

QUANTITATIVE ANALYSIS OF HANGING GARDEN
ENDEMIC SPECIES RICHNESS IN THE
MOAB REGION, UTAH

by

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A dissertation submitted to the faculty of
The University of Utah
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Geography
The University of Utah
August 1996

ABSTRACT

Much of the previous research concerning hanging gardens has been of a descriptive nature. This work quantifies the relationship between those plant species that are primarily restricted to hanging gardens (endemic species) and selected environmental, spatial, and structural aspects of the gardens at the microhabitat (individual plot), local (garden), and regional scale (Moab region). Furthermore, it investigates the effects of environmental, spatial and structural factors on the species richness of the endemics in which species richness is the number of endemic species per area unit. Data on the hanging gardens were collected in the Moab, Utah, area where Navajo and Entrada sandstones occur over wide areas. Consequently, there are numerous and varied hanging gardens. An intensive sample of 25 hanging gardens was conducted in July and August of 1994. In each garden, four 4-m square plots (100 plots) were sampled according to a random stratified sampling design with disproportionate sampling in areas where endemics were expected to occur.

The results of the analysis indicate that gardens with high numbers of endemics are gardens that have lower light levels, are not subjected to flooding, have coarse soil textures due to the dominance of groundwater erosion (as well as no flooding), are the more mature gardens, and have water available from the seep line in more than half the perimeter of the garden. The low light environment and availability of water tend to indicate that some of these species are shade-adapted, moisture-loving species. The lower number of endemics in flood prone gardens indicates that some of these species are not adapted to frequent disturbance. The fact that high species richness occurs in gardens

where groundwater erosion is dominant and flooding does not occur indicates that the endemic species are adapted to small scale disturbances caused by rock spalling that occurs as a result of groundwater erosion in these sandstone alcoves. It is concluded that if the area is held constant a set of environmental and spatial factors can be found that will predict the number of endemics in the gardens.

The prediction equation developed appears to be related to the importance of succession in species richness where the disturbance regime is controlled by groundwater erosion. The light environment and seepline predictors indicate the successional stage of the garden, and the position of the garden and the soil texture predictors indicate the disturbance level. In gardens with high endemic richness, the disturbances tend to be frequent small-scale disturbances and temporally rare large-scale disturbances. In other words, the disturbance is frequent enough to keep the later successional species from excluding the earlier successional species but infrequent enough to allow later successional species to become established in the garden.

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I. INTRODUCTION

Hanging gardens are defined as a type of vegetation community that occurs where subsurface water flows out of solid rock. In addition to being a vegetation community, gardens are considered to be a geomorphic and hydrologic unit. Many researchers in ecology and botany have examined hanging gardens in southern Utah. Welsh and Toft (1981) described the geomorphology, geologic strata, and plant communities of the hanging gardens of southeastern Utah. Welsh (1989) provided descriptive information of the hanging gardens of the Colorado Plateau and the Virgin River drainage including geography, geomorphology, aspects of species distribution and diversity, and summaries of the principal vascular and algae species. Other research has provided information about specific endemic plant species such as their characteristics and details of their sites (Franklin, 1992). Additionally the above material includes speculation about the distribution and the floristic affinities of the species that occur in the gardens (Franklin, 1992; Welsh, 1981). Much of the previous research concerning hanging gardens has been of a descriptive nature. The only research that has attempted to quantify and analyze the distributions of the plant species has been that of Nebeker, Harper, Brotherson, and Welsh (1977); Malanson (1978, 1982); and Malanson and Kay (1980). Malanson (1978, 1982) found that in the hanging gardens of Zion Narrows the disturbance variables of flood frequency and soil depth segregate dispersal types whereas the spatial variables of area, distance to possible seed sources, and relative isolation do not. Nebeker et al. (1977) found the hanging gardens in Arches National Park to be dissimilar, random assortments with the

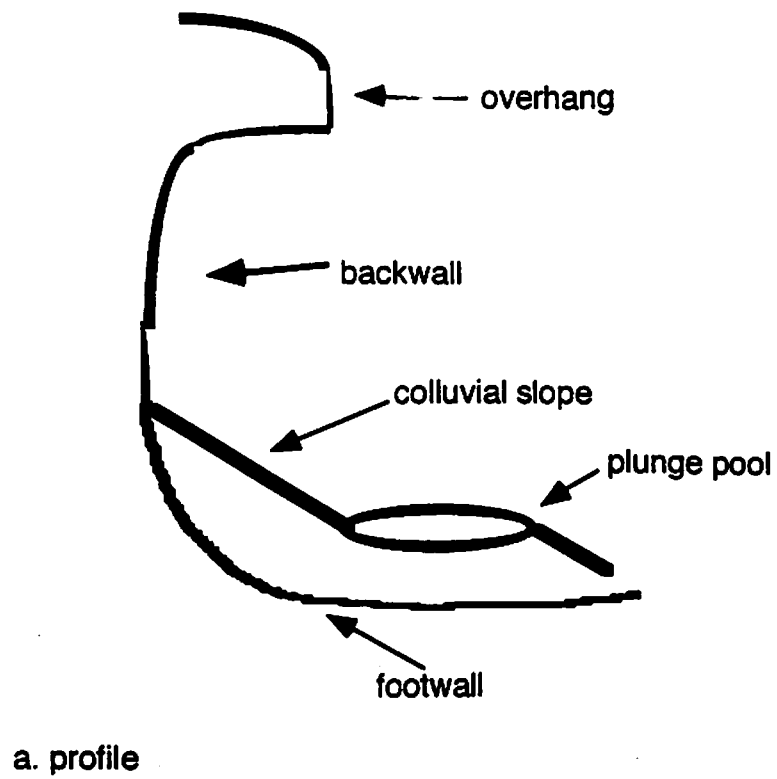
most common species being those adapted to dispersal by birds or wind. However, their investigations did not focus on the endemic plant species that occur in the gardens; rather they focused on the common species of the gardens.

These gardens are isolated from each other and from other plant communities by vertical expanses of sandstone, and their vegetation consists mostly of herbaceous species. Additionally, the habitats are relatively shaded, enclosed, or entrenched sites that promote high humidity, provide shelter from drying winds and intense sunlight, and contribute to cooler summer temperatures. The abundant water in many gardens should help moderate high day time and low night time temperatures (Clover & Jotter, 1944). Furthermore, Welsh (1989) reported that a hydrothermograph placed within Step Garden in Glen Canyon recorded smooth, rounded curves of temperature and humidity, as if the instrument had been placed within a house. It has been noted that there is a tendency for vegetation on the footwall to be stratified with the more mesophytic plants occurring along the line of contact between the backwall and the colluvial slope. Down slope these species give way to less mesophytic grasses, forbs, and low shrubs. Near the margin of the detrital slope, the vegetation gives way to tree and shrub species that provide added protection from sun and wind (Welsh, 1981). Hanging gardens are not generally rich in species, but as a group they are diverse and dissimilar. The gardens of the Colorado Plateau contain various combinations of the endemic species *Carex curattorum*, *Aquilegia micrantha*, *Primula specuicola*, *Habenaria zothecina*, *Cirsium rydbergii*, *Erigeron kachinensis*, *Perityle specuicola* and *Zigadenus vaginatus* (Table 1).

Table 1. Characteristics of endemic species.

Species	flowers	elevation range	habit	position
<i>Carex curatorum</i>	May-Aug.	1150-1340 m	perennial	backwall
<i>Zigadenus vaginatus</i>	Apr-Jun	_____	perennial	backwall
<i>Habenaria zothecina</i>	Jun-July	994-1829 m	perennial	detrital slope
<i>Erigeron kachinensis</i>	Apr-Jul	1630-1730 m	perennial	detrital slope
<i>Perityle specuicola</i>	Jul-Sept	1125-1220 m	perennial	backwall detrital slope
<i>Aquilegia micrantha</i>	May-Jun	1125-1895 m	perennial	backwall detrital slope
<i>Primula specuicola</i>	Mar-May	1210-1520 m	perennial	backwall detrital slope
<i>Mimulus eastwoodiae</i>	Jul-Sept	940-1370 m	perennial	backwall detrital slope
<i>Cirsium rydbergii</i>	Jul-Sept	1150-1370 m	perennial	backwall detrital slope

In addition, the most fully developed hanging gardens consist of an overhang that is arched or sloping and an arched or flat face or backwall (Figure 1). The footwall angles out from the bottom of the backwall and is sloping at an angle less than the angle of repose. It is covered by vegetated colluvium and/or alluvium (colluvial slope). Seepines occur on the face and are sometimes buried under the colluvial slope. Clinging vegetation occurs on the backwall



b. plan view

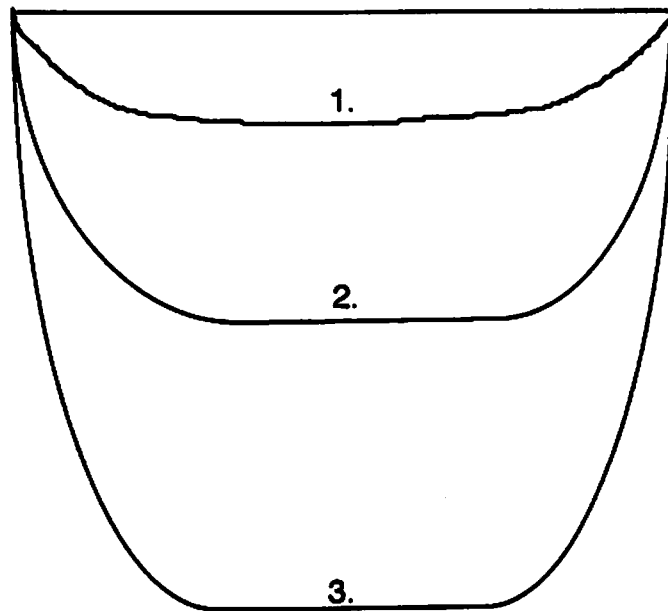


Figure 1. Profile(a) and plan view(b) of hanging garden. Plan view shows that configuration can be (1) linear, (2) moderately deep, or (3) parabolic.

and sometimes on the overhang. Gardens that are in stream channels occur at knickpoints or have retreated from plateau edges and often have plunge pools that are formed by waterfalls during stream flow. These pools are surrounded by alluvium and colluvium that are usually saturated with water from the nearby seep lines. The endemic plants occur on both the backwall, footwall, and detrital slope area (Welsh & Toft, 1981). The formations with the greatest development of hanging gardens are the Navajo and Entrada sandstones, both of which are crossbedded, massive formations composed of windblown sand and which contain ancient pond bottoms that serve as impervious bedding planes. According to Welsh (1989) water flows into the gardens along these bedding planes or between a lower, less permeable layer and these overlaying sandstones.

Furthermore, individual gardens support different endemic plant species and different numbers of the endemic species, i.e., exhibit different levels of species diversity or species richness. Researchers have noted that species occur in patterns in the gardens and have found that for common garden species factors such as disturbance and dispersal type are related to their occurrence. The primary focus of this work is the investigation of species richness of the hanging garden endemics through application of the principles of island biogeography. The theory of island biogeography is attractive for use in the examination of the endemic species diversity in the hanging gardens of the Colorado River drainage, because it provides a method to analyze the species diversity through testable predictions based on general ecological processes. This work, therefore, quantifies the relationship between those plant species that are primarily restricted to hanging gardens (endemic species) and selected environmental, spatial, and structural aspects of the gardens at the microhabitat (individual plot), local (garden), and regional scale (Moab region).

Furthermore, it investigates the effects of environmental, spatial, and structural factors on the species richness of the endemics in which species richness is the number of endemic species per area unit.

In addition, the primary environmental factors that control diversity at all scales are identified and their importance is explained. Environmental, spatial, and fragmentation effects, disturbance, and species richness vary at the microhabitat, local, and regional scale; therefore, the hypotheses were investigated at the appropriate scale or scales. According to theory, species richness increases with area; therefore the following hypothesis was tested. Area is a factor in the endemic species richness (local). Although a plethora of studies has involved species-area effects, MacArthur and Wilson (1967) never intended using area as a variable. Spatial, environmental diversity implies that the environment is diverse if a chosen quantitative or qualitative factor such as vegetation cover, soil salinity, or available moisture assumes different values at different locations (Kolasa & Rollo, 1991). It is reasoned that species diversity increases with area primarily because the diversity of the habitat increases with area. Habitat diversity may be a more important parameter because it includes area and environmental factors (Hart & Horwitz, 1991). Harner and Harper (1976) suggest that environmental habitat diversity may be a more powerful determinant of species diversity than area if their independent influences are separated.

With these concepts in mind, sampling of the gardens was designed to separate area effects from environmental and spatial effects to test hypotheses concerning these latter effects alone. The following hypotheses were tested: (a) A set of environmental and spatial variables can be used to predict the endemic species richness of the gardens or plots. (b) If sample plots or gardens display the same environmental and spatial characteristics, they will contain the same

endemic species (microhabitat, local) and they will contain the same number of endemic species. The sampling design also allows for separating fragmentation effects from environmental and spatial effects. Fragmentation effects imply that area affects temporal dynamics and relationships with other areas through effects on colonization, extinction, speciation, and catastrophic disturbance (Hart & Horwitz, 1991). Fragmentation effects were tested with the following hypotheses. (c) The species diversity of the endemic species is related to the location of the garden in space (local, regional). (d) In addition, if the diversity is held constant, larger areas will have greater species richness than smaller areas. Both processes and environmental factors operate at different scales; therefore scale effects were investigated. (e) The hypothesis that was addressed was that there are different, important explanations for distribution at each scale--microhabitat, local, and regional. Finally, the alcoves in which hanging gardens develop are the result of a type of groundwater erosion known as spring sapping erosion. (f) The following hypothesis was tested to examine the relationship of this process to species diversity. The dominance of spring sapping erosion is related to the species diversity of the endemic species (local, regional).

To test these hypotheses, data on the hanging gardens were collected in the Moab, Utah, area where Navajo and Entrada sandstones occur over wide areas. Consequently, there are numerous and varied hanging gardens. An intensive sample of 25 hanging gardens was conducted in July and August 1994. In each garden, four 4-m square plots (100 plots) were sampled according to a random stratified sampling design with disproportionate sampling in areas where endemics were expected to occur. In each sample plot, all species present were recorded. Soil samples were collected in each plot by sampling the first 15 cm of soil at each corner and at the center of the

plot. The soil samples were later analyzed for soil color, soil water salinity, soil water pH, and soil texture. The aspect of the plot was determined by compass. In each garden, data were recorded on a text form, and a schematic drawing was made of the garden. The depth, width, and aspect of the garden; the length of the visible seep lines; and the average slope of the colluvial slope were measured. Other factors recorded include depth of the overhang and location of plots. The location of the garden was recorded on 1:24,000 scale maps to be used to determine distance to nearest neighbor, distance to a channel that flows directly to the Colorado River, and distance to the Colorado River. All variables that were angle readings were converted to sine functions or dummy variables--aspect, slope of colluvium, and overhang angle--making them suitable for use as an independent variable in statistical analysis.

Finally, the data were analyzed primarily through multiple regression analysis of factors obtained through principal components analysis of the environmental and spatial variables. These factors were also used to obtain categories of gardens to test fragmentation effects through application of t tests.

In conclusion, the subsequent chapters detail the conceptual framework, analysis, and conclusions of this research. The following chapter is a conceptual framework of various aspects of the hanging gardens and investigations into species diversity. This framework includes investigations of general hanging garden characteristics, the endemic species, hydrology and geomorphology, species diversity, and spatial analysis methods. Chapter III includes the discussion of the methodology. Chapters IV to VI discuss the various aspects of the analysis of the regional and local data. Chapter VII presents the conclusions that are drawn from the analysis. Chapter VIII discusses the analysis of the microhabitat data. Chapter IX presents the conclusions that were drawn from this analysis. Chapter X discusses the

relationships between the levels of organization. The final chapter presents a summary of the conclusions of the research and future research questions.

II. THE CONCEPTUAL FRAMEWORK

The conceptual framework for examining species diversity in the hanging gardens involves several topics. These topics include the hanging gardens, endemic species, the theory of island biogeography, groundwater geomorphology, and spatial analysis. Each of these topics will be examined in this chapter.

A. Hanging Gardens

The existing literature provides an invaluable amount of descriptive material concerning the hanging gardens. Along with these descriptive works, there is speculation about the distribution of the plant species that occur in the gardens. The only research that has attempted to quantify and analyze the distributions has been that of Nebeker et al. (1977), Malanson (1978, 1982), and Malanson and Kay (1980). Malanson's research in the Zion Narrows, however, involved only the common species of the gardens, i.e., he noted that for common species the greatest diversity was in the stable sites and the gardens maintain their dissimilar, fugitive assemblages through the response of dispersal types to frequent disturbance (1978). More explicitly, he found that the disturbance variables of expected flood frequency and soil depth segregate dispersal types, whereas the spatial variables of area, distance to possible seed sources and relative isolation do not (Malanson & Kay, 1980). Nebeker et al. (1977), also working with common species of the gardens, concluded that garden assemblages are random collections of plants and found plants whose seeds are dispersed by birds are the most common in hanging gardens of Canyonlands and Arches.

Moreover, Nebeker et al. (1977) and Malanson (1982) concluded that the hanging garden vegetation is a random assortment of individuals. They were, however, considering all common species and not just the endemic species. In this research, the definition of hanging garden endemics excludes *Perityle specuicola* that occurs rarely in gardens and occurs in a very large population in Pole Canyon on sites that are not hanging gardens. It is a Colorado Plateau endemic but not a hanging garden endemic. In addition, the researchers did not control for differences in the area of the gardens. It has been known to botanists since the 1920s that the number of species increases in samples of larger area and that the rate of increase of species number decreases with progressively larger area (Myers & Giller, 1988). The slopes of the curves generated when the number species is plotting by area vary widely. Most studies of species-area relationships have failed to resolve their causal factors.

Furthermore, the stability of the gardens varies, with the backwall being very stable and the colluvial slope (Figure 1) being generally unstable; i.e., it is subjected to flooding (Malanson, 1978). Malanson's research was conducted in the Zion Narrows area which is subject to frequent flooding. Gardens on the Colorado Plateau do not appear to be flooded frequently. Malanson found that the stable areas of the garden are dominated by K-selected species. K-selected species are characterized by being perennial, showing late maturity, producing fewer seeds, and often exhibiting many chemical and/or mechanical defenses (Mauseth, 1991). In contrast, r-selected species are fast growing annuals with few defensive compounds or structures, flower quickly, and produce many small seeds. Their seeds are also adapted to widespread dispersal. Stable gardens or more stable portions of gardens have more diverse vegetation and contain more rare species. All of the hanging garden endemics in this study are K-selected species. Malanson (1978) concluded that these stable sites appear to

support the deduction that hanging gardens are relictual refugia. Refugia are geographic areas whose limits are distinct. They are habitats that protect species from certain extinction during some series of environmental disturbance. As such, they tend to be small areas within a larger ecogeographic unit (Myers & Giller, 1988).

However, Welsh (1981) states that the plants with boreal and Southwestern affinities in hanging gardens do not represent "transads," i.e., plants that exist on both sides of desert communities and must have extended through those communities at some time in the past. He describes these species as opportunists that are in the gardens as a result of long-distance dispersal; he further doubts that boreal or southwestern elements were ever directly tied to a widespread flora; i.e., they were always disjunct.

The deduction that these species are opportunists and are the result of long distance-dispersal does, in fact, appear to be the case with the common species of the gardens (Nebeker et al., 1977). This may not, however, be the case with the K-selected endemic species of the gardens.

Furthermore, it has been noted that many riparian species (*Betula*, *Alnus*, *Acer*, *Populus*, *Salix*, *Celtis*, *Cercis* species) in the western U.S. have affinities with Tertiary floras (Chaney, 1947). Chaney (1947) and Axelrod (1958) divide the early Tertiary vegetation of North American into three geofloras. Each of these geofloras was said to represent a major vegetation type and to have wide geographic extent and uniformity. In the southern half of North America was the broadleaf, evergreen, Neo-Tropical Geoflora. In the north was the temperate, mixed deciduous Arcto-Tertiary Geoflora. Between the two, in the southern Rocky Mountains and Mexico was the sclerophyllous and microphyllous Madro-Tertiary Geoflora (Axelrod, 1958).

In addition, Daubenmire (1978) and Wolfe (1987) have examined the composition of the temperate mesophytic forest regions and its subsequent segregation as the western United States became increasingly arid. Deciduous trees and shrubs that occurred when these forests extended from coast to coast across North America included *Acer*, *Betula*, *Ostrya*, *Quercus*, *Cornus*, *Crataegus*, *Rhamnus*, *Philadelphus*, *Sambucus*, and *Fraxinus*. These are all common riparian species in the western United States and most occur in hanging gardens. These forests became three separate entities, the eastern forests that became predominantly deciduous hardwood forests, except at high latitudes or altitudes, and two western components (Daubenmire, 1978; Wolfe, 1987). The first western component is the *Tsuga heterophylla* component that extends from Alaska to Central California. The second is the *Pseudotsuga menziesii* component. It occurs mainly at midaltitudes in the mountains where the heat supply is better than at subalpine forest elevations, but moisture is not as deficient as in the lowlands. The occurrence of these temperate forests parallels the subhumid climate zones. In the area of the Colorado Plateau, there are now two areas with subhumid climates that support temperate mesophytic components--the *Pseudotsuga menziesii* zone in the mountains and some riparian areas, including hanging gardens.

In addition, during the Miocene, as the western United States became more arid with the continuing rise of the Sierra Nevada and the Rocky Mountains, the various climatic stresses are believed to have stimulated the evolution of the herbaceous life form. Before the Miocene, there was little evidence of the existence of herbs (Daubenmire, 1978). These species do not occur west of Peach Springs in the Grand Canyon, and they are intimately connected to the Colorado River drainage system northeast of this point. If some upper Colorado River species are compared with species in the gardens of Zion

National Park, it is found that in the Zion gardens there are *Aquilegia formosa* and *A. chrysantha*, but no *A. micrantha*; *Mimulus cardinalis*, but no *M. eastwoodiae*; *Dodecatheon pulchellum*, but no *Primula specuicola*. Species that do occur in gardens in both areas include *Calamagrostis scopulorum*, *Carex aurea*, and *Adiantum capillus-veneris* (Welsh, 1989). The development of the eastern Colorado drainage would appear to be an important part of the development of the flora of these gardens. The Colorado River drainage is believed to have become integrated between 3.8 and 5.9 millions years ago (Nations, Wilt, & Helvey, 1985). These temperate forest species and their associated herbaceous species apparently occurred in the Colorado Plateau region before the complete integration of the river system, especially the integration with the portions of the river below the Grand Canyon.

B. The Endemic Species

The hanging gardens contain various combinations of the endemic species *Carex curatorum*, *Aquilegia micrantha*, *Primula specuicola*, *Cirsium rydbergii*, *Erigeron kachinensis*, *Habenaria zothecina*, *Perityle specuicola*, and *Zigadenus vaginatus* (Table 1). *Carex curatorum* is listed as a separate species by several researchers (Albee, Shultz, & Goodrich, 1988; Welsh, Atwood and Reveal, 1975) whereas Cronquist, Holmgren, Holgren, Reveal and Holmgren (1977) lists it as a variety of *Carex scirpoides*. The other variety, *Carex scirpoides pseudosciroidea*, occurs at high elevations in the mountains, often above treeline. *C. curatorum*, however, occurs only in hanging gardens of the Colorado and San Juan Rivers above their confluence and on the Kaibab Plateau in Arizona (Atwood et al., 1991). *Zigadenus vaginatus* is listed as a separate species by Welsh (1975) but is considered to be synonymous with *Z. elegans* by other researchers such as Albee et al. (1988); in fact, Welsh et al.

(1975) maintain that it is related to *Z. elegans* and notes that it occurs in gardens in Grand, San Juan, and Kane counties in Utah. *Habenaria zothecina* is listed by Welsh et al. (1975) and Albee et al. (1988). Cronquist et al. (1977) include it as synonymous with *H. sparsifolia*. *Habenaria zothecina* is found in hanging gardens from Arch Canyon, west of Comb Ridge, north to Arches National Park; it is also found on moist stream banks near hanging gardens. It occurs in Emery, Garfield, San Juan, Grand, and Uintah Counties of Utah and in Moffat County, Colorado (Atwood et al., 1991). *Erigeron kachinensis* grows in hanging gardens in White, Armstrong, and Dark Canyons, as well as along the Dolores River (Welsh, 1989). It also occurs on sandy sites in ponderosa at high elevations in the Abajo Mountains. It is closely related to *E. subglaber* (Atwood et al., 1991). *Perityle specuicola* is endemic to Grand and San Juan County, Utah. Its southern most occurrence is just north of Dark Canyon in Cataract Canyon. It is known mostly from gardens in the Moab area (Welsh, 1989) with the largest population found in Pole Canyon near the Dewey Bridge (Franklin, 1993). It is believed to be related to *P. tenella* (Atwood et al., 1991), which grows only in Washington County, Utah. *Aquilegia micrantha* occurs in most hanging gardens and is found in Emery, Garfield, Grand, Kane, San Juan, and Wayne Counties of Utah, as well as in Colorado and Arizona on the Colorado Plateau (Welsh, 1989). *Primula specuicola* is found in gardens in Grand, Garfield, Kane, San Juan, and Wayne Counties of Utah, and in northern Arizona. *Mimulus eastwoodiae* occurs in Grand, Kane, and San Juan Counties of Utah and in adjacent areas of northern Arizona (Welsh et al., 1975). *Cirsium rydbergii* is distributed in Garfield, Grand, Kane, San Juan, and Wayne Counties of Utah and in the Black Mesa area of Apache County Arizona (Welsh et al., 1975). It occasionally grows outside the gardens in the adjacent drainages (Welsh, 1989).

According to Rabinowitz (1981) narrow endemics are locally abundant in a specific habitat but are restricted geographically. This definition is used to distinguish narrow endemism from other forms of rarity. In order to clarify the distinction between endemics and common species, hanging garden endemics are defined in this work as those species that occur primarily in hanging gardens or adjacent habitats. Common species are defined as those species that are not primarily restricted to hanging garden habitats. Major (1988) defines a taxon as endemic if it is confined to a particular area through historical, ecological, or physiological reasons. Each of these reasons and their relevance to the hanging garden endemic plants are discussed in the following section.

1. Historical Factors

The age of a taxon is often described with the terms neoendemic and paleoendemic. Neoendemics are described as youthful species while paleoendemics are relatively old relict species (Cain, 1944). Stebbins and Major (1965) recast this classification by considering the way that narrow endemics have achieved their restricted distributions. Their system includes the age of the endemic, its systematic position, and its chromosome number and ploidal level (number of sets of chromosomes). In groups of related species, diploids are older than derivative low polyploids, whereas high polyploids and diploids are paleoendemics. Endemics with more than one disjunct population are likely to be paleoendemics. Paleoendemics are ancient remnants of taxa that were once more widespread. Their specialized habitats have constricted over time. Neoendemism lacks generic endemism (Tolmachev, 1974). Neoendemics are recent origin and may expand their range and gene pool (Stebbins & Major, 1965). In California paleoendemics are found in mild

climate, in high precipitation areas, and in the most arid deserts whereas neoendemics are found in border regions between arid and humid climates (Stebbins & Major, 1965).

In addition, geologic processes such as mountain building, connection and disconnection of land masses, soil genesis, and other processes that create discontinuities often result in the isolation that is necessary for the genesis of unique biotas (Kruckeberg & Rabinowitz, 1985). Connection of land masses provides new avenues of migration, whereas disconnection isolates formerly connected biotas. These same forces may create changes in climate such as the dry shadow that resulted from the creation of the Sierra Nevada. Other climate-induced changes may result from glacial and interglacial episodes.

Additionally, evolutionary history includes the effects of past climatic changes, mode of origin of species, and phyletic momentum or inertia (Fiedler & Ahouse, 1992). One effect of climate change could be the isolation of a species adapted to a mesic habitat in small enclaves within an arid area. Such a species may not have the phyletic momentum to ever expand its range under present climate conditions. If it has the ability it might evolve sympatrically ("in the same location") at the edge of its range or allopatrically ("in separated locations") if several populations are isolated from one another.

Although it is not known if the hanging garden endemics are paleoendemics, the habitat in which they occur has been evolving since the initial formation of the Colorado Plateau. These species could have been evolving right along with the habitat. The broadleaf deciduous trees characteristic of riparian areas include genera and species that were once part of widespread early Tertiary mixed mesophytic forests. As climates became more arid in the western United States from middle to late Tertiary, these forests

fragmented and disappeared over wide areas (Raven & Axelrod, 1978). *Populus-Salix* associations are known to have diversified during the Tertiary and now occupy a wide variety of regions, all of which share the common features of running water and shifting substratum (Reichenbacher, 1984). These broadleaf deciduous forests undoubtedly had understory species some of which came to occupy riparian areas and perhaps hanging gardens. In a study of *Mimulus*, Vickery and Wullstein (1987) found *Mimulus eastwoodiae* to be more closely related to *M. lewisii* than is *M. cardinalis* (which is found outside the Colorado Plateau in Arizona and Zion National Park). *Mimulus lewisii* is widespread in the western United States and in Utah at high elevations (Spellenburg, 1979). Many of the hanging garden endemics appear to be related to high elevation species. These species could then be very old, having developed from Tertiary forest understory species and retreating to hanging gardens while related species retreat to high elevations as the climate became more and more arid.

However, these endemics do not correspond to some of the characteristics of paleoendemics. They do not display generic endemism. In Vickery and Wullstein's work (1987), the six *Mimulus* species included all displayed the same ploidy level $n=8$. According to Stebbins and Major (1965) neoendemics retain the same ploidy level as their progenitors. As noted above in California paleoendemics are found in moisture rich, equitable climates whereas neoendemics are found at humid-arid boundaries. Both of these conditions describe the hanging garden environment. The age of these taxa and their evolutionary history appear to be unanswerable at this point. However, if I make an educated assumption that they are old species and apply the categorization of endemics developed by Fiedler and Ahouse (1992), these species would be included in the narrow (distribution)/ long (persistence)

category. This would indicate that the primary causes of rarity are long-term processes such as evolutionary history and earth history, and the second order of probable causes includes taxon age, stochasticity and taxon ecology. If they are in the category of short/narrow, the first order causes are small-scale events such as taxon ecology, life history strategies, and stochasticity, and the second order causes include reproductive biology, genetics, and population dynamics.

To summarize, in the historical factors category, the only aspect that is well known is the earth history. The formation of the Colorado Plateau, the retreat and fragmentation of mesophytic deciduous forests, and the integration of the Colorado River system (which may have been as little as 4-5 million years ago) all point to a habitat and flora that may be quite old.

2. Ecological Factors

The ultimate success of an organism in occupying space is its tolerance to environmental factors (Kruckeberg & Rabinowitz, 1985). Differences in microclimate may evolutionarily select for the persistence of a species. For example, Young and Smith (1979) found that for the two subalpine congeners, *Arnica cordifolia* and *A. latifolia*, the small-scale distribution of both species appeared to be coupled to the sunfleck dynamics of their respective microclimates due to the lack of stomatal action that would reduce transpiration. Differences in microclimate provide variation of habitats to be exploited by distinct biotas. When local climates are highly discontinuous or very different than the prevailing climate, some plants will become endemic to those sites. The ultimate causes of the multitude of discontinuities in space and time are geological processes. These processes create microclimates and irregularities in the landscape that result in physical and chemical irregularities that in turn provide an assortment of discrete habitats (Kruckeberg & Rabinowitz, 1985). An

abundance of cliff crevice plants in arid and humid mountains and on islands are endemics. According to Major (1988), open, rocky cliff and rapidly eroding sites are often the most stable sites (least disturbed).

Moreover, edaphic conditions (chemical, physical, and biological properties of soils) have long been linked to endemic taxa. Plants endemic to soils derived from serpentinite and ferromagnesian rocks are found in sites around the world--Zimbabwe, New Caledonia, Yugoslavia, California, and Oregon. Other endemics are found on substrates like gypsum, limestone, alkaline, and heavy metal soils (Kruckeberg & Rabinowitz, 1985).

Furthermore, population dynamics and structure include factors that influence recruitment and mortality and the status of populations (declining, stable, increasing) (Fiedler & Ahouse, 1992). There have been few studies on population dynamics of endemics. One study on rarity (Wells 1981) concerning orchids found that brush clearing and grazing that occurred a decade earlier affected the population recruitment and current dynamics. Small populations may be more prone to extinction than larger populations (Simberloff, 1974). However, Rabinowitz (1981) has shown that natural selection can favor traits that offset the disadvantages of small population.

In addition, endemics coexist with other organisms. They are often members of distinctive communities. Though community status, competitive ability, and interactions with other species are often included in accounts of taxa attributes, they have rarely included endemics (Kruckeberg & Rabinowitz, 1985). Studies that have been done have found some endemics occurring in specific successional habitats (Mahler, 1983). The community in which an endemic occurs can be either rare or common. Some endemics have been found to be poor competitors (Grime, 1979) whereas others have not (Rabinowitz, 1981).

Moreover, lack of control of stomata opening and therefore lack of control of transpiration may account for shade-adapted species distributions. From my personal observation, it has been noted that in one garden these endemic species were only exposed to the sun for 15 min to less than 2 hrs. Outside of the garden most species are exposed to the sun for long periods of time at high temperatures and low humidities. Temperatures in the gardens are several degrees lower and the humidity is higher throughout the day. These hanging garden endemics may be restricted to hanging gardens because they cannot tolerate long exposure to the sun, high temperatures, and low humidities. Ehrlinger (1993) noted that *Cirsium rydbergii* functions with its stomata wide open even when it is in full sun. If these endemics are all able to do this, they are then able to maximize their photosynthesis during their brief exposures to sunlight.

Furthermore, the hanging gardens are geologically and edaphically different than the surrounding landscape. The substrates are sometimes much less saline, the perched water tables provide adequate to abundant water, and this same groundwater creates a distinctive erosion surface. These erosion surfaces appear to be quite stable. They are subjected to occasional small-scale rock spalling from the backwall and the removal of material from the toe of the colluvial slope by runoff that pours into the plunge pool. The flooding of the plunge pool affects a very small portion of the garden only, but it perpetuates the development of the hanging garden by transporting the colluvium downstream. If colluvium buries the seep lines or seep lines, the development of the garden will cease (Baker, 1990). The large-scale rock falls that result from undercutting appear to be relatively rare.

Finally, little is known of the population dynamics of these endemics. The previous records of these endemics appear to show that the populations

fluctuate up and down over a period of years in a particular location. It was noted above that population fluctuations may be the result of sporadic reproduction which in turn could be the result of some environmental fluctuation, i.e., changes in the availability of water. It could also be related to small or large-scale disturbances. For example, in a garden in Cordova Canyon there appears to have been a relatively recent large rock fall. There are very many more juvenile *Habenaria zothecina* than adults. In general, the opposite is true. There are more adults than juveniles. Nothing is known about the competitive abilities or community interactions of these endemics. A log assembly ratio (Caswell & Cohen, 1991) does indicate that these endemics tend to occur together (Table 2).

3. Physiological Factors

Major (1988) hypothesizes that mode or rates of photosynthesis and transpiration rates may be distinct in endemic species. In some subalpine understory species, transpiration was not controlled because the stomata did not close in response to sunflecks. Perhaps some species lack stomatal control and would be endemic to understory type habitats. C₄ species (species with an alternative photosynthetic pathway) might be endemic to habitats with high temperatures and frequent drought (Major, 1988). Other physiological responses might be the ability to take up and dispose of heavy metals or salts that would be toxic to other species.

In addition, the number and type of seed produced may affect the rarity of a species. For example, Wiens (1984) has found that for the rare paleoendemic *Dedeckera eurekaensis* the percentage of viable seed produced averages about 2.0% (below 4% is critical) and that spontaneous seed germination averaged only 3.5% in seven trials. Plants that do produce seedlings die when

Table 2. Log-assembly ratio values (Caswell & Cohen, 1991).

	<i>Aquilegia</i>	<i>Primula</i>	<i>Mimulus</i>	<i>Cirsium</i>	<i>Habenaria</i>	<i>Zigadenus</i>
<i>Aquilegia</i>	X	-.26*	-.09	-.75	.39	.12
<i>Primula</i>	-.26	X	.37	.28	-.10	.44
<i>Mimulus</i>	-.09	.37	X	-.35	.48	.75
<i>Cirsium</i>	-.75	.28	-.35	X	-.79	.45
<i>Habenaria</i>	.39	-.10	.48	-.79	X	.36
<i>Zigadenus</i>	.12	.44	.75	.45	.36	X
**	+2	+3	+3	+2	+3	+5

*A negative value indicates that the species tend not to occur together. A positive value indicates the species tend to occur together. A zero value indicates the species are distributed independently.

* *The number of species that tend to occur together.

they are still quite small. The seed dispersal mode of a species may contribute to rarity. For example, if a species is wind dispersed in a very patchy environment it may have little chance of landing in a site where it can successfully germinate. Some species in patchy environments may resort to vegetative reproduction to ensure their persistence. Pollination biology may be influential in rare taxa. Harper (1979) using lists of rare and endemic plants

from Utah, California, and Colorado found woody plants to be underrepresented and herbs to be over represented. He also found that rare species exhibit bilateral more often than radial symmetry. Bilateral species must depend on healthy insect populations for pollination.

For the hanging garden endemics, stomatal closure and photosynthesis characteristics of shade-adapted plants may be important physiological characteristics. Of these endemics *Aquilegia micrantha* appears to occur in the most microhabitats within the gardens. It also appears to be the most variable in the color, size, and shape of the leaves, all of which would be adaptive to various amounts of sunlight. *Habenaria zothecina* appears to occur only very near or in running water. *Primula specuicola* exhibits variable leaf size. *Habenaria zothecina* and *Zigadenus vaginatus* have vertically oriented leaves which result in less exposure to sunlight. Of these six endemics, only two are bilaterally symmetrical. As noted above those that are bilaterally symmetrical are dependent on healthy insect populations. There are generally very healthy populations of insects in the gardens especially mosquitoes. I have also seen hummingbirds in the gardens and many *Mimulus* species are pollinated by hummingbirds. In Vickery and Wullstein's (1987) work on *Mimulus* they found that all the species studied normally outcross although they are self-compatible. Modes of seed dispersal have not been document for these endemics. From personal observation and according to other researchers (Franklin, 1992), it appears that these species may be reproducing vegetatively. If this is the case, it could be a strategy for filling spaces opened by small-scale disturbances caused by rock spalling. Wiens (1993) found that *Mimulus eastwoodiae* produced an average of 4% viable seeds. I investigated the number of viable seeds produced by *Primula specuicola* and found it to be about 50%. I have

seen no indication in any studies that these species have problems with seed germinate and establishment.

From the above discussion, it is apparent that as with most endemics little is known about the causes of their rarity or which factors may have selected for their occurrence in the hanging gardens. If these endemics are in the narrow/long category discussed above, as I believe they are, then the ultimate causes of their rarity or restriction are mainly long-term processes such as earth history that created and continues to create their unique habitat and their evolutionary history from mesophytic deciduous forest understory species to hanging garden species. If this is the case, then the second order causes include taxon ecology and stochasticity. These species are adapted to a rare habitat and to an active erosion surface that is very stable over time in some gardens.

C. Species Diversity and the Theory of Island Biogeography

The concept of species diversity resulted from studies of species-area relationships. Species richness is the number of species per unit area. Likewise, area has become a major independent variable for prediction of the number of species per unit area. It is suggested that increased area increases the number of possible habitats and, therefore, the number of species. Research in island systems has used area as a basis for species prediction, but precision is gained by the inclusion of other variables (Johnson & Raven, 1970; MacArthur & Wilson, 1967). Two models of differences in species-area relationships are fragmentation models and habitat heterogeneity models. Fragmentation effects imply that area affects temporal dynamics and relationships with other areas through affects on colonization, extinction,

speciation, and catastrophic disturbance (Hart & Horwitz, 1991). Spatial environmental heterogeneity implies that the environment is heterogeneous if a chosen quantitative or qualitative factor such as vegetation cover, soil salinity, or available moisture assumes different values at different locations (Kolasa & Rollo, 1991). It is reasoned that species diversity increases with area primarily because the heterogeneity of the habitat increases with area. Furthermore, heterogeneity may be a more important parameter because it includes area and other parameters (Hart & Horwitz, 1991). Harner and Harper (1976) suggested that environmental heterogeneity may be a more powerful determinant of species diversity than area if their independent influences are separated.

Additionally, species richness is related to disturbance frequency. The concept is that species richness is maximized at intermediate disturbance frequency (Connell, 1978; Huston, 1979). If disturbance is infrequent, local competition proceeds to equilibrium and fugitive species are eliminated. If disturbance is common, it eliminates all species. At intermediate frequencies, the combination of fugitive species and equilibrium species produces a maximum in species richness. It has been suggested that gardens that are not frequently flooded have a greater species richness and contain more rare species. Some hanging gardens of the Colorado Plateau experience very little flooding, i.e., in this sense they are very stable sites.

However, gardens occur at active erosion sites. Many of these gardens are dominated by spring sapping erosion processes rather than general fluvial processes. Groundwater outflow and sapping are proposed to be the most significant processes in the formation of theater-headed valleys in Navajo sandstone (Laity, 1990). As the valley develops, lateral retreat by sidewall seepage approaches that of the headward retreat (Dunne, 1990). These erosion sites may produce intermediate frequency disturbance.

Islands have been important to evolutionists, biogeographers, and ecologists since the time of Darwin and Wallace. With their well-defined boundaries and differences in size, shape, and distance from mainland species source areas, they have been viewed as natural experiments with biological communities. The main premise of the equilibrium theory of island biogeography is that each island is in dynamic equilibrium with species numbers between the processes of immigration and extinction, i.e., rates of immigration and extinction are a function of species number. The condition of equilibrium ($\underline{S}^*$) is found at the intersection point of the rate curves for immigration and extinction. Change is continual, and turnover of species composition is expected because the equilibrium is dynamic. The quantitative predictions of the equilibrium theory concern island size or distance from a source of potential colonists (MacArthur & Wilson, 1967). The colonization rate is a decreasing function of the distance to a source of colonists whereas the extinction rate is a decreasing function of island size. Furthermore, the immigration rate drops off rapidly as the best colonists become established on the island. The extinction rate increases more rapidly at high species numbers because of increased competition between species. According to the theory, small islands support fewer species due to higher extinction rates and islands close to the mainland support more species due to higher immigration rates. The theory can be extended to habitat islands, such as ponds and mountain tops. The theory provides a relatively simple and very importantly a quantitative approach to explaining patterns of species distributions. It emphasizes species richness; i.e., species are treated as equivalent (Schoener, 1988).

1. Immigration in Island Biogeography

Colonization rates or immigration rates decline with increasing species densities on islands because more and more species are already present on the island. Rates of colonization decline exponentially since, as the equilibrium density (S^*) is approximated, the species with the highest rates of colonization are already there. Only species with low probabilities of successful colonization are absent. In practice it is extremely difficult to determine the number of individuals or the sex of colonists. Generally the criterion used is the presence of a new species on an island. Censuses are conducted over discrete time intervals, and immigration curves are constructed from the data. These curves only approximate the actual rate because immigration and extinction can occur between census periods (Schoener, 1988).

Moreover, Simberloff and Wilson (1969) in their experiments on mangrove islands were able to construct actual rate curves for immigration after islands were fumigated. Rate curves have been obtained that support the theory (Rey, 1981) even though some do not (Osman, 1982). Other experiments suggest that the shape of the curve fluctuates seasonally in regions with seasonal variability (Osman, 1978). It is difficult to compare immigration rate curves from different studies because of the problems with census periods that were mentioned above.

2. Distance Effects in Island Biogeography

The theory predicts that the isolation of an island is the deciding factor in the arrival of a new species on an island. The descent of the curve is steeper for islands nearer a source (the initial rate of colonization is greater). Islands that are further from a source area have a lower number of potential colonizing species and less frequent arrival of new species. The immigration rate curve for

far islands has a lower intercept and a more gradual slope than that for a near island. If islands of similar size but at different distances from sources are paired, the theory holds that the near islands will maintain a greater number of species at equilibrium. A major problem with distance as a parameter is determining the source (Schoener, 1988). In their work on mangrove islands, Simberloff and Wilson (1969) found that species accumulated more slowly and achieved lower equilibrium numbers on more distant islands.

In addition, agreement with the predictions has also been obtained experimentally. The source area was a sponge fully colonized by freshwater microscopic organisms in a laboratory tank. Uncolonized substrates were placed at various distances from the source (Cairns & Henebry, 1982). In studies that have not agreed with the predictions it may be due to problems with spatial or time scales or the determination of the source or sources of colonists (Schoener, 1988).

3. Extinction and Turnover in Island Biogeography

Extinction rates are obviously zero when no species are present and the rates increase as more and more species are present on the island (and more time has elapsed). As population densities become individually smaller, it is thought that competitive exclusion causes extinction rates to increase. Extinction rates increase exponentially when the number of species is greater than the equilibrium number of species because species with higher extinction rates make up an increasing proportion of the biota (Schoener, 1988). The definition of extinction is relatively clear, but the measurement of extinction rates suffers from the same problems as colonization. Another problem encountered with extinction rates is the "rescue effect" which has been observed among Arizona desert thistles (Brown & Kodric-Brown, 1977). When immigration rates

are high, populations can be saved from extinction by the continual influx of individuals and new genetic material.

In practice, turnover rates (the number of species replaced by new species per unit time at equilibrium) are extremely difficult to measure. For confirmation of the theory, species constancy must coincide with species turnover. To test confidently the theory, one must measure the constancy of species densities in the presence of species turnover and find the predicted ordering of species densities and turnover rates. Logistically, turnover is extremely difficult to measure because of problems with transient species and unnoticed extinctions. Simberloff (1976) and Simberloff and Wilson (1969) have accomplished these measurements, the most completely in their experimental studies. Simberloff (1976) demonstrated both area and distance effects as well as turnover at approximately 1.5 extinctions or colonizations per year. Turnover rates can be scaled by the average number of species on an island when relative rates are desired for comparative purposes (Diamond, 1969). Under most natural conditions (Williamson, 1981), extinctions and colonizations occur in approximately the patterns predicted by the theory, but there is enormous scatter in short-term relationships.

4. Area Effects in Island Biogeography

According to the theory, island area influences population size and therefore extinction probabilities. Because a smaller island has a small population, it has a greater probability of species extinction. The extinction rate curve rises more rapidly than that of a larger island. If both large and small islands are equidistant from their source, their colonization curves will be similar, and the intersection of the extinction curve for the small island with the colonization curve will predict a lower number of species than the number

expected for a small island at equilibrium. Land masses that were once connected and have become isolated are expected to undergo "relaxation" to a lower number of species because of their reduced area (Diamond, 1972).

In addition, a plethora of studies have involved species-area effects. MacArthur and Wilson never intended using area itself as a variable. It was used as a surrogate for other factors, such as habitat diversity, which in turn controls species diversity (MacArthur & Wilson, 1967). Many believe erroneously that the theory predicts a linear relationship when species and area are plotted as log-log. The theory makes no assumptions about the shape or the slope of species-area curves (Williamson, 1988).

5. Species Composition

Data from Simberloff's (1976) experimental studies suggest a pattern of change in diversity as community species richness increases. Simberloff and Wilson (1969) suggest that equilibrium should pass through noninteractive, interactive, assortative, and evolutionary phases. It has long been recognized that island biotas are often overrepresented in species with high vagility and dispersal ability (Diamond, 1972). That is, organisms are represented in different proportions on islands than on mainlands. Differences in extinction probabilities also contribute to disharmony. Any condition that causes rarity (specialized habitat, high trophic level) contributes to higher extinction probabilities.

For example, Brown (1971) assumed that boreal mammals reached the mountain top islands in the Great Basin during the Pleistocene and since then there have been extinctions but no colonization. Therefore, species richness or density is not in equilibrium but is declining or "relaxing" as the extinction process dominates. The Sierra Nevada are considered to be the species

source area for these islands and are assumed to be saturated with species (to have as many as they can hold or the equilibrium species density). When species-area curves are compared for mainland and island areas, islands are undersaturated at all island sizes (operationally defined by elevation considerations). In other words, the slope of the species-area curve is greater for habitat islands. If it is assumed that all boreal mammals were once on all islands, extinction rates have been proportionally higher for large mammals, predatory species, and species with specialized habitat requirements.

In addition, when the percentage saturation versus distance from the source area is graphed, the distance effect was not found to be significant. Brown concludes that colonization is not now occurring and plays no role in determining species richness. Island areas are not in equilibrium with their faunas of boreal mammals. For these species, desert valleys constitute absolute barriers to dispersal. Nonequilibrium patterns should be most common for poor dispersers and on land bridge islands.

According to Diamond (1972) species diversity on islands may be displaced from equilibrium in either direction: volcanic activity or declining sea levels (number of species is less than equilibrium) or increased sea levels make islands small or increase their isolation with the extreme case being the creation of land bridge islands (number of species is greater than equilibrium). He found that the islands of Long and Krakatou have relaxed upward after complete volcanic disturbance during recent time. Contracted islands (Diamond, 1969) should be relaxing from supersaturation. Contracted islands have occurred with the end of the last glaciation. These islands show longer relaxation times for larger islands. Land bridge islands (Diamond, 1972) start with a great disparity with equilibrium species diversity. Faunas of first order land bridge islands (those once connected to New Guinea) should be relaxing

toward densities characteristic of oceanic islands of similar size. The largest of these islands were found to be greatly supersaturated and their calculated relaxation times range from 6200-8200 years. Faunas on smaller islands were close to equilibrium with relaxation rates very much smaller than 10,000 years. Extinction rates are higher on smaller islands. Second-order land bridge islands have relaxation times resembling those of contracted islands.

6. Potential Relevance of the Theory of Island Biogeography to Hanging Gardens

Hanging gardens are habitat islands. They are mesic enclaves that are widely separate by a sea of aridity. It is, therefore, appropriate to make use of island biogeography theories in an examination of the species distributions in these gardens. A paucity of knowledge concerning the hanging gardens and long-term sampling that would be required preclude directly using extinction rates, immigration rates, and turnover rates in the hanging gardens. However, using distance to a source or degree of isolation as a surrogate for immigration and area as a surrogate for extinction probabilities can be used to construct some testable hypotheses. Species composition theories also may be relevant to the hanging gardens.

Regarding hanging gardens, distance to a source of colonists can be measured in several ways. If it is posited that the Colorado River is the main corridor for dispersal, even though the initial source of colonists is unknown, then gardens of the same area that are far from the Colorado should have fewer species than gardens that are near the Colorado. Islands that are far from a source will have fewer species at equilibrium than near islands. Other distance measures that can be used are distance to a stream channel that is connected to the Colorado and distance to the garden's nearest neighbor. Distance to

nearest neighbor may be the most important measure. Hanging gardens appear to be created by headward erosion of channels. In the process of headward channel erosion, other seep lines are exposed and new gardens formed. These newly formed gardens were therefore at one time virtually a part of the original garden. This could be stated: gardens of the same size that are near a neighbor will have greater numbers of species at equilibrium than those that are farther from a neighbor.

The area of the gardens varies a great deal and so can be used as a surrogate for extinction probability. Small gardens should have a greater probability of extinction. If a small garden and a large garden are at equal distances (their colonization rates would then be the same) from a source (nearest neighbor/Colorado River), then the small garden will have a lower number of species than the number expected for a small garden at equilibrium. This presents the problem of determining the equilibrium number of species. Following Diamond's (1972) method, the area of the gardens could be regressed on the total number of species in the garden. The resulting equation is then used to calculate the equilibrium number of species according to the area of the garden. Once this equilibrium number of species is calculated for all gardens, they can be examined to see if all or some are at equilibrium. A hypothesis to be tested could be that gardens that exhibit evidence of a recent, large-scale rock fall (rear garden in Cordova Canyon) will have higher species numbers than equilibrium. It is possible to develop an equation to predict the equilibrium number of endemic species in the same manner as above. A hypothesis to be tested would be that the gardens exhibit a lower number of endemic species than equilibrium. This could indicate that there is presently no colonization of the gardens by endemics and that extinction factors are dominant, as in Brown's study (1971). If gardens are assumed to be

experiencing immigration and their degree of isolation is assumed to have increased since the Pleistocene, the gardens should be relaxing downward from supersaturation. The gardens are now more isolated because there appears to have been more gardens during glacial periods. The hypothesis to be tested would be that the species number is greater than the species number at equilibrium. The theory of island biogeography is attractive for use in the examination of the distribution of species numbers in the hanging gardens of the Colorado River drainage, because it provides a method to analyze these insular species distributions through testable predictions based on general ecological processes.

7. Species Diversity Measurements

Species diversity measures can be divided into three categories--species richness, species abundance, and proportional species abundance. Species richness measures the number of species in a defined sampling unit. Species abundance measures the distribution of species population. Indices based on the proportional abundance of species seek to combine richness and evenness of abundance into a single figure (Magurran, 1988). Species richness indices can be either numerical species richness defined as the number of species per specified number of individuals or biomass (Kempton, 1979) or species density which is the number of species per specified collection area (Hurlbert, 1971). Species density is the most common measure of species richness and is favored by botanists. Hill (1993) observed that diversity measures can be arranged according to whether they emphasize species richness (weights in favor of uncommon species) or dominance (weights towards abundant species). The number of species per unit area weights in favor of uncommon species.

D. Geomorphology and Hydrology of Hanging Gardens

Another important aspect of hanging gardens is that they are geomorphic and hydrologic units (Welsh & Toft, 1981). Gardens often occur in alcoves that have developed in sandstone formations. Two important sandstone units that occur in the Moab area of the Colorado Plateau are the Navajo and Entrada. They are mainly flat lying or gently warped over large areas. Alcove development appears to be principally related to the nature, occurrence, and attitude of these formations. These sandstones are excellent aquifers, yielding water at seeps and springs throughout the region. The recharge potential of these sandstones is high because of their widespread exposure at low dip angles, relatively uniform permeability of the rock, and pervasive fracturing. Small discontinuous bodies of perched groundwater occur throughout the formations. Perched water tables that are associated with alcove development are important in modifying the canyon walls. Furthermore, the evolution of canyon networks in the area is often dependent on sustained seepage at valley headwalls fed by regional aquifers (Laity, 1990). The development of alcoves in sandstones is promoted by the flow of groundwater at an exposed seepage face. Many regional processes and controls effect the flow and dominance of groundwater including the geological structure of the landscape, the characteristics of the lithologies, and the macroclimate as well as small-scale processes at the seepage face.

1. Large-Scale Processes--Geology, Lithology, Climate, Regional Denudation, and Valley Morphology

The overall structural controls of the region provide the ultimate control of the drainage of both surface and groundwater flow. The dominant control of drainage in the region is the Colorado River. All waters, surface and

groundwater, ultimately flow toward it. Other structural controls on regional drainage are the synclines, collapsed salt anticlines, and the LaSal Mountains. These features control the regional direction and degree of dip of the sedimentary units. The processes that created these structures also resulted in the creation of many faults, joints, and fractures in the sediments which exert control on overland and subsurface flow, i.e., toward the Colorado River, through collapsed anticlines, and toward and through synclines. Low angle dips (1 to 4 degrees) favor groundwater flow due to facilitated infiltration. Steeper angles favor surface flow (Baker, 1990).

Two major sedimentary units in this region exhibit the best expression of alcove formation, the Navajo and Entrada sandstones. Navajo sandstone is considered to be an extensive dune deposit. It is underlain by the Kayenta formation of mudstone, siltstone, and sandstone that acts as an aquiclude for downward moving groundwater. Small discontinuous bodies of perched groundwater occur extensively throughout the formation over thin, impermeable units of limestone, siltstone, and shale (Doelling, 1985). Entrada sandstone is made up of mostly quartz grains weakly cemented by calcium carbonate and iron oxide (Schumm & Chorley, 1966). These sandstones have relatively uniform permeability and pervasive fracturing and jointing. Joints may have any attitude including vertical, horizontal, inclined at various angles, or curved. These joints and fractures enhance infiltration on shallow slopes and provide conduits for groundwater flow. In Entrada sandstone groundwater seeps into partings within the members or at the contact of the members (Baker, 1990; Doelling, 1985). This pervasive jointing and its exploitation by groundwater form a very deep regional weathering front within the formations (Twidale, 1990).

The region has been relatively arid since the Tertiary. There is evidence that there has been greater available water in the area in the past, but there is no consensus on whether there was increased precipitation or cooler temperatures. Regardless of the cause many features such as dry alcoves and tafoni are considered to be relictual of greater groundwater flow. Erosion is believed to be proceeding more slowly now than in the past. At the present time, winter precipitation is chiefly frontal and relatively evenly distributed. Summer rain is more sporadic, convectional in nature and often results in flashfloods (Baker, 1990; Oberlander, 1980).

Furthermore, precipitation ranges from 13 to 38 cm depending on elevation. Over large areas snowmelt can occur numerous times during the winter months. There is no one single spring runoff except at high elevation. This promotes infiltration rather than overland flow. Precipitation varies from year to year. Basins composed of surface Navajo or Entrada sandstone that have a large drainage area will not be affected by this variability but areas draining local perched groundwater will. Evapotranspiration is high during the warm months. Sandy deposits that collect in exposed joints and low lying areas can protect the groundwater from rapid evaporation (Baker, 1990; Doelling, 1985).

Regional denudation is controlled by the Colorado River which is deeply incised in the region. Its deep incision in turn leads to incision in its tributary channels. Its most rapid incision should have occurred after the integration of the Colorado system through the Grand Canyon dated at between 4-10 million years ago (Luchitta, 1988). Incision episodes also rapidly expose seepage faces. However, rapid lowering of base level could increase overland flow by increasing the hydraulic gradient. Other base-level changes would have been caused by changes in sea level or regional precipitation. It has been noted that

since the 1800s, channels in the region have experienced alluviation (Oberlander, 1980). Regional erosion is proceeding into younger deposits to the north in the Moab area. It could be that presently the entire system above Lake Powell may be undergoing increased alluviation due to the buildup of sediment in that reservoir.

In addition, the hydraulic gradient for both surface and groundwater flow is a product of the regional slope. Surface flow dominates when the regional slope is greater than 4 degrees. Surface flow is also promoted if large portions of the basin consist of exposures of less permeable rock. The subsurface flow in Navajo and Entrada sandstone is largely controlled by jointing, and there may be several different levels of groundwater flow. Hydraulic head is nevertheless a function of slope though the flow path may be stepped.

Furthermore, increases in recharge rates of groundwater in the past would have resulted in greater prominence of groundwater as an erosive force. Many features in the region are believed to be relicts of enhanced recharge of the groundwater (Baker, 1990). If the groundwater recharge area is regional, the flow is not affected by short-term drought whereas groundwater areas that are locally recharged may dry up during drought years.

Within the region there are two distinct valley types. Valleys or canyons that are eroded by groundwater maintain a constant width; have u-shaped valleys, steep headcuts that are cusped, relatively straight longitudinal profile; and exhibit strong controls on network pattern. Valleys or canyons where surface runoff dominates are characterized by narrow v-shaped valleys with tapering first-order tributaries, relatively smooth concave upward profiles, and a more dendritic network pattern (Baker, 1990). The structural control on the development of groundwater-eroded canyons is a result of the direction of the joints. Canyons that develop parallel to monoclines develop in an

asymmetrically branched pattern. Tributaries that grow up the monocline are stubby or unbranched. In a gently plunging syncline, canyons tend to be elongated and symmetrically branched. Within these networks the tributaries have a strong constancy of junction angle into the main channel and are largely parallel over wide areas. Groundwater-dominated channels grow in an updip direction and parallel to the strike of exposed joints (Laity & Malin, 1985).

Moreover, groundwater discharge is greatest at headwall seeps. Inflow decreases in a downstream direction. This is compatible with general models of drainage extension by groundwater erosion; i.e., groundwater flow is focused at the valley heads (Figure 2) and the relative outflow decreases downstream (Dunne, 1990). This focusing also tends to stabilize surfaces between indentations. If several valley heads are competing in an area for groundwater and one is at a lower elevation, it may grow faster and leave the others dry as a result of subsurface piracy (Dunne, 1990). As these canyons extend to the drainage divide, overland flow will become dominant. A moderate amount of overland flow is required to remove sediment downstream. If sediment is not removed, the seepage face will be sufficiently buried resulting in the cessation of groundwater erosion (Baker, 1990; Dunne, 1990). Overland flow over the lip of the headcut creates plunge pools below the headcut. Plunge pools activity is thought to sustain the form of a knickpoint as it migrates upstream whether the erosion is from groundwater or surface flow (Thornes, 1994). Too much flow over the lip will degrade the cusped morphology and cut a v-shaped notch in the lip that concentrates the flow and increases the velocity (Thornes, 1994). Headcuts without plunge pools may be on their way to burial. In advanced stages of network development, the development of side channels and main channels proceeds at about the same rate due to the smaller drainage area of

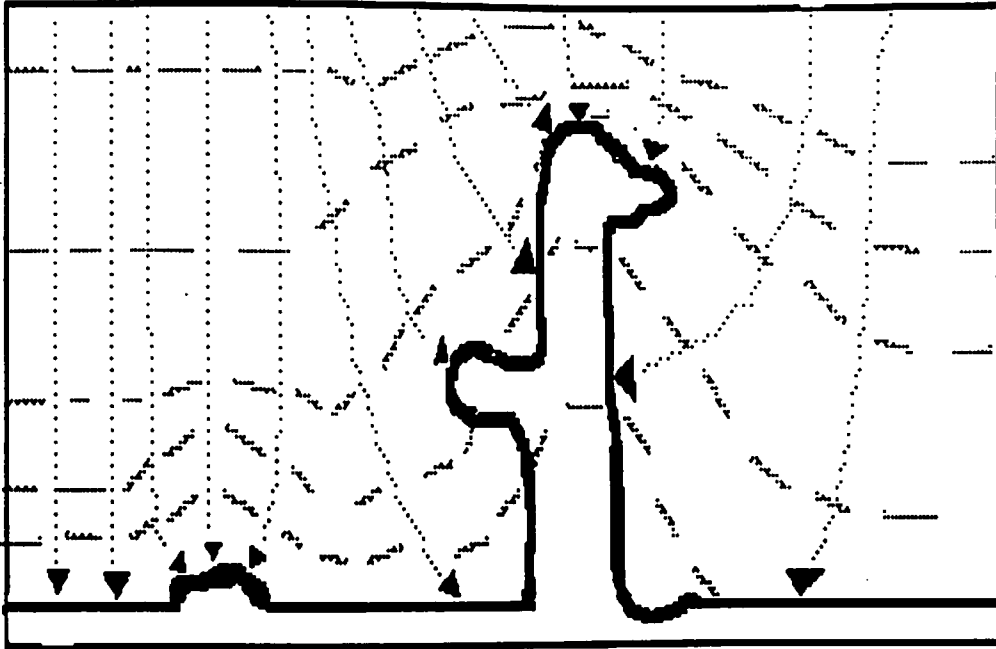


Figure 2. The focus of groundwater erosion (adapted from Dunne, 1990).

the main channel. At this stage the valley widens (Dunne, 1990). The channels may continue to grow until adjacent tributaries merge leaving isolated buttes (Baker, 1990). Seepage faces can be exposed in various ways. Incision of a channel, undercutting at the outside of a meander bend, along an exposed fault line and the progressive development of a runoff channel may all expose seepage faces (Dunne, 1990).

2. Small-Scale Processes--Erosion at the Seepage Face and Mass Wasting

As previously noted, groundwater is concentrated at the seepage face. The seeping groundwater eventually weakens the material that provides basal support of the sandstones. Seepage pressure on individual grains is said to be the erosion process in unconsolidated materials. In massive sandstones this does not appear to be a dominant process. Seeps in sandstone alcoves are covered with a layer of algae, mosses, and other vegetation that binds the grains. The dominant process in this setting appears to be spalling. The exposed faces are chemically and mechanically weathered by several processes. The growth of algae and other vegetation in near surface pores and within microsheeting pores that are parallel to the wall acts chemically and mechanically on the sandstone. The deposition of calcite from the groundwater near the evaporative surface acts to wedge grains and microsheeting joints apart and decreases the strength of the sandstone (Baker, 1990). The groundwater is often slightly acidic, which acts to dissolve the sandstone cement (Doelling, 1985). Deposits of salt on the wall surface are sometimes 100 to 200 mm in thickness. The loss of wall material is caused by sloughing as the layer of calcite-separated grains thickens, by weakening and failure of microsheeting joints through wetting and drying cycles or through biological processes, and by the formation of ice sheets and icicles in winter that fall through thawing or as a result of the weight of the ice. As the weathering front thickens, the weakened material sloughs off in flakes or thin sheets. The removal of this material can be enhanced in winter by diurnal freeze-thaw cycles. The result of this sloughing, grain release, and plucking is the enlargement of cavities and alcoves in the cliff faces. This enlargement undermines the basal support and eventually causes slab failure (Baker, 1990).

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Slab failure is enhanced by and causes the development of pressure release joints parallel to the wall and in tension fractures (Baker, 1990; Doelling, 1985). The slabs of sandstone generally disintegrate on impact and the material is moved down valley by the flooding of surface waters and the wind (Baker, 1990). These large slab failures do not appear to occur very often (Schumm & Chorley, 1966). In the 25 gardens I surveyed only one appeared to have had a relatively recent slab failure.

Furthermore, if the eroded materials are not moved away from the slope in sufficient quantities, the seepage face will be deeply buried and seepage erosion will cease. The existence of a plunge pool appears to facilitate the removal of colluvium by limiting the growth of the toe of colluvial slope. The colluvial slopes and their vegetation also provide some additional basal support to the sandstone walls. It appears that large volumes of water converging on the seepage face in some gardens may be accommodated by flow through macroscopic tunnels that are relatively straight (Baker, 1990). This introduces internal tunnel scour, an erosion process. Little is known about the exact mechanisms involved (Dunne, 1990).

Finally, the development of alcoves in massive sandstones of southeastern Utah is the result of the convergence of multiple processes over all temporal and spatial scales. Abundant seeps and collapse features in the area indicate that groundwater erosion is and has been an important process in valley and channel development. Other evidence of groundwater erosion in the region is the high transmissivity of the Navajo and Entrada sandstones, the observed alcove formation or undermining of cliff faces at sites of seepage along canyon walls that agrees with theoretical groundwater outflow models, the strong structural control of canyon growth, and the development of drainage networks that are different in pattern and development from those formed by

surface water erosion. The endemic species addressed in this work are intimately connected to the alcoves formed by this groundwater erosion process

E. Spatial Analysis Methods and Problems

With Spatial Data

Spatial autocorrelation is often a problem in biogeographic data. Autocorrelation is present when the random error terms are correlated or are not normal, random, independent variables. In other words, successive error terms are related to each other. This violates a basic assumption of many multivariate modeling and validation techniques used in spatial analysis. Most environmental conditions and geological processes tend to be more similar at near points in space than at points far distant from each other. Soil variability offers a good example of both ecological and geologic processes over space. Jenny (1941) proposed the idea of five soil-forming factors, i.e., parent material, climate, topography, vegetation, and time. With the exception of time, the factors are all geographically distributed. These spatial variables can be anticipated to have autocorrelated error terms if they are used in multivariate analysis, modeling, or validation techniques. Because the variables are expected to generate autocorrelation, transformation could be performed to attempt to remove the autocorrelation (Neter, Wasserman, & Kutner, 1990). However, this should only be done if the addition of spatially ordered variables does not remove the autocorrelation. An additional solution may be the addition of a distance variable such as nearest neighbor distance. This would be similar to dummy variables used for seasonal data to remove temporal autocorrelation.

Another alternative is to employ geostatistical theory and specifically designed sampling techniques (vanEs, 1993). Geostatistical theory incorporates the distance between observations into its hypotheses. This results

in spatially structured variables that can be used to investigate variability and in optimizing estimation efforts. Sample designs can be constructed that consider the spatial structure of variables. If the aim is to characterize the spatial structure of a variable, then observations need to be made close enough together to allow for a good description of a semivariogram. Observations also need to include an equivalent number of both large and small distances. A nested sampling design would accomplish this objective (vanEs, 1993). If spatial correlation structure is not of interest, then optimizing sample efficiency may be the objective. Observations at short distance may provide redundant information due to spatial autocorrelation. To optimize the design and the number of true degrees of freedom, the researcher needs to have knowledge of the range of spatial autocorrelation and assign sampling locations outside this range (vanEs, 1993).

Multiple regression analysis is used to analyze the relationship between a single dependent variable and several independent variables. It can describe/explain and predict the relationship between two or more interval scaled variables and can be used to examine the incremental and total explanatory power of many variables (Hair, Anderson, & Tatham, 1992). When multiple regression is used for predictive purposes, it is important that the researcher refrain from choosing a smaller set of variables from a large set. This results in far fewer actual degrees of freedom than the researcher assumes. Mallow's C_k can be used as a measure that minimizes the effect of underfitting and overfitting. In prediction it is also important to investigate the relationship of the sample size to population. The magnitude of the population multiple correlation strongly affects how many observations are needed for a reliable prediction equation. If the estimate of the squared population value is .50, then about 15 observations per predictor are needed. If the estimate of the squared

population value is substantially larger than .50, then far less than 15 observations per predictor are needed. An assumption in multiple regression is that the independent variables are not correlated. Principal components factor analysis can be used to remove the correlation between terms.

III. METHODOLOGY

A. The Purpose of the Study

Individual hanging gardens support different endemic plant species and different numbers of the endemic species, i.e., exhibit different levels of species richness. The primary focus of this work is the investigation of species richness of the hanging garden endemics through application of the principles of island biogeography. The theory of island biogeography is useful in the examination of the hanging gardens of the Colorado River drainage, because it provides a method to analyze the species richness through testable hypotheses based on general ecological and physical processes. This work (Table 3), therefore, quantifies the relationship between those plant species that are primarily restricted to hanging gardens (endemic species) and selected environmental, spatial and structural aspects of the gardens at the microhabitat (individual plot), local (garden), and regional scale (Moab region).

B. Endemic Species Diversity Hypotheses

The primary environmental factors that control diversity at all scales are identified and their importance is explained. Environmental, spatial, and fragmentation effects and species richness vary at the microhabitat, local, and regional scale; therefore, all hypotheses are investigated at the appropriate scale or scales. According to theory, species diversity increases with area; therefore the following hypothesis was tested: an increase in area will exhibit an increase in the endemic species richness at the local and microhabitat scale.

Table 3. Architecture of the study.

Conduct literature review of hanging gardens, groundwater erosion, species diversity, and island biogeography.

Select a study area where many gardens with known endemic occurrences exist.

Develop a sampling method that will control for area and select for sites where endemics are expected to occur.

Based on theories developed from literature review select measurements and data to be collected.

Conduct field work and lab analysis of samples collected.

Organize and conduct preliminary analysis of the data to discover meaningful relationships. Develop new variables from the data.

Apply multivariate techniques, including test for multicollinearity, linear relationships, variance, etc.

Develop multivariate equations to predict level of endemic richness and tests for area effects.

Investigate and provide explanations for the results and these analyses.

Investigate limitations of the study and possible solutions to those limitations.

Suggest further research directions based on the findings of this study.

Although a plethora of studies (Brown, 1977; Diamond, 1969; Schoener, 1988; Simberloff, 1976; Simberloff & Wilson, 1969) has involved species-area effects, MacArthur and Wilson (1967) never intended using area as anything other than a surrogate variable for other factors, such as habitat diversity, which in turn controls species diversity. Habitat diversity implies that the environment is diverse if a chosen quantitative or qualitative factor such as vegetation cover, soil salinity, or available moisture assumes different values at different locations (Kolasa & Rollo, 1991). It is reasoned that species richness increases with area

primarily because the diversity of the habitat increases with area. Furthermore, habitat diversity may be a more important parameter because it includes area and environmental factors (Hart & Horwitz, 1991). Harner and Harper (1976) suggest that habitat diversity may be a more powerful determinant of species diversity than area if their independent influences are separated.

With these concepts in mind, sampling of the gardens was designed to separate area effects from environmental and spatial effects to test hypotheses concerning these latter effects alone. This was accomplished by holding the area sampled constant. According to theory, species diversity increases with area. With the data, the following habitat effect hypotheses were tested. A set of environmental and spatial variables such as light environment, salinity of the soil, distance to a seed source can be found to predict the endemic species richness of the gardens or plots. This was accomplished with various multivariate analysis techniques. Furthermore, if sample plots or gardens display the same environmental and spatial characteristics, they should in theory contain the same number of endemic species. The relationship was tested with t tests. The sampling design also allows for separating fragmentation effects from environmental and spatial effects. Fragmentation effects imply that area affects temporal dynamics and relationships with other areas through effects on colonization, extinction, speciation, and catastrophic disturbance (Hart & Horwitz, 1991). Fragmentation effects were tested with the following hypotheses. If habitat characteristics are held constant, larger areas will have more species than smaller areas (local, regional), because, among other reasons, larger areas have lower extinction rates. If area is held constant, gardens near the Colorado River will have greater species diversity, because distant gardens should have lower immigration rates. These area comparisons were made with t tests.

Processes and environmental factors operate at different scales; therefore, scale effects were investigated. The hypothesis addressed is that there are different, important explanations for distribution at each scale--microhabitat, local, and regional. This was determined by examining the variables that are used to predict species richness at the local, regional and microhabitat scale. Finally, the alcoves in which hanging gardens develop are the result of a type of groundwater erosion known as spring sapping erosion. To examine the relationship of this process to species diversity, I tested the following hypothesis: the dominance of spring sapping erosion is related to the presence and species richness of the endemic species (local, regional). This was examined by determining if the important variables in predicting a high species richness were related to groundwater erosion processes.

C. Study Area and Data Collection

To test these hypotheses, data on the hanging gardens were collected in the Moab, Utah, (Figure 3 and 4) area where jointed and faulted Navajo and Entrada sandstones (regional groundwater flow) occur over wide areas with many synclinal features. Consequently, there are numerous and varied hanging gardens. A sample of 25 hanging gardens was conducted in July and August 1994. A measure of sampling adequacy applied to the data (Equation 2 and 3) indicates that a sample of 22 gardens is adequate for representation of gardens in the Moab region (the model cannot be generalized to gardens outside of this region). In each garden, four 4-m square plots (100 plots) were sampled according to a random stratified sampling design with disproportionate sampling in areas of the gardens where endemics were expected (Figure 5).

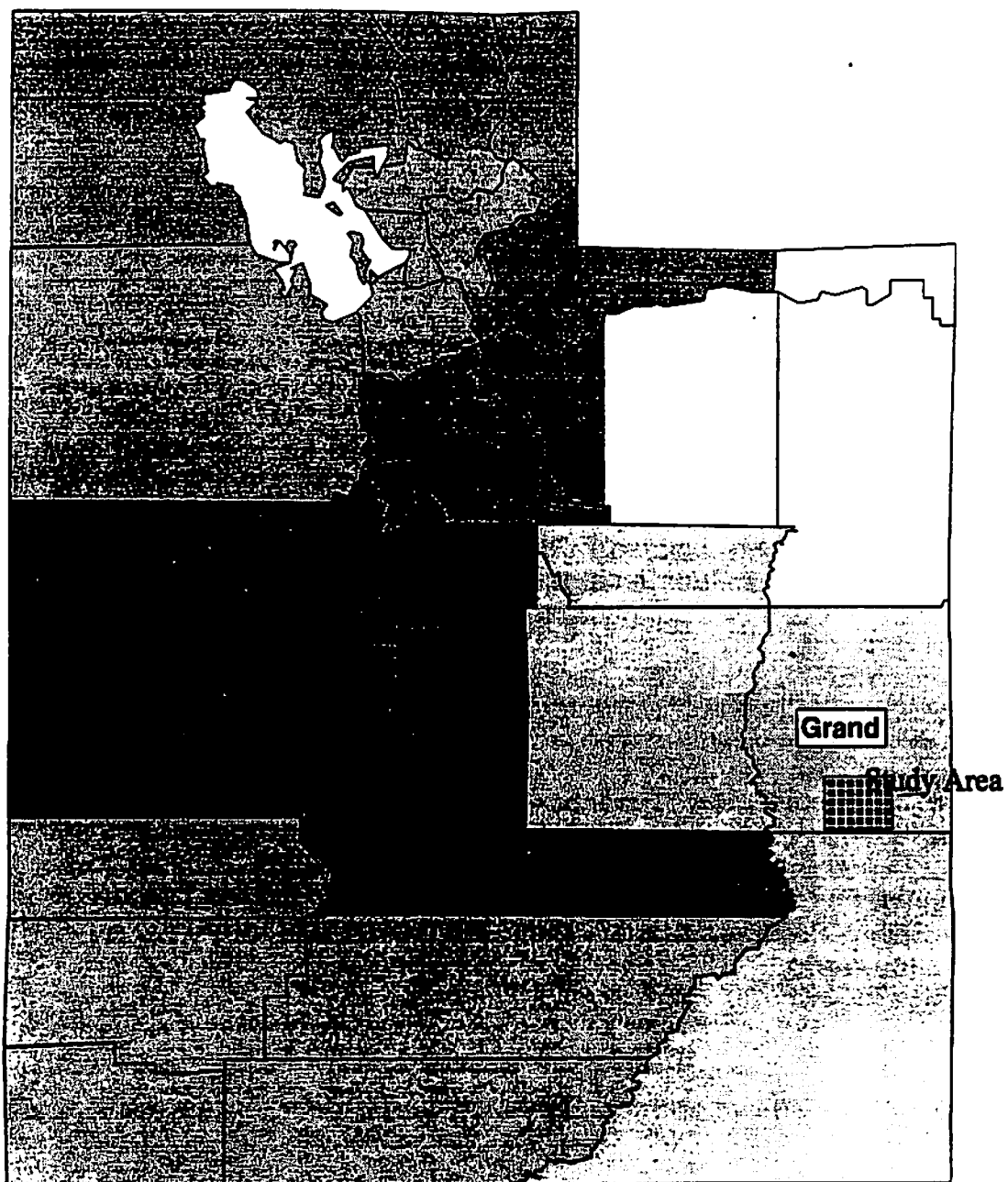
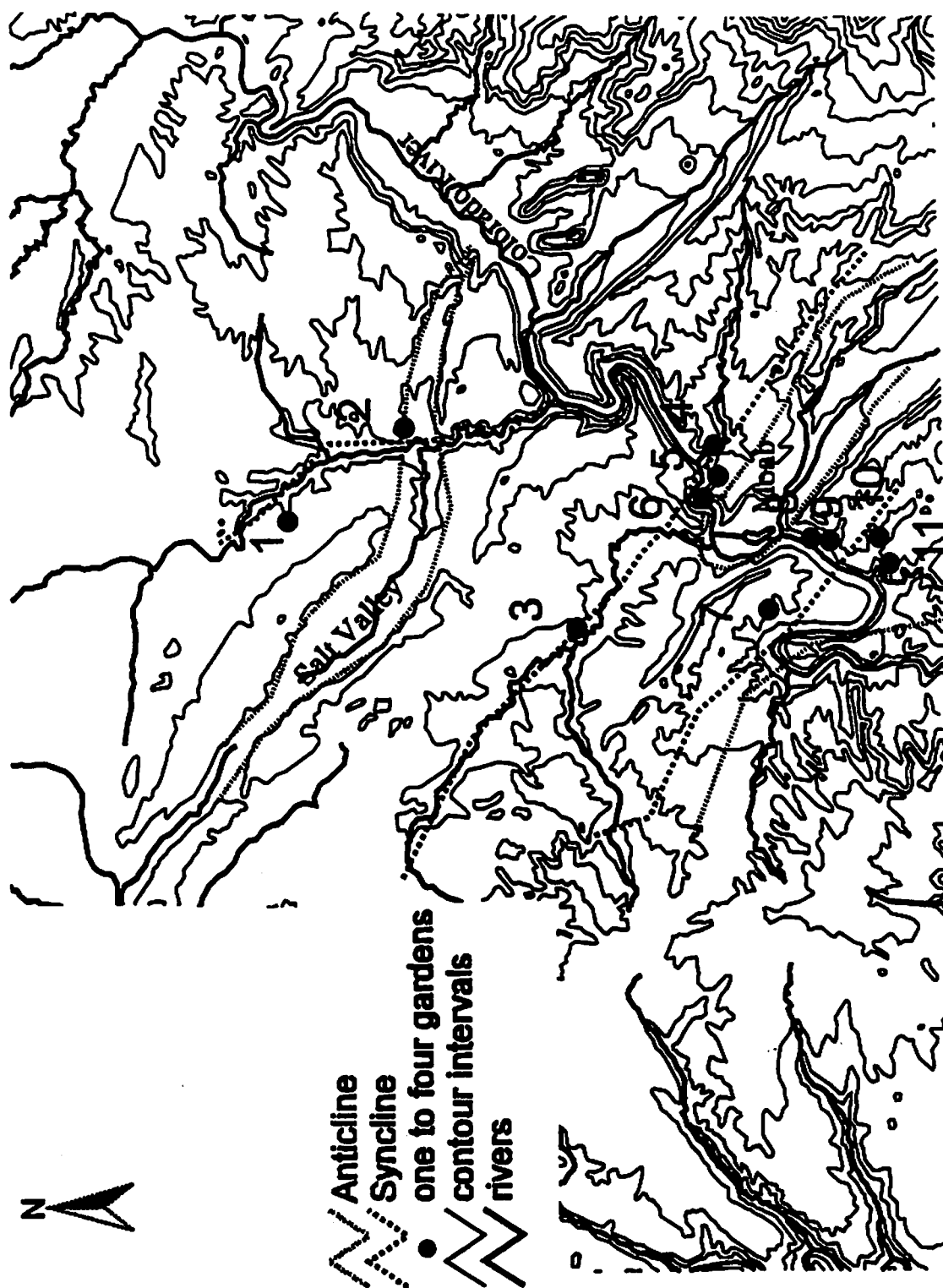


Figure 3. Location of study area in Utah.

Figure 4. Moab area structural features and location of gardens.

- 1. Cordova Canyon:** Two gardens--1 large garden at the rear that has had a large rock fall near the center (CRR) and 1 medium garden on the right-hand side (CRS).
- 2. Gardens along the collapsed anticline near Delicate Arch:** Four gardens--3 medium (D1, D2, D3) and 1 small linear garden (D4).
- 3. Courthouse Wash:** Two gardens--1 medium (CH1) and 1 large garden both on right hand side (CH2).
- 4. Negro Bill Canyon:** Four gardens--3 medium (N1, N2, N4) and 1 small linear garden (N3) all on the left-hand side.
- 5. Sheep Canyon:** One large garden at the rear of the canyon.
- 6. Alcoves along the Colorado:** Two gardens--1 small garden at milepost 2 (Road) and a medium garden slightly upstream (Camp) from the small garden.
- 7. Bootlegger Canyon:** Four gardens--3 medium (B1, B2, B4) and 1 small linear garden (B3).
- 8. Garden near King's Bottom:** Large garden at rear of short canyon (Kings).
- 9. Moonflower Canyon:** Two gardens--1 very large garden at rear of canyon with the entire overhang collapsed onto colluvial slope (MR) and a medium garden along the right-hand side (MS).
- 10. Prichett Canyon:** Two gardens--1 medium (PU) and 1 small linear garden (PL) up a short drainage on the left-hand side of the canyon. Gardens are on the right-hand side of the drainage.
- 11. Unnamed Canyon:** One garden--a large garden up the first drainage into Kane Spring Creek on the left-hand side (Lost). Garden is up the right-hand side of the canyon.



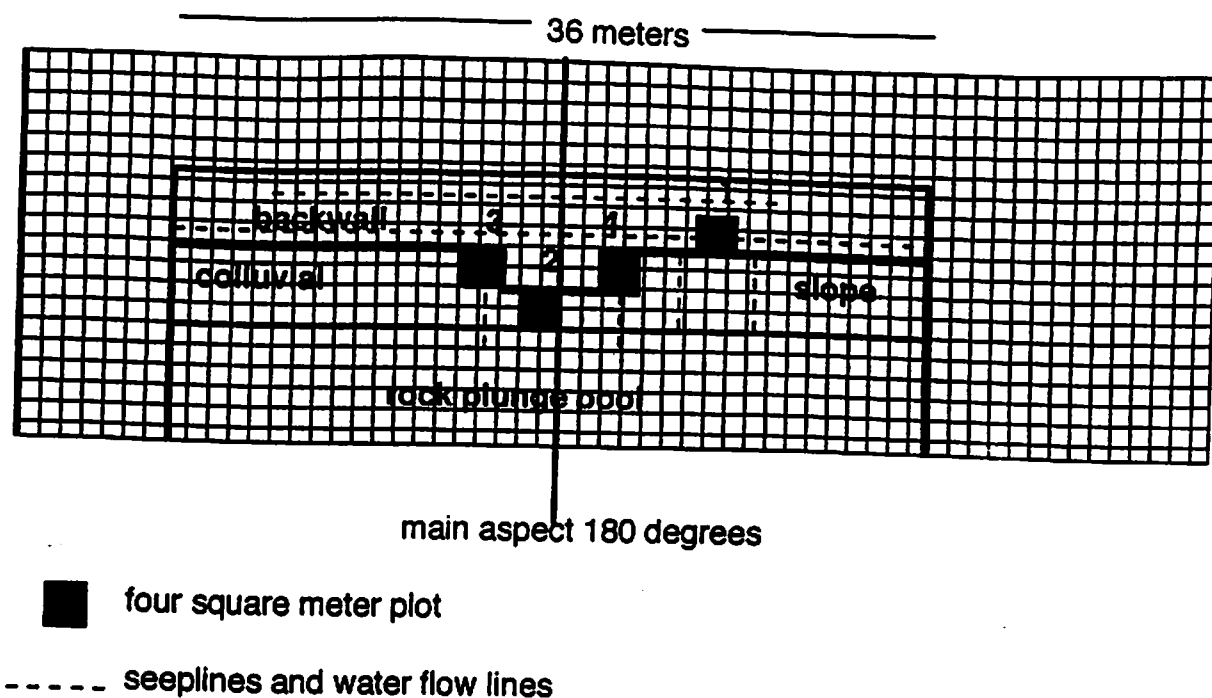


Figure 5. Garden projected onto two-dimensional surface. Information was taken from actual working field documents. This garden is near Delicate Arch (D2).

In each sample plot, all species present were recorded. Soil samples were collected in each plot by sampling the first 15 cm of soil at each corner and at the center of the plot. The soil samples were later analyzed for soil color, soil water salinity, soil water pH, and soil texture. The aspect of the plot was determined by compass. In each garden, data were recorded on a text form, and a schematic drawing was made of the garden. The depth, the width, and the aspect of the central axis, the length of the visible seepines, and the average slope of the colluvial slope were measured. Other factors recorded include depth of the overhang and location of sample plots. The location of the garden was recorded on 1:24,000 scale maps to determine distance to nearest neighbor, distance to a channel that flows directly to the Colorado River, and

distance to the Colorado River. Several variables have been developed from the data collected and are included along with an explanation of the variable in Table 4. All variables that were angle readings were converted to sine functions or dummy variables--ratio of the seepline length and perimeter of the garden, aspect, slope of colluvium, and overhang angle--making them suitable for use as independent variables in statistical analysis.

Table 4. Variables used in the analysis

Local and regional variables

pos-Position is the elevation above the channel adjacent to the garden and that is a tributary of the Colorado River. The elevation difference is measured in meters and divided by 1000 meters to keep it proportional to other variables.

itex-Inverse of soil texture is the inverse of the percentage of sand in the soil sample. The value of the four plots is averaged.

lcat-Light environment category is a variable created by multiplying aspect (north=1, east and west=2, south=3) of the main axis of the garden, a position category (1 is near the canyon floor, 3 is elevated high on the canyon wall) and the cosine of the angle between the backwall and a line from the contact of the upper colluvial slope and the back wall to the outer edge of the overhang. If there is no overhang the angle is 90 degrees and the cosine is 1. The variables was then divided into groups to create a dummy variable where the lowest light=-1, moderate light=0 and high light=1.

dcr-Distance to the Colorado River is the approximate distance (km) to the river from the garden.

d2-Ratio of the seepline to the perimeter is a dummy variable. If the drip to perimeter ratio is less than 50%, the value is 0 and if greater than 50% the value is 1.

Microhabitat variables

drp-Proximity to the seepline is the distance in feet to the seepline.

itex-Inverse of soil texture is same as in the garden variables.

llgt-Light environment is formed in the same manner as in the garden data except that the aspect is that of the sample plot. The logarithm to the base 10 is taken for normality purposes.

salinity- Soil salinity is the salinity of a mixture of soil and distilled water measured in μmhos .

sat-Soil saturation is a dummy variable. If the soil is saturated sat=1, if not saturated sat=0.

IV. INTRODUCTION TO THE ANALYSIS OF THE DATA

The environmental and spatial variables such as light environment, position, and length of the seepline were first investigated at the garden level. The endemic plant species are considered to be a community of associated species. Therefore, a log-assembly ratio (Caswell & Cohen, 1991) was calculated for each pair of endemics (Table 2). This ratio is based on the following :

$$\text{Log-assembly ratio} = \frac{x_1 x_4}{x_2 x_3} \quad (1)$$

where x_1 is the number of gardens in which neither species occurs, x_2 and x_3 are the number of gardens in which only one of the species occurs and x_4 is the number of gardens in which both species occur. The ratio is negative if the 2 species do not tend to occur together, zero if they are independently distributed, and positive if they tend to occur together. All endemics tend to occur with at least two other endemic species.

To determine the garden sample size required, the equation

$$B = z(s^2/n * N-n/n)^{1/2} \quad (2)$$

was used with $z=1.96$ (95% confidence interval), $N=70$ (population), $n=25$ (sample), and $s=1.22$ (the calculated standard deviation of the sample mean number of endemics). The lower bound of the population mean is found to be

2.24 and the upper bound is found to be 3.52. If $\underline{B}=.64$, I could be 95% confident that the population mean lies between these bounds. To estimate the sample size needed, the equation

$$n' = (z^2 \cdot s^2) / B^2 \quad (3)$$

estimates that the sample size required is 23. Twenty-five gardens were sampled. This sample size adequately estimates the number of species per garden in the Moab region.

The species richness variable, number of endemics (end) was used as the dependent variable in the analysis. A species diversity measure (dv) based on relative abundance of the species *Primula specuicola*, *Habenaria zothecina*, and *Zigadenus vaginatus* and the number of species was found to be so closely related to species richness that it provides no additional insight (Figure 6). The species richness variable in the sense of species density tends to be weighted in favor of the uncommon species whereas abundance tends to be weighted in favor of the common species (Magurran, 1988). In other words, the measurement of diversity depends on the objective of the research. In this research the rarer species were expected to have more specific habitat requirements; therefore the species richness variable was determined to be the more useful variable.

The following chapters present the analysis of the data and discussion of that analysis. Analysis at the local and regional scale includes analysis of the environmental and spatial variables that determine the number of endemic species followed by an analysis of fragmentation and area effects on the

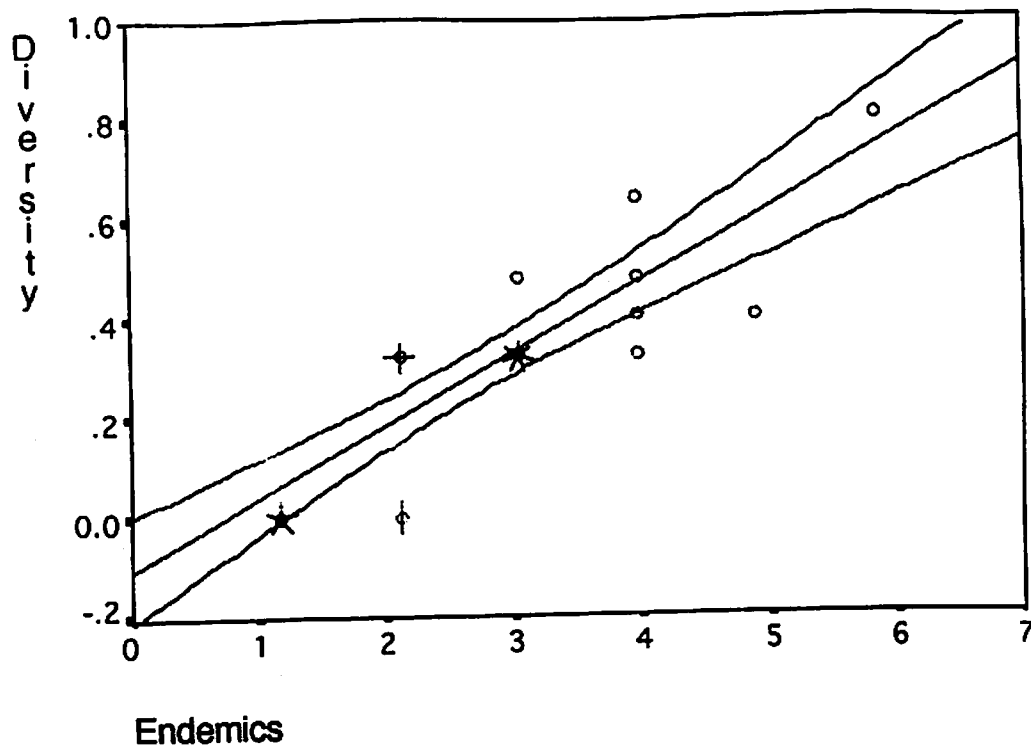


Figure 6. Plot of the relationship between diversity and number of endemics. More diverse gardens have a greater number of endemics.

species richness of the gardens. A discussion of the regional and local analysis is then presented. The same approach is taken with the analysis at the microhabitat level. The environmental and spatial factors are analyzed, followed by an analysis of fragmentation and area effects and a discussion of the results. The subsequent chapter discusses the relationships between the three levels of organization.

V. ENVIRONMENTAL AND SPATIAL ANALYSIS AT THE LOCAL AND REGIONAL SCALE

Pearson correlation analysis was used to determine the strength of the relationships between the dependent (END) and independent variables and to detect any multicollinearity (Table 5). The dependent variable is significantly correlated with D2 (a dummy variable that indicates that 50 % or more of the perimeter has an exposed seep line) with $P=.000$, POS (elevation of the garden above the adjacent stream channel) with $P=.002$, ITEX (the inverse of the ratio of sand to silt and clay) with $P=.000$, LCAT (low, moderate or high light environment) with $P=.013$, and DCR (the distance to the Colorado River) with $P=.015$. All other variables have P values greater than .05.

The Pearson correlations indicate that endemic richness increases as distance to the Colorado and elevation above the adjacent channel increase

Table 5. Pearson correlation coefficients of local
and regional variables.

	D2	DCR	DNN	DTRIB	DW	SOILSA
END	.6868 $P=.000$	.4797 $P=.015$	-.0394 $P=.852$	.2630 $P=.204$	-.1297 $P=.537$	-.3932 $P=.052$
	ITEX	LCAT	OTHER	POS	SINSLOPE	SOILPH
END	-.7118 $P=.000$	-.4887 $P=.013$	-.2216 $P=.287$	.6002 $P=.002$	-.0074 $P=.972$	.0759 $P=.718$

and the number of endemics decreases as the soil texture becomes more silty and as the light environment increases. The number of endemics increases if the seepline covers 50 % or more of the garden perimeter.

Variables that appear to have no correlation with endemic richness are distance to nearest neighbor $P=.852$, the shape of the garden $P=.537$, the number of nonendemic species $P=.287$, the slope of the colluvium $P=.972$, and the pH of the soil $P=.718$. The salinity of the soil has a negative correlation with endemic richness $P=.052$; however, its distribution is very flat and it is correlated with D2 $P=.032$ and LCAT $P=.076$.

There is a great deal of multicollinearity between the variables (Table 6). In fact, there is only one pair of variables that is not significantly correlated, LCAT and POS. To minimize the effects of the multicollinearity and because of nonlinearity problems, DCR was eliminated as a variable. Relative linearity of

Table 6. Pearson correlations between variables.

	D2	DCR	ITEX	LCAT	POS
D2	1.0000 $P=.$	.4237 $P=.035$	-.6373 $P=.001$	-.8108 $P=.000$	.4198 $P=.037$
DCR	.4237 $P=.035$	1.0000 $P=.$	-.6248 $P=.001$	-.4007 $P=.047$	.7403 $P=.000$
ITEX	-.6373 $P=.001$	-.6248 $P=.001$	1.0000 $P=.$	.4107 $P=.041$	-.7911 $P=.000$
LCAT	-.8108 $P=.000$	-.4007 $P=.047$	.4107 $P=.041$	1.0000 $P=.$	-.2500 $P=.228$

the relationship between the dependent variable, END, and each independent variable was graphed as presented in Figure 7. All independent variables have a relatively linear relationships with the dependent variable except DCR which exhibits a quadratic relationship with endemic richness.

Initially, it was intended that there be a separate analysis at the regional and local levels of organization. This, however, leaves too few variables in each group with DCR and POS at the regional level, and LCAT, D2, and ITEX are the local level. If factor analysis is employed on these few variables, they cannot be

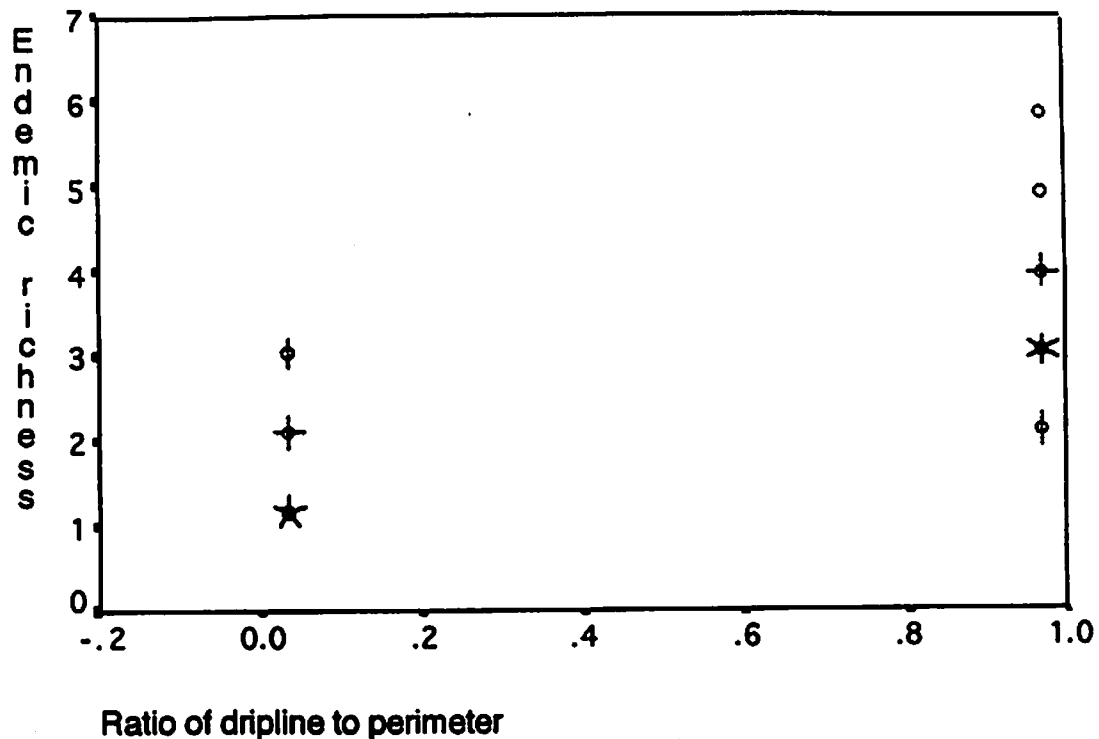


Figure 7. The scatterplot of the relationship between the number of endemics and the seepline category.

separated into meaningful factors. For example, DCR and POS result in two equal and opposite factors. For this reason, the regional variable of POS was employed with the local variables of D2, ITEX, and LCAT.

To eliminate the effects of multicollinearity, the remaining variables of POS, D2, ITEX, and LCAT were used in a principal components factor analysis requesting four variables. A varimax rotation was employed to determine if the variables were adequately separated (uncorrelated) and to aid in naming the resulting factors (Table 7). Factor 1 has the highest loading, .97118, for LCAT, Factor 2 is .94695 for POS, Factor 3 is .79184 for ITEX, and Factor 4 is .65921 for D2.

Using principal components analysis introduces a problem into the interpretation of the variables. When using components analysis, the total variance (common, unique and error variance combined) is considered. Hybrid factors are derived that contain small proportions of unique variance and error variance. It is not known what proportion of the total variance is made up of this unique and error variance portion. This introduces unreliability into the derived

Table 7. Varimax rotation of the principal components analysis factors.

	Factor 1	Factor 2	Factor 3	Factor 4
LCAT	<u>.97118</u>	-.10524	.12918	-.17044
POS	-.10726	<u>.94695</u>	-.28867	.09189
ITEX	.22160	-.52324	<u>.79184</u>	-.22383
D2	-.65796	.17041	-.32171	<u>.65921</u>

factors, but not enough in the first few factors to distort the overall factor structure (Hair et al., 1992).

The resulting factors were used as independent variables in a stepwise multiple regression analysis. Regression analysis was chosen because the dependent variables is normally distributed, there is a linear relationship between the dependent and independent variables, and regression analysis can be used to predict the level of the dependent variable. The regression analysis was based on the model:

$$Y = \beta_0 + \beta_1 \text{lc}at + \beta_2 \text{pos} + \beta_3 \text{it}ex + \beta_4 \text{D}2 \quad (4)$$

The following equation was obtained:

$$Y' = 2.72 - .434X_1 + .567X_2 - .532X_3 + .532X_4 \quad (5)$$

where X_1 = the factor that represents the light category(lcat)

X_2 = the factor that represents position of the garden(pos)

X_3 = the factor that represents the inverse of soil texture(itex)

X_4 = the factor that represents the seepline category(D2)

Table 8 includes the parameters, significance tests, and degrees of freedom. From the Beta values (standardized regression coefficients for direct comparison of explanatory power), it can be seen that POS has the greatest explanatory power (Beta= .43), followed by ITEX (Beta=-.41) and D2 (Beta= .40). The variable LCAT has the least explanatory power with Beta =-.33. The B values or regression coefficients reflect basically the same results (Equation 5) as does

Table 8. Multiple regression results.

Variable	<u>B</u>	Beta	<u>T</u>	Sig <u>T</u>
LCAT	-.434011	-.331897	-2.419	.0252
POS	.566815	.433455	3.159	.0049
ITEX	-.531593	-.406519	-2.963	.0077
D2	.523254	.400142	2.916	.0085
(Constant)	2.72000		15.471	.0000

R Square = .62341 F = 8.27704 Significance of F = .0004
 Degrees of freedom = 20

the significance of the *t* values. The equation is significant at the .05 level and yields an $\bar{R}^2$ of .62. The normal probability plot, residual plot, and the four partial probability plots are seen in Figures 8 to 13. Figure 13 is the normal probability plot of the standardized residuals for the overall equation. If the residuals fall along a straight line, the residuals represent a normal distribution. The residuals for the most part do represent a normal distribution. Figure 8 is a residual plot with the studentized residual versus the predicted values. The residuals fall in a generally random pattern as they should. Figures 9-12 are standardized partial regression plots for each of the four variables. For all four variables, no nonlinear pattern is shown. Each predictor variable meets the linearity assumption.

A final consideration is the possibility residuals are correlated sequentially over space. Spatial autocorrelation is often a problem in biogeographic data. Autocorrelation is present when the random error terms are correlated or are not normal, random, independent variables. In other words, successive error terms are related to each other. This violates a basic

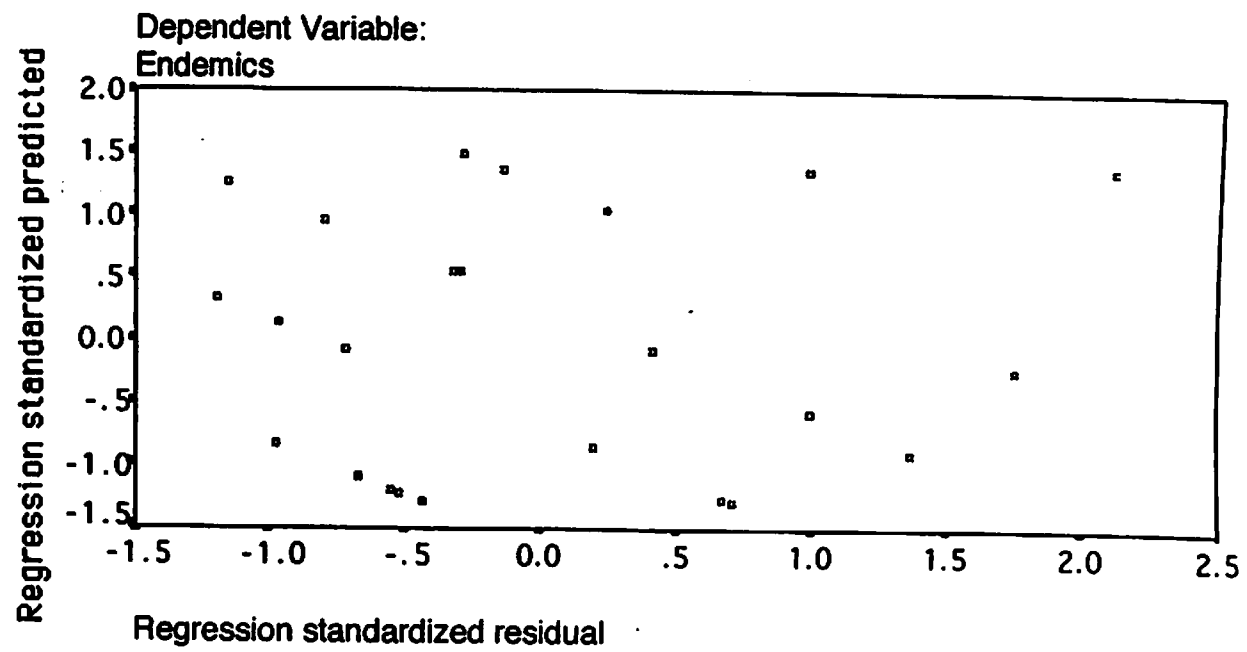


Figure 8. Scatterplot of the predicted and residual values.

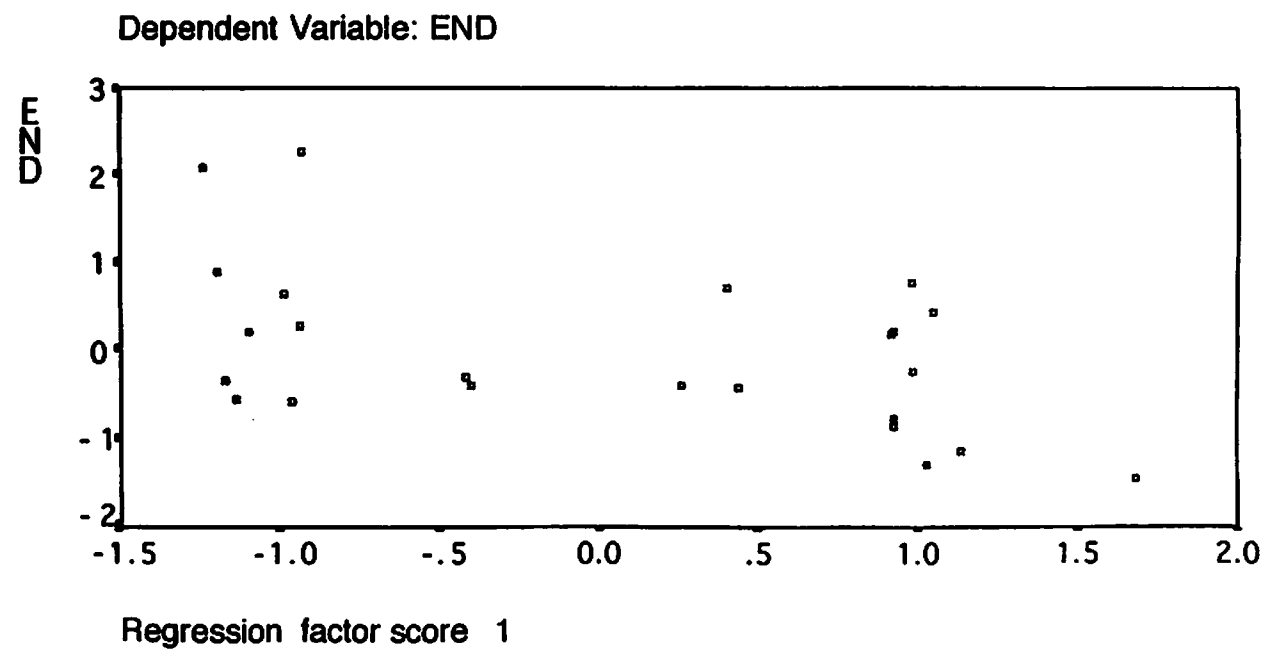


Figure 9. Partial residual plot of Factor 1.

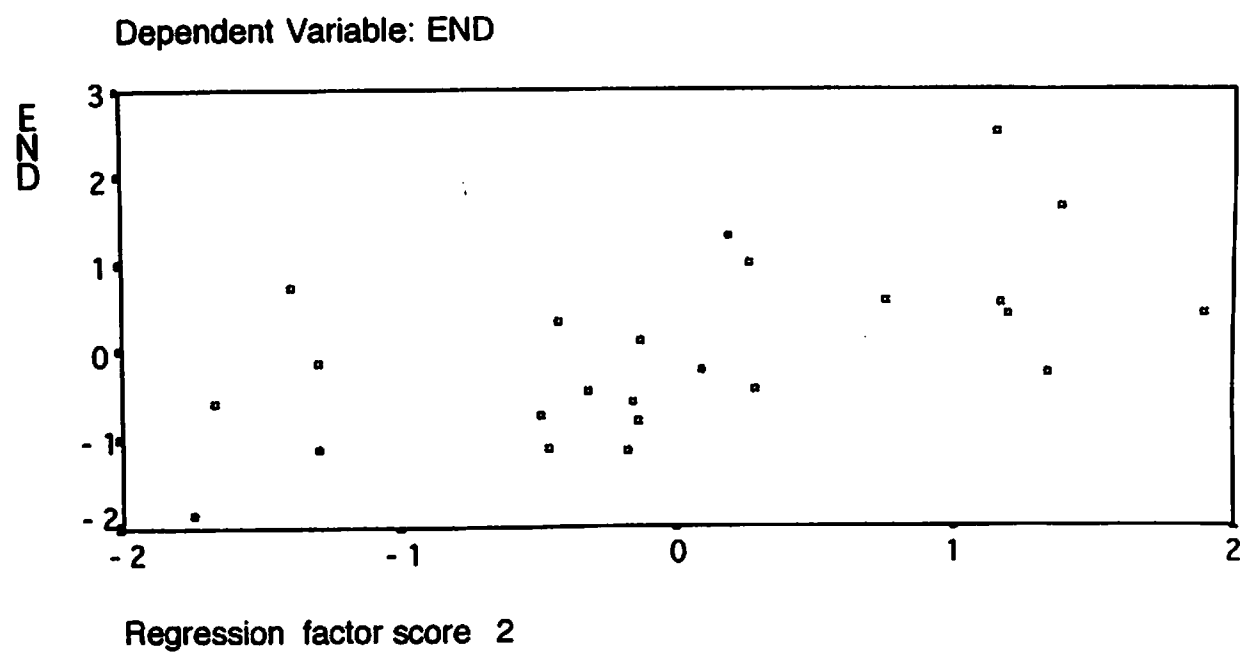


Figure 10. Partial residual plot of Factor 2.

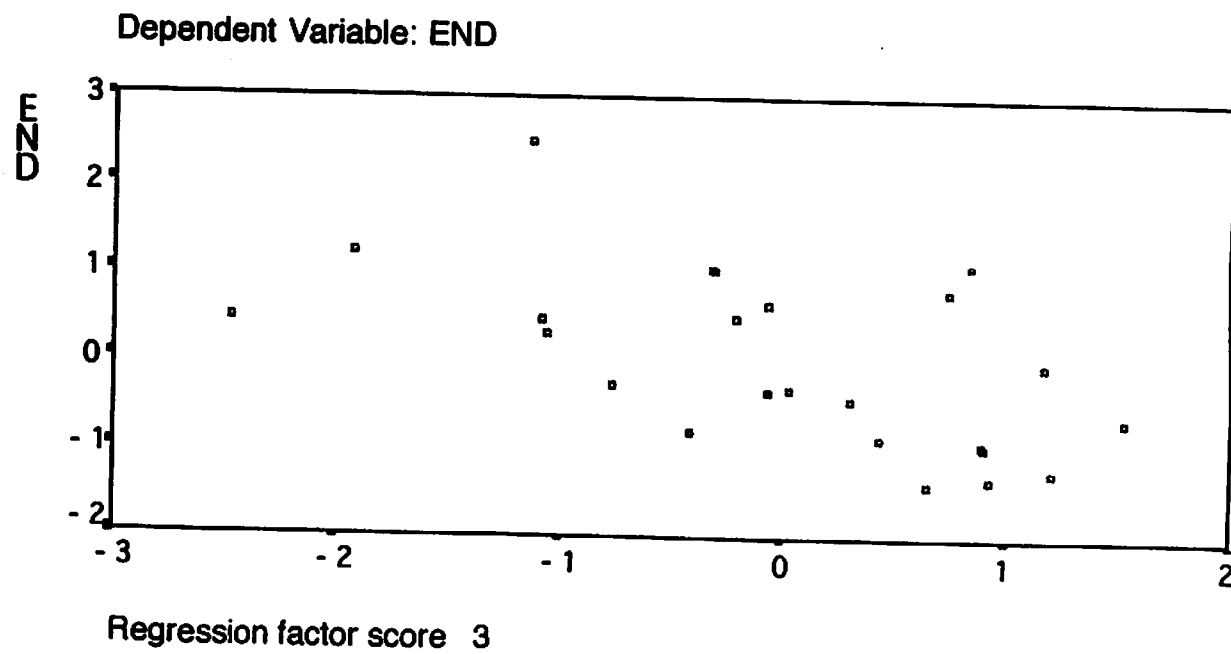


Figure 11. Partial residual plot of Factor 3.

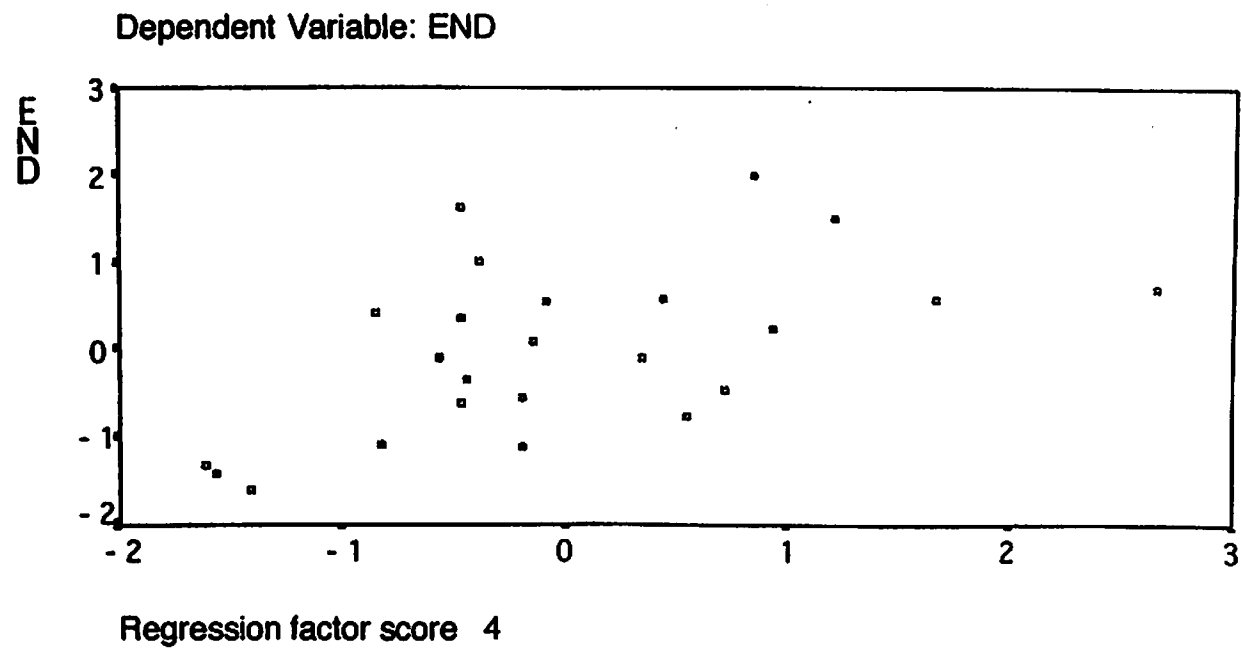


Figure 12. Partial residual plot of Factor 4.

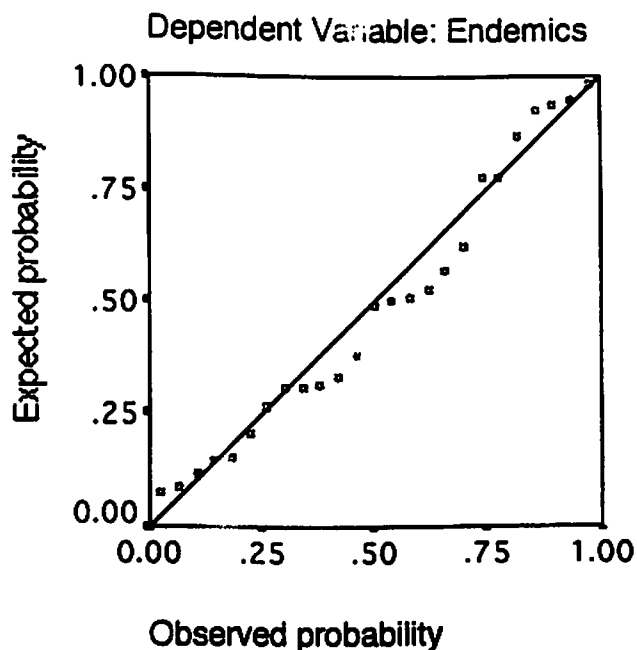


Figure 13. Normal probability plot .

assumption of many multivariate modeling, and validation techniques used in spatial analysis. Most environmental conditions and geological processes tend to be more similar at near points in space than at points far distant from each other. Spatial variables can be anticipated to have autocorrelated error terms if they are used in multivariate analysis, modeling or validation techniques. The addition of spatially ordered variables generally removes the autocorrelation (Neter et al., 1990). This is similar to dummy variables used for seasonal data to remove temporal autocorrelation. Coordinates were assigned to each garden and regressed on the standardized residuals to test for spatial autocorrelation. The results are in Table 9. There is no evidence of spatial autocorrelation.

Table 9. Regression to test for spatial autocorrelation.

Variable	<u>B</u>	<u>SE B</u>	Beta	<u>t</u>	Sig <u>t</u>
X	.033126	.092580	.082136	.358	.7239
Y	.002445	.035665	.015736	.069	.9460
(Constant)	-.185925	.481959		-.386	.7034
<u>R</u> Square = .00798 <u>F</u> = .08844 Significance of <u>F</u> = .9157 Degrees of freedom= 22					

The X and Y parameter t values have no significance, and the F value (F=.94) for the equation also shows no relationship between the location and the residual value. The autocorrelation is controlled by using a spatial-ordered variable in the equation (pos).

The regression equation predicts that the number of endemic species decreases if the garden is exposed to high light, increases if the elevation of the garden above the adjacent channel increases, decreases as the texture of the soil becomes less sandy, and increases if the seepline covers 50 % or more of the perimeter of the garden. Gardens that have high endemic species richness are gardens with low-light environments, are elevated above the adjacent channel, have sandy soil textures, and have a seepline that covers more than half of the garden perimeter.

The interrelationships between the predictor variables can be used to develop additional equations. The soil texture variable can be predicted from the position and seepline variables. Position and seepline are highly correlated and cannot be separated through factor analysis. A factor analysis was used to create one factor from these two variables (Table 10).

Table 10. Relationship between factor and variables.

Pos	D2	Factor1
.040	.00	-.77538
.005	.00	-1.47120
.030	.00	-.97419
.010	.00	-1.37180
.020	.00	-1.17299
.030	1.00	.21162
.050	.00	-.57658
.005	.00	-1.47120
.040	1.00	.41043
.090	.00	.21864
.020	.00	-1.17299
.005	1.00	-.28539
.050	1.00	.60923
.050	.00	-.57658
.050	1.00	.60923
.050	1.00	.60923
.040	1.00	.41043
.040	.00	-.77538
.090	1.00	1.40445
.005	1.00	-.28539
.090	1.00	1.40445
.090	1.00	1.40445
.060	1.00	.80803
.090	1.00	1.40445
.090	1.00	1.40445

This factor was then used to generate a regression equation to predict soil texture.

$$\text{itex}' = 2.25 - .482 \text{ Factor 1} \quad (6)$$

The equation has a Beta value for Factor 1 of $-.84$ with a t value significance of $.0000$. The significance of the F value for the equation is $.0000$, and it has an R^2 of $.71$ at a $.05$ significance level (Table 11). In other words, the soil texture

becomes more sandy (less silty) as the elevation of the position increases and if the seepage line is greater than 50 % of the perimeter.

In addition, the position variable can be predicted from the distance from the Colorado River with the following nonlinear equation:

$$\text{pos}' = .006 + .018\text{dcr} - .0009\text{dcr}^2 \quad (7)$$

The Beta values for dcr and dcr2 are respectively 3.21 (significance of t value = .0000) and -2.52 (significance of t value = .0003), and the significance of the F value for the equation is .0000. The equation has an R^2 of .76 at a .05 significance level (Table 12). In other words, the position of the garden increases as distance from the Colorado River increases up to a point. The position then begins to decrease. Equations 6 and 7 are included to illustrate the multiple and complex relationships between the variables.

Table 11. Regression of factor representing position and seepage line on inverse of soil texture.

Variable	<u>B</u>	Beta	<u>t</u>	Sig <u>t</u>
FAC1_3	-.482377	-.844467	-7.561	.0000
(Constant)	2.248793		35.981	.0000
<u>R</u> Square = .71312	<u>F</u> = 57.17407	Significance of <u>F</u> = .0000		
	Degrees of freedom= 23			

Table 12. Nonlinear regression of dcr on position.

Variable	<u>B</u>	Beta	<u>t</u>	Sig <u>t</u>
DCR	.017527	3.215096	5.511	.0000
DCR**2	-.0008967	-2.516300	-4.313	.0003
(Constant)	.006464		1.088	.2886
<u>R</u> Square = .75510 <u>F</u> = 33.91578 Significance of <u>F</u> = .0000 Degrees of freedom = 22				

These results confirm that if area is held constant, there are environmental and spatial variables that explain the number of endemics in the gardens. The following hypothesis is confirmed; if the area is held constant, a set of environmental and spatial variables can be obtained that will predict the number of species in a garden. The environmental and spatial variables that can be used to predict the endemic richness of a garden are the elevation of the garden above the adjacent channel, the ratio of the seepline to the perimeter of the garden, the light environment, and the soil texture. A second hypothesis addressed by this analysis is that if the area is held constant, gardens near the Colorado River will have greater numbers of endemic species. This is found not to be the case. The number of endemics increases as position increases. Position increases, to a point, as distance from the Colorado increases. Gardens near the Colorado tend to have fewer endemics.

VI. REGIONAL AND LOCAL FRAGMENTATION EFFECTS

In order to test the hypothesis that the number of endemics will increase as area increases, if environmental and spatial variables are held constant, the gardens were grouped into five categories. The clusters (environmental categories) were obtained by using a k-mean cluster technique on the factors used in the regression equation as the independent variables (Table 13). Cluster analysis groups or classifies objects so that each object is similar to others in the group according to the selected criteria, in this case the spatial and environmental variables of pos, d2, lcat, and itex. The resulting clusters should have high internal homogeneity and high external heterogeneity. K-mean cluster analysis is a nonhierarchical procedure that uses random cluster seeds to group the objects that are within a specified distance of the seeds (Neter et al., 1992). It was used because it is a parallel threshold procedure that selects several cluster seeds at the same time, and objects within the threshold distance are assigned to the closest seed. Threshold distances are adjusted as the process proceeds, and fewer or more objects are included in the clusters. The results of k-mean cluster are not susceptible to the distance measure used; therefore the standard Euclid distance measure was used (Table 13). Five categories were selected because that was the lowest number of categories that displayed high significance for each factor ($P=.0000$) in an ANOVA (Table 14).

Table 13. Distances between final cluster centers.

Cluster	1	2	3	4	5
1	.0000				
2	2.3972	.0000			
3	2.3903	2.301...	.0000		
4	2.5039	2.9980	2.9795	.0000	
5	3.1579	2.8921	2.8257	3.2721	.0000

Table 14. Analysis of variance of clusters for each factor.

Variable	Cluster <u>MS</u>	<u>DF</u>	Error <u>MS</u>	<u>DF</u>	<u>F</u>	Prob
FAC1_1	4.3712	4	.325	20.0	13.4190	.000
FAC2_1	3.8342	4	.433	20.0	8.8516	.000
FAC3_1	3.8838	4	.423	20.0	9.1765	.000
FAC4_1	4.2388	4	.352	20.0	12.0335	.000

In each environmental category generated by the cluster analysis, a new "garden" was created by randomly combining gardens in the environmental category (CAT) and determining the number of endemics in these new, larger areas (32 m²). Within three of the environmental categories (category 5 had only two members and category 4 had only three members), the mean of the smaller area was compared to the mean of the larger area using a *t* test (Table 15). The *t* test assesses the significance of the difference between two independent sample means. The null hypothesis is that there is no difference in the mean number of endemics in large and small gardens when the environmental factors are held constant. At a .05 significance level, the means are not found to be equal in small and larger areas for categories 3 and 4 (those gardens with an average of three or fewer endemics). In fact, the number of endemics is larger in the larger areas. In the category of gardens with an average of three endemics, the mean number of endemics is found to increase with area with a two-tailed significance of .000, whereas in the category of gardens with a mean number of endemics of two, the mean number of

Table 15. *t* tests for equality of means in which environmental factors are held constant.

Variable	Mean area 1/2	df	<i>t</i> value*	.05 critical <i>t</i> value	2 tail significance
CAT 2	4/5	12	1.53	2.18	.153
CAT 3	2.72/3.86	12	4.90	2.18	.000*
CAT 4	1.80/2.60	18	2.68	2.10	.015*

* the equality of means is rejected if *t* value is greater than the critical *t* value

endemics is found to increase with area with a two-tailed significance of .015. For gardens with three or fewer endemics, the number of endemics increases as the area increases when environmental factors are held constant. In the environmental category 2 gardens (those with high endemic richness and average number of endemics is four), the hypothesis that the means are equal cannot be rejected. The t value (1.53) is less than the critical t value (2.18), and any difference in the means is not due to an increase in the area. In gardens with high endemic richness, an increase in area does not increase the number of endemics when environmental factors are held constant.

The same garden environmental categories were used to test the hypothesis that gardens with different environmental and spatial characteristics will have the same number of endemics if area is held constant. Ten mean comparisons were required for the five environmental categories. In six of the comparisons, the hypothesis that the means are equal is rejected (Table 16). The four comparisons in which the hypothesis that the means are equal cannot be rejected are those in which the means of the two categories are very close in value and the degrees of freedom are low (Cat 1/4 means = 1.88/1.33 $df=9$, Cat 1/5 means = 1.88/3.00 $df=8$). In general, gardens with different spatial and environmental characteristics and equal area do not have the same number of endemics.

Finally, environmental categories 1-3 were each randomly split into two groups to compare the means of groups where the area and environmental factors were held constant. Groups 4 and 5 have too few members to use in this analysis. The hypothesis that the means of the groups are equal cannot be rejected (Table 17). However, the significance level is very poor due to the small sample sizes. In gardens with the same area and environmental factors,

Table 16. t tests for equality of means in which environmental factors vary and equal areas are compared.

Variable	Mean area 1/2	<u>df</u>	<u>t</u> value*	.05 critical <u>t</u> value	2 tail significance
CAT 1/2	1.88/4.33	12	4.94	2.18	.000*
CAT 1/3	1.88/2.83	12	2.21	2.18	.047*
CAT 1/4	1.88/1.3	9	1.02	2.26	.335
CAT 1/5	1.88/3.00	8	1.82	2.31	.106
CAT 2/3	4.33/2.83	10	2.87	2.23	.017*
CAT 2/4	4.33/1.33	7	4.58	2.37	.003*
CAT 2/5	4.33/3.00	6	1.73	2.45	.134
CAT 3/4	2.83/1.33	7	3.00	2.37	.020*
CAT 3/5	2.83/3.00	6	.30	2.45	.776
CAT 4/5	1.33/3.00	3	3.87	3.18	.030*

Table 17. t tests for equality of means in which environmental factors are constant and equal areas are compared.

Variable	Mean area 1/2	<u>df</u>	<u>t</u> value*	.05 critical <u>t</u> value	2 tail significance
CAT 1	1.75/2.00	6	.40	2.45	.705
CAT 2	4.00/4.67	4	.76	2.78	.493
CAT 3	2.67/3.00	4	.50	2.78	.643

the number of endemics appears to be equal (Cat 1 means= 1.75/2.00, Cat 2 means = 4.00/4.67, and Cat 3 means = 2.67/3.00).

VII. DISCUSSION OF REGIONAL AND LOCAL ANALYSIS

A. Environmental and Spatial Factors

The initial hypothesis tested was that a set of environmental and spatial factors can be found that will predict the number of endemics in a garden, if the area is held constant. Equation 5 is the result of testing this hypothesis. It predicts that the number of endemics will be highest in those gardens where the light environment is low, the seepline is greater than 50% of the perimeter, the soil texture is sandy, and the garden is elevated above the adjacent channel. The light environment in this equation is based on a category, and all gardens with four or more endemics are in the lower light categories of -1 and 0. There are never four endemics in gardens in the high light category of 1. The light category is based on the position of the garden relative to the channel, i.e., the amount of shading that the garden would be receiving from canyon walls, the overhang size, and the aspect of the main axis of the garden. The light category factor has the lowest B (-.434) and significance of the t value (.0252) of all of the factors. The light environment is an important factor but not as important as the other three factors. If the light environment were measured in a more precise fashion, for example, with data loggers, this factor might be found to be more significant.

The factors representing position, inverse of soil texture, and the seepline category are all closely related and have similar β values and significance levels (Table 18).

Table 18. Close relationships between variables.

Variable	β	Significance of t
pos	+ .567	.0049
itex	- .532	.0077
d2	+ .523	.0085

In addition Equation 6 ($itex' = 2.25 - .482 \text{ Factor } 1$) in the garden analysis indicates the interrelationship. In other words, the soil texture becomes more sandy (less silty) as the elevation of the position increases and if the seepage line is greater than 50 % of the perimeter. Their relationships with each other can be seen further in their Pearson correlations (Table 19).

The high correlation between the position of the garden and soil texture is due to the position being an indicator of flooding potential in the garden. If the garden is elevated above the adjacent channel, it is not going to be flooded; therefore there will not be silt deposited in the garden by flooding events. The texture of the soil is then controlled by the groundwater erosion occurring in the garden, and this erosion is creating substrates that are coarse in texture. Groundwater erosion is occurring along the seepage line, hence the correlation of *itex* with *d2*.

The variable, *pos*, has a spatial dimension as well as an environmental dimension as demonstrated by its relationship to the variable, *dcr*, distance to the Colorado River (Equation 7). The Pearson correlation between the two variables is .7351 ($P = .000$). In other words, gardens farther from the Colorado tend to be more elevated above the adjacent channels and tend to have higher numbers of endemics. According to island biogeography, gardens of equal size

Table 19. Pearson correlations of the variables.

	itex	d2
pos	-.7684	.3854
	P=.000	P=.057
itex		-.6373
		P=.001

and near the mainland or corridor should have greater numbers of species, and islands close to the mainland or corridor should support more species due to higher immigration rates. Here the opposite is found to be the case. Gardens that are further from the Colorado tend to have greater numbers of endemics. These gardens also tend to be elevated. Channel erosion is occurring in two dimensions in this area, from the Colorado outward and downward through the stratigraphic layers. Therefore, gardens that are removed from the Colorado and elevated above the adjacent channel are older, more mature gardens than those that are near the Colorado and situated lower in their channels. It appears that gardens that have high numbers of endemics species are the more mature gardens and immigration rates are not higher in gardens that are near the Colorado River. Another possible conclusion is that the Colorado River is not the mainland or corridor for dispersal of these species. It would seem, however, that if that were the case there would be no correlation between distance to the river and the number of endemics. An alternative explanation is that the Colorado was originally the mainland or corridor but it is not now. The corridors now are channels that contain later successional gardens.

Position is largely controlled by the location of regional groundwater flow. In this sample, the gardens are in Entrada and Navajo sandstones. The regional groundwater flow occurs near the contact between the Navajo and the underlying Kayenta sandstones and at the contact between the Slick Rock and Dewey Bridge Members of the Entrada sandstone. The general regional slope of flow surface is toward the Colorado River. As distance increases from the river, therefore, the elevation of the contact tends to increase. Position is then an expression of the regional structural geology (synclines, anticlines, and channel of the Colorado) and regional groundwater flow paths.

This analysis indicates that gardens with high numbers of endemics are gardens that have lower light levels, are not subjected to flooding, have coarse soil textures due to the dominance of groundwater erosion (as well as no flooding), are the more mature gardens, and have water available from the seep line in more than half the perimeter of the garden. The low-light environment and availability of water tend to indicate that some of these species are shade-adapted, moisture-loving species. The lower number of endemics in flood prone gardens indicates that some of these species are not adapted to frequent disturbance. The fact that high species diversity occurs in gardens where groundwater erosion is dominant and flooding does not occur indicates that the endemic species are adapted to small-scale disturbances caused by rock spalling that occurs as a result of groundwater erosion in these sandstone alcoves. It is concluded that if the area is held constant, a set of environmental and spatial factors can be found that will predict the number of endemics in the gardens.

The final hypothesis to be addressed was whether the dominance of spring sapping erosion is related to the number of endemics. In other words, the dominance of spring sapping erosion is related to the occurrence of higher

endemic species richness. Three of the four variables in the regression prediction equation appear to be related to groundwater erosion: D2, POS, and ITEX. The D2 variable indicates that for endemic richness to be high one half or more of the garden must have an exposed seepage line; i.e., half or more of the garden is undergoing active erosion by groundwater. The variables of POS and ITEX appear to be related to the susceptibility of a garden to flooding. If a garden is susceptible to flooding, fluvial erosion has become the dominant erosion mechanism. Gardens that are not susceptible to flooding have an elevated position and sandy soil. These are also the gardens that tend to have high endemic richness. Based on these three variables, POS, D2, and ITEX, the dominance of groundwater erosion appears to be related to high endemic richness. It is concluded that the dominance of groundwater erosion or spring sapping erosion is related to high numbers of endemic species.

It is tempting to conclude that gardens with high endemic richness are gardens that are subject to moderate disturbance regimes. However, disturbance and succession each exert control on the species diversity of a habitat (Huston, 1994). This is a dynamic equilibrium model of species diversity. In this model, species diversity can be reduced by either of the two processes of competitive displacement (succession) or disturbance. This model is a smaller scale analogy of the dynamic equilibrium model of island biogeography where the opposing forces are immigration and extinction (Huston, 1994). For understory forest vegetation, species that are drought tolerant are early successional species whereas species that are shade-tolerant are middle to later successional species. With the correlations of the individual species to the variables for seepage category as a surrogate for drought tolerance and light category as a surrogate for shade tolerance, a rough approximation to successional stage can be determined (Figure 14). *Aquilegia micrantha* and

disturbances. In other words, the disturbance is frequent enough to keep the later successional species from excluding the earlier successional species but infrequent enough to allow later successional species to become established in the garden. Malanson (1978) found that stable gardens (gardens not subject to frequent flooding) or more stable portions of gardens have more diverse vegetation and contain more rare species. He concluded that these stable sites appear to support the deduction that hanging gardens are relictual refugia. Refugia are geographic areas whose limits are distinct. They are habitats that protect species from certain extinction during some series of environmental disturbance.

If disturbance frequencies were very low, the later successional species would exclude the other species because local processes like competition would dominate. In early successional gardens where disturbance is frequent local processes such as mortality, reproductive failure, and local extinction are dominant. Malanson's research in the Zion Narrows noted that for common species the greatest diversity was in the stable sites and the gardens maintain their dissimilar, fugitive assemblages through the response of dispersal types to frequent disturbance (1978). More explicitly, he found that the disturbance variables of expected flood frequency and soil depth segregate dispersal types, whereas the spatial variables of area, distance to possible seed sources, and relative isolation do not (Malanson & Kay, 1980). In other words, local processes are dominant. Under conditions in which neither disturbance nor competitive exclusion dominates, the effect of these local processes is weak and the highest species diversity occurs. The effect of large-scale processes, such as the heterogeneity of the landscape, regional species pool, rates of immigration, among others, determine the maximum number of species that can coexist in the system of all possible habitats ("metahabitat") (Huston, 1994).

The final hypothesis to be addressed was whether the dominance of spring sapping erosion is related to the number of endemics. In other words, the dominance of spring sapping erosion is related to the occurrence of higher endemic species richness. Three of the four variables in the regression prediction equation appear to be related to groundwater erosion: D2, POS, and ITEX. The D2 variable indicates that for endemic richness to be high one half or more of the garden must have an exposed seepage line; i.e., half or more of the garden is undergoing active erosion by groundwater. The variables of POS and ITEX appear to be related to the susceptibility of a garden to flooding. If a garden is susceptible to flooding, fluvial erosion has become the dominant erosion mechanism. Gardens that are not susceptible to flooding have an elevated position and sandy soil. These are also the gardens that tend to have the high endemic richness. Based on these three variables: POS, D2, and ITEX, the dominance of groundwater erosion appears to be related to high endemic richness.

B. Area Effects on Species Richness at the Regional and Local Scale

According to theory, the number of species will increase as area increases. The hypothesis is that if the environmental and spatial variables are held constant, the number of endemic species will increase as the area increases. The environmental and spatial characteristics were held constant by clustering the gardens according to seepage category, light environment category, soil texture, and position of the garden, i.e., the same factors used in the regression analysis. In those clusters in which the average number of species in the garden (16 sq m) was less than four species, the larger gardens (32 sq m) were found to have higher numbers of endemics. However in the

environment are the factors that determine the number of endemics in a garden. Gardens with high endemic diversity are those with 50 % or more of the garden under the influence of a seep line which indicates not only that half or more of the garden has available moisture but also at least half of the garden is under the influence of groundwater erosion. The groundwater erosion, sandy texture of the substrate, and elevated position of these gardens indicate that flooding or fluvial erosion is not the dominant erosional process. The dominance of groundwater erosion creates a habitat with small-scale disturbances. This allows the habitat to develop to a later successional stage. The light environment is the least important of the environmental factors. Gardens with high endemic species diversity are not those with the highest light environment. The light environment is always low to moderate. This favors the late and midsuccessional species that are shade-tolerant and not drought-tolerant. Area effects were found not to be significant in gardens with high endemic diversity.

VIII. ANALYSIS OF THE MICROHABITAT DATA

A. Environmental Factors

At the microhabitat level, the number of endemic species is not normally distributed. This eliminates multiple linear regression as a technique to predict the number of endemics. The distribution appears to be a Poisson distribution. The dominance of ones and zeros in the data precludes using Poisson regression as an analysis technique.

The approach taken was to look only at the extremes, the sample plots with no endemics and those with high numbers of endemics. The species *Aquilegia micrantha* and *Cirsium rydbergii* were eliminated from the count of endemic species richness because they have no correlation with any predictor variable. The new variable of endemic richness was named e2. The Pearson correlations for e2 and the spatial and environmental factors are shown in Table 20. The dependent variable is correlated with proximity to the seepline ($P=.000$), soil texture ($P=.000$), the light environment ($P=.000$), soil salinity ($P=.002$), and soil saturation ($P=.000$).

Table 20. Pearson correlations endemics and independent variables.

	DRP	ITEX	LLGT	NN	PH	SALINITY	SAT
E2	-.4879 $P=.000$	-.3455 $P=.000$	-.4630 $P=.000$	.0576 $P=.570$	.0429 $P=.672$	-.3031 $P=.002$	.3713 $P=.000$

correlation with proximity to the seepline as a surrogate for drought tolerance and light environment as a surrogate for shade tolerance (Figure 16). The results are basically the same as those in the garden analysis with *Aquilegia micrantha* and *Cirsium rydbergii* as early successional species, *Primula specuicola* and *Mimulus eastwoodii* as midsuccessional, and *Habenaria zothecina* and *Zigadenus vaginatus* as later successional species.

B. Microhabitat Fragmentation and Area Effects

At the microhabitat level only one test was made to determine area effects. A new group of sample plots was created by adding two environmental category 2 plots together and calculating the number of endemics to create a new group with larger area. The means of the larger (8 sq m) and small area (4 sq m) plots were compared using a *t* test (Table 23).

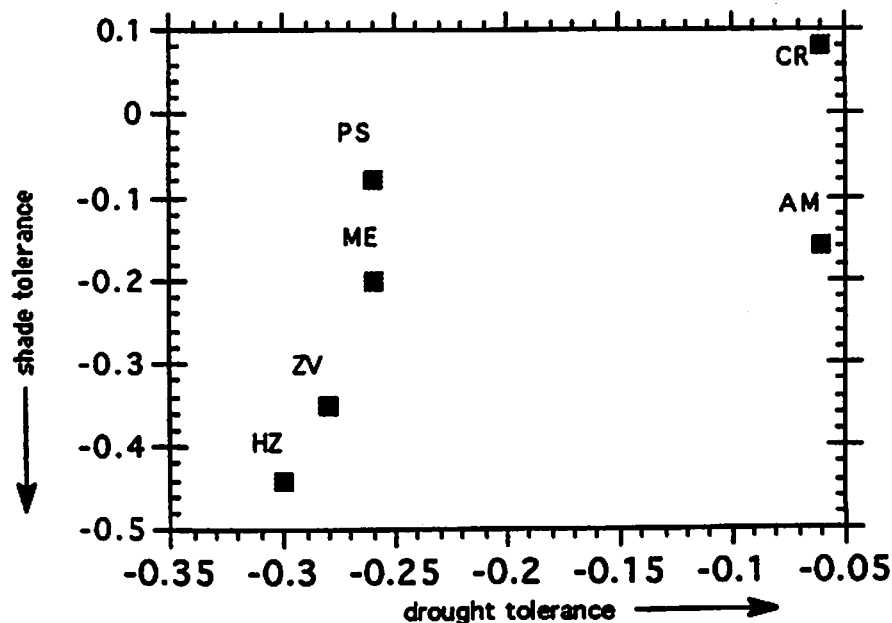


Figure 16. Plot of species correlations with proximity to seepline and light environment.

Table 23. t tests for equality of means of endemics in large and small areas with environmental factors held constant.

Cat	Df	t value	t critical	significance
Area 1/2	26	4.84	2.06	.000*

*the hypothesis that the means are equal is rejected

The hypothesis that the mean number of endemics of the large and small areas is equal was rejected (significance of t value = .000). When the environmental factors are held constant and area is increased, the number of endemics increases. Fragmentation or area effects are evident in the sample plots that have high endemic richness. At the microhabitat level, small areas appear to have higher extinction rates than larger plots as suggested by theory.

IX. DISCUSSION OF THE MICROHABITAT ANALYSIS

It is apparent that the sample plot data are somewhat lacking. There are two problems with the plot-level data. In the first case, the sample of plots with high endemic diversity is too small. In most gardens there are many more than four sampling plots available. At the sample plot level, area is already controlled by the size of the sample plot. Since gardens vary greatly in size a better approach at the plot level would be to sample equally plots with no endemics and those with two or more endemics not including *Aquilegia micrantha* and *Cirsium rydbergii*. This data set would require an additional 36 plots with two or more endemics. Second, the measurements taken are rather coarse. At the plot level, finer grain measurements such as those that could be collected with data loggers would probably detect more discrete differences among the plots. However, with 100 sample plots, the expense would be prohibitive. Another approach would be best. If sample plots included an equal number of those with no endemics and those with endemics (100 plots) and measurements were taken at a finer scale, differences might be more discernible. For example, the light environment could be calculated using aspect, location, angle to the horizon, among others, to produce a more exact measure of solar energy over the month of July.

The comparison of extremes in number of endemics provides the only method for using the environmental factors to predict the occurrence of endemics. This is a result of the data inadequacies discussed above. This, in turn, forced a modification of the original hypothesis. The categories were

created by dividing the plots according to the number of endemics, excluding *Aquilegia micrantha* and *Cirsium rydbergii*. Comparisons were made between gardens with no endemics and those with two or more. Five factors were found to have good correlations with the two groups. Those factors were proximity to seepline, $\log_{10}$ of light, saturation of the soil, inverse of soil texture, and soil salinity. The endemic richness will be highest in microhabitats that are near the seepline with saturated, nonsaline, sandy soil and with a shady light environment. Being close to the seepline indicates that the plot is moist to saturated with water and that it is in an area of the garden that is subject to groundwater erosion processes; i.e., small-scale disturbances. Soil salinity is related to soil texture, light environment, and the availability of light. This can be illustrated by forming a new variables, *Idi*, by adding *itex*, *drp*, and $\log_{10}$ of the light. The Pearson correlation between soil salinity and *Idi* is .2587 ($P=.009$). In other words, soil salinity is low when the plot is near the seepline, exposed to low light, and has a sandy soil texture.

As in the garden analysis this seems to indicate an environment favorable to later successional species. An indication of the successional stage of each species was estimated by plotting for each individual species the correlation with proximity to the seepline as a surrogate for drought tolerance and light environment as a surrogate for shade tolerance (Figure 16). The results are basically the same as those in the garden analysis with *Aquilegia micrantha* and *Cirsium rydbergii* as early successional species, *Primula specuicola* and *Mimulus eastwoodii* as midsuccessional and *Habenaria zothecina* and *Zigadenus vaginatus* as later successional species.

To further illustrate the relationship between environmental factors and the occurrence of endemics, the plots with no endemics (1) and those with two or more endemics were used as the a priori categories to perform a discriminant

At the landscape level, the position and distance from the Colorado are controlled by the overall geologic structure of the region. These processes began in the Tertiary period (Doelling, Oviatt, Oviatt, & Huntoon, 1988) with the creation of the synclines and the integration of the Colorado River system. The structure of the landscape and the Colorado River channel control the regional groundwater flow that results in the formation of the sandstone alcoves in which gardens exist.

At the ecosystem or local scale, position is again important, though at this scale along with soil texture it indicates the level of flooding disturbance and the dominance of groundwater or fluvial erosion processes. If fluvial erosion dominates the garden, it will never reach the high levels of endemic diversity even in later successional stages. The highest levels of diversity are attained in later successional gardens dominated by groundwater erosion that produces small-scale disturbances. The low light environment and availability of water also are related to the later successional gardens having high endemic diversity because later successional species are not drought tolerant but are shade-tolerant. Although the effects of disturbance and succession are operating at the ecosystem scale, they are controlled by regional processes. The structural geology of the region controls the position of the garden which determines if it will be subjected to flooding. The immigration of the later successional species, *Zigadenus vaginatus*, is controlled by the existence of a limited number of later successional gardens in which it occurs. This greatly limits the possible seed sources for later successional gardens. Even at the ecosystem scale, regional processes exert great control on the endemic species richness.

At the microhabitat scale, the availability of water and low light environment are the critical determinants for high endemic diversity. These are the factors that are important to later successional species. Furthermore,

succession is largely determined by the regional existence of seed sources for later successional species. At all levels of organization, regional processes appear to be strong determinants of the level of endemic richness. As noted in a previous chapter, if neither succession or disturbance dominants, local processes such as competition and extinction are weak. The effect of large-scale processes such as the heterogeneity of the landscape, regional species pool, rates of immigration, regional groundwater flow paths, regional geologic structure, among others, determine the maximum number of species that can coexist in the system of all possible habitats ("metahabitat") (Huston, 1994).

XI. CONCLUSIONS AND RECOMMENDATIONS

A. Regional and Local Level

The initial hypothesis tested was that a set of environmental and spatial factors can be found that will predict the number of endemics in a garden, if the area is held constant. Equation 5 is the result of testing this hypothesis. It predicts that the number of endemics will be highest in those gardens where the light environment is low, the seepline is greater than 50% of the perimeter, the soil texture is sandy, and the garden is elevated above the adjacent channel. The light environment in this equation is based on a category, and all gardens with four or more endemics are in the lower light categories of -1 and 0. There are never four endemics in gardens in the high light category of 1. The light category is based on the position of the garden relative to the channel; i.e., the amount of shading that the garden would receive from canyon walls, the overhang size, and the aspect of the main axis of the garden. The low light environment and availability of water tend to indicate that some of these species are shade-adapted, moisture-loving species. The light category factor as the lowest B (-.434) and significance of the T value (.0252) of all of the factors. The light environment is an important factor but not as important as the other three factors. If the light environment were measured in a more precise fashion this factor might be found to be more significant.

The high correlation between the position of the garden and soil texture is due to position being an indicator of flooding potential in the garden. If the garden is elevated above the adjacent channel it is not going to be flooded; therefore there will not be silt deposited in the garden by flooding events. The

texture of the soil is then controlled by the groundwater erosion occurring in the garden, and this erosion is creating substrates that are coarse in texture. Groundwater erosion is occurring along the seepage line. The fact that high species diversity occurs in gardens where groundwater erosion is dominant and flooding does not occur indicates that the endemic species are adapted to small-scale disturbances caused by rock spalling that occurs as a result of groundwater erosion in these sandstone alcoves.

The variable, pos, has a spatial dimension as well as an environmental dimension as demonstrated by its relationship to the variable, dcr, distance to the Colorado River (Equation 7). The Pearson correlation between the two variables is .7351 ($P=.000$). In other words, gardens farther from the Colorado tend to be more elevated above the adjacent channels and tend to have higher numbers of endemics. According to island biogeography, gardens of equal size and near the mainland or corridor should have greater numbers of species and islands close to the mainland or corridor should support more species due to higher immigration rates. Here the opposite is found to be the case. Gardens that are further from the Colorado tend to have greater numbers of endemics. These gardens also tend to be elevated. Channel erosion is occurring in two dimensions in this area, from the Colorado outward and downward through the stratigraphic layers. Therefore gardens that are removed from the Colorado and elevated above the adjacent channel are older, more mature gardens than those that are near the Colorado and situated lower in their channels. It appears that gardens that have high numbers of endemic species are the more mature gardens and extinction rates are higher in gardens that are near the Colorado River (due to flooding). Under high disturbance frequencies and low population growth rates, local processes like mortality and local extinction are dominant. Under

low disturbance frequencies in later successional gardens, regional processes regulate the level of species diversity (Huston, 1994).

Position is largely controlled by the location of regional groundwater flow. In this sample, the gardens are in Entrada and Navajo sandstones. The regional groundwater flow occurs near the contact between the Navajo and the underlying Kayenta sandstones and at the contact between the Slick Rock and Dewey Bridge Members of the Entrada sandstone. The general regional slope of flow surface is toward the Colorado River. As distance increases from the river, therefore, the elevation of the contact tends to increase. Position is then an expression of the regional structural geology (synclines, anticlines, and channel of the Colorado) and regional groundwater flow paths.

The final hypothesis at the garden level to be addressed was that the dominance of spring sapping or groundwater erosion is related to the number of endemics. In other words, the dominance of spring sapping erosion is related to the occurrence of higher endemic species richness. Three of the four variables in the regression prediction equation appear to be related to groundwater erosion: D2, POS, and ITEX. The D2 variable indicates that for endemic richness to be high one half or more of the garden must have an exposed seepage line; i.e., half or more of the garden is undergoing active erosion by groundwater. The variables of POS and ITEX appear to be related to the susceptibility of a garden to flooding. If a garden is susceptible to flooding, fluvial erosion has become the dominant erosion mechanism. Gardens that are not susceptible to flooding have an elevated position and sandy soil. These are also the gardens that tend to have high endemic richness. Based on these three variables: POS, D2, and ITEX, the dominance of groundwater erosion appears to be related to high endemic richness. It is concluded that the

dominance of groundwater erosion or spring sapping erosion is related to high numbers of endemic species.

At the habitat or garden level, environmental and spatial factors are the most important contributors to high endemic diversity. Area effects are not present in gardens with high endemic diversity. In these favorable habitats, the smaller gardens do not appear to have higher extinction rates. This is due to their lack of frequent, large-scale disturbances. The important environmental factors at the habitat level for high endemic species diversity are related to lower light environments, nonsusceptibility to flooding, dominance of groundwater erosion, and the availability of water. The dominance of groundwater or spring sapping erosion over flooding or fluvial erosion creates a habitat that is subjected to only small-scale disturbance and rare large-scale disturbances. Frequent disturbance such as flooding can decrease species diversity.

A general classification of hanging garden types can be developed by using a position category and a percentage of the seepline to the perimeter of the garden category (Table 25). Position and seepline are related to regional processes. This classification of the gardens can be used to predict gardens that will have high endemic diversity. From this sample, the position categories would be low (less than 20 m), medium (21 to 50 m) and high (greater than 50 m). The seepline to perimeter ratio would be defined as low if the ratio is less than 50 % and high if greater than 50 %. This results in six classes of gardens with each of the sample gardens in its class and the number of endemics in each garden.

soil saturation, inverse of soil texture, and soil salinity as the independent variables. The analysis was able to predict the correct category in 90% of the cases. A set of environmental factors can be found that will predict the plots that have no endemics and those that will have two or more endemics, if *Aquilegia micrantha* and *Cirsium rydbergii* are excluded from the endemics.

At the sample plot or microhabitat level, environmental factors again play the dominant role in determining where endemic species diversity is highest. The availability of water, being located near the groundwater erosion surface, lower light environments, sandy soil, and low salinity of the soil all contribute to the occurrence of high numbers of endemic species. Unlike the garden, area effects are present in plots with high endemic diversity. According to theory, smaller plots have higher extinction rates than larger plots. This was not found to be true at the garden level for gardens with high species richness. At the plot level, small-scale disturbances can cause extinction in small areas.

C. Regional Processes and All Levels of Organization

At all levels of organization, regional processes that influence flooding and the flow paths of groundwater and the existence of possible seed sources for later successional species are determinants of the level of species richness. The level of flooding disturbance and the successional stage each exert control on the species makeup of the ecosystem and the microhabitat. In later successional gardens with small-scale disturbance regimes, endemic species diversity is highest. Neither disturbance or succession dominates the habitat (Figure 17).

At all levels of organization, regional processes appear to be strong determinants of the level of endemic richness. As noted in a previous chapter, if neither succession nor disturbance dominants, local processes such as

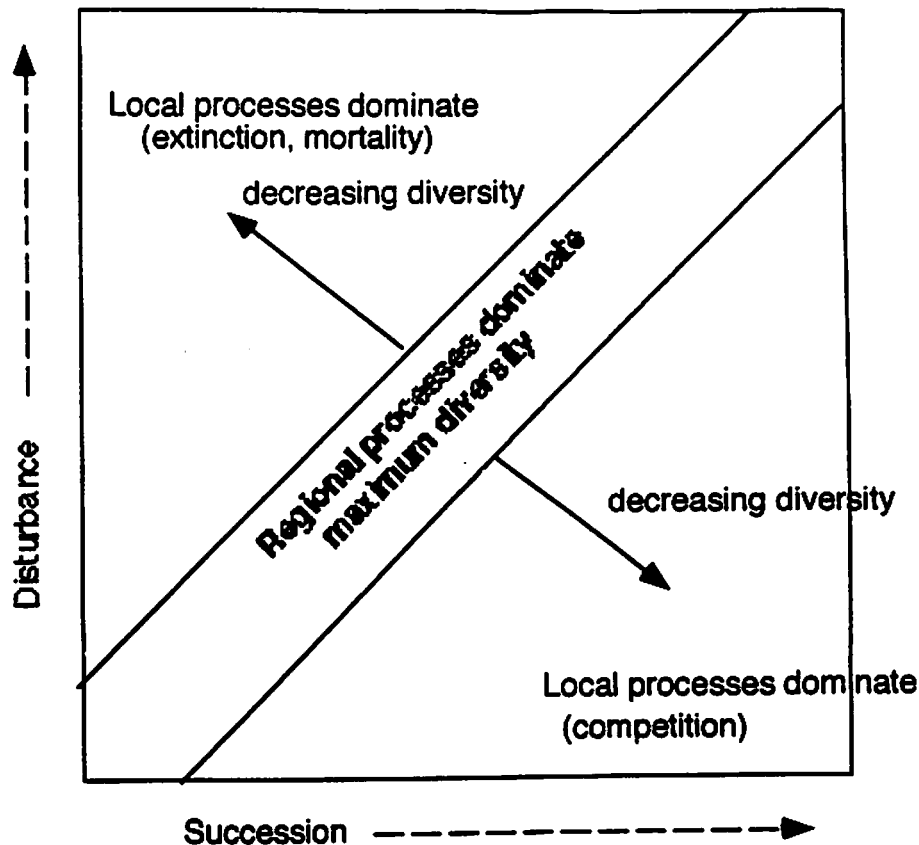


Figure 17. Domains of the two primary processes that reduce species diversity in the dynamic equilibrium model. Diversity is highest when neither process dominates (adapted from Huston, 1994).

competition and extinction are weak. The effect of large-scale processes such as the heterogeneity of the landscape, regional species pool, rates of immigration, regional groundwater flow paths, regional geologic structure, among others, determine the maximum number of species that can coexist in a "metahabitat" (Huston, 1994). It is interesting to recall that according to the classification of endemics developed by Fiedler and Ahouse (1992), for species that are included in the narrow distribution/long persistence category the primary causes of rarity are long-term processes such as evolutionary history

APPENDIX B

GARDEN DATA

Garden	pos	axis	dw	dp	over	ph	salin	text	dnn	hab
Road	0.01	2	0.31	0.25	0.17	6.8	1.23	0.35	0.25	0
N3	0.005	2.5	0.1	0.08	0.01	6.8	1.2	0.36	0.1	0
PU	0.03	5	1.2	0.37	0.34	6.7	1.53	0.35	0.13	0
PL	0.01	5	0.25	0.33	0.01	6.7	1.55	0.51	0.13	0
B3	0.02	5	0.3	0	0.03	6.7	1.13	0.34	0.02	0
Camp	0.03	2.5	1.15	0.8	0.62	6.7	1.25	0.39	0.25	1
N4	0.05	2.5	0.21	0.26	0.01	6.8	1.3	0.35	0.13	0
MR	0.005	2.5	1	0.1	0.01	7	1.33	0.36	0.27	1.
Kings	0.04	2.5	0.83	0.8	0.62	6.6	1.33	0.42	0.25	0
D4	0.09	3	0.08	0.17	0.22	6.6	1.98	0.47	0.01	0
B4	0.02	2	0.2	0	0.03	6.7	1.25	0.33	0.15	0
Sheep	0.005	1	1.18	1	0.71	6.9	1.2	0.41	0.75	1
NB1	0.05	2.5	0.58	0.5	0.21	6.7	1.25	0.55	0.1	0
NB2	0.05	2.5	0.33	0	0.01	6.6	1.18	0.44	0.1	0
CRS	0.05	2	0.46	0.5	0.71	7	1.33	0.46	0.06	1
CRR	0.05	1	0.79	1	0.64	7	1.33	0.46	0.06	1
B1	0.04	3	0.18	0.5	0.5	6.9	1.23	0.46	0.02	0
B2	0.04	3	0.11	0.4	0.1	6.7	1.35	0.37	0.02	0
CH2	0.09	3	0.57	1	0.71	6.9	1.1	0.64	0.3	0
MS	0.005	1	0.3	0.76	0.35	6.6	1.13	0.36	0.27	1
D2	0.09	3	0.35	0.83	0.6	6.7	1.15	0.74	0.02	0
CH1	0.09	3	0.3	1	0.74	6.8	1.1	0.74	0.3	1
Lost	0.06	1	0.57	1	0.77	6.9	1.08	0.73	0.25	1
D1	0.09	3	0.3	0.92	0.6	6.8	1.23	0.63	0.05	0
D3	0.09		0.3	0.6	0.71	6.7	1.18	0.75	0.02	1

Garden	zig	pri	cir	mim	aqu	end	other	itex	lgt	lcat	dcr
Road	0	0	0	0	1	1	11	2.86	1.66	0	1.61
N3	0	0	1	0	0	1	10	2.78	2.5	1	1.45
PU	0	0	0	0	1	1	8	2.86	1.65	0	2.42
PL	0	0	1	0	1	2	3	1.96	2.5	1	2.21
B3	0	0	0	1	0	1	8	2.94	2.91	1	1.21
Camp	0	0	0	0	1	2	6	2.56	0.95	-1	0.4
N4	0	0	1	0	1	2	8	2.86	2.5	1	1.42
MR	0	0	0	0	1	2	13	2.3	2.5	1	0.81
Kings	0	1	1	0	0	2	9	2.3	0.95	-1	0.4
D4	0	0	0	1	1	2	6	2.13	2.34	1	11.27
B4	0	1	0	0	1	2	5	3.03	1.94	1	0.97
Sheep	0	1	0	0	1	3	7	2.44	0.29	-1	0.81
NB1	0	1	0	1	1	3	8	1.82	1.98	1	1.61
NB2	0	1	0	1	1	3	6	2.27	2.5	1	1.45
CRS	0	0	0	1	1	3	4	2.17	0.58	-1	16.1
CRR	0	0	0	1	1	3	9	2.17	0.36	-1	16.1
B1	0	1	1	1	0	3	8	2.17	1.5	0	2.17
B2	0	1	0	1	1	3	13	2.7	2.7	1	1.69
CH2	1	0	0	1	1	3	10	1.56	0.87	-1	13.36
MS	0	1	0	1	1	4	6	2.76	0.65	-1	0.21
D2	1	1	1	0	1	4	7	1.35	1.2	0	11.27
CH1	1	1	0	1	0	4	8	1.35	0.78	-1	13.36
Lost	1	0	0	1	1	4	3	1.37	0.23	-1	2.03
D1	1	1	1	1	1	5	7	1.59	1.2	0	11.27
D3	1	1	1	1	1	6	6	1.33	0.87	-1	11.27

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