571.5 **	-82.9	-146.9	119.2	-571.5 **	-571.5 **			
14	-528.2 **	-121.4	-154.8	39.6	-528.2 **	-528.2 **			
15	-414.0 **	-77.7	-103.6	54.4	-414.0 **	-414.0 **			
16	-263.1	-60.0	-80.3	19.8	118.6				
17	-1683.5 **	248.0	168.5	852.0	-1683.5 **	-1683.5 **			
18	-1226.8 **	-33.3	-89.3	288.2	-1226.8 **	-1226.8 **			
19	-26.2	-31.1	-48.1 **	-8.1	-26.2	-26.2			
20	-148.3 **	-54.2	-64.1	-10.1	-148.3 **				
21	-107.5	-59.1	-76.3	-3.5	-107.5	-107.5			
22	-654.7 **	-76.2	-116.6	102.0	-430.8				
23	-629.4	-83.1	-126.9	145.5	-629.4	-629.4			
24	-128.0 **	6.0	-7.6	65.5		-128.0 **			
25	-385.2	74.6	42.8	251.4	-385.2	-385.2			
All Islands		76.7	87.0	79.6			76.7	77.0	

Note: Values with asterisks denote best-fit functions. Empty cells did not converge to a solution.

Table 3.4A. AIC values for convex species-area functions fit to herbaceous species quadrat data.

Site ID	Exponential	Power	Monod	Negative Exponential	Asymptotic Regression	Rational
1	-46.9	32.5		33.7		-119.4
2	-5.6	-2.4	-10.8	-27.6	1.7	-16.9
8	-14.2	-14.6	-10.8	6.9		-72.1 **
9	-35.4	-34.8	-14.0	3.5		-60.3
11	-28.1	7.2		15.6		-59.5
13	-57.0	-5.0		-11.0		-103.0
14	-25.1	-3.9	-78.3	-6.7		-90.7
15	-37.4	1.9	-27.1	5.8		-86.4 **
16	-48.1	-0.5		22.0		-41.5
17	-33.7	-0.4	-35.3	2.3		-73.7
19	-12.8	-24.1		-8.2		
24	-37.8	-11.7	-18.1	1.3		-59.7 **
All Islands	46.5	48.8	40.9 **	41.6	43.4	42.9

Note: Values with asterisks denote best-fit functions. Empty cells did not converge to a solution.

Table 3.4B. AIC values for sigmoidal species-area functions fit to herbaceous species quadrat data.

Site ID	Logistic	Tjorve Logistic	Gompertz	Extreme Value Function	Hill	Lomolino	Chapman-Richards	Cumulative Weibull	Cumulative Beta-P
1	-171.3 **	18.1	2.0	90.6		-171.3 **			
2	-19.1	-33.1	-36.6 **	-1.4	-19.1			3.7	
8	-71.4	-8.2	-18.4	24.8					
9	-84.5 **	-22.4	-30.2	7.9					
11	-82.0 **		-6.5	38.6		-82.0 **			
13	-108.5 **	-13.9	-25.4	26.0		-108.5 **			
14	-97.0 **	-20.0	-27.5	26.2					
15	-64.0	-9.8	-21.5	37.6					
16	-67.2 **	7.7	-1.1	43.4					
17	-84.1 **	-9.0	-16.7	24.2				-63.8	
19	-36.6 **	-22.4	-24.6	-13.1					
24	-57.9	-18.0	-23.6	6.8					
All Islands	42.9	44.2	43.9			42.9		43.1	

Note: Values with asterisks denote best-fit functions. Empty cells did not converge to a solution.

Figure 3.2A. Comparison of the logistic and rational functions with the empirical sample curve for woody species at the Outer Union patch.

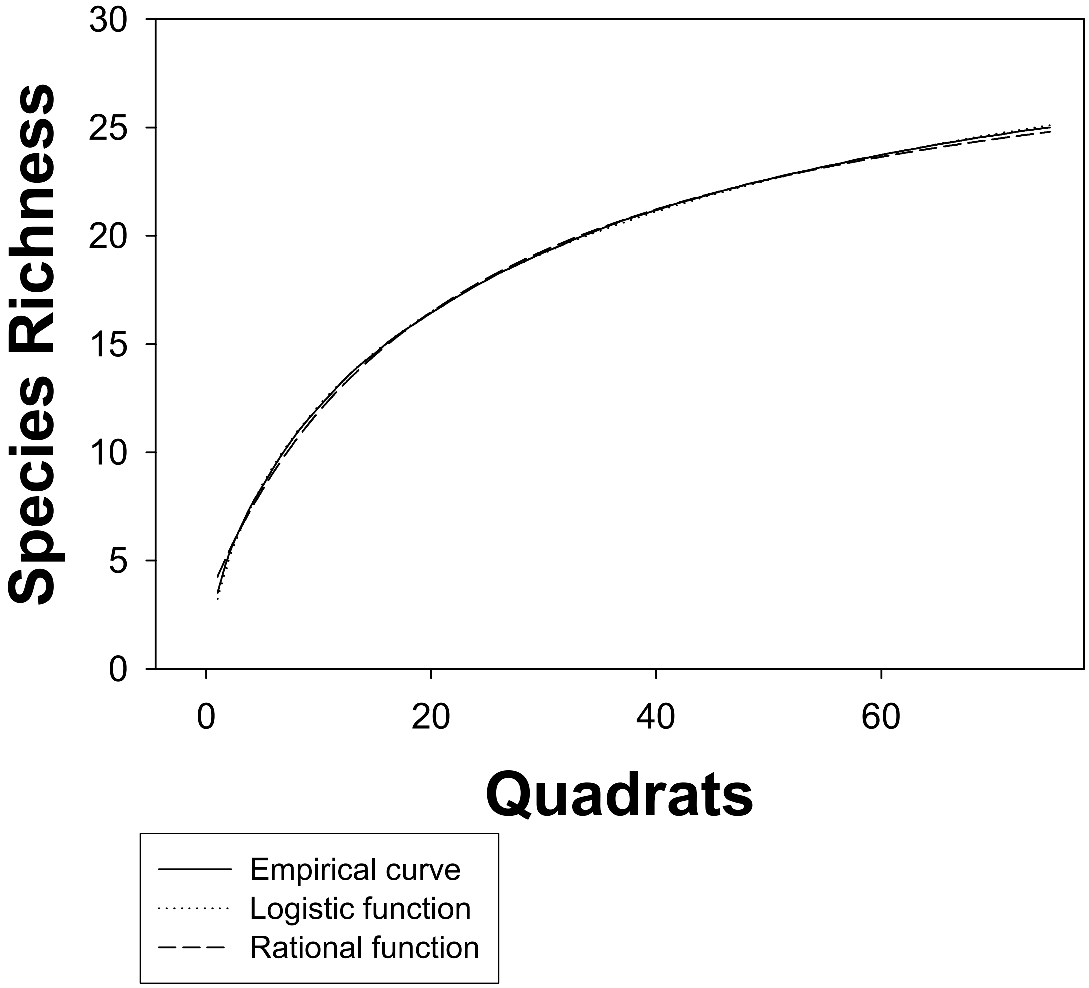


Figure 3.2B. Comparison of the logistic and rational functions with the empirical sample curve for woody species at Twin Buttes.

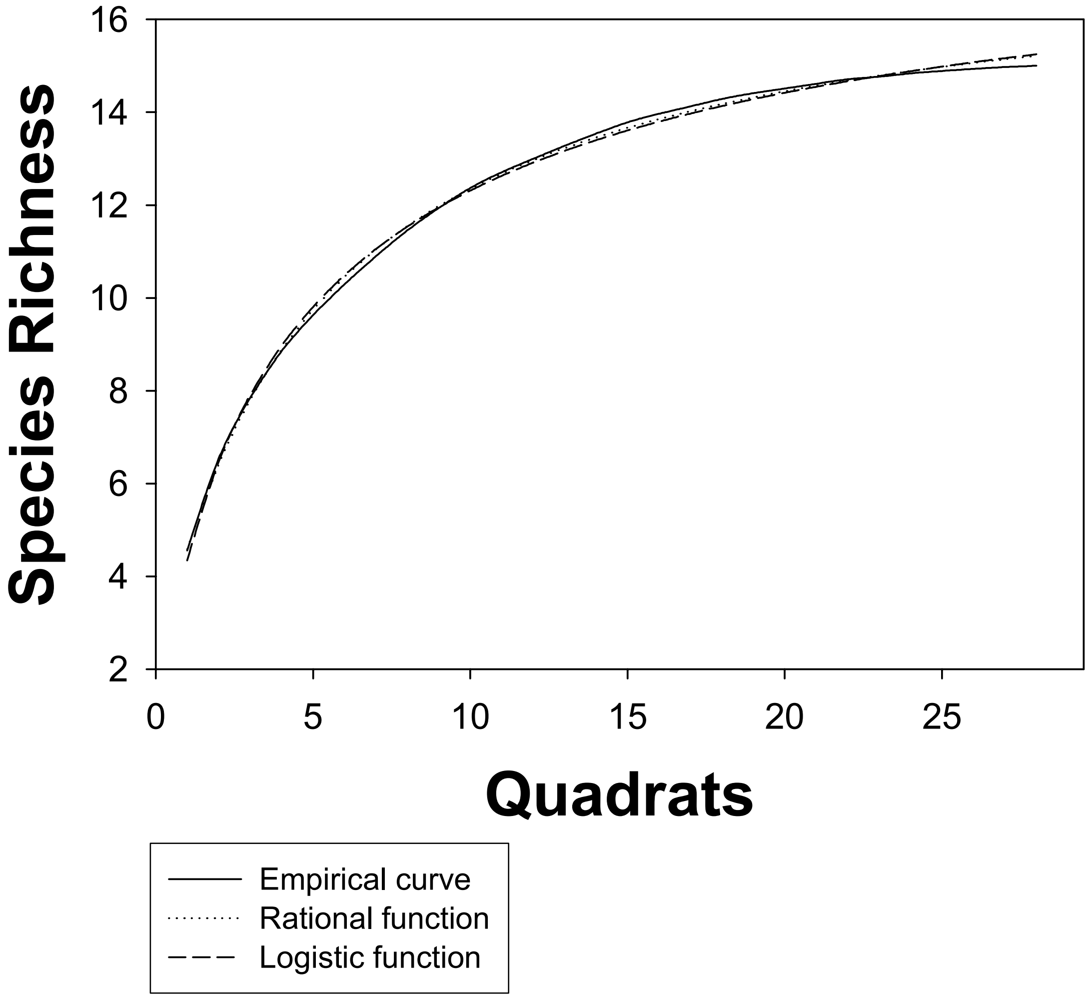


Figure 3.3A. Comparison of the logistic and rational functions with the empirical sample curve for herbaceous species at Adobe Dam Recreation Area.

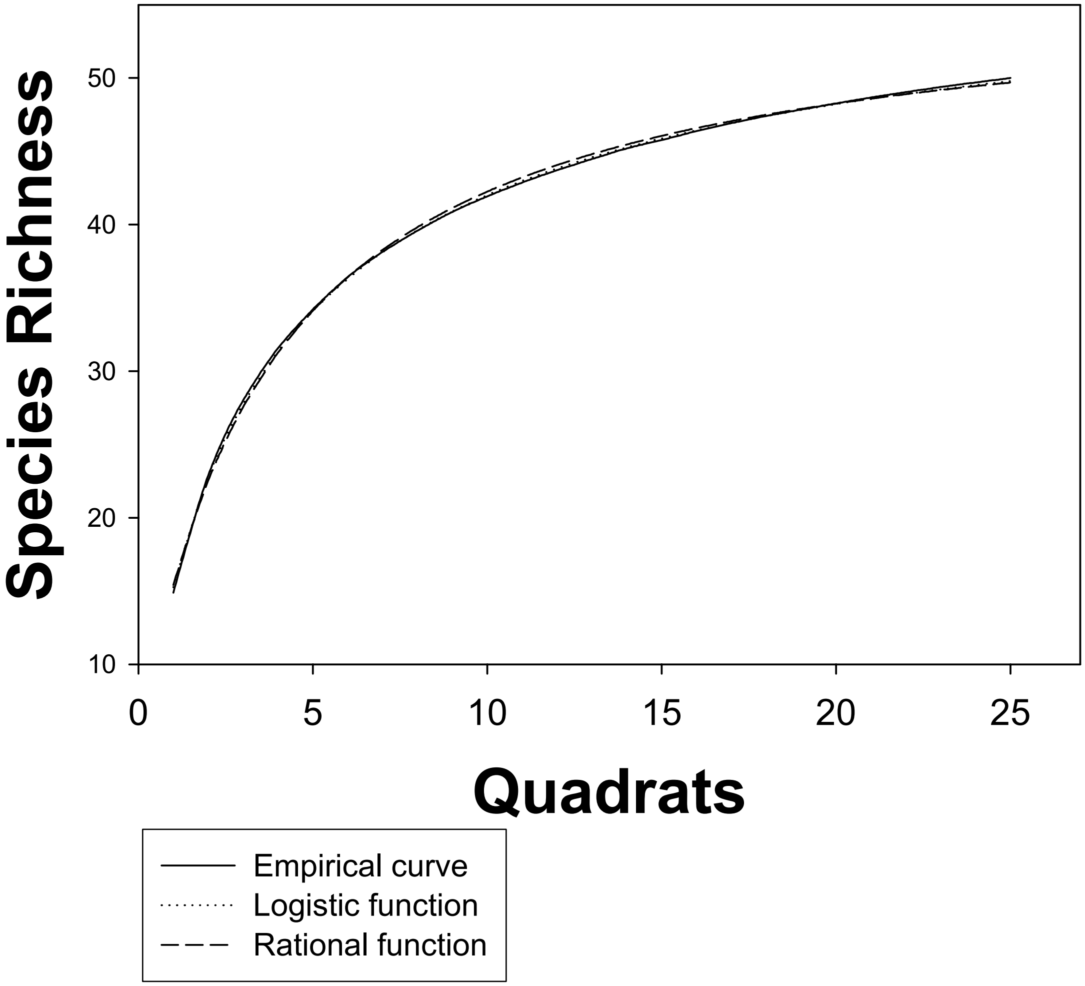


Figure 3.3B. Comparison of the logistic and rational functions with the empirical sample curve for herbaceous species at Lookout Mountain Park.

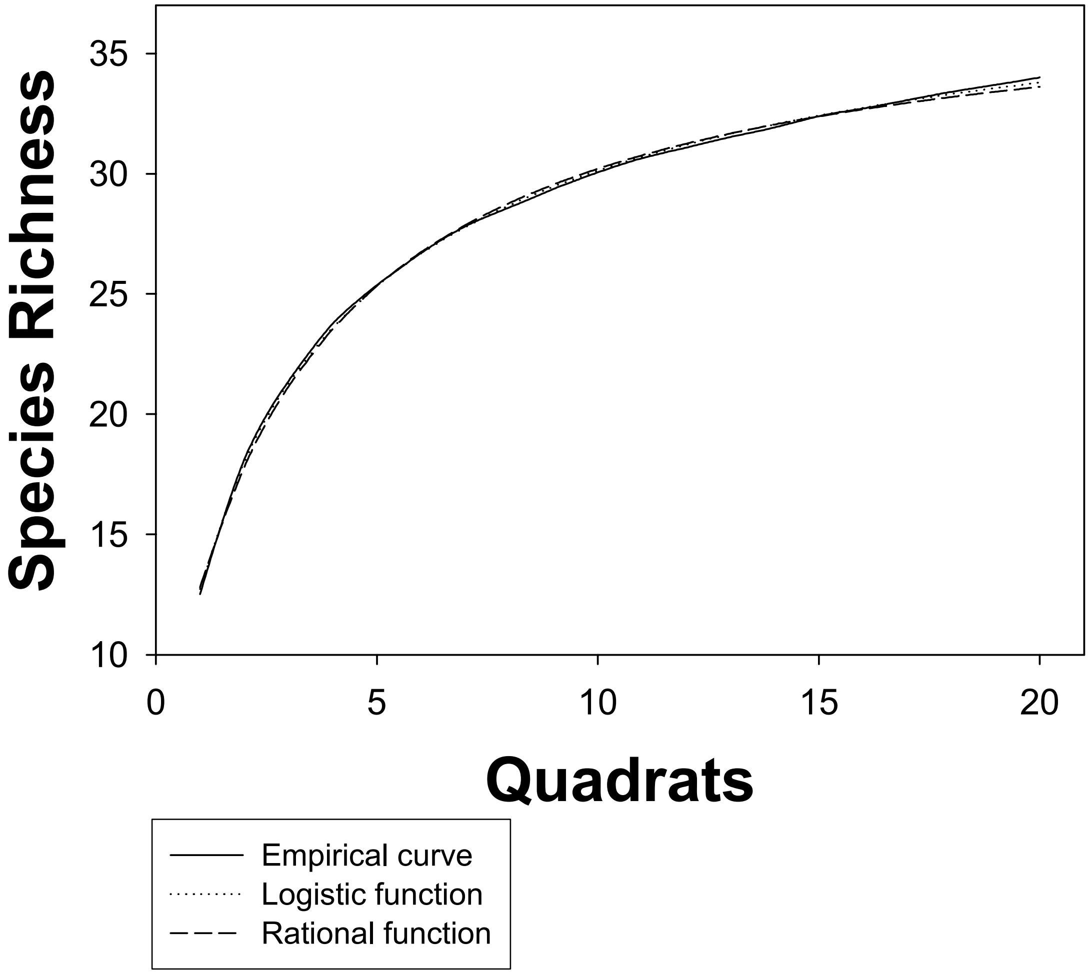


Figure 3.3A. The exponential function best describes the relationship between island area and woody species richness. The semi-log plot is used to better depict the range in point values.

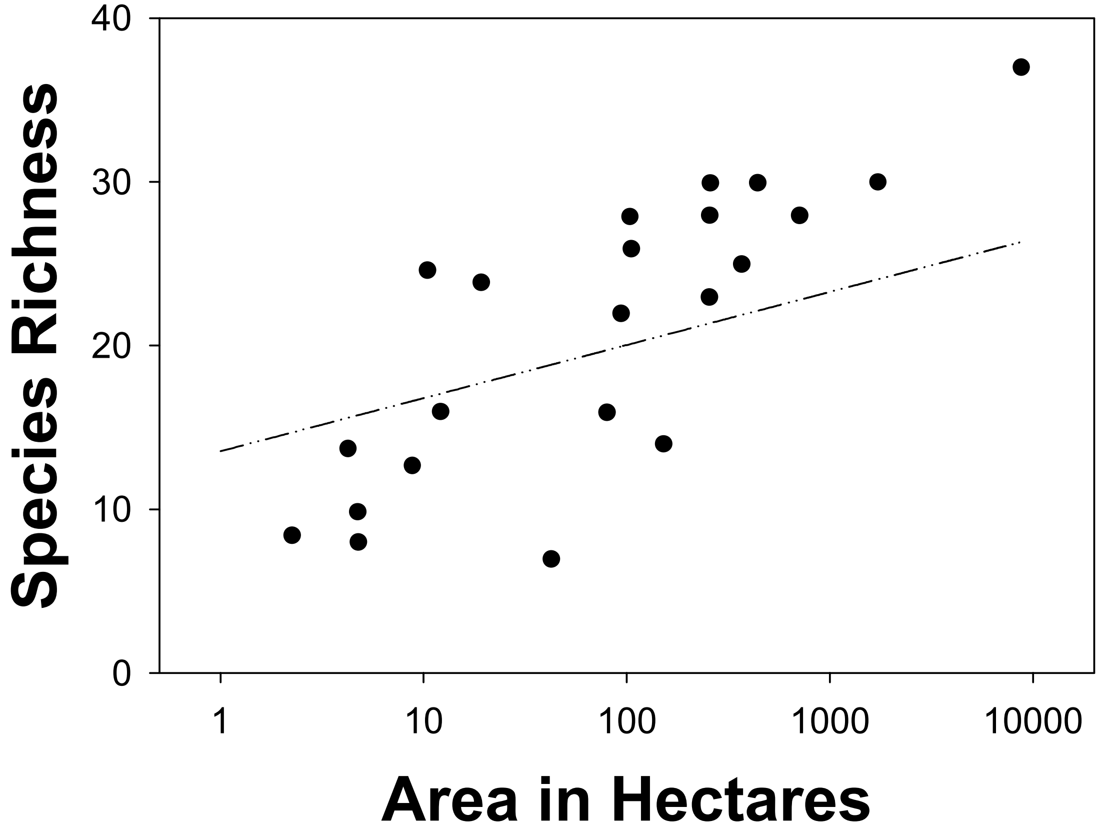


Figure 3.3B. The Monod function best describes the relationship between island area and herbaceous species richness. The semi-log plot is used to better depict the range in point values.

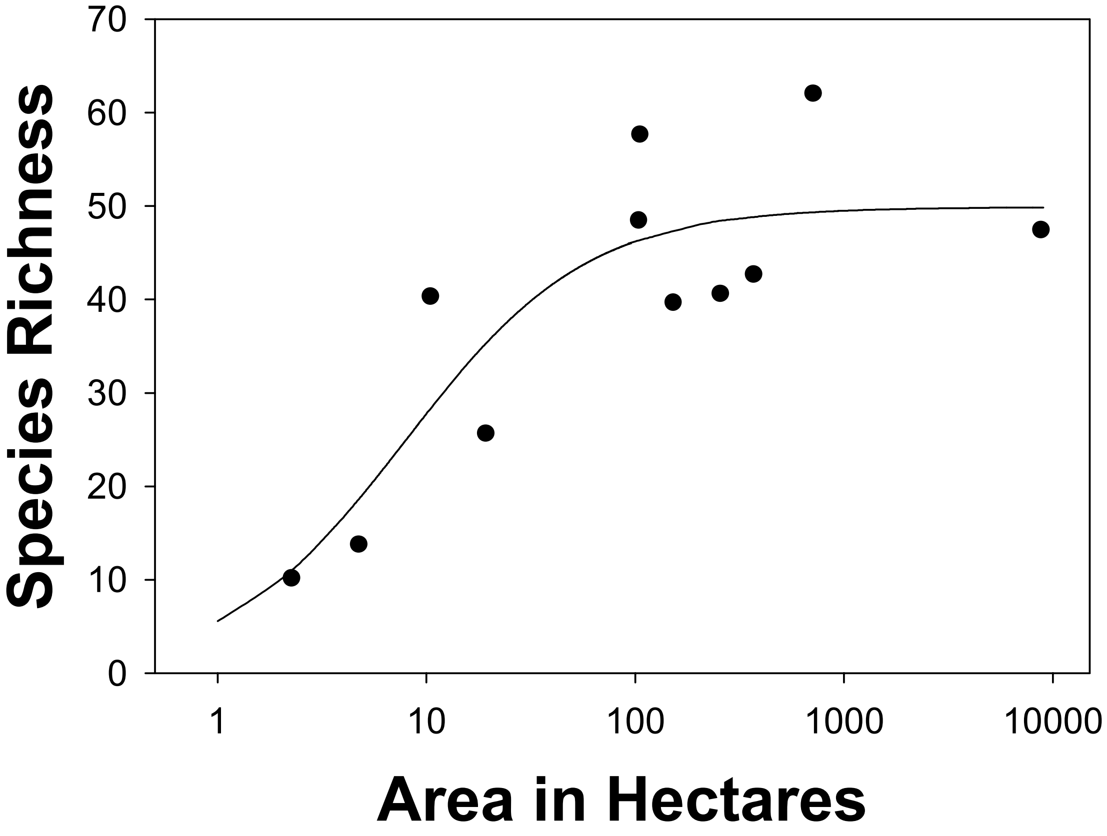


Table 3.5A. Best-fit functions and estimates of woody species richness for the study sites.

Site ID	Best-fit Function	Function Estimate	First-Order Jackknife Estimate	Species Sampled
1	Logistic, Hill, Lomolino	26.1	25.9	22
2	Logistic, Hill	16.4	9.8	8
3	Rational	23.5	22.0	20
4	Gompertz	8.0	8.0	8
5	Logistic, Hill, Lomolino	31.7	28.0	24
6	Logistic		12.7	8
7	Logistic, Hill	18.6	13.7	11
8	Logistic, Hill	92.3	24.6	17
9	Logistic, Hill	26.8	23.9	18
10	Logistic, Hill, Lomolino	8.1	7.0	6
11	Logistic, Hill, Lomolino	32.0	14.0	12
12	Logistic, Hill, Lomolino	37.8	29.9	25
13	Logistic, Hill, Lomolino	31.2	25.0	21
14	Logistic, Hill, Lomolino	23.2	23.0	16
15	Logistic, Hill, Lomolino	63.2	27.9	21
16	Power	109.4	27.9	19
17	Logistic, Hill, Lomolino	38.7	37.0	33
18	Logistic, Hill, Lomolino	33.0	30.0	26
19	Gompertz	7.0	8.4	6
20	Logistic, Hill	21.9	15.9	13
21	Rational	17.6	16.0	15
22	Logistic	57.3	29.9	23
23	Rational	23.6	24.0	22
24	Logistic, Lomolino	48.8	35.8	28
25	Exponential	36.2	37.0	31

Notes: When there is a tie between the logistic, Hill, and / or Lomolino functions, the logistic is used in order to generate a species richness estimate. For site ID 6 (Park of Canals), the best-fitting logistic does not yield a non-negative estimate for areas much larger than the sampled area since the 'c' constant is negative; the second best-fitting power function yields 89.1 species.

Table 3.5B. Best-fit functions and estimates of herbaceous species richness for the study sites.

Site ID	Best-fit Function	Function Estimate	First-Order Jackknife Estimate	Species Sampled
1	Logistic, Lomolino	59.0	57.7	50
2	Gompertz	13.2	13.8	13
8	Rational	42.4	40.3	31
9	Logistic	38.5	25.7	21
11	Logistic, Lomolino	40.3	39.7	34
13	Logistic, Lomolino	47.3	42.7	37
14	Logistic	29.2	40.6	26
15	Rational	43.6	62.1	35
16	Logistic	57.4	48.5	39
17	Logistic	49.7	47.5	40
19	Logistic	9.3	10.2	7
24	Rational	43.7	41.4	36

Notes: When there is a tie between the logistic, Hill, and / or Lomolino functions, the logistic is used in order to generate a species richness estimate. For site ID 9 (Tempe Saltbush patch) herbaceous data, the best-fitting logistic function yields a negative estimate for the total species richness since the ‘c’ constant is negative; the second best-fitting Gompertz estimate of 9.3 is presented here instead.

Table 3.6A. Comparison of abundances and frequencies for species in South Mountain Park sampled for this study and the flora listed in Daniel and Butterwick (1992). Abundance refers to mean number of individuals per quadrats; frequency refers to the percentage of the total 556 quadrats occupied by each species.

Species	Abundance	Frequency (%)	Paper Comments
Acacia greggii	1.7	2.0	Occasional along washes
Ambrosia ambrosoides	1.5	0.7	Occasional to common along washes
Ambrosia deltoidea	18.6	36.5	Occasional to common on slopes
Ambrosia dumosa	2.6	4.7	Occasional to locally common
Argythamnia lanceolata	1.0	3.2	Rare to occasional; (Kearney and Peebles 1960): low shrub
Baccharis sarothroides	1.0	0.2	Rare to common in washes
Bebbia juncea	1.0	0.2	Locally occasional, especially in washes
Brickellia coulteri	1.0	0.2	Rare to occasional
Bursera microphylla	1.5	5.0	Rare to occasional
Carnegia gigantea	1.0	6.5	Occasional to common
Cylindropuntia acanthocarpa	1.8	31.7	Occasional on slopes
Cylindropuntia bigelovii	4.1	10.1	Occasional to locally common
Cylindropuntia leptocaulis	1.0	0.7	Rare to locally occasional
Echinocereus engelmannii	1.4	14.4	Occasional
Encelia farinosa	11.5	62.9	Common throughout, esp. on slopes
Ephedra fasciculata	2.2	7.7	Rare to locally common
Eriogonum fasciculatum	5.1	4.5	Occasional to locally common
Eriogonum wrightii	1.8	0.9	Occasional
Ferocactus cylindraceus	2.5	32.7	Occasional to locally common
Fouquieria splendens	1.3	10.4	Occasional to common
Hibiscus denudatus	2.5	3.1	Rare to occasional
Hymenoclea salsola	2.5	0.7	Occasional to common in washes
Hyptis emoryi	1.8	2.2	Occasional to locally common
Krameria grayi	2.1	32.0	Occasional to common
Larrea tridentata	4.6	78.2	Occasional to common
Lycium sp.	2.2	21.4	Occasional
Mammillaria microcarpa	2.1	9.0	Rare to occasional to locally common
Olneya tesota	1.3	4.9	Occasional to locally common
Parkinsonia microphylla	1.5	32.7	Occasional to common
Senna covesii	2.0	0.4	Rare to occasional
Tamarix ramosissima	2.0	0.2	Locally occasional in washes
Trixis californica	1.0	0.5	Occasional
Viguieria deltoidea	2.2	4.7	Occasional

Table 3.6B. Species listed in Daniel and Butterwick (1992) that were not sampled in this study. Those species that were observed in South Mountain but not captured within quadrats are indicated.

Species	Observed Off Plot	Paper Comments
Abutilon abutiloides	No	Rare
Abutilon incanum	No	Rare to occasional
Aloysia wrightii	No	Rare to locally occasional
Atriplex canescens	Yes	Rare to occasional
Atriplex polycarpa	Yes	Rare to locally common
Bernardia incana	No	Rare to locally occasional
Celtis pallida	No	Rare to occasional along washes
Crossosoma bigelovii	Yes	Occasional to common on slopes
Forestiera shrevei	No	Rare along washes
Galium stellatum	Yes	Rare to occasional
Gymnosperma glutinosum	No	Locally occasional
Isocoma acradenius	Yes	Rare to occasional
Justicia californica	No	Rare along wash (single locality)
Opuntia chlorotica	Yes	Rare to occasional on slopes
Opuntia phaecantha	Yes	Rare to occasional
Parkinsonia florida	Yes	Rare on slopes, locally common in washes
Peniocereus greggii	No	Only one plant seen (minor wash in creosote flats)
Phorodendron californicum	Yes	Occasional in Acacia, Parkinsonia, and Olneya
Prosopsis velutina	Yes	Rare to occasional along washes
Salazaria mexicana	No	Only one plant seen (canyon bottom)
Sueda torreyana	No	Locally occasional
Ziziphus obtusifolia	No	Rare to occasional

Chapter 4: USING LANDSAT ETM IMAGERY TO MAP SONORAN DESERT PLANT COMMUNITY DISTRIBUTION IN THE CAP-LTER STUDY AREA, PHOENIX, ARIZONA

ABSTRACT

Rapid growth of urban areas threatens natural ecosystems occupying the outlying areas beyond the advancing urban fringe. Remote sensing methods offer an opportunity to map this landscape before it is altered by development. This study represents an effort to map the distribution of plant community types across the Central Arizona – Phoenix Long Term Ecological Research (CAP-LTER) site centered in metropolitan Phoenix using Landsat ETM data. A vegetation classification was carried out based on woody vegetation. A system was devised which represented a compromise between providing floristic information and enabling maximal spectral discrimination among community types. Image classification used reference spectra derived from training sites and was carried out on subsets defined by soil surface texture in order to control for the strong background soil signature inherent to arid regions. While groundtruthing revealed that vegetation on clayey soils was mapped to 91% accuracy, other sections produced maps with less accuracy. This study demonstrates that image classification of desert vegetation using only Landsat ETM data is problematic and may not be practical without supporting data, such as radar imaging.

INTRODUCTION

Habitat destruction and development associated with growing populations is a common phenomenon in the modern world. As natural ecosystems are destroyed or their integrity is compromised, it becomes all the more urgent to record ecological resources before they are lost. Additionally, landscape structure is an important influence on the character and functioning of an area's ecosystem. For these reasons, it is particularly crucial to analyze and inventory the landscape elements susceptible to alteration or removal, which are especially threatening at the fringes of urban zones. I produced a vegetation distribution map of Sonoran Desert habitats around the Phoenix metropolitan area using remote sensing methods. Since remote sensing of vegetation in arid regions has been difficult on account of interference from background soil spectra, several steps were taken to maximize the probability of success, including the mapping of vegetation types hypothesized to be spectrally distinguishable and stratification of the image classification process by soil characteristics.

Background

With recent population growth in the United States, metropolitan areas have spread over large proportions of the country so that urbanization now dominates the ecology of many regions. Urban areas are defined as possessing a population density greater than 620 people per square kilometer (Bourne and Simmons 1982); 74% of Americans lived in urban zones in 1989, which is expected to increase 6% by 2025 (Fox 1987, Haub and Kent 1989). This increase in population has been accompanied by an expansion of the urbanized landscape. Between 1960 and 1970, urban land cover increased by nine million acres, and then by 13 million acres in the following decade (Frey 1984).

Rapid urbanization has drastic impacts upon an area’s ecological integrity by eliminating some habitats through development and altering others by introducing or intensifying environmental stressors (McDonnell and Pickett 1990, Rebele 1994). Cities are usually dominated by anthropogenic disturbances that may differ in nature, frequency, or amplitude from natural disturbance regimes. Native species in remnant communities often must resist intense competitive pressures from exotic species benefiting from altered disturbance events and immigration of colonizers from nearby source areas. Trophic imbalances and physiological stressors, including air and water pollution, may imperil the viability of some populations. Political policies can have subtle effects that change the landscape structure, affecting such ecological factors as availability of recruitment sites or the stability and character of the soil.

Given the rapidity of urbanization, remote sensing provides a useful means by which to assess large-scale patterns and track changes through time. Ground-based mapping is time consuming and expensive. New maps must include recently developed areas on the periphery as well as provide updates about existing urban land covers. Satellite images are created continuously, providing a potential source for contemporaneous data. While cities are enormously complicated landscapes, researchers have successfully produced maps of urban land cover from satellite images, usually with the aid of other spatially-explicit data. For example, Ward et al. (2000) classified land cover in Queensland, Australia by assigning types based on the proportion of pixel area covered by vegetation, impervious surface, and exposed soil (Ridd 1995), yielding a map that was 88% accurate. Stefanov et al. (2001) produced a land cover map of Phoenix, Arizona with comparable accuracy in which preliminary class assignments were evaluated and reassigned based on an expert system approach. This method uses GIS data from other sources to construct a series of decision rules allowing the appropriateness of individual pixel assignments to be determined.

Assessment of landscape structure for a large area of interest is a basic requirement for understanding system functioning and implementing sound conservation priorities. Knowledge of landscape structure is the first step for quantitatively understanding how patches interact with each other and is necessary for predicting effects of habitat fragmentation. Remote sensing is immensely useful for tracking changes in time by facilitating comparison of images taken on different dates (e.g. Palmer and van Rooyen 1998, Ward et al. 2000, Robbins 2001, Rudel et al. 2002, Wilson and Sadler 2002). Structural information about the landscape is also useful for implementing a ground-based sampling regime for large-scale studies: without cognizance of resource distribution on the landscape, over- or undersampling of selected patches is a risk (Stohlgren et al. 1997).

Remote sensing is ideally suited for obtaining information about landscape structure that is relevant to conservation priorities. For example, Harris and Asner (2003) analyzed images taken of arid lands of southern Utah and determined that grazing gradients around water sources were evident, even in well-watered years; they observed an increase in photosynthetically-active vegetation with increasing distance from the water source, contrary to what would be observed in the absence of cattle grazing. Tanser and Palmer (1999) used a moving filter, based on the standard deviation of pixel values, to identify areas on an arid South African landscape that had been disturbed. Yool (1998) studied the Trinity site of the first nuclear detonation and found that, after decades, the long-term, lower-intensity impact of cattle grazing had altered the desert vegetation structure more than the quick and extensive disturbance of the blast.

Purpose of Study

The Phoenix metropolitan area is currently one of the largest and most rapidly growing urban centers in the United States. Its population has doubled in the last thirty years (Grimm et al. 2000) and has increased by 40% between 1985 and 1995 to over 2.5 million people (Baker et al. 2001). This population explosion has been accompanied by the large-scale development of agricultural and desert lands for residential, industrial, and commercial uses (Stefanov et al. 2001), which has resulted in the exponential expansion of urbanized area (Jenerette and Wu 2001). Between 1995 and 1998, development extended the urban fringe by about 1 km per year to an average of approximately 30.5 km from the metropolitan center (Gober and Burns 2002). Most new construction occurs at the rural-urban fringe, serving to expand the urban matrix by creating new nodes of urbanization (Whyte 1968, Gober and Burns 2002). With this rampant growth, it is necessary to document the ecological resources lying beyond the city before this landscape is developed.

This project produced a woody vegetation distribution map across undeveloped parcels of outlying desert wilderness, as well as remnant mountain parks throughout the city, contained within the Central Arizona Phoenix Long Term Ecological Research (CAP-LTER) study area (Figure 4.1). This effort sought to create the first accurate classification map of Sonoran Desert vegetation derived from satellite imagery. This map is the first fine-scale depiction of plant community types in the Phoenix region. The map allows for a calculation of the land area covered by each vegetation class, and shows which of these classes are exposed to development pressures.

METHODS

Vegetation classification

In order to determine which vegetation classes were appropriate for use in mapping desert areas of the CAP-LTER site, classification analysis was carried out using woody vegetation data collected throughout the study area. Two datasets were used in this analysis. The Survey 2000 consisted of a stratified random design in which 204 sample plots measured vegetation and other ecological parameters in a multitude of land-covers, including outlying desert environments (Hope et al. 2003, Grimm and Redman 2004). From this set, 72 plots located in undeveloped desert habitat were employed in the analysis. Each plot was a square measuring 30 x 30 m, from which woody individuals (i.e. trees, shrubs, and cacti) were counted and identified to species; the width and length of up to five randomly selected individuals per species were recorded in each plot. The second dataset consisted of a set of 104 samples, collected between 1998 and 2001, concentrated on remnant desert habitat islands embedded within the urban matrix. Samples with five 100-m^2 circular quadrats arrayed along a transect consisted of counts of woody individuals identified to species. For this analysis, data were aggregated by transect (500 m^2).

Since the objective was to determine vegetative classes resolvable by remote sensing methods, the classification represented a compromise between containing the most floristic information possible and having a set of classes that are spectrally distinguishable. The advantage of a cover-based vegetation classification, particularly for use in remote sensing, is that plant cover more adequately represents biomass present in a community than density does (Mueller-Dombois and Ellenberg 1974, Shupe and Marsh 2004). Toward this end, the coverage of each species was estimated as the average area of a circle with diameter equal to the mean of the width and length of each measured individual, and then averaged for each species (Table 4.1). Total coverage for species within each plot was calculated as the mean individual coverage multiplied by the density of individuals. Analyses utilized the relative coverage of each species as a percentage of total vegetative coverage. Vegetative classes were based on analyses using TWINSPAN (PCord; McCune and Mefford 1999), which classifies samples based on iterative dichotomous separation of groups. Nomenclature followed the USDA Plants Database (http://plants.usda.gov).

Image analysis

A Landsat ETM image from August 1999, projected in UTM NAD 27 coordinates, was selected (Figure 4.1). August 1999 was a wet period during the late summer monsoon season in Arizona during which woody vegetation is photosynthetically active and ephemeral herbs and grasses are present. Although an abundant layer of herbaceous groundcover can obscure spectral signatures of woody plants and decrease potential discrimination between communities, the summer herbaceous vegetation is relatively sparse, particularly compared with herbaceous species of the winter / spring assemblage. Hence, late summer offers the potential for a high degree of photosynthetic activity in the woody vegetation without inference from dense herbaceous groundcover.

The image was processed and analyzed using ERDAS Imagine software (2002). Prior to image classification, all ground cover features not associated with undeveloped desert land were extracted from the scene (Figure 4.2). This includes all impervious and landscaped surfaces associated with urban areas and exposed soil related to industrial sites, clearings for new urban development, and major disturbances (Ward et al. 2000). A LANDISCOR color aerial photograph (2000) covering the study area was used as an interpretive guide for ground features in order to aid in extraction of urban features. A supervised classification procedure was used in order to assign vegetation classes to the image pixels. This method involves creation of spectral signatures for each candidate class based on training sites in the field, which contain vegetation indicative for each class. These class signatures are used as a reference for the assigning of community types to pixels by the classifier tool. The maximum likelihood decision rule was used to discriminate between vegetation types, which incorporates variability of classes into the process and generally offers the highest accuracy of the ERDAS Imagine alternatives (ERDAS Field Guide 1997).

A pilot study, which used field sampling locations used in the TWINSPAN classification as training sites, yielded poor results, so several corrective actions were instituted in order to increase accuracy. Given the area of pixels (900 m^2), the original field sample plots were too small to use as training sites without significant risk of mixing vegetation types. Therefore, a separate effort was made to collect training samples of each vegetation type over an area encompassing multiple pixels, which were recorded with GPS and designated during the training process. Since these samples formed the reference source for all vegetation in the study area, each training site was selected as an unambiguous representative of a given community type. Multiple training sites, scattered across the landscape as much as possible, were used for each reference signature. Whenever feasible, a minimum set of pixels equal to ten times the number of bands in the image, 70 in this case, was utilized in order to create reference spectra, as recommended by Congalton (1991).

The larger-scale thermal band 6, which has a resolution of 120 m rather than 30 m inherent to the other bands, was dropped and replaced with a Soil Adjusted Vegetation Index (SAVI) layer calculated from the Landsat image. SAVI is a modification of the Normalized Difference Vegetation Index (NDVI), which is commonly used to detect photosynthetically active vegetation by virtue of relatively high reflectance of near-infrared and low reflectance of visible red light. SAVI includes a correction for soil reflectance, which is especially useful given desert surfaces' high proportion of exposed soil.

Efforts were made to control for the soil substrate in the image classification so that the vegetation would be the dissimilar variable between pixels. Surface soil texture influences the scattering of incident light. GIS-based soil maps were obtained from the Natural Resources Conservation Service (Soil Survey Geographic Database 2002). These maps were used to divide the total study area into sections based on texture characteristics: sandy, loamy, clayey, and coarse particle dominated soils (Figure 4.3).

An additional unlabeled class, roughly coinciding with the shallow bedrock of mountainous areas, was divided further into sections for individualized treatment based on predominant reflectance character. The intention of this step was to aggregate sites with similar geological reflectance features into a common classification effort. Each separate patch was analyzed using unsupervised classification in which reference spectra are not determined by the user. Instead, the classifier groups pixels based on spectral similarity apparent from the image itself with only the total number of classes selected by the user (eight classes in this case). A GIS layer depicting geology (Arizona Land Resources Information System) was utilized in order to visually ascertain correspondence between geological formations and the image classification. If there was a correlation, the candidate area was split into separate parts; if there was no apparent correlation, the whole patch was retained. Next, separate patches were combined into a common view, the unsupervised classification was repeated, and areas without evidence of spectral divergence were aggregated. This process resulted in seven different study sections, each of which was mapped on its own with reference spectra derived from training sites located within each section, if possible. If a hypothesized vegetation type was not located during field surveys, a signature from another section was used; this was necessary for the final map in one case: remnant habitat islands excluding South Mountain Park, Squaw Peak Recreation Area, and Papago Park.

Assessment of image classification accuracy was performed through field sampling in a stratified random manner. Given the large extent of the study area and prohibitions for access in many locales, a multitude of groundtruthing points were selected from accessible areas. From this set, 700 points were randomly chosen for the field survey. Registration of Landsat pixels is not perfect; image rectification and restoration from raw data necessarily distorts actual positioning of pixels to a slight degree. For this reason, points were designated from clusters of similarly classed pixels. Coordinates were chosen from each image section, which allowed for a separate accuracy assessment for each section's map. Vegetation within a 20 m radius from each point was surveyed to determine the appropriate community type. Since the pixel array represents a two-dimensional depiction of the landscape, training site radius was lengthened on slopes to allow for a horizontal distance of 20 m. Post-groundtruthing procedures were used in order to maximize accuracy, including refinement of training areas, deletion of classes found to be absent or rare in each study section, and aggregation of classes lacking strong discrimination as revealed by groundtruthing results, followed by reclassification of the scene.

Accuracy assessment was reported using an error matrix (Congalton and Green 1999). Overall accuracy is a holistic summary of how predicted class membership agrees with field observations from the groundtruthing effort, and is calculated as the sum of the diagonal cells divided by the total survey sites used to assess that particular classification. Producer's accuracy demonstrates how well survey site pixels of a particular vegetation type are classified, and equals the number of correctly classified sites divided by the total number of survey sites for that type, the column total (Lillesand and Kiefer 2000). User's accuracy represents the probability that a classified pixel indicates the correct vegetation type in the field, and equals the number of correctly classified sites divided by the total number of sites that actually belong to that class, the row total. Since accuracy assessment was not feasible for the more remote or inaccessible locations of the Sierra Estrella Mountains, the McDowell Mountains, and the sandy soil of the Hassayampa River, vegetation maps for these areas were not included in this paper since their accuracy is unknown.

RESULTS

Vegetation classification

Initial vegetation classification yielded ten vegetation types (Table 4.2A). Three types with a single species attaining greater than 60% of the total vegetation cover were designated as *Larrea*-, *Ambrosia*-, or *Encelia*-dominated scrub. If two of these common species occupied the same vegetation with (1) neither species surpassing 60% and (2) the coverage ratio equaling less than 2:1, the community was designated as being either *Larrea-Ambrosia* or *Larrea-Encelia* scrub. There were no samples containing *Ambrosia* and *Encelia* as codominants. Vegetation containing an abundance of large shrubs, trees, and / or cacti not dominated by the previous three species was classified as mixed scrub. The Lower Colorado River Valley (LCRV) and Arizona Upland mixed scrub were separated by the presence of species endemic to or more frequent in the Arizona Upland subdivision of the Sonoran Desert, such as *Calliandra eriophylla*, *Simmondsia chinensis*, and *Eriogonum fasciculatum*.

Use of these community types in a pilot project produced poor results. It was hypothesized that the multitude of classes and their spectral ambiguity contributed to poor discrimination between vegetation types. It was originally expected that the greater biomass and density observed in the Arizona Uplands vegetation in concert with dissimilar, widespread species would distinguish the two communities. However, this was not the case and the LCRV and Arizona Upland types were combined into a single category: mixed scrub. Distinguishing between dominant and codominant types was also problematic. It was hypothesized that this difficulty arises as a result of the sparse nature of *Larrea* foliage, with long spreading branches and relatively low leaf cover. This scarcity of vegetative tissue counteracts the relatively large size of *Larrea* in terms of canopy width and length. With the goal of maximizing spectral divergence, communities with codominance between *Larrea* and *Encelia* or *Ambrosia* were reclassified into either *Encelia*- or *Ambrosia*-dominated scrub, under the assumption that *Larrea* would not significantly interfere with these spectral signatures. This aggregation of classes resulted in six vegetation types, five of which were used for mapping (Table 4.2B).

Riparian woodlands and *Atriplex*-dominated scrub are two communities with more limited distribution than the other four. *Atriplex polycarpa* had once covered large sections of the Salt and Gila River valleys (Turner and Brown 1982). This species and its associated vegetation type have since been converted to croplands and *Atriplex*-dominated scrub is now very rare in the study area. Accordingly, the *Atriplex*-dominated scrubland was not included in the image classification. Riparian woodlands currently exist in the Phoenix area, but their distribution is limited to strands along the Salt and Gila Rivers. There were only two samples from riparian area, one of which surveyed the less common *Sarcobatus*-*Lycium* community, compared with more widespread deciduous forest stands. Training sites for the image classification were located in riparian communities and included stands of other riparian species, such as *Populus fremontii*, *Salix gooddingii*, and *Tamarix ramosissima*.

Image classification

Accuracy of the classified images ranged from very good to very poor. The most accurate classification (overall accuracy 91%, Table 4.3) was for vegetation on clayey soils (Figure 4.4), which occupies a limited area primarily located on the plains northwest of the White Tank Mountains as roughly parallel linear strands. This favorable result was almost certainly influenced by the simplicity of vegetation on these soils. The two classes found to occupy this habitat, *Larrea*-dominated scrub and mixed scrub, represent low and high extremes of vegetative biomass, respectively. In Papago Park, where the same two vegetation types were mapped (Figure 4.5), overall accuracy was 70% (Table 4.4). Most of the error in this classification arose from overestimation of the coverage of the mixed scrub. Papago Park was likely more problematic because of its greater topographical heterogeneity and lower vegetation density of the mixed scrub, providing less contrast between class spectral signatures.

Other sites' accuracies, which used three or more classes, appeared to suffer from a diversity of reference signatures from which to select. All other sites had lower accuracies than Papago Park, with the exception of the portions of the White Tank Mountains dominated by TKgm geology (Figure 4.6, Table 4.5), which was 73% accurate overall. The TKgm substrate is dominated by light colored granitic rocks commonly containing muscovite and garnet and associated with abundant pegmatic dikes. This map's success is likely attributable to high vegetation densities allowing dominant plants to form a more robust signature.

For many of the maps, post-classification revisions were able to improve classification accuracy. The simplest revision involved excluding classes that analysis showed to be very rare or absent in that section; their inclusion greatly lowered overall accuracy for the maps. For example, excluding *Encelia*-dominated scrub from the classification of vegetation on coarse-particle soils allowed the overall accuracy to increase from 55 to 63% (Figures 4.7, 4.8; Tables 4.6, 4.7). Groundtruthing found that only 1 out of 30 survey sites predicted to be this vegetation type was correct. Overall accuracy for the Squaw Peak Recreation Area increased from 41 to 57% when the *Encelia*-dominated scrub was excluded (Figures 4.9, 4.10; Tables 4.8, 4.9).

South Mountain Park was split into an eastern and western half due to spectral divergence and dissimilar geology. The west is dominated by Precambrian metamorphic rocks formed about 1.7 billion years ago and the east is primarily Cenozoic igneous rocks developed about 25 million years ago (Daniel and Butterwick 1992). Since *Ambrosia*-dominated scrub was not found in the western half, it was dropped from the classification (Figures 4.11, 4.12; Tables 4.10, 4.11). However, overall accuracy was minimally increased by five percent to 66%. The nine points originally attributed to this community were split roughly equally between the *Larrea*-dominated scrub and mixed scrub with negligible improvement.

Several steps were taken to improve accuracy for the eastern half of South Mountain Park (Figures 4.13, 4.14; Tables 4.12, 4.13). Initial scouting located no suitable training sites to generate the *Larrea*-dominated scrub reference signature. Therefore, the signature from the western half of the park was used in order to detect this vegetation type in the eastern half. The groundtruthing survey failed to find any of this vegetation in the field. All pixels assigned to *Larrea*-dominated scrub were located on the rocky, steep north-facing slope of the mountain, which was actually dominated by mixed scrub. While the mixed scrub signature had performed perfectly in terms of user's accuracy, it failed to respond to this particular slope habitat. A second mixed scrub signature, sampled from the slope and treated as a separate class, performed well in matching this north-facing slope habitat and was integrated into a composite mixed scrub class with the original. This resulted in favorable producer's and user's accuracies for the mixed scrub, at 88 and 82%, respectively. A refinement to the *Ambrosia*-dominated scrub signature was also made by incorporating two additional training sites located at the base of the south-facing slope. Producer's accuracy increased somewhat for *Ambrosia*-dominated scrub, though at the expense of *Encelia*-dominated scrub. Overall accuracy in the eastern half of South Mountain Park increased from 50 to 68%.

Similar refinements to the *Ambrosia*-dominated scrub signature in the loamy soils habitat failed to yield improvements for this map, which had an overall accuracy of 60% (Figure 4.15, Table 4.14).

By far, the worst classification results occurred for the remainder of the remnant habitat islands (Figure 4.16; Table 4.15). By virtue of their limited size and the paucity of favorable training sites for use in generating reference signatures from within each remnant, training sites were shared among the aggregate. Geological maps indicated that these islands were dominated by undifferentiated metamorphic rock (Xm), which, along with general field observations, suggested they could be treated and classified en masse. However, overall accuracy for the group was 40%, with overall accuracy of individual islands ranging from 19 to 50%.

The individual maps revealed appreciable differences in vegetation type distribution across the study area (Table 4.16A, B). *Larrea*-dominated scrub was common (> 44%) on plains chiefly composed of loamy and clayey soils and in Papago Park; *Ambrosia*-dominated scrub was most frequent on coarse particle soils and in the Squaw Peak Recreation Area. *Encelia*-dominated scrub was observed in the more rocky areas, such as the White Tank mountains and several of the remnant patches, but lacking in the plains. Mixed scrub was found in all map sections to varying degrees. Overall, mixed scrub and *Ambrosia*-dominated scrub were the most common vegetation types, with *Larrea*-

dominated scrub attaining intermediate frequency. Riparian woodland and *Encelia*-dominated scrub were the rarest vegetation types.

DISCUSSION

Vegetation classification

Several authors have produced Sonoran Desert vegetation classifications (Table 4.16). The main difference between these systems is the scale to which each characterizes the vegetation and the degree of floristic detail conferred. Turner's (1974) classification is the most general and corresponds to the large-scale geomorphology of the Salt River valley and the surrounding mountains. Turner generally named desert communities by the most common, representative species. Thus, the paloverde-saguaro community is so named despite the fact that, at small-scales, these species may be absent. The present study's classification is similar Turner's system, with the exception that Turner lacks vegetation types dominated by *Ambrosia deltoidea* or *Encelia farinosa*. Since the *Encelia*-dominated scrub is virtually restricted to topographically heterogeneous habitats, it would likely have been considered a variant stand of the paloverde-saguaro community. The *Ambrosia*-dominated scrub was undifferentiated between the paloverde-saguaro and the creosotebush communities, and overlaps with both types on the Turner (1974) map.

Brown et al. (1982) produced a vegetation classification that is comprehensive for the Southwest region and represents every type detected in the Phoenix area. It contains a much higher level of detail with attention given to the more specific assemblages of species observable in a localized area. Brown's classification communicates more floristic information than this study's system. However, Brown's classification would be difficult, if not impossible, to implement using the remote sensing methods available for this analysis.

Image classification

Image analysis and classification in desert environments is truly a challenge due to the low absolute coverage of vegetation and high soil reflectance, which can obscure vegetation signatures. This scarcity becomes problematic for image analysis below about 30% plant cover (Okin et al. 2001). Additionally, nonlinear mixing of light can obscure vegetation spectra whereby reflected light interacts with multiple surfaces (Ray and Murray 1996). The nature of desert vegetation can also complicate classification since spectral characteristics can vary between and among species, and some desert plants possess adaptations that avoid surface contact with light in order to reduce heat load (Gates et al. 1965, Okin et al. 2001). Standing plant litter and living non-photosynthetic tissues also add variability to pixel reflectance (Asner et al. 2000, Harris and Asner 2003). Nagler et al. (2000) reported that the cellulose and lignin of plant materials contains an absorptive feature at a 2.1 micron wavelength, the depth of which can be used to assess contribution of plant litter; however, this information is only useful when using sophisticated techniques, such as spectral mixture analysis, and likely would have limited applicability to supervised image classification.

Stratification by soil texture class sought to compensate for the strong background signature from the soil, though this may have limited utility when vegetation is especially sparse. Despite the bright soil reflectance, vegetation indices are capable detecting patterns if the background is fairly constant (Harris and Asner 2003). Use of the SAVI layer in this study was intended to take advantage of this possibility. Additionally, the vegetation types derived for this study were designated with spectral separability in mind. It was hypothesized that a gradient in biomass from *Larrea*-dominated scrub to mixed scrub would facilitate classification. While accuracies were not optimal, the classifier was able to designate the majority of pixels correctly for most of the subset classifications.

There have been other efforts to map Sonoran Desert vegetation. Border (1999) used Landsat TM imagery and Reeves (1999) used the hyperspectral Airborne Visible Infrared Imaging Spectrometer (AVIRIS) in order to map vegetation in the McDowell Mountains northeast of Phoenix and Scottsdale. Both authors obtained poor accuracy. Remote sensing in extremely mountainous terrain can be difficult since cast shadows on north-facing slopes yield less light to sensors than sunlit south-facing slopes, which increases spectral variability (Giles 2001). Correcting this topographical shadowing effect involves complex procedures. This complication can be mediated to some extent, however, if vegetative type and slope are highly correlated. Their efforts were also complicated by the designation of numerous, finely-divided vegetative types that are not resolvable in this environment.

On the other hand, Shupe and Marsh (2004) successfully generated a map of Sonoran vegetation on the US Army Yuma Proving Grounds. Their overall accuracy for their map of 12 vegetation classes attained 88%. However, this achievement was only possible when they used Landsat TM imagery in conjunction with elevation data and synthetic aperture radar (SAR) imagery. When only the Landsat TM data was analyzed, accuracy was 56% for cover-based communities and 61% for density-based communities. SAR requires expertise for use and is far less available than Landsat TM data. These authors were also assisted by their location being exclusively in the Lower Colorado River Valley (LCRV) subdivision of the Sonoran Desert (Shreve and Wiggins 1964, Turner and Brown 1982), which has the most arid conditions and simplest botany of the subdivisions. Phoenix occurs at the transition between the LCRV and the Arizona Upland, which is the wettest and physiognomically most complex of the subdivisions. While the authors used 12 classes, some of these were redundant and were bundled into four groupings for alternative classifications.

Conclusion

This effort attempted to construct a fine-scale vegetation distribution map for undeveloped portions of the CAP-LTER study area in and around metropolitan Phoenix. Using empirical data on vegetation gathered within this area, community types were delineated to be used as reference for a supervised classification of a Landsat ETM image of the vicinity’s desertlands. The plant community types derived were designed to provide floristic information while enabling the spectral discrimination essential to perform an image classification. In order to control for the dominating effect of exposed soil reflectance that has complicated remote sensing in arid environments, the image was divided and classified separately using training and groundtruthing sites from within each area. Accuracy was highly variable, with only vegetation in clayey soils attaining a high accuracy of 91%. Other subsets were 70% accurate or less. Other studies have had difficulty mapping desert vegetation using Landsat images alone. Use of other supporting data, such as elevation data and radar images, is likely necessary for producing accurate vegetation maps in desert environments.

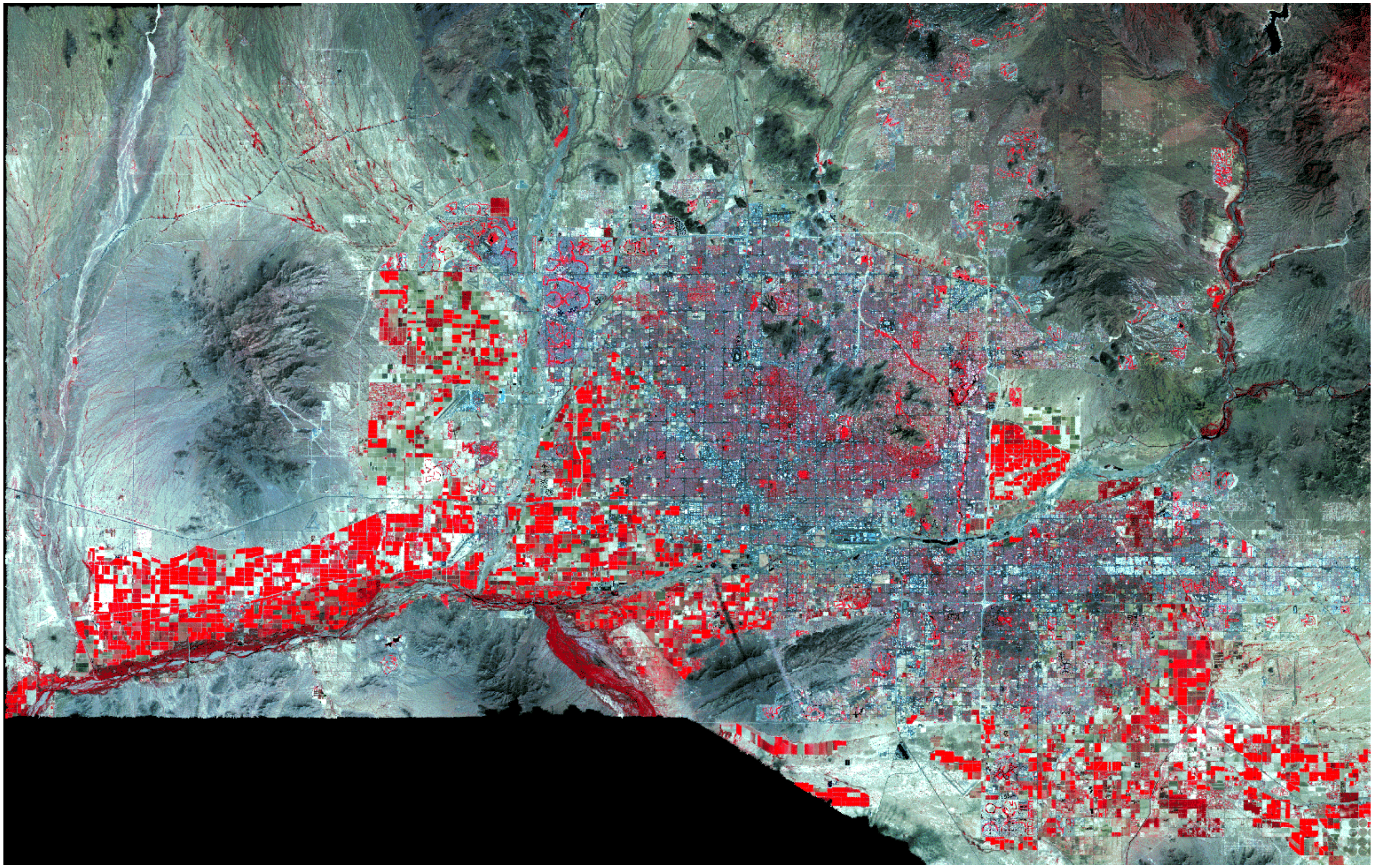


Figure 4.1. Landsat ETM image of the CAP-LTER study area from August 1999.

Table 4.1. Statistics for the individual plant coverage of common woody species.

Species	Mean (m^2)	Standard Deviation
Acacia greggii	4.72	5.18
Ambrosia deltoidea	0.67	0.40
Ambrosia dumosa	0.63	1.44
Baccharis sarothroides	0.53	0.45
Calliandra eriophylla	0.53	0.41
Cylindraceus acanthocarpa	0.91	1.13
Cylindraceus bigelovii	0.34	0.40
Cylindraceus fulgida	0.39	0.41
Echinocereus engelmanii	0.08	0.08
Encelia farinosa	0.62	0.54
Ephedra fasciculata	1.05	0.69
Eriogonum fasciculatum	0.58	0.54
Ferocactus cylindraceus	0.36	1.42
Fouquieria splendens	1.74	1.60
Hymenoclea salsola	0.44	0.29
Hyptis emoryi	1.21	1.15
Krameria grayi	1.13	0.79
Larrea tridentata	3.98	3.82
Lycium sp.	2.48	2.48
Olneya tesota	17.18	9.98
Parkinsonia microphylla	14.66	13.40
Prosopsis velutina	12.28	12.90
Simmondsia chinensis	3.02	1.94

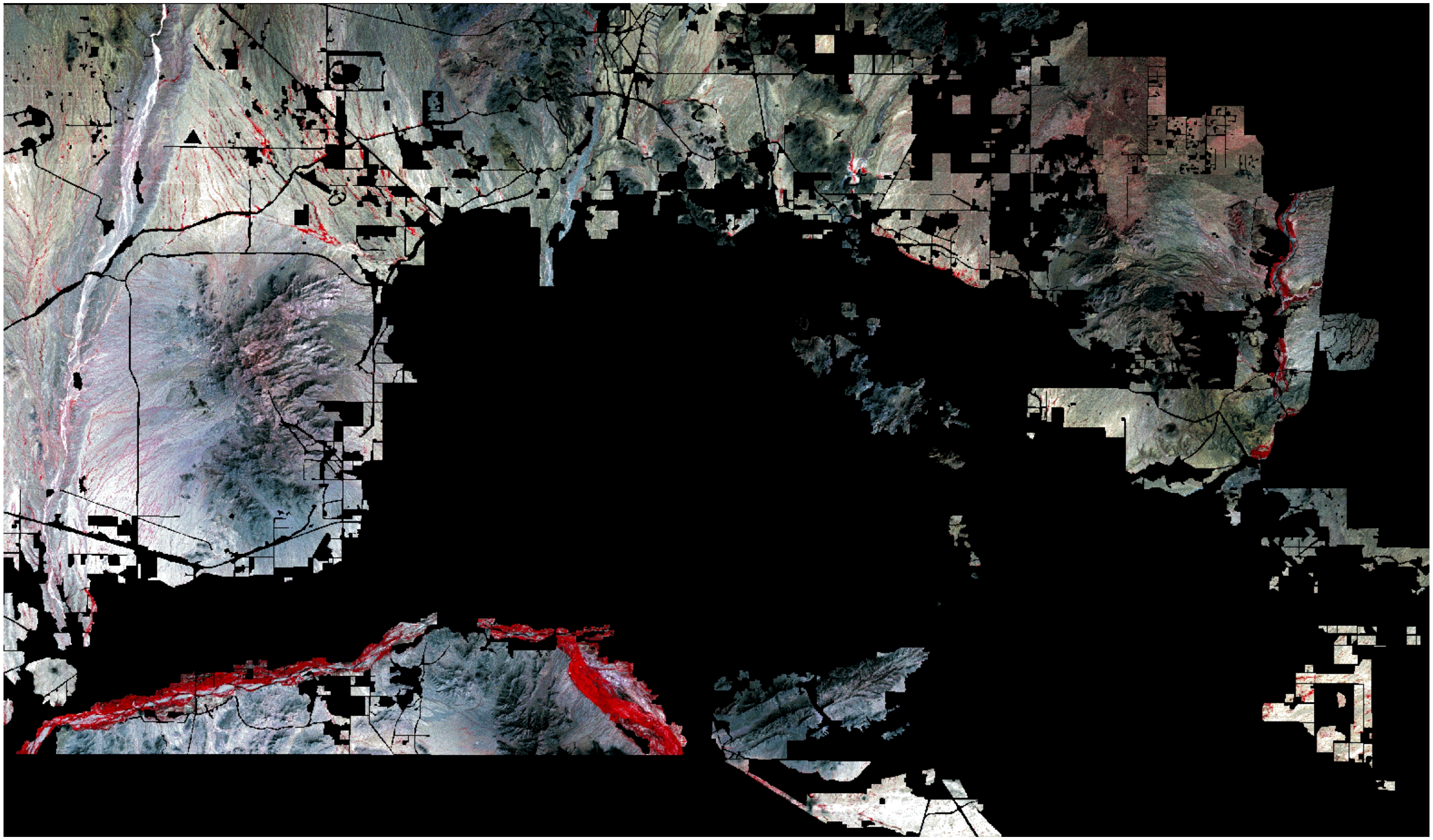


Figure 4.2. Landsat ETM image after extraction of urban features.

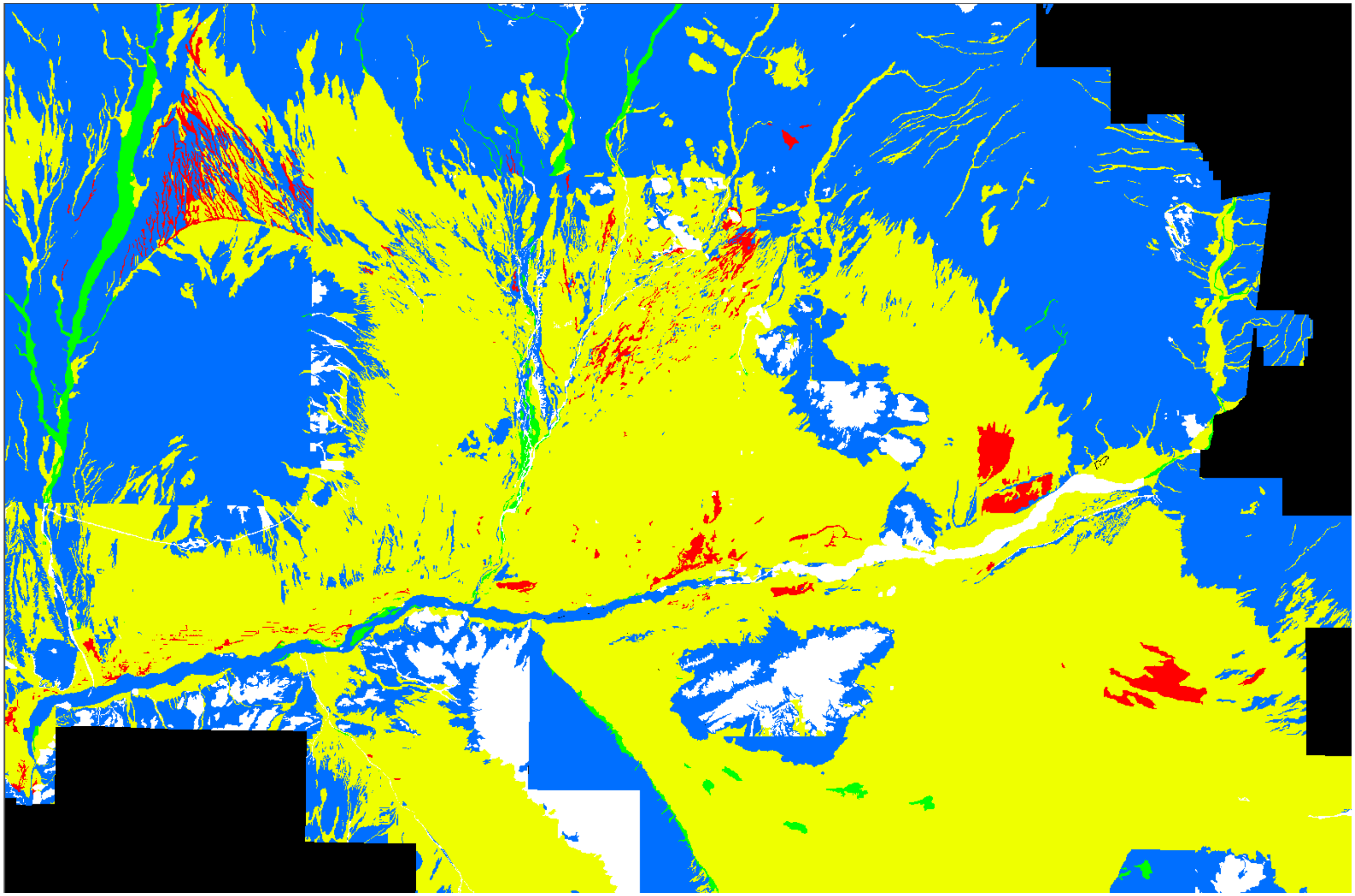


Figure 4.3. Distribution of soil surface texture classes in the CAP-LTER study area. Clayey soils are red, sandy soils are green, loamy soils are yellow, coarse particle soils are blue, and unlabeled polygons are white.

Table 4.2A. Comparison between the preliminary and finalized plant community classification.

Original Classification	Revised final classification
Larrea-dominated scrub	*Larrea*-dominated scrub
Ambrosia-dominated scrub *Larrea-Ambrosia* codominant scrub	*Ambrosia*-dominated scrub
Encelia-dominated scrub *Larrea-Encelia* codominant scrub	*Encelia*-dominated scrub
Lower Colorado River Valley mixed scrub Arizona Upland mixed scrub	Mixed scrub
Sarcobatus-Lycium riparian community	Riparian woodland
Atriplex-dominated scrub	*Atriplex*-dominated scrub

Table 4.2B. Vegetation classification used for mapping.

Community Type	Common Species	Frequency (%)	Mean Relative Cover
Larrea-Dominated Scrub 55 samples	*Larrea tridentata*	100	0.81
	Ambrosia deltoidea	64	0.07
	Parkinsonia microphylla	34	0.04
	Ferocactus cylindraceus	33	0.001
	Krameria grayi	27	0.01
Ambrosia-Dominated Scrub 34 samples	*Ambrosia deltoidea*	100	0.54
	Larrea tridentata	91	0.26
	Cylindropuntia acanthocarpa	68	0.02
	Parkinsonia microphylla	53	0.07
	Encelia farinosa	35	0.01
Encelia-dominated Scrub 7 samples	*Encelia farinosa*	100	0.52
	Larrea tridentata	86	0.29
	Parkinsonia microphylla	86	0.11
	Ferocactus cylindraceus	86	0.01
	Ambrosia deltoidea	43	0.03
Mixed scrub 75 samples	*Larrea tridentata*	76	0.19
	Lycium sp.	71	0.04
	Parkinsonia microphylla	69	0.23
	Ambrosia deltoidea	67	0.11
	Encelia farinosa	67	0.06
Riparian woodland 2 samples	*Sarcobatus vermiculatus*	50	0.47
	Salix gooddingii	50	0.27
	Prosopsis velutina	50	0.17
	Baccharis sarothroides	50	0.04

Note: Riparian woodlands are less common than other community types and what is sampled here is somewhat atypical; other widespread species include *Populus fremontii*, *Tamarix ramosissima*, *Suaeda torreyana,* and *Platanus wrightii.*

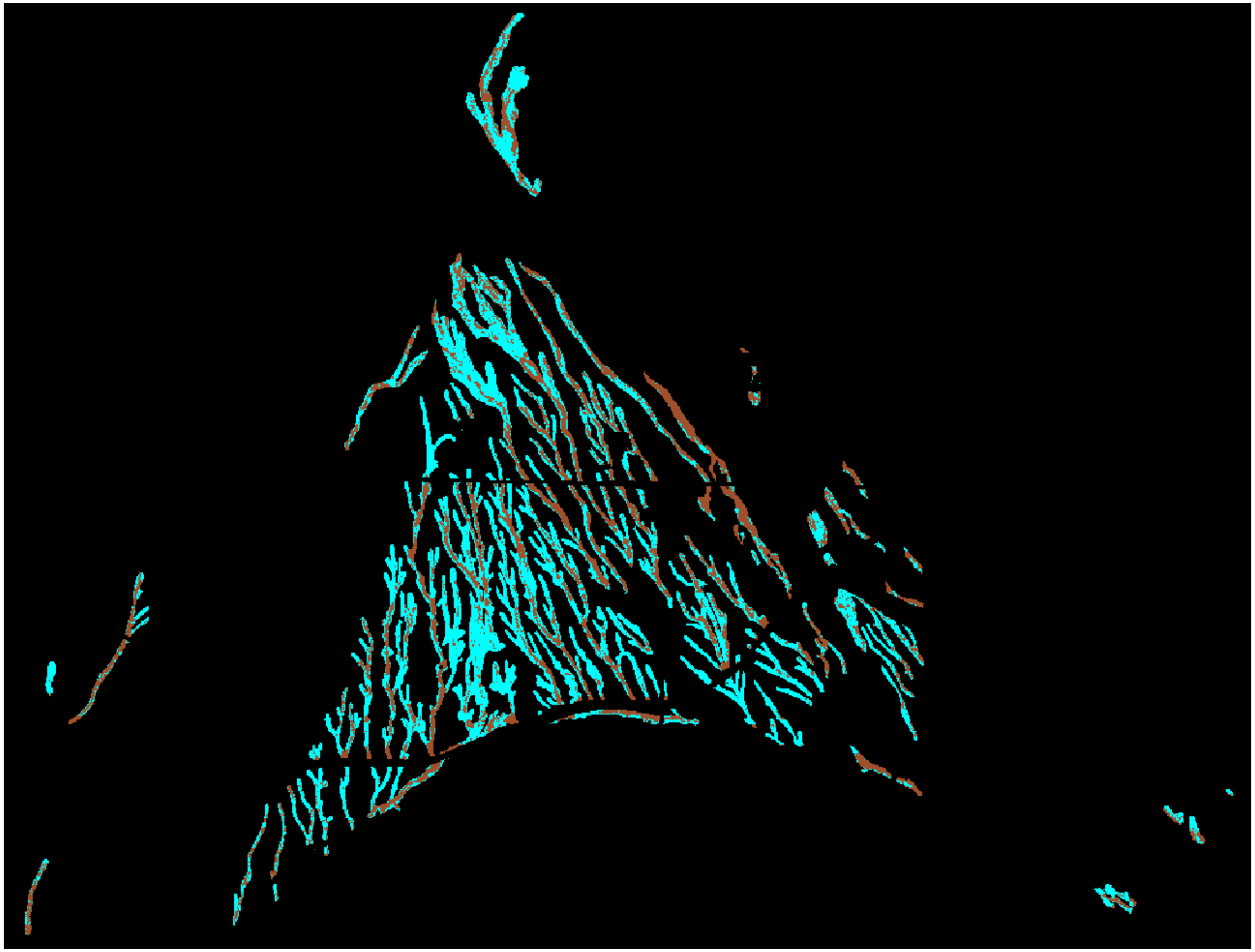


Figure 4.4. Vegetation map for desert land dominated by clayey soils. This area is located on the plains northwest of the White Tank Mountains. *Larrea*-dominated scrub is cyan and mixed scrub is brown.

Table 4.3. Error matrix for the classification of vegetation in environments with clayey soils.

	Field Observations		
Predictions	*Larrea*-dominated	Mixed scrub	Row Total
Larrea-dominated	15	2	17
Mixed scrub	1	15	16
Column Total	16	17	33

	Producer's Accuracy	User's Accuracy
Larrea-dominated scrub	94%	88%
Mixed scrub	88%	94%
		Overall accuracy: 91%

Figure 4.5. Vegetation map of Papago Park. Larrea-dominated scrub is indigo; mixed scrub is brown.

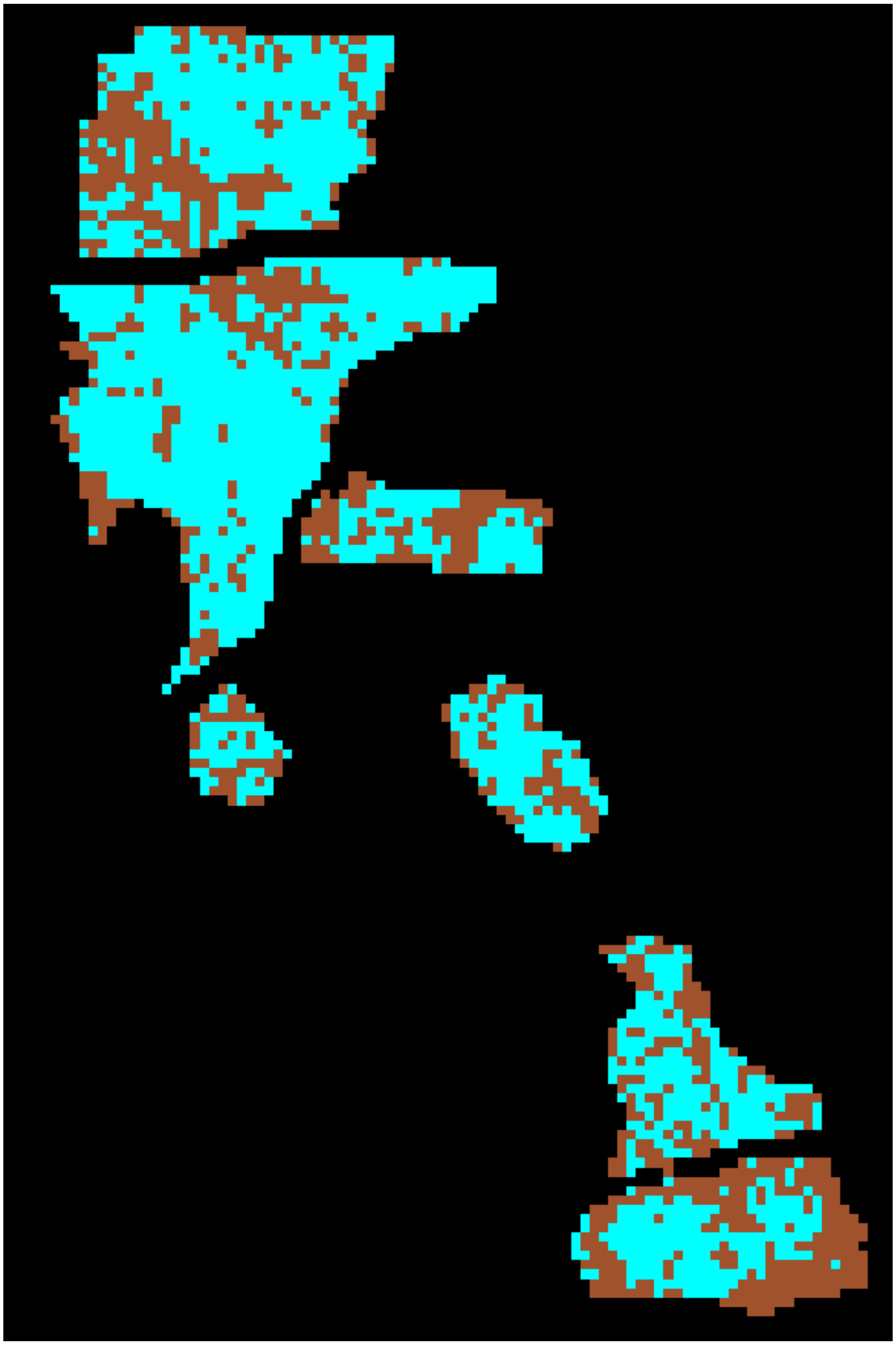


Table 4.4. Error matrix for the classification of vegetation in Papago Park.

Predictions	Field Observations *Larrea*-dominated	Mixed scrub	Row Total
Larrea-dominated	12	1	13
Mixed scrub	4	4	8
Column Total	16	4	23

	Producer's Accuracy	User's Accuracy
Larrea-dominated scrub	75%	92%
Mixed scrub	80%	50%
		Overall accuracy: 70%

Figure 4.6. Vegetation map of the White Tank Regional Park. Encelia-dominated scrub is grey, Ambrosia-dominated scrub is green, and mixed scrub is brown.

Table 4.5. Error matrix for the classification of vegetation in the White Tank Mountains Regional Park.

	Field Observations			
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	14	1	2	17
Encelia-dominated	2	5	2	9
Mixed scrub scrub	3	0	14	17
Column Total	19	6	18	45

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	74%	82%
Encelia-dominated scrub	83%	56%
Mixed scrub	78%	82%

Overall accuracy: 73%

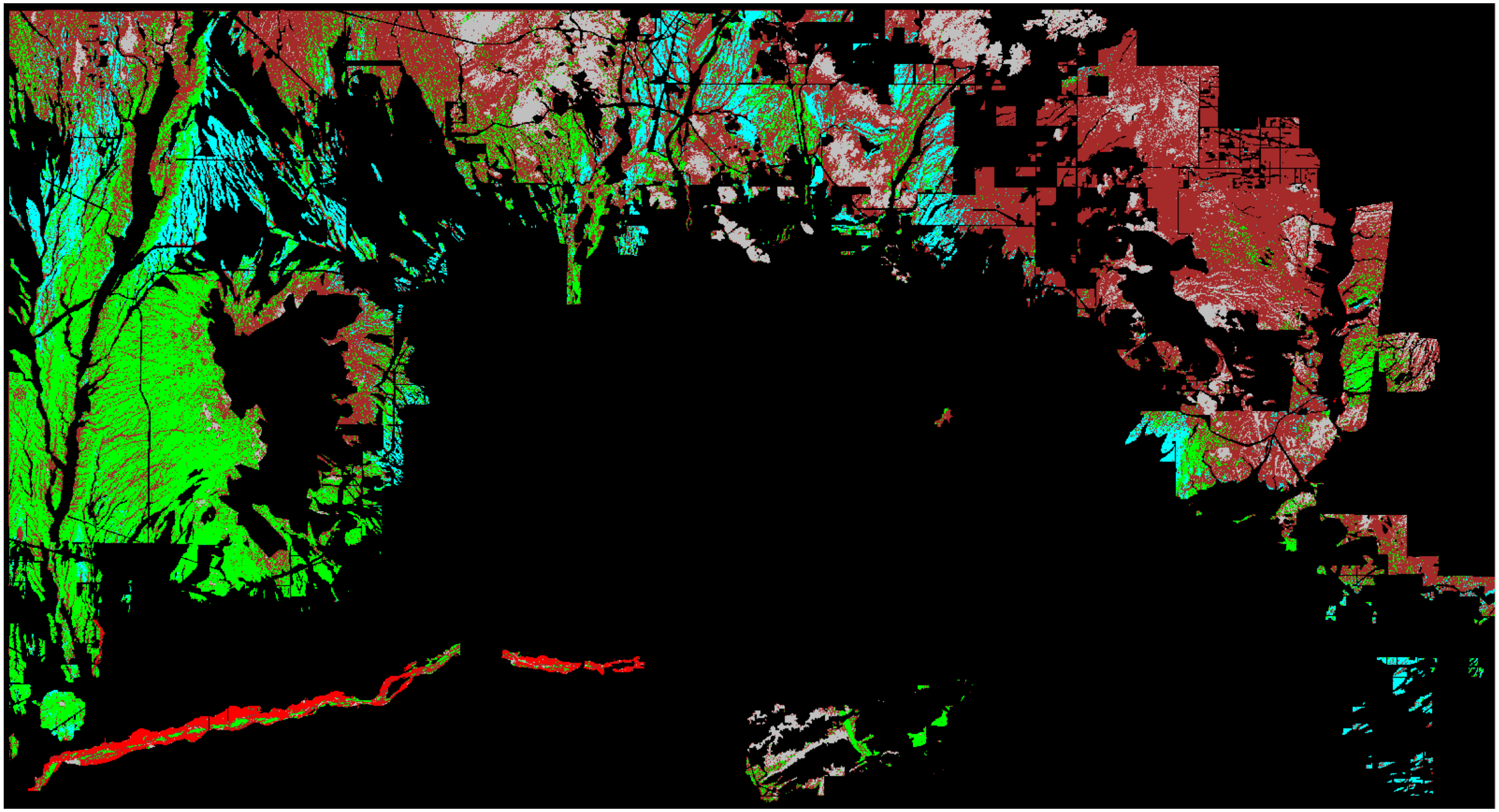


Figure 4.7. Initial vegetation map for desert land dominated by coarse-particle soils. *Ambrosia*-dominated scrub is green, *Encelia*-dominated scrub is grey, *Larrea*-dominated scrub is cyan, riparian woodland is red, and mixed scrub is brown.

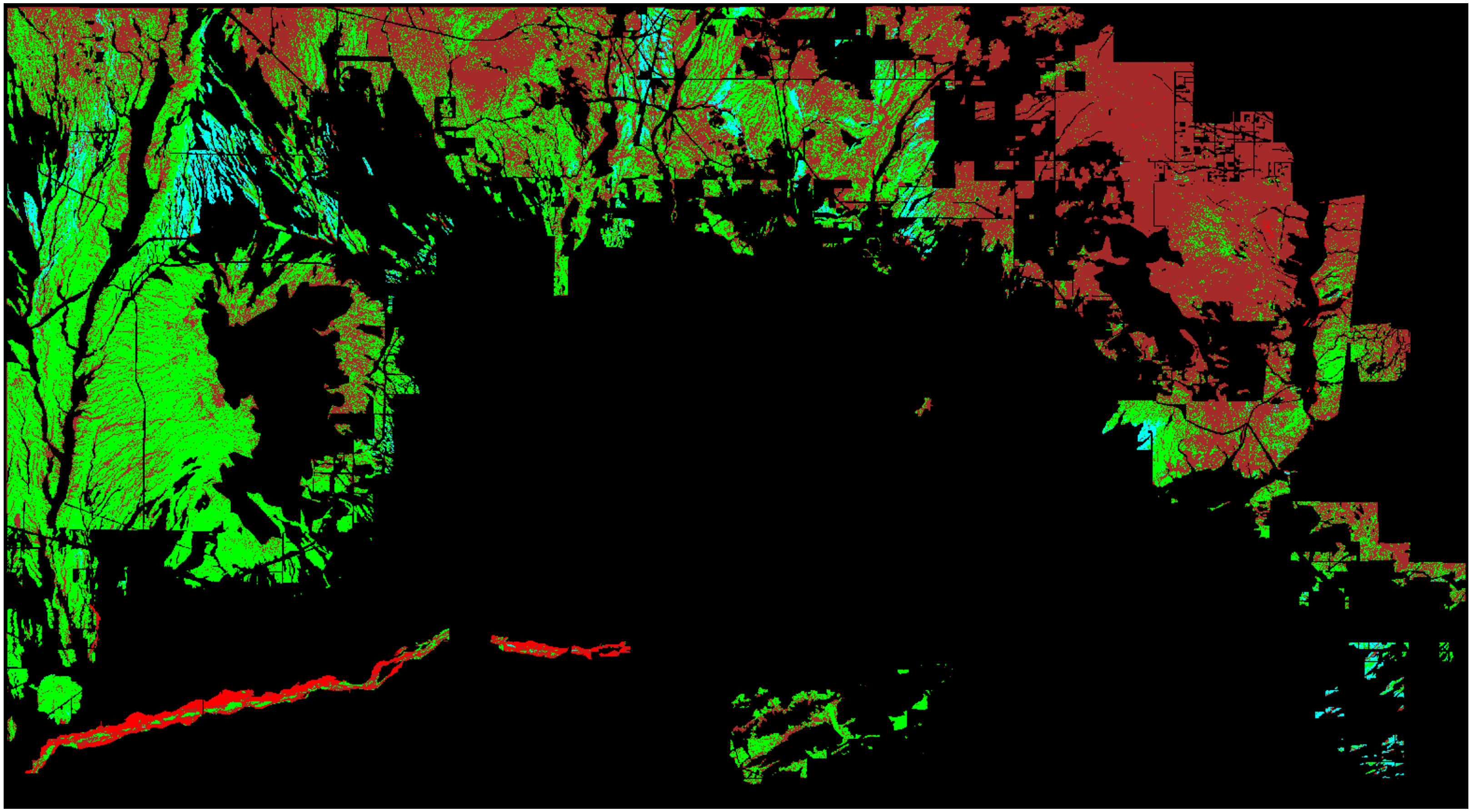


Figure 4.8. Revised vegetation map for desert land dominated by coarse-particle soils. *Ambrosia*-dominated scrub is green, *Larrea*-dominated scrub is cyan, riparian woodland is red, and mixed scrub is brown.

Table 4.6. Error matrix for the initial classification of vegetation in environments with coarse-particle soils.

	Field Observations					
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	*Larrea*-dominated	Riparian woodland	Mixed scrub	Row Total
Ambrosia-dominated	11	0	9	3	8	31
Encelia-dominated	12	1	2	0	15	30
Larrea-dominated	3	0	20	0	0	23
Riparian woodland	0	0	0	14	2	16
Mixed scrub	13	0	3	3	49	68
Column Total	39	1	34	20	74	174

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	28%	31%
Encelia-dominated scrub	100%	3%
Larrea-dominated scrub	59%	83%
Riparian woodland	70%	88%
Mixed scrub	66%	72%

Overall accuracy: 55%

Table 4.7. Error matrix for the revised classification of vegetation in environments with coarse-particle soils. *Encelia*-dominated scrubland was excluded.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Larrea*-dominated	Riparian woodland	Mixed scrub	Row Total
Ambrosia-dominated	16	12	3	11	42
Larrea-dominated	4	19	0	0	23
Riparian woodland	0	0	13	2	15
Mixed scrub	19	3	4	61	87
Column Total	39	34	20	74	174

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrubland	41%	38%
Larrea-dominated scrubland	56%	83%
Riparian woodland	65%	87%
Tree-shrub-cactus scrubland	82%	70%

Overall accuracy: 63%

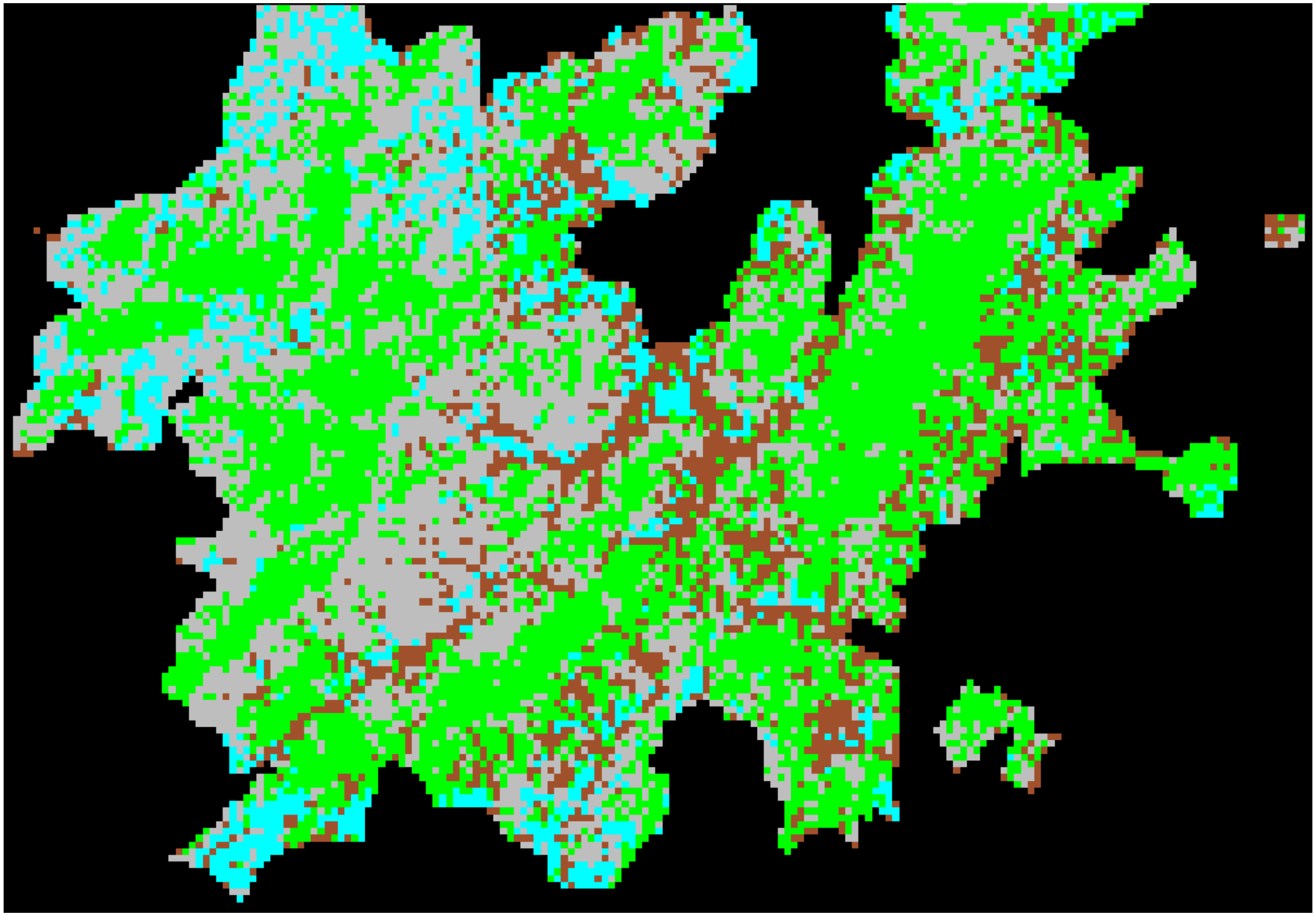


Figure 4.9. Initial vegetation map of Squaw Peak Recreation Area. *Encelia*-dominated scrub is grey, *Ambrosia*-dominated scrub is green, *Larrea*-dominated scrub is cyan, and mixed scrub is brown.

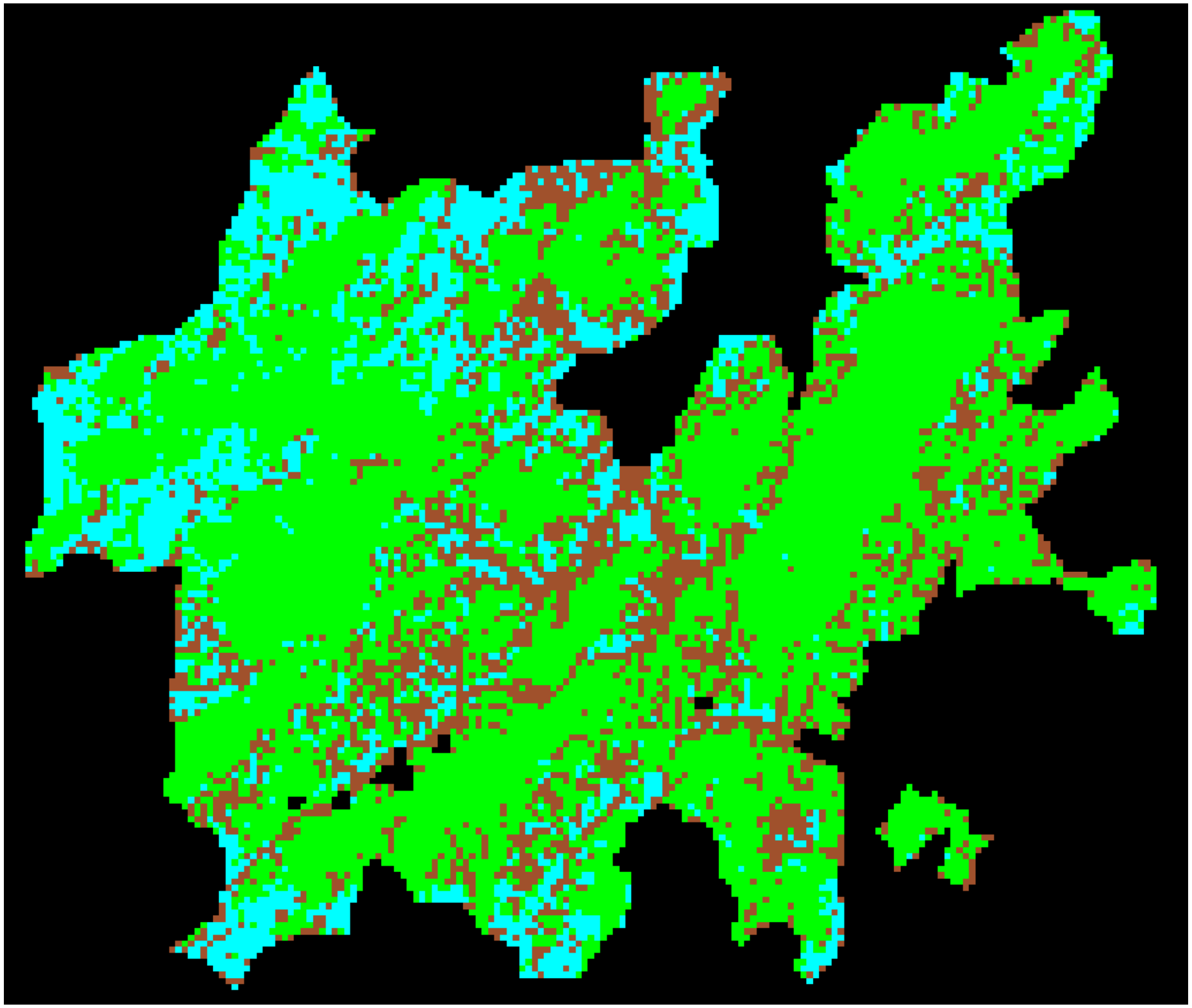


Figure 4.10. Revised vegetation map of Squaw Peak Recreation Area. *Ambrosia*-dominated scrub is green, *Larrea* dominated scrub is cyan, and mixed scrub is brown.

Table 4.8. Error matrix for the initial classification of vegetation in the Squaw Peak Recreation Area.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	12	1	0	3	16
Encelia-dominated	13	2	1	3	19
Larrea-woodland	10	0	3	2	15
Mixed scrub	4	0	1	9	14
Column Total	39	3	5	17	64

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	31%	75%
Encelia-dominated scrub	67%	11%
Larrea-dominated scrub	60%	20%
Mixed scrub	53%	64%

Overall accuracy: 41%

Table 4.9. Error matrix for the revised classification of vegetation in the Squaw Peak Recreation Area. Encelia-dominated scrubland was excluded.

	Field Observations			
Predictions	*Ambrosia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Ambrosia-dominated scrub	20	0	1	21
Larrea-dominated scrub	13	3	4	20
Mixed scrub	6	2	12	20
Column Total	39	5	17	61

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	51%	95%
Larrea-dominated scrub	60%	15%
Mixed scrub	71%	60%

Overall accuracy: 57%

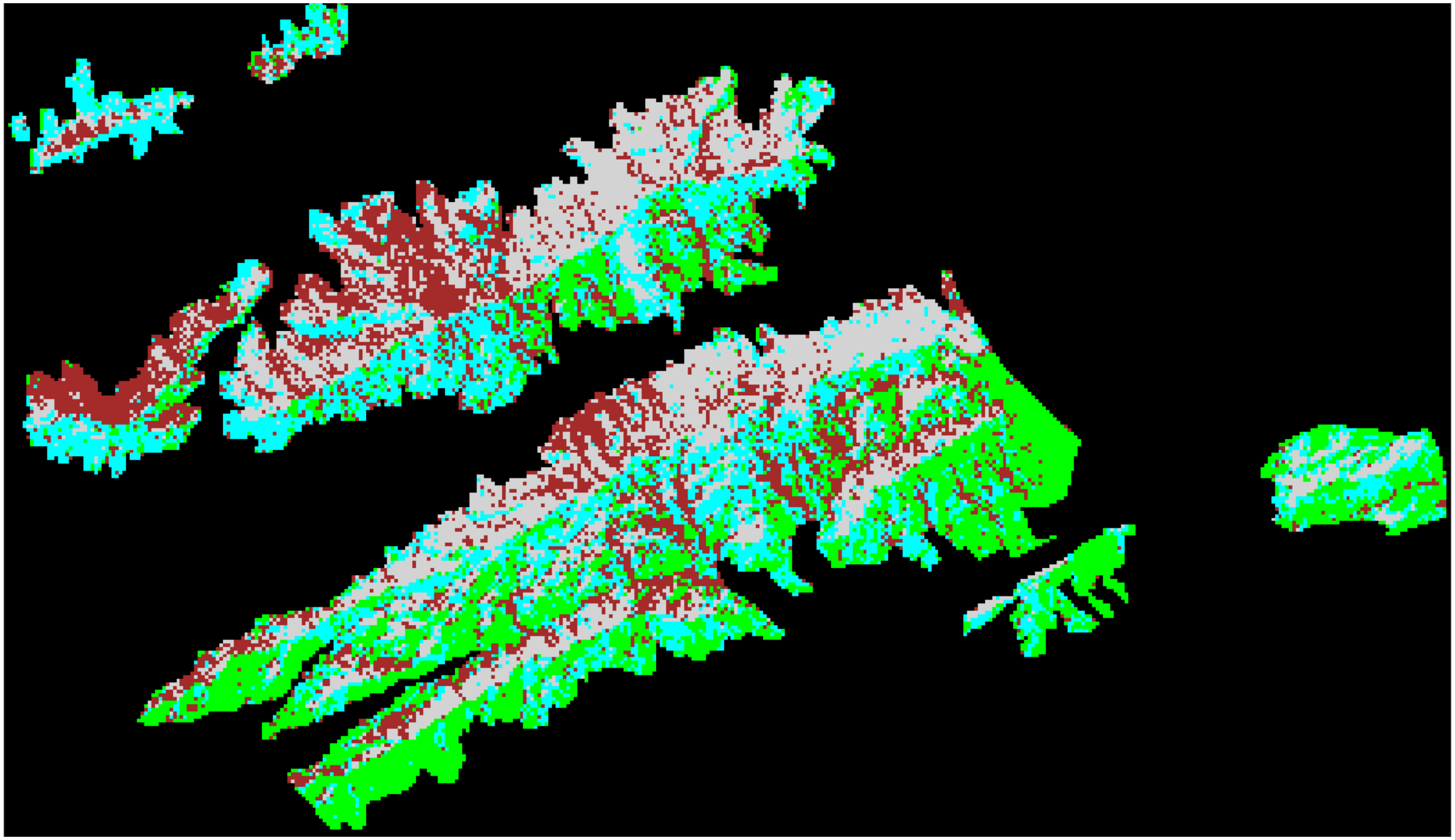


Figure 4.11. Initial vegetation map of the western half of South Mountain Park. *Encelia*-dominated scrub is grey, *Ambrosia*-dominated scrub is green, *Larrea*-dominated scrub is cyan, and mixed scrub is brown.

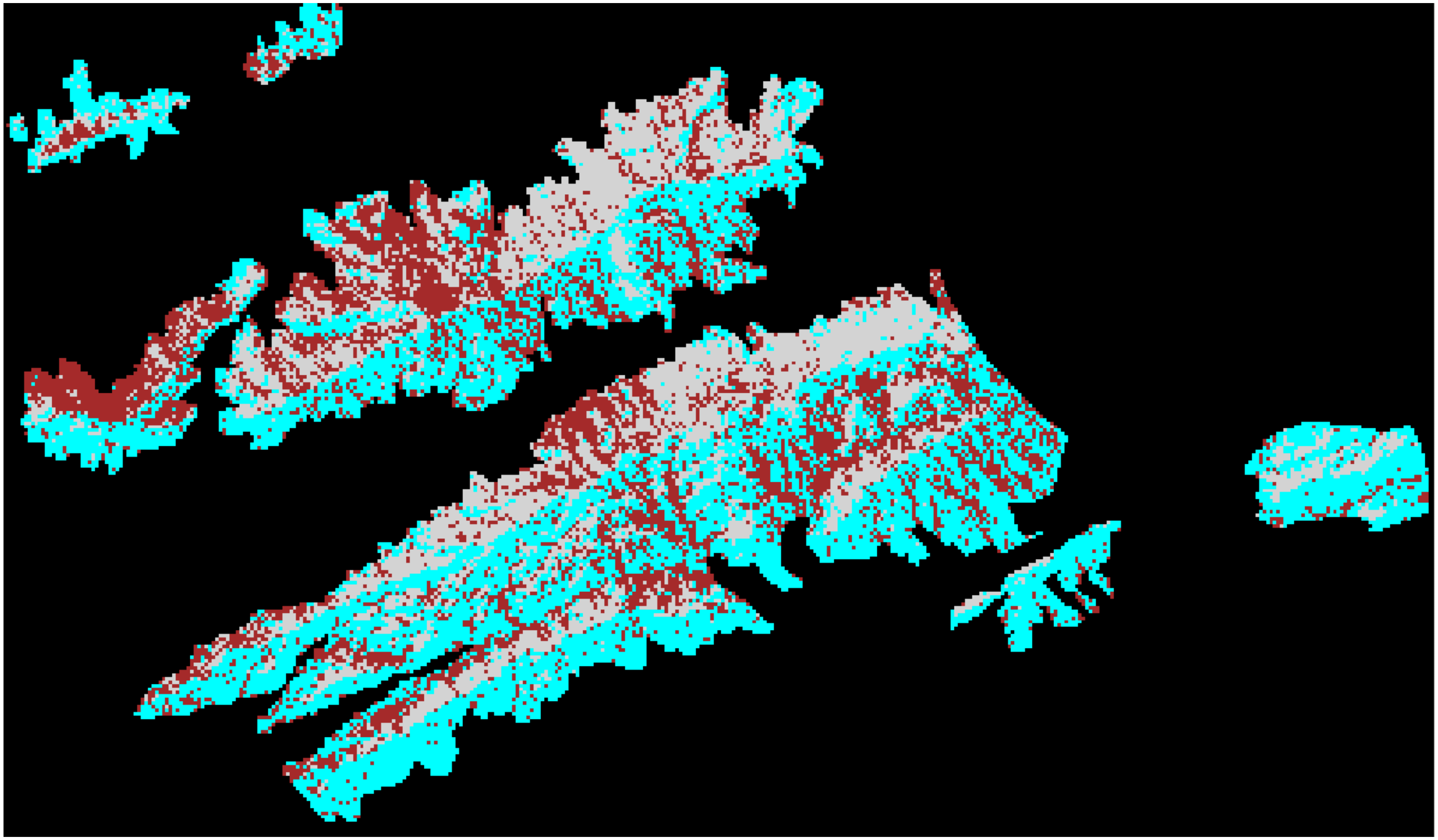


Figure 4.12. Revised vegetation map of the western half of South Mountain Park. *Encelia*-dominated scrub is grey, *Larrea*-dominated scrub is cyan, and mixed scrub is brown.

Table 4.10. Error matrix for the initial classification of vegetation in the western half of South Mountain Park.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	0	3	4	2	9
Encelia-dominated	0	12	3	1	16
Larrea-dominated	0	2	5	1	8
Mixed scrub	0	0	1	10	11
Column Total	0	17	13	14	44

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	undefined	0%
Encelia-dominated scrub	71%	75%
Larrea-dominated scrub	38%	63%
Mixed scrub	71%	91%

Overall accuracy: 61%

Table 4.11. Error matrix for the revised classification of vegetation in the western half of South Mountain Park. Ambrosia-dominated scrubland was dropped from the classification.

	Field Observations			
Predictions	*Encelia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Encelia-dominated	12	3	1	16
Larrea-woodland	4	6	2	12
Mixed scrub	1	4	11	16
Column Total	17	13	14	44

	Producer's Accuracy	User's Accuracy
Encelia-dominated scrub	71%	75%
Larrea-dominated scrub	46%	50%
Mixed scrub	79%	69%

Overall accuracy: 66%

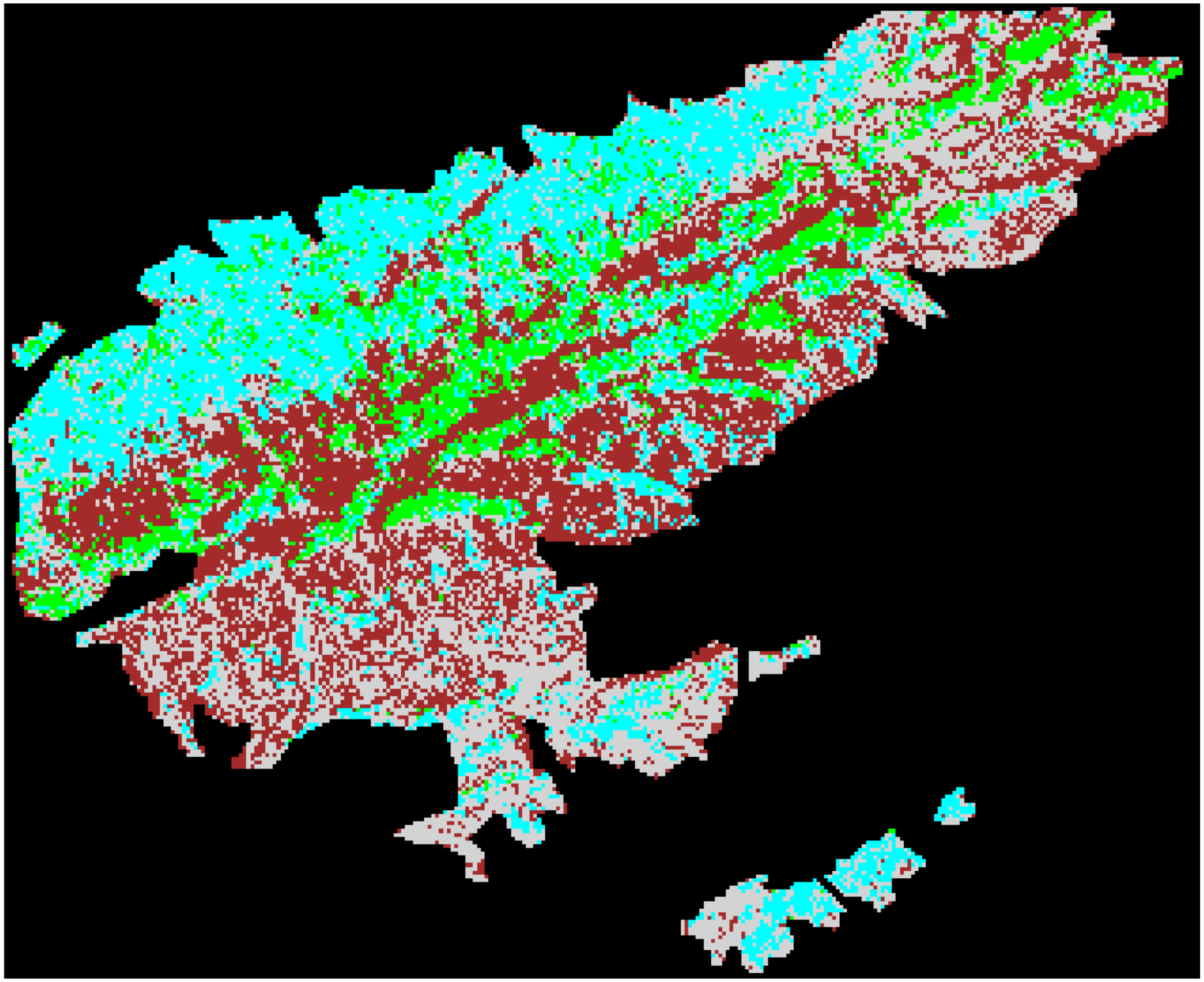


Figure 4.13. Initial vegetation map of the eastern half of South Mountain Park. *Encelia*-dominated scrub is grey, *Ambrosia*-dominated scrub is green, *Larrea*-dominated scrub is cyan, and mixed scrub is brown.

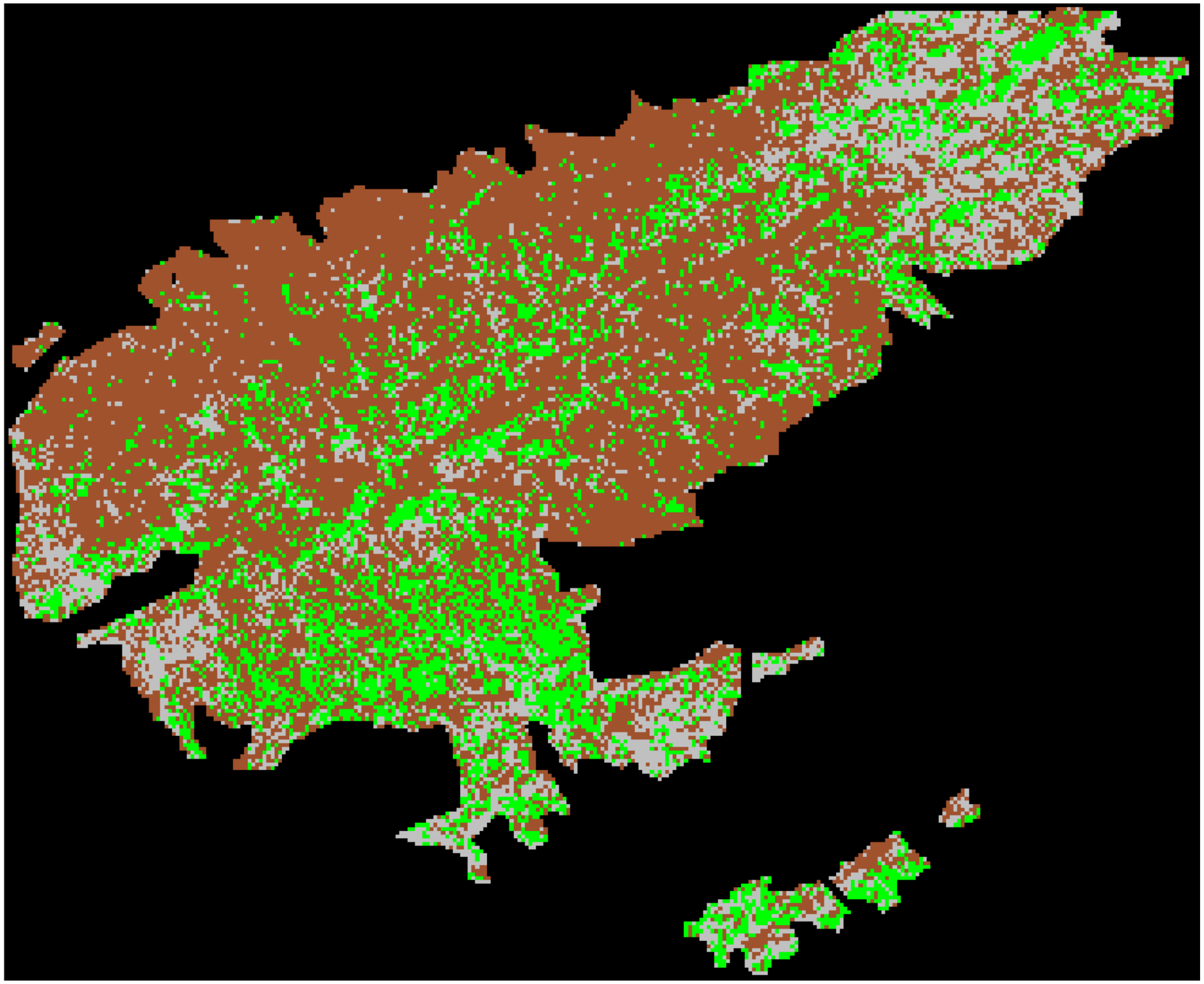


Figure 4.14. Revised vegetation map of the eastern half of South Mountain Park. *Encelia*-dominated scrub is grey, *Ambrosia*-dominated scrub is green, and mixed scrub is brown.

Table 4.12. Error matrix for the initial classification of vegetation in the eastern half of South Mountain Park.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	4	0	0	3	7
Encelia-dominated	9	8	0	0	17
Larrea-woodland	0	3	0	10	13
Mixed scrub	0	0	0	13	13
Column Total	13	11	0	26	50

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	31%	57%
Encelia-dominated scrub	73%	47%
Larrea-dominated scrub	undefined	0%
Mixed scrub	50%	100%

Overall accuracy: 50%

Table 4.13. Error matrix for the revised classification of vegetation in the eastern half of South Mountain Park. Larrea-dominated scrubland was dropped, the training site for Ambrosia-dominated scrubland was revised by adding new sites, and a second Tree-shrub-cactus scrubland class was added to describe habitats on the steep, rocky north-facing slope of South Mountain which was misclassified as Larrea-dominated scrubland in the initial classification.

	Field Observations			
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	6	3	2	11
Encelia-woodland	5	5	1	11
Mixed scrub	2	3	23	28
Column Total	13	11	26	50

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	46%	55%
Encelia-dominated scrub	45%	45%
Mixed scrub	88%	82%

Overall accuracy: 68%

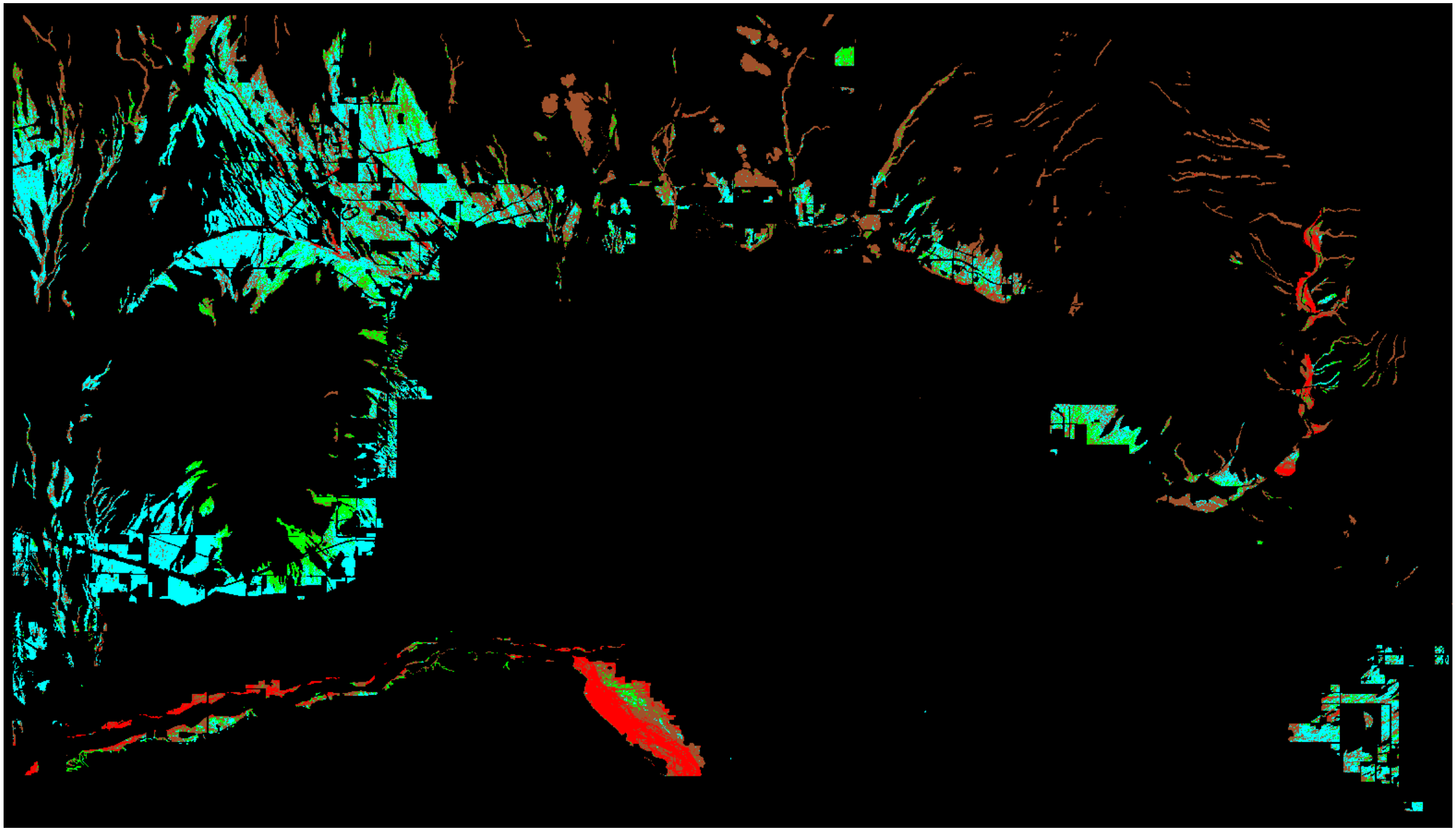


Figure 4.15. Vegetation map for desert lands dominated by loamy soils. *Ambrosia*-dominated scrub is green, *Larrea*-dominated scrub is cyan, riparian woodland is red, and mixed scrub is brown.

Table 4.14. Error matrix for the classification of vegetation in environments with loamy soils.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Larrea*-dominated	Riparian woodland	Mixed scrub	Row Total
Ambrosia-dominated	5	12	0	5	22
Larrea-dominated	8	32	0	2	42
Riparian woodland	0	0	13	7	20
Mixed scrub	1	5	1	15	22
Column Total	14	49	14	29	108

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrub	36%	23%
Larrea-dominated scrub	65%	76%
Riparian woodland	93%	65%
Mixed scrub	52%	68%

Overall accuracy: 60%

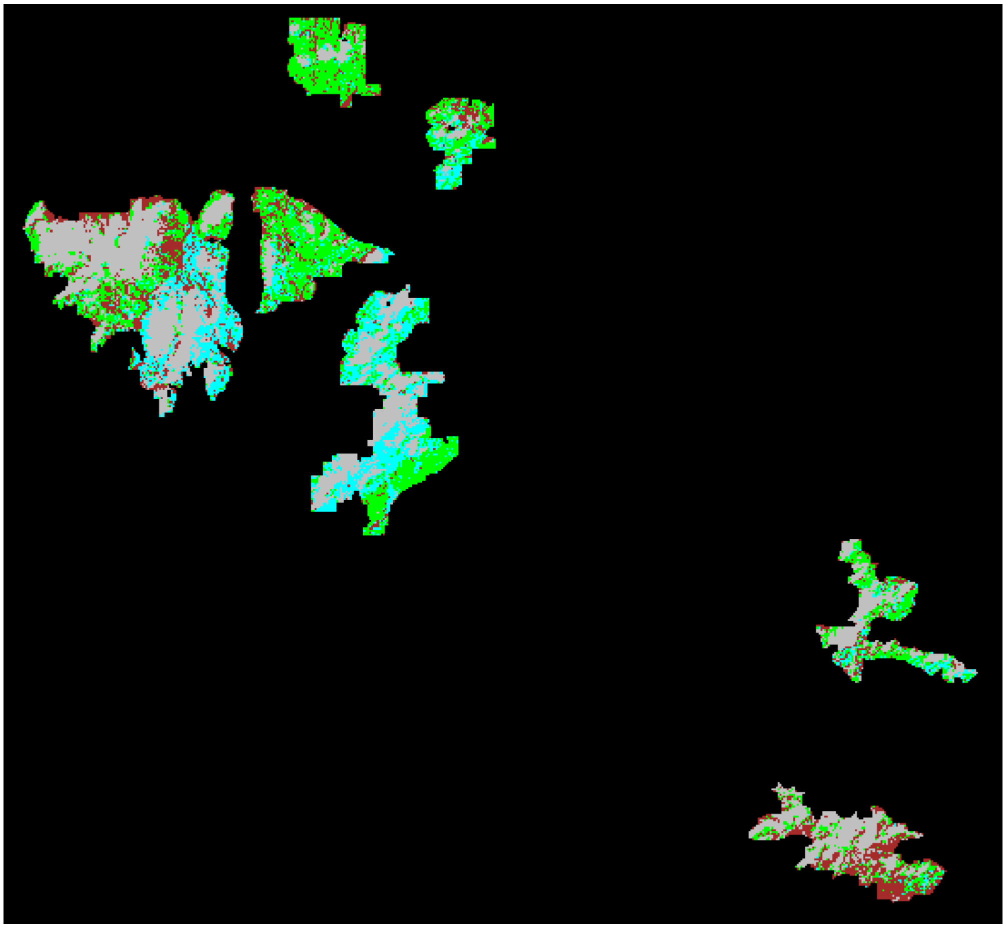


Figure 4.16. Vegetation map for assorted remnant habitat islands embedded in the urban matrix. This view includes the following sites: Camelback Mountain, Mummy Mountain, Lookout Mountain, Shadow Mountain, West Squaw patch, Phoenix Mountain Preserve West, and Phoenix Mountain Preserve East. Encelia-dominated scrub is grey, Ambrosia-dominated scrub is green, Larrea-dominated scrub is cyan, and mixed scrub is brown.

Table 4.15. Error matrix for the classification of remnant habitat islands within the urban matrix, all islands considered together.

	Field Observations				
Predictions	*Ambrosia*-dominated	*Encelia*-dominated	*Larrea*-dominated	Mixed scrub	Row Total
Ambrosia-dominated	25	4	5	9	43
Encelia-dominated	15	14	2	21	52
Larrea-woodland	8	5	9	8	30
Mixed scrub	9	5	2	16	32
Column Total	57	28	18	54	159

	Producer's Accuracy	User's Accuracy
Ambrosia-dominated scrubland	44%	58%
Encelia-dominated scrubland	50%	27%
Larrea-dominated scrubland	50%	30%
Mixed scrub	30%	50%

Overall accuracy: 40%

Table 4.16. Comparison between published Sonoran Desert plant community type systems.

Turner (1974)	Brown et al. (1982)	Initial Classification	Final Classification
Creosotebush community	*Larrea tridentata* association	*Larrea tridentata* dominated scrub	*Larrea tridentata* dominated scrub
(Not defined)	*Ambrosia deltoidea* – *Carnegia gigantea* mixed scrub association	*Ambrosia deltoidea* dominated scrub *Larrea tridentata* – *Ambrosia deltoidea* dominated scrub	*Ambrosia deltoidea* dominated scrub
(Not defined)	*Encelia farinosa* – mixed scrub association	*Encelia farinosa* dominated scrub *Encelia farinosa* – *Larrea tridentata* dominated scrub	*Encelia farinosa* dominated scrub
Paloverde-Saguaro Community	Mixed scrub – *Parkinsonia microphylla* – *Olneya tesota* association *Simmondsia chinensis* – mixed scrub association *Opuntia bigelovii* association *Larrea tridentata* – mixed scrub association *Ambrosia deltoidea* – *Parkinsonia microphyllum* mixed scrub association	Lower Colorado River Valley (LCRV) mixed scrub Arizona Uplands mixed scrub	Mixed scrub
Deciduous riparian forest	*Populus fremonti* – *Salix* sp. association *Prosopsis velutina* association *Prosopsis velutina* – mixed short tree association	Riparian woodland	Riparian woodland
Desert saltbush community	*Atriplex polycarpa* – mixed shrub association	*Atriplex polycarpa* – dominated scrub	*Atriplex polycarpa* – dominated scrub

Table 4.17A. Summary of land cover for each vegetation map. Area covered by each vegetation type are estimated by multiplying the number of pixels by 900 m^2, the area contained within each pixel.

Vegetation Map	Number Of Pixels	Area in km^2	Percentage of Surface Covered
Surface composed of coarse particle soils			
Ambrosia-dominated scrub	950,664	855.6	44.6
Larrea-dominated scrub	87,573	78.8	4.1
Mixed scrub	1,055,697	950.1	49.6
Riparian woodland	35,779	32.2	1.7
Surface composed of loamy soils			
Ambrosia-dominated scrub	96,321	86.7	13.1
Larrea-dominated scrub	326,256	293.6	44.3
Mixed scrub	270,226	243.2	36.7
Riparian woodland	43,498	39.1	5.9
Surface composed of clayey soils			
Larrea-dominated scrub	30,328	27.3	62.0
Mixed scrub	18,575	16.7	38.0
White Tank Mountains (TKgm geology)			
Ambrosia-dominated scrub	19,375	17.4	33.6
Encelia-dominated scrub	20,921	18.8	36.3
Mixed scrub	17,333	15.6	30.1
Papago Park			
Larrea-dominated scrub	1926	1.7	65.3
Mixed scrub	1022	0.9	34.7

Table 4.17B. Summary of land cover for each vegetation map. Area covered by each vegetation type are estimated by multiplying the number of pixels by 900 m^2, the area contained within each pixel.

Vegetation Map	Number Of Pixels	Area in km^2	Percentage of Surface Covered
South Mountain Park (Eastern Section)			
Ambrosia-dominated scrub	7030	6.3	20.7
Encelia-dominated scrub	6578	5.9	19.4
Mixed scrub	20,365	18.3	59.9
South Mountain Park (Western Section)			
Encelia-dominated scrub	7598	6.8	27.2
Larrea-dominated scrub	12,690	11.4	45.4
Mixed scrub	7688	6.9	27.5
Squaw Peak Recreation Area			
Ambrosia-dominated scrub	9976	9.0	63.3
Larrea-dominated scrub	2772	2.5	17.6
Mixed scrub	3007	2.7	19.1
Other remnant patches			
Ambrosia-dominated scrub	6000	5.4	28.4
Encelia-dominated scrub	7856	7.1	37.2
Larrea-dominated scrub	3839	3.5	18.2
Mixed scrub	3434	3.1	16.2
Entire Mapped Area			
Ambrosia-dominated scrub	1,089,366	980	35.4
Encelia-dominated scrub	42,953	39	1.4
Larrea-dominated scrub	465,384	419	15.1
Mixed scrub	1,397,347	1258	45.5
Riparian woodland	79,277	71	2.6
Total	3,074,327	2,767	100.0

LITERATURE CITED

Abrams, P. 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics **14**: 359-376.

Aho, J. M. 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. Pages 157-196 *in* G. W. Esch, A. O. Bush, and J. M. Aho, editors. Parasite communities: patterns and processes. Chapman and Hall, London.

Aho, J. M. and A. O. Bush. 1993. Community richness in parasites of some freshwater fishes from North America. Pages 185-193 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois.

Anderson, M. J. 1998. Effects of patch size on colonization in estuaries: revisiting the species-area relationship. Oecologia **118**: 87-98.

Anderson, W. B. and A. Wait. 2001. Subsidized island biogeography hypothesis: another new twist on an old theory. Ecology Letters **4**: 289-291.

ArcGIS. 2002. Environmental Research Institute, Inc., Redlands, California.

ArcView 3.3. 2002. Environmental Research Institute, Inc., Redlands, California.

ArcMap 9.0. 2002. Environmental Research Institute, Inc., Redlands, California.

Arizona Land Resources Information System. Geological Formations. Arizona State Land Department. Phoenix, Arizona.

Arrhenius, O. 1921. Species and area. Journal of Ecology **9**: 95-99.

Arrhenius, O. 1923. On the relation between species and area – a reply. Ecology **4**: 90-91.

Asner, G. P., C. A. Wessman, C. A. Bateson, and J. L. Privette. 2000. Impact of tissue, canopy, and landscape factors on the hyperspectral reflectance variability of arid ecosystems. Remote Sensing of Environment **74**: 69-84.

Atmar, W. and B. D. Patterson. 1993. On the measure of order and disorder in the distribution of species on archipelagos. Oecologia **96**: 373-382.

Bahre, C. J. and M. L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. Journal of Biogeography **20**: 489-504.

Baker, L. A., D. Hope, Y. Xu, J. Edmonds, and L. Lauver. 2001. Nitrogen balance for the Central Arizona – Phoenix (CAP) Ecosystem. Ecosystems **4**: 582-602.

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 Ecosystems **6**: 183 – 203.

Baldi, A. and T. Kisbenedek. 1999. Orthopterans in small steppe patches: an investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches. Acta Oecologica **20**: 125-132.

Baltanas, A. 1992. On the use of some methods for the estimation of species richness. Oikos **65**: 484-492.

Barbour, M. G. 1968. Germination requirements of the desert shrub *Larrea tridentata*. Ecology **49**: 915-923.

Barbour, M. G. 1973. Larrea plant communities on bajada and moisture gradients in the United States and Argentina. Vegetatio **28**: 335-352.

Barrett, K., D. A. Wait, and W. B. Anderson. 2003. Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. Journal of Biogeography **30**: 1575-1581.

Berglund, H. and B. G. Jonsson. 2003. Nested plant and fungal communities: the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. Biological Conservation **112**: 319-328.

Blossey, B. 1999. Before, during, and after: the need for long-term monitoring in invasive plant species management. Biological Invasions **1**: 301 – 311.

Bond, W. J., J. Midgley, and J. Vlok. 1988. When is an island not an island – insular effects and their causes in fynbos shrublands. Oecologia **77**: 515-521.

Border, S. 1999. An attempt to classify Sonoran Desert vegetation in the McDowell Mountains using thematic mapper simulator data. Master's thesis. Arizona State University, Tempe, Arizona.

Bourne, L. S. and J. W. Simmons. 1982. Defining the area of interest: definition of the city, metropolitan areas, and extended urban regions. Pages 57-72 *in* L. S. Bourne, editor. Internal structure of the city. Oxford University Press, New York.

Bowers, J. E. 2005. Effects of drought on shrub survival and longevity in the northern Sonoran Desert. Bulletin of the Torrey Botanical Society **132**: 421 – 431.

Bowers, J. E. and R. M. Turner. 2002. The influence of climatic variability on local population dynamics of Cercidium microphyllum (foothill paloverde). Oecologia **130**: 105 – 113.

Bowers, J. E., R. M. Turner, and T. L. Burgess. 2004. Temporal and spatial patterns in emergence and early survival of perennial plants in the Sonoran Desert. Plant Ecology **172**: 107 – 119.

Bowers, M. A. and C. H. Lowe. 1986. Plant-form gradients on Sonoran Desert bajadas. Oikos **46**: 284-291.

Brown, D. E., C. H. Lowe, and C. P. Pase. 1982. A digitized classification system for the biotic communities of North America, with community (series) and association examples for the Southwest. Pages 302-315 *in* D. E. Brown, editor. Biotic communities of the American Southwest-United States and Mexico. University of Arizona Press, Superior, Arizona.

Brown, R. F. and D. G. Mayer. 1988. Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. Annals of Botany **61**: 127-138.

Brunn, H. H. and J. Moen. 2003. Nested communities of alpine plants on isolated mountains: relative importance of colonization and extinction. Journal of Biogeography **30**: 297-303.

Burbidge, A. A., M. R. Williams, and I. Abbott. 1997. Mammals of Australian islands: factors influencing species richness. Journal of Biogeography **24**: 703-715.

Caley, M. J. and D. Schluter. 1997. The relationship between local and regional diversity. Ecology **78**: 70-80.

Carillo-Garcia, A., J. L. Leon de la Luz, Y. Bashan, and G. J. Bethlenfalvay. 1999. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. Restoration Ecology **7**: 321 – 335.

Caswell, H. and J. E. Cohen. 1993. Local and regional regulation of species-area relations: a patch occupancy model. Pages 99-107 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois.

Cave, G. H. and D. T. Patten. 1984. Short-term vegetation responses to fire in the upper Sonoran Desert. Journal of Range Management **37**: 491 – 496.

Chown, S. L., N. J. M. Gremmen, and K. J. Gaston. 1998. Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. The American Naturalist **152**: 562-575.

Clench, H. K. 1979. How to make regional lists of butterflies: some thoughts. Journal of the Lepidopterists' Society **33**: 216-231.

Coleman, B. 1981. On random placement and species-area relationships. Mathematical Biosciences **54**: 191-215.

Coleman, B. D., M. A. Mares, M. R. Willig, and Y. H. Hsieh. 1982. Randomness, area, and species richness. Ecology **64**: 1121-1133.

Colwell, R. K. 1999. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5.0.1. User's guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Congalton, R. G. 1991. A review of the accuracy of classifications of remotely sensed data. Remote Sensing of Environment **37**: 35-46.

Congalton, R. G. and K. Green. 1999. Assessing the accuracy of remotely sensed data: principles and practices. CRC Press, Boca Raton, Florida.

Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. The American Naturalist **113**: 791-833.

Connor, E. F., E. D. McCoy, and B. J. Cosby. 1983. Model discrimination and expected slope values in species-area studies. The American Naturalist **122**: 789-796.

Cornell, H. V. 1985. Local and regional richness of cynipine gall wasps on California oaks. Ecology **66**: 1247-1260.

Cornell, H. V. 1999. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. Ecoscience **6**: 303-315.

Cornell, H. V. and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology **61**: 1-12.

Cornell, H. V. and R. H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. Journal of Animal Ecology **65**: 233-241.

Cutler, A. H. 1991. Nested faunas and extinction in fragmented habitats. Conservation Biology **5**: 496-505.

Cutler, A. H. 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. Landscape and Urban Planning **28**: 73-82.

Daniel, T. E. and M. L. Butterwick. 1992. Flora of the South Mountains of south-central Arizona. Desert Plants 10: 99 – 119.

Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. John Wiley, New york.

de Candolle, A. 1855. Géographie botanique raisonnée: ou l'exposition des faits principaux et des lois concernant la distribution géographique des plates de l'epoque actuelle. Maisson, Paris.

de Caprariis, P., R. H. Lindeman, and C. M. Collins. 1976. A method for determining optimum sample size in species diversity studies. Mathematical Geology **8**: 575-581.

Drayton, B. and R. B. Primack. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. Conservation Biology **10**: 30-39.

Drezner, T. D., P. L. Fall, and J. C. Stromberg. 2001. Plant distribution and dispersal mechanisms at the Hassayampa River Preserve, Arizona, USA. Global Ecology and Biogeography **10**: 205 – 217.

Dzwonko, Z. and S. Loster. 1988. Species richness of small woodlands on the western Carpathian foothills. Vegetatio **76**: 15-27.

Dzwonko, Z. and S. Loster. 1989. Distribution of vascular plant species in small woodlands on the western Carpathian foothills. Oikos **56**: 77-86.

Dzwonko, Z. and S. Loster. 1992. Species richness and seed dispersal to secondary woods in southern Poland. Journal of Biogeography **19**: 195-204.

ERDAS Field Guide. 1997. ERDAS Inc., Atlanta, Georgia. Fourth edition.

ERDAS Imagine 8.6. 2002. Leica Geosystems GIS and Mapping LLC, St. Gallen, Switzerland.

Evans, F. C., P. J. Clark, and R. H. Brand. 1955. Estimation of the number of species present on a given area. Ecology **36**: 342-343.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. Bioscience **55**: 399 – 407.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology **12**: 42-58.

Flather, C. H. 1996. Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. Journal of Biogeography **23**: 155-162.

Fleishman, E., C. J. Betrus, R. B. Blair, R. MacNally, and D. D. Murphy. 2002. Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups. Oecologia **133**: 78-89.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, New York.

Fox, J. W., J. McGrady-Steed, and O. L. Petchey. 2000. Testing for local species saturation with nonindependent regional species pools. Ecology Letters **3**: 198-206.

Fox, R. 1987. Population images. United Nations Fund for Population Activities.

Frey, H. T. 1984. Expansion of urban area in the United States: 1960-1980. United States Department of Agriculture Economic Research Service Staff Report Number **AGES830615**.

Gardner, J. L. 1951. Vegetation of the creosotebush area of the Rio Grande valley in New Mexico. Ecological Monographs **21**: 379-403.

Gates, D. M., H. J. Keegan, J. C. Schleter, and V. R. Weidner. 1965. Spectral properties of plants. Applied Optics **4**: 11-20.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkens, Baltimore, Maryland.

Gering, J. C. and T. O. Crist. 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. Ecology Letters **5**: 433-444.

Giles, P. T. 2001. Remote sensing and cast shadows in mountainous terrain. Photogrammetric Engineering and Remote Sensing **67**: 833-839.

Gilpin, M. E. and J. M. Diamond. 1976. Calculation of immigration and extinction curves from species-area-distance relation. Proceedings of the National Academy of Sciences of the United States of America **73**: 4130-4134.

Gleason, H. A. 1922. On the relation between species and area. Ecology **3**: 158-162.

Gleason, H. A. 1925. Species and area. Ecology **6**: 66-74.

Gober, P. and E. K. Burns. 2002. The size and shape of Phoenix's urban fringe. Journal of Planning Education and Research **21**: 379 – 390.

Goldberg, D. E. and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology **67**: 695-712.

Gould, S. J. 1979. An allometric interpretation of species-area curves: the meaning of the coefficient. The American Naturalist **114**: 335-343.

Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. Journal of Vegetation Science **8**: 21-28.

Grassle, J. F. and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. The American Naturalist **139**: 313-341.

Grimm, N. B. and C. L. Redman. 2004. Approaches to the study of urban ecosystems: the case of Central Arizona-Phoenix. Urban Ecosystems **7**: 199 – 213.

Grimm, N. B., J. M. Grove, S. T. A. Pickett, and C. L. Redman. 2000. Integrated approaches to long-term studies of urban ecological systems. Bioscience **50**: 571-584.

Gurd, D. B. and T. D. Nudds. 1999. Insular biogeography of mammals in Canadian parks: a re-analysis. Journal of Biogeography **26**: 973-982.

Halvorson, W. L. and D. T. Patten. 1974. Seasonal water potential changes in Sonoran Desert shrubs in relation to topography. Ecology **55**: 173-177.

Harris, A. T. and G. P. Asner. 2003. Grazing gradient detection with airborne imaging spectroscopy on a semi-arid rangeland. Journal of Arid Environments **55**: 391-404.

Haub, C. and M. M. Kent. 1989. 1989 world population data sheet. Population Reference Bureau, Washington, D. C.

He, F. and P. Legendre. 1996. On species-area relations. The American Naturalist **148**: 719-737.

Hill, J. L. and P. J. Curran. 2001. Species composition in fragmented forests: conservation implications of changing forest area. Applied Geography **21**: 157-174.

Hobbs, E. 1988. Using ordination to analyze the composition and structure of urban forest islands. Forest Ecology and Management **23**: 139-158.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang and J. A. Tosi. 1971. Forest environments in tropical life zones. Pergamon Press, Oxford.

Honnay, O., M. Hermy, and P. Coppin. 1999a. Effects of area, age, and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. Biological Conservation **87**: 73-84.

Honnay, O., M. Hermy, and P. Coppin. 1999b. Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? Oikos **84**: 119-129.

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. Proceedings of the National Academy of Sciences **100**: 8788 – 8792.

Hubbell, S. P. and R. B. Foster. 1983. Diversity of canopy trees in a Neotropical forest and implications for conservation. Pages 25-41 *in* S. Sutton, T. C. Whitmore, and A. Chadwick, editors. Tropical rain forest: ecology and management, Blackwell, Oxford.

Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos **86**: 393-401.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. The American Naturalist **93**: 145-159.

Jarvinen, O. 1982. Conservation of endangered plant populations: single large or several small reserves? Oikos **38**: 301-307.

Jenerette, G. D. and J. Wu. 2001. Analysis and simulation of land-use change in the central Arizona-Phoenix region, USA. Landscape Ecology **16**: 611 – 626.

Kadmon, R. 1995. Nested species subsets and geographic isolation – a case study. Ecology **76**: 458-465.

Kadmon, R. and H. R. Pulliam. 1993. Island biogeography: effect of geographical isolation on species composition. Ecology **74**: 977-981.

Kearney, T. H. and R. H. Peebles. 1960. Arizona flora. University of California Press, Berkeley, California.

Keely, J. E. 2003. Relating species abundance distributions to species-area curves in two Mediterranean-type shrublands. Diversity and Distributions **9**: 253-259.

Keely, J. E. and C. J. Fotheringham. 2003. Species-area relationships in Mediterranean-climate plant communities. Journal of Biogeography **30**: 1629-1657.

Kenney Aerial Mapping, Inc. 2000. Phoenix aerial photography. Phoenix, Arizona.

Kerr, J. T., A. Sugar, L. Packer. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conservation Biology **14**: 1726-1734.

Kilburn, P. D. 1966. Analysis of species-area relation. Ecology **47**: 831-843.

Kinzig, A. P., P. Warren, C. Martin, D. Hope, and M. Katti. 2005. The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. Ecology and Society **10**: 23 – 36.

Koerner, B. and J. Klopatek. 2002. Anthropogenic and natural CO2 emission sources in an arid urban environment. Environmental Pollution **116**: S45 – S51.

Kotzen, B. 2003. An investigation of shade under six different tree species of the Negev Desert towards their potential use for enhancing micro-climatic conditions in landscape and architectural development. Journal of Arid Environments **55**: 231-274.

Lack, D. 1976. Island birds. Blackwell, Oxford.

LANDISCOR Aerial Information. 2000. Phoenix aerial photography. Phoenix, Arizona.

Laurance, W. F. 2002. Hyperdynamism in fragmented habitats. Journal of Vegetation Science **13**: 595-602.

Lawesson, J. E., G. de Blust, C. Grashof, L. Firbank, O. Honnay, M. Hermy, P. Hobitz, and L. M. Jensen. 1998. Species diversity and area-relationships in Danish beech forests. Forest Ecology and Management **106**: 235-245.

Lawrey, J. D. 1991. The species-area curve as an index of disturbance in saxicolous lichen communities. Bryologist **94**: 377-382.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos **84**: 177-192.

Levenson, J. B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pages 13-39 *in* Burgess, R. L. and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer Verlag, New York.

Lillesand, T. M. and R. W. Kiefer. 2000. Remote sensing and image interpretation. Fourth edition. John Wiley and Sons, New York.

Lomolino, M. V. 1989. Interpretations and comparisons of constants in the species-area relationship: an additional caution. The American Naturalist **133**: 277-280.

Lomolino, M. V. 1996. Investigating causality of nestedness of insular communities: selective immigration or extinctions? Journal of Biogeography **23**: 699-703.

Lomolino, M. V. 2000. Ecology’s most general, yet protean pattern: the species-area relationship. Journal of Biogeography **27**: 17-26.

Lomolino, M. V. 2001. The species-area relationship: new challenges for an old pattern. Process in Physical Geography **25**: 1-21.

Lomolino, M. V. 2002. ‘There are areas too small, and areas too large, to show clear diversity patterns’: R. H. MacArthur. Journal of Biogeography **29**: 555-557.

Lomolino, M. V. and M. D. Weiser. 2001. Towards a more general species-area relationship: diversity in all islands, great and small. Journal of Biogeography **28**: 431-445.

Loo, S. E., R. McNally, and G. P. Quinn. 2002. An experimental examination of colonization as a generator or biotic nestedness. Oecologia **132**: 118-124.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MacArthur, R. H. and R. Levins. 1967. Limiting similarity, convergence, and divergence of coexisting species. The American Naturalist **101**: 377-385.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Makse, H. A., S. Havlin, and H. E. Stanley. 1995. Modeling urban-growth patterns. Nature **377**: 608-612.

Martin, C. A., P. S. Warren, and A. P. Kinzig. 2004. Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in residential neighborhoods and embedded small parks of Phoenix, AZ. Landscape and Urban Planning **69**: 355 – 368.

Martin, T. E. 1981. Species-area slopes and coefficients – a caution on their interpretation. The American Naturalist **118**: 823-837.

Marui, Y., S. Chiba, J. Okuno, and K. Yamasaki. 2004. Species-area curve for land snails on Kikai Island in geological time. Paleobiology **30**: 222-230.

Matlack, G. R. 1994. Plant species migration in a mixed history forest landscape in eastern North America. Ecology **75**: 1491-1502.

Matter, S. F., I. Hanski, and M. Gyllenberg. 2003. A test of the metapopulation model of the species-area relationship. Journal of Biogeography **29**: 977-983.

May, R. M. 1975. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey.

McAuliffe, J. R. 1986. Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. Ecology **67**: 276-280.

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. Ecological Monographs **64**: 111-148.

McAuliffe, J. R. 1995. The aftermath of wildfire in the Sonoran Desert. The Sonoran Quarterly **4**: 4-8.

McAuliffe, J. R. 1999. The Sonoran Desert: landscape complexity and ecological diversity. Pages 68-114 *in* Robichaux, R. H., editor. Ecology of Sonoran Desert plants and plant communities. University of Arizona Press, Tucson, Arizona.

McCune, B. and M. J. Mefford. 1999. PCOrd: Multivariate analysis of ecological data. Version 4.0. MjM Software, Gleneden Beach, Oregon.

McDonald, H. A. and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology **6**: 409-415.

McDonnell, M. J. and S. T. A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology **71**: 1232-1237.

McKinney, M. L. 1998. On predicting biotic homogenization: species-area patterns in marine biota. Global Ecology and Biogeography Letters **7**: 297-301.

McKinney, M. L. and D. L. Frederick. 1999. Species-time curves and population extremes: ecological patterns in the fossil record. Evolutionary Ecology Research **1**: 641-650.

McLaughlin, S. P. 2002. Exotic plant species in the western United States. Pages 47 – 62 *in* B. Tellman, editor. Invasive exotic species in the Sonoran region. University of Arizona Press, Tucson, Arizona.

Mielke, P. W. J., and E. S. Johnson. 1974. Some generalized distributions of the second kind having desirable application features in hydrology and meteorology. Water Resources Research **10**: 223-226.

Mikkelson, G. M. 1993. How do food webs fall apart – a study of changes in trophic structure during relaxation on habitat fragments. Oikos **67**: 539-547.

Miller, R. I. and R. G. Wiegert. 1989. Documenting completeness, species-area relations, and the species-abundance distribution of a regional flora. Ecology **70**: 16-22.

Monod, J. 1950. La technique de culture continue, theorie, et applications. Annales de l'Institut Pasteur **79**: 390-410.

Mooney, H. A. and F. S. Chapin. 1994. Future directions of global change research in terrestrial ecosystems. Trends in Ecology and Evolution **9**: 371-372.

Morgan, P. H., L. P. Mercer, and N. W. Flodin. 1975. General model for nutritional responses of higher organisms. Proceedings of the National Academy of Science **72**: 4327-4331.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

Mulugeta, D., D. E. Stoltenberg, and C. M. Boerboom. 2001. Weed species-area relationships as influenced by tillage. Weed Science **49**: 217-223.

Myklestaad, A. and M. Saetersdal. 2004. The importance of traditional meadow management techniques for conservation of vascular plant species richness in Norway. Biological Conservation **118**: 133-139.

Nabe-Nielsen, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuni National Park, Ecuador. Journal of Tropical Ecology **17**: 1-19.

Nagler, P. L., C. S. T. Daughtry, and S. N. Goward. 2000. Plant litter and soil reflectance. Remote Sensing of Environment **71**: 207-215.

Natuhara, Y. and C. Imai. 1999. Prediction of species richness of breeding birds by landscape-level factors of urban woods in Osaka Prefecture, Japan. Biodiversity and Conservation **8**: 239-253.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science **142**: 15-23.

Okin, G. S., D. A. Roberts, B. Murray, and W. J. Okin. 2001. Practical limits on hyperspectral vegetation discrimination in arid and semiarid environments. Remote Sensing of Environment **77**: 212-225.

Palmer, A. R. and A. F. van Rooyen. 1998. Detecting vegetation change in the southern Kalahari using Landsat TM data. Journal of Arid Environments **39**: 143-153.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology **71**: 1195-1198.

Palmer, M. W. 1991. Estimating species richness – the second order jackknife reconsidered. Ecology **72**: 1512-1513.

Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. Conservation Biology **1**: 323-334.

Patterson, B. D. 1990. On the temporal development of nested subset patterns of species composition. Oikos **59**: 330-342.

Patterson, B. D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnaean Society **28**: 65-82.

Patterson, B. D. and J. H. Brown. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. Journal of Biogeography **18**: 395-402.

Peterken, G. F. and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology **72**: 155-182.

Phillips, D. L. and J. A. MacMahon. 1978. Gradient analysis of a Sonoran Desert bajada. The Southwestern Naturalist **23**: 669-680.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic areas. Annual Review of Ecology and Systematics **32**: 127-157.

Pierson, E. A. and R. M. Turner. 1998. An 85-year study of saguaro (*Carnegia gigantea*) demography. Ecology **79**: 2676-2693.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. Ecology **43**: 185-215.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist **149**: 875-902.

Ratkowsky, D. A. 1990. Handbook of nonlinear regression models. Marcel Dekker, New York.

Ray, T. W. and B. C. Murray. 1996. Nonlinear spectral mixing in desert vegetation. Remote Sensing of Environment **55**: 59-64.

Rebele, F. 1994. Urban ecology and special features of urban ecosystems. Global Ecology and Biogeography Letters **4**: 173-187.

Rees, W. E. 2000. Eco-footprint analysis: merits and brickbats. Ecological Economics **32**: 371-374.

Reeves, M. C. 1999. Mapping Sonoran Desert vegetation using hyperspectral imagery. Master's thesis. Arizona State University, Tempe, Arizona.

Reid, D. 1978. The effects of frequency of defoliation on the yield response of a perennial ryegrass sward to a wide range of nitrogen application rates. Journal of Agricultural Science **90**: 447-457.

Reynolds, J. F. 1986. Adaptive strategies in desert shrubs with special reference to the creosote bush [*Larrea tridentata* (D. C.) Cov.]. Pages 19-49 *in* W. G. Whitford, editor. Pattern and process in desert ecosystems. University of New Mexico Press, Albuquerque, New Mexico.

Ricklefs, R. E. 1987. Community diversity – relative roles of local and regional processes. Science **235**: 167-171.

Ricklefs, R. E. 2000. The relationship between local and regional species richness in birds of the Caribbean Basin. Journal of Animal Ecology **69**: 1111-1116.

Ridd, M. 1995. Exploring a V-I-S (Vegetation-Impervious Surface-Soil) model for urban ecosystem analysis through remote sensing – comparative analysis for cities. International Journal of Remote Sensing **16**: 2165-2185.

Robbins, P. 2001. Tracking invasive landcovers in India, or why our landscapes have never been modern. Annals of the Association of American Geographers **91**: 637-659.

Rorslett, B. 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany **39**: 173-193.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univesity Press, Cambridge, New York.

Rudel, T. K., D. Bates, and R. Machinguiashi. 2002. A tropical forest transition? Agricultural change, out-migration, and secondary forests in the Ecuadorian Amazon. Annals of the American Association of Geographers **92**: 87-102.

Sagar, R., S. Raghubanshi, and J. S. Singh. 2003. Asymptotic models of species-area curve for measuring diversity of dry tropical forest tree species. Current Science **84**: 1555-1560.

Scanlan, M. J. 1981. Biogeography of forest plants in the prairie forest ecotone in western Minnesota. Pages 97-124 *in* Burgess, R. L. and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer Verlag, New York.

Scheiner, S. M. 2003. Six types of species-area curves. Global Ecology and Biogeography **12**: 441-447.

Scheiner, S. M. and M. R. Willig. 2005. Developing unified theories in ecology as exemplified with diversity gradients. The American Naturalist **166**: 458-469.

Scheiner, S. M., S. B. Cox, M. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari. 2000. Species richness, species-area curves, and Simpson's paradox. Evolutionary Ecology Research **2**: 791-802.

Schmid, M. K. and G. F. Rogers. 1988. Trends in fire occurrence in the Arizona Upland subdivision of the Sonoran Desert, 1955 to 1983. Southwestern Naturalist **33**: 437 – 444.

Schoener, T. W. 1976. The species-area relationship within archipelagos: models and evidence from island land birds. Proceedings of the XVI International Ornithological Conference: 629-642.

Sharpe, D. M., G. R. Guntenspergen, C. P. Dunn, L. A. Leitner, and F. Stearns. 1987. Vegetation dynamics in a southern Wisconsin agricultural landscape. Pages 137 - 155 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

Shreve, F. and I. L. Wiggins. 1964. Vegetation and flora of the Sonoran Desert. Stanford University Press, Stanford, California.

Shupe, S. M. 2005. Multivariate characterization of Sonoran Desert vegetation in southwest Arizona using US Army field data. Plant Ecology **176**: 215-235.

Shupe, S. M. and S. E. Marsh. 2004. Cover- and density-based vegetation classifications of the Sonoran Desert using Landsat TM and ERS-1 SAR imagery. Remote Sensing of Environment **93**: 131-149.

Simberloff, D. and J. L. Martin. 1991. Nestedness of insular avifaunas – simple summary statistics masking complex species patterns. Ornis Fennica **68**: 178-192.

Simberloff, D. S. and N. Gotelli. 1984. Effects of insularization on plant species richness in the prairie-forest ecotone. Biological Conservation **29**: 27-46.

Soil Survey Geographic Database. 2002. Maricopa county. National Cartographic and Geospatial Center, Fort Worth, Texas.

Solbrig, O. T., M. A. Barbour, J. Cross, G. Goldstein, C. H. Lowe, J. Morello, and T. W. Yang. 1977. The strategies and community patterns of desert plants. Pages 67-106 *in* G. H. Orians and O. T. Solbrig, editors. Convergent evolution in warm deserts. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.

Soule, M. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos **63**: 39-47.

Soule, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect: a model of faunal collapse in the game reserves of East Africa. Biological Conservation **15**: 259-272.

Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. Journal of Animal Ecology **68**: 1-16.

Stefanov, W. L., M. S. Ramsey, and P. R. Cristensen. 2001. Monitoring urban land cover change: an expert system approach to land cover classification of semiarid to arid urban centers. Remote Sensing of Environment **77**: 173-185.

Stohlgren, T. J., M. B. Coughenour, G. W. Chong, D. Binkley, M. A. Kalkhan, L. D. Schell, D. J. Buckley, and J. K. Berry. 1997. Landscape analysis of plant diversity. Landscape Ecology **12**: 155-170.

Sugihara, G. 1981. $S=CA^z$, z congruent to ¼ - reply. The American Naturalist **117**: 790-793.

Sullivan, B. K. and M. Flowers. 1998. Large iguanid lizards of urban mountain preserves in northern Phoenix, Arizona. Herpetological Natural History **6**: 13 – 22.

Suzan, H., G. P. Nabhan, and D. T. Patten. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. Journal of Vegetation Science **7**: 635 – 644.

SYSTAT 6.1 for Windows. SPSS Inc., Chicago, Illinois.

Tanser, F. C. and A. R. Palmer. 1999. The application of a remotely sensed diversity index to monitor degradation patterns in a semi-arid, heterogeneous South African landscape. Journal of Arid Environments **43**: 477-484.

Terborgh, J. W. and J. Faaborg. 1980. Saturation of bird communities in the West Indies. The American Naturalist **116**: 178-195.

Tewksbury, J. J. and J. D. Lloyd. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients, and benefactor size. Oecologia **127**: 425 – 434.

Tjorve, E. 2003. Shapes and functions of species-area curves: a review of possible models. Journal of Biogeography **30**: 827-835.

Tokeshi, M. 1993. Species abundance patterns and community structure. Advances in Ecological Research **24**: 111-186.

Turner, R. M. 1974. Map showing vegetation in the Phoenix area, Arizona. US Geological Survey Map I-845-I.

Turner, R. M. and D. E. Brown. 1982. Sonoran desertscrub. Pages 181-221 *in* D. E. Brown, editor. Biotic communities of the American Southwest-United States and Mexico. University of Arizona Press, Superior, Arizona.

Ulrich, W. and J. Buszko. 2003. Species-area relationships of butterflies in Europe and species richness forcasting. Ecography **26**: 365-373.

Valone, T. J. and C. D. Hoffman. 2002. Effects of regional pool size on local diversity in small-scale annual plant communities. Ecology Letters **5**: 477-480.

Van Ruremonde, R. H. A. C. and J. T. R. Kalkhoven. 1991. Effects of woodlot isolation on the dispersion of plants with fleshy fruits. Journal of Vegetation Science **2**: 377-384.

Ward, D., S. R. Phinn, and A. T. Murray. 2000. Monitoring growth in rapidly urbanizing areas using remotely sensed data. Professional Geographer **52**: 371-386.

Weibull, W. 1951. A statistical distribution function of wide applicability. Journal of Applied Mathematics **18**: 293-296.

Weiher, E. 1999. Relative abundance and evenness patterns along diversity and biomass gradients. Journal of Ecology **87**: 1005-1011.

Went, F. W. 1948. Ecology of desert plants: I. Observations on germination in the Joshua Tree National Monument, California. Ecology **29**: 242-253.

Whitford, W. G., R. Nielson, and A. de Soyza. 2001. Establishment and effects of establishment of creosote bush, *Larrea tridentata*, on a Chihuahuan Desert watershed. Journal of Arid Environments **47**: 1-10.

Whyte, W. H. 1968. The last landscape. Doubleday, Garden City, New Jersey.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience **48**: 607 – 615.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95-118 *in* M. E. Soule and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Massachussetts.

Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy – the effects of fragmentation on extinction. The American Naturalist **125**: 879-887.

Williams, C. B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, Orlando, Florida.

Williams, M. R. 1995. An extreme-value function model of the species incidence and species-area relations. Ecology **76**: 2607-2616.

Williams, M. R. 1996. Species-area curves: the need to include zeroes. Global Ecology and Biogeography Letters **5**: 91-93.

Williamson, M. 1981. Island populations. Oxford University Press, Oxford.

Williamson, M., K. J. Gaston, and W. M. Lonsdale. 2001. The species-area relationship does not have an asymptote. Journal of Biogeography **28**: 827-830.

Wilson, E. H. and S. A. Sader. 2002. Detection of forest harvest type using multiple dates of Landsat TM imagery. Remote Sensing of Environment **80**: 385-396.

Wilson, M. F., L. Leigh, and R. S. Felger. 2002. Invasive exotic plants in the Sonoran Desert. Pages 81 – 90 *in* B. Tellman, editor. Invasive exotic species in the Sonoran region. University of Arizona Press, Tucson, Arizona.

Worthen, W. B. 1996. Community composition and nested-subset analysis: basic descriptors for community ecology. Oikos **76**: 417-426.

Wright, D. H. and J. H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia **92**: 416-428.

Wright, D. H., B. D. Patterson, G. M. Mikkelson, A. Cutler, and W. Atmar. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia **113**: 1-20.

Yang, R. C., A. Kozak, and J. H. G. Smith. 1978. The potential of Weibull-type functions as flexible growth curves. Canadian Journal of Forest Research **8**: 424-431.

Yang, T. W. and C. H. Lowe. 1956. Correlation of major vegetation climaxes with soil characteristics in the Sonoran Desert. Science **123**: 542.

Yool, S. R. 1998. Multi-scale analysis of disturbance regimes in the northern Chihuahuan Desert. Journal of Arid Environments **40**: 467-483.

Zschau, T., S. Getty, C. Gries, Y. Ameron, A. Zambrano, and T. H. Nash. 2003. Historical and current atmospheric deposition to the epilithic lichen *Xanthoparmelia* in Maricopa County, Arizona. Environmental Pollution **125**: 21 – 30.