Determinants of the structural niches of columnar cacti in the Southwest

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Determinants of the structural niches of columnar cacti in the Southwest

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DETERMINANTS OF THE STRUCTURAL Niches
OF COLUMNAR CACTI IN
THE SOUTHWEST

By
Joseph G. Hentz

A thesis submitted in partial fulfillment
of the requirements for the degree of
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LIMITING SIMILARITY AND ALTERNATIVE HYPOTHESES THAT MAY EXPLAIN PATTERNS OF VARIATION IN THE 'STRUCTURAL NICHES' OF COLUMNAR CACTI IN THE SOUTHWEST WERE EVALUATED. EVOLUTIONARY ADAPTATION HAS BEEN APPLIED TO CACTUS COMMUNITIES IN THE SOUTHWEST BY SEVERAL AUTHORS. I EVALUATED WHETHER MORPHOLOGICAL DIFFERENCES AMONG POPULATIONS OF *Carnegiea gigantea* AND *Pachycereus pringlei* ACTUALLY REPRESENT EVOLUTIONARY ADAPTATION, DIFFERENT DEVELOPMENTAL RESPONSES TO THE ENVIRONMENT, OR SIMPLY DIFFERENCES IN POPULATION AGE STRUCTURE. THE USE OF 'NATURAL EXPERIMENTS' IN HYPOTHESIS TESTING IS DESCRIBED. A METHOD TO AVOID DEMOGRAPHIC BIAS WHEN COMPARING POPULATIONS IS ALSO DESCRIBED.

POPULATIONS OF *Carnegiea* RUNNING EAST TO WEST ACROSS SOUTHERN ARIZONA DIFFER PRIMARILY IN SIZE STRUCTURE, NOT IN GROWTH FORM. WHERE GROWTH FORM DIFFERENCES DO EXIST, THEY ARE CORRELATED WITH VARIATION IN MEASURES OF ARIDITY. *Carnegiea* AND *Pachycereus* IN LESS XERIC ENVIRONMENTS HAVE MORE BRANCHES, GREATER TOTAL BRANCH LENGTH, AND EARLIER INITIATION OF BRANCHING THAN THOSE OF EQUAL HEIGHT IN MORE XERIC ENVIRONMENTS. I FOUND NO EVIDENCE OF EVOLUTIONARY DIVERGENCE AMONG *Carnegiea* OR *Pachycereus* POPULATIONS. NATURAL EXPERIMENTS COMPARING ADJACENT STANDS SUPPORT THE HYPOTHESIS THAT THE GROWTH FORM VARIATION IS A DEVELOPMENTAL RESPONSE TO ARIDITY, AND NOT AN EVOLUTIONARY ADAPTATION.
Also, the presence of a similar competitor was not associated with divergence of *Carnegiea* or *Pachycereus* populations from the growth form of populations without similar competitors. Other evidence, mechanisms, and implications for community theory are discussed.
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INTRODUCTION

Theoretical Setting

The questions of central interest in community ecology are whether biotic communities are organized in a predictable structure, and if so, what forces determine this structure. The structure of biotic communities includes patterns of distribution of species, relative abundance of species, and the types of species that coexist. For most of the history of natural science, emphasis has been on descriptive studies. As world exploration accelerated in the nineteenth century, more studies began to address observed patterns of species distribution and abundance. Attempts to explain these patterns increased after publication of *The Origin of Species*. Typically, historical explanations were emphasized. These explanations attempted to answer where taxa originated phylogenetically and geographically, how the taxa diversified, and what were the routes of dispersal leading to present distribution patterns (history in Brown and Gibson 1983).

What has become known as the revolution of modern ecology was a shift from studies of specific historical explanations to a search for general ecological explanations. This shift in emphasis would make ecology more a predictive science, and less a mere historical record. Are
there laws of ecology (comparable to laws of physics) which govern the assembly of communities? This search for generality was also a transition to the study of abstract forces. Biotic interactions such as competition began to be considered independently of the phylogenetic relationships of the species involved.

Hutchinson was one of the greatest influences in bringing about a shift toward generality (Hutchinson 1959, Brown 1981). He focused attention on the question "What determines the number of species that can coexist in a given area?" In theory, competition between species had been considered a force promoting diversification since Darwin's theory of natural selection. In the 1920's, the logistic equation for population growth had been extended into the Lotka-Volterra model of interspecific competition. In the 1930's, Gause's competitive exclusion principle was a result of the Lotka-Volterra model. According to this principle, competing species can coexist only if intraspecific competition is greater than interspecific competition. To achieve this, coexisting competitors must differ in their resource use. But how much must they differ? Hutchinson (1959) observed that coexisting competitors seemed to differ greatly in their resource use, and that there is little overlap in resource use. So although competition may promote the diversification of species, it may also limit the maximum number of competitors that can coexist in a given
area due to limits in the similarity of coexisting competitors. MacArthur and Levin (1967) translated this observation into mathematical and graphical models. Whether there are theoretical maxima to the number of coexisting species, and whether present communities are at their maxima, has since been the subject of a large body of literature (Brown 1981).

Many studies have assumed that morphological differences serve as an index of differences in resource use. These studies have attempted to show there is a lower limit to the morphological similarity of competing species (Roth 1981, Simberloff 1983). Competition theory predicts that the coexistence of morphologically similar competing species leads to coevolutionary change. The main predictions are character displacement and character release. Character displacement is the divergence of similar characters in competing species (Connell 1980, Arthur 1982). Character release is the evolution of species toward the character of a competitor that was present but becomes absent in a community (Grant 1972). These studies of morphological differences have been controversial. Morphological differences between species that coexist were often accepted as evidence supporting competition theory (Roth 1981, Simberloff 1983). This acceptance was countered with the question whether each set of coexisting competitors is more dissimilar than a (null model) set randomly assembled from
a larger, noninteractive pool of species. This more critical view offers a potentially valuable means of hypothesis testing. However, the difficulty in practice is determining what the noninteractive species pool should be. Simberloff (1983) and Harvey et al. (1983) provide reviews of criticism and defense (respectively) of these kinds of studies.

An important question at the heart of this debate is what constitutes critical testing of competition hypotheses? Can morphological differences between coexisting species always be used to provide evidence supporting competition theory? Even where morphological differences occur in a manner predicted by competition theory, one must ask whether there are hypotheses other than competition that would predict the same pattern of differences. If so, the differences do not constitute adequate evidence for competition theory.

There are many alternatives to consider. Coexisting species do not necessarily compete, even if they overlap in resource use. Factors other than competition may limit their populations, such as parasitism (Price 1980, May 1983). The community may not have reached equilibrium following an environmental perturbation. Or, the pace of environmental change may exceed the rate of evolutionary change, or even the rate of dispersal. So, nonoverlap in resource use may result from species 'missing' from a community because they have not reached it yet (e.g. Brown 1971). Even if the
species do compete, Abrahms (1976) has shown that if the competition occurs on several niche dimensions rather than on a single dimension as in the MacArthur and Levin model, stable coexistence can occur.

Another possibility is that the 'adaptationist program' often does not apply (Gould and Lewontin 1979). Species may differ for reasons other than natural selection: 1) the trait may be influenced by the environment, rather than entirely genetically determined; 2) the trait may have been affected by genetic drift; 3) the trait may be linked to, or pleiotropic with, another character undergoing selection; 4) the evolution of a species may be developmentally constrained by its history; and 5) even if selection is acting, the adaptive landscape may have multiple peaks, so that different combinations of traits may only represent different strategies achieving the same adaptive result. Futuyma (1986) presented an extensive review of alternative causes of morphological differences.

**Columnar Cacti**

In this study I evaluate limiting similarity and alternative hypotheses that may explain patterns of variation in the 'structural niches' (Rand 1964) of columnar cacti in the Southwest. Columnar cacti, especially *Carnegiea gigantea* (Engelm.) Britt. & Rose (saguaro) and *Pachycereus*
pringlei (S.Wats.) Britt. & Rose (cardon), are particularly suitable for study of community structure because their growth form is more easily quantified than other plants. Evolutionary adaptation, especially limiting similarity, has been applied to cactus communities in the Southwest by several authors. Several patterns of variation in the structural niches of columnar cacti have been reported.

Cody (1984, 1986) reported that branching patterns of columnar cacti change "amongst species that coexist at a certain desert site." He attributed the divergence in branching pattern to limiting similarity of coexisting competitors because, "populations of a single species at different sites differ in such a way as to provide morphological differences within each particular set of coexisting species at each site." For example, "Further south [than Tucson] in Organ Pipe Cactus National Monument, the sauguros are taller and more branched. Here they are joined by St [sic Lemaireocereus thurberi (Engelm.) Britt. & Rose (organ pipe)], which as before fills the ecomorphological niche of lower and prolifically branched plants that show little change in branch number over most of their height." A number of other examples were given. But, is there a simpler explanation? Are these differences also correlated with differences in the physical environment, such as variation in aridity?

Yeaton et al. (1980) compared a Carnegiea subpopulation
on a rocky mountainside with that of a relatively flat bajada. They report:

"the major difference between the two subpopulations was the lack of branching of individuals on the more moisture-stressed slopes. The branching habit appears to be an adaptation to increase the reproductive potential of those saguaro occupying the less moisture-stressed end of the gradient (on the flats), while the non-branching habit of those individuals on the slopes represents an adaptation to reduce cuticular and transpirational water losses and increase individual survivorship by a reduction in stem surface area."

(Italics mine). However, it is difficult to imagine how gene flow is prevented between the adjacent subpopulations in order for the differing adaptations to occur. Also, it is likely that the slopes were actually less moisture stressed than the flats due to the differences in the substrates.

Steenbergh and Lowe (1983) report this same pattern between steep slopes and bajadas for Carnegiea populations at Organ Pipe Cactus National Monument, Saguaro National Monument-West Unit, and Saguaro National Monument-East Unit. But, they draw a different conclusion. They report that there is actually no difference in the growth form of the two subpopulations (and hence no differing adaptations). Rather, the subpopulations differ demographically in their age structure. Large, old plants predominate in the nonrocky flats. Small, juvenile and young adult plants predominate in the higher elevation, rocky slopes. The ratio of juveniles to adults increases with density, and the rocky slopes have the highest densities. Lower densities exist on the flats because of higher juvenile mortality to freezing
temperatures. Freezing temperatures occur more frequently in the valley bottoms in the Basin and Range province because of cold air drainage. They report these demographic differences in age structure between subpopulations on slopes of north versus south aspect as well. The question remains whether there are any allometric differences in the growth forms between the subpopulations.

Steenbergh and Lowe (1983) also report variation in *Carnegiea* growth form from east to west across southern Arizona. Although they attribute differences between nearby subpopulations to differences in age structure, they attribute the differences between separate populations from east to west to adaptation, using essentially the same argument used by Yeaton for differences between slopes and flats:

"Saguaro populations growing in dissimilar climatic environments exhibit large order differences in branching characteristics. ...the frequency of branched stems and the number of branches per stem increases across the species' distribution from west to east. The production of branches increases with faster rates of stem growth associated with the gradient of increasing summer precipitation from west to east and greater plant-available soil moisture during the principle period of saguaro growth. ...Natural selection has favored those saguaro genotypes that provide greater differential reproduction and survival, i.e., the more greatly branched plants over the less productive, less branched and unbranched plants. ...Selection for the branched form, which provides greater differential survival, thereby concomitantly selects for higher growth rate potential."

(Italics mine.) In other words, Steenburgh and Lowe claim that *Carnegiea* populations in less moisture stressed
environments have higher growth rates and more branches because they have undergone evolutionary adaptation for greater reproductive potential.

The growth rate of those *Carnegiea* undamaged by freezes decreases from east to west (Steenburgh and Lowe 1983). However, a large fraction of *Carnegiea* have been affected by frost conditions which reduce growth rates as well as survivorship (Steenburgh and Lowe 1983). Do each of these morphological differences in columnar cacti actually represent evolutionary adaptation, different developmental responses to the environment, or simply differences in population age structure?
METHODS

Natural Experiments

Studies that lack artificial experimental manipulations are not necessarily merely observational or correlative. Experiments actually fall on a continuum from laboratory experiments to manipulative field experiments to natural experiments (Diamond 1986). Each type has different advantages and disadvantages, and no type is necessarily superior.

Laboratory experiments are desirable for their close control of variables. Close control makes it easier to infer cause and effect relationships. However, laboratory experiments are the least realistic representations of natural communities. Variables that are shown to be significant in a laboratory setting are only potentially significant in the natural community. Other variables not included in the laboratory may far outweigh the experimental variables.

Field experiments are intermediate in realism and inferential power. In field experiments, artificial manipulations are imposed on natural communities rather than in laboratory communities. However, the scale or nature of the necessary manipulations are often unfeasible and in many cases unethical.
Natural experiments result from searches for sites where the desired experimental manipulations have naturally occurred on their own. Agents such as volcanoes, environmental gradients, or construction companies may serve the experimenter as unwitting research assistants in much the same way as a graduate assistant might manipulate conditions in a laboratory greenhouse. How well the variables are controlled is determined by how carefully the study sites are selected. Natural experiments are weakest in control of variables since some variable may go unnoticed, and because one cannot alter which plant will get which treatment. This concern is overcome by using multiple study sites. Natural experiments are the strongest in realism because no variables are accidentally excluded. Since no artificial manipulations occur, there are no unethical disturbances. Because each type of experiment has both advantages and disadvantages, no single method is ideal. Rather, a combination of methods can yield the highest confidence in the conclusions. For the growth form of columnar cacti, manipulative experiments are not practical because the lifespans of the organisms exceed that of the experimenter, and because of ethical concerns for the plants as protected species.

Experimentation does not necessarily require artificial manipulations. Experimentation can be defined as a reasoning process using the hypothetico-deductive method. Furthermore,
the 'scientific method' is not merely the use of experiments (hypothetico-deduction), but is a way to devise critical experiments to answer causal questions by differentiating between multiple hypotheses (Platt 1964, Chamberlain 1965).

Null Model Tests of Competition Hypotheses

Null models have been used to counter uncritical acceptance of competition hypotheses. However, there is a marked difference between testing multiple hypotheses, and the comparison of results to statistical 'null hypotheses'. 'Statistical hypotheses' are actually predictions. Tests that differentiate between null and alternative 'statistical hypotheses' do not necessarily constitute critical tests of real alternative hypotheses. For example, limiting similarity is one hypothesis explaining morphological variation in columnar cacti. An experiment might be devised to test whether the variation is greater than that in a set of species assembled randomly from a larger, noninteractive pool. The 'null prediction' is that the morphological variation is no greater than in the random pool. The 'alternative prediction' is that the variation does differ significantly from the random pool. However, this experiment cannot be considered critical because it does not distinguish between alternative explanations (real hypotheses). For even if the variation differs from the
random pool, the same pattern of variation can be predicted by alternatives named in the last section, particularly by variation in environmental variables such as aridity.

**Hypothesis Testing**

Since different populations of columnar cacti typically differ in their age structure, frequency distributions of parameters such as the number of arms cannot be used to critically compare growth forms. To do so would be biased by the age of the stand. To avoid this bias and distinguish between growth form variation and demographics, one can compare various height-specific (allometric) relationships. For each of the measured growth form parameters, the relationship between the parameter and the height of the central stem can be determined. This represents the rate of branch production per unit height. These relationships are then compared between sites. Only one growth form parameter is not dependent on the height of the central stem. That is the insertion height of the lowest branch. The lowest branch is the first one produced, barring injury to the apex. The distribution of this parameter at each site can be directly compared.

For each cactus, the following measurements were made: insertion height of each arm \((I_i, i=1\) for the lowest arm), length of each arm \((L_i)\), number of arms \((N)\), and the height
of the central stem (H). From these measurements, the growth form of cactus populations can be described by the following parameters: the insertion height of the lowest arm, the height-specific sum of arm lengths, and the height specific number of arms. The terms arm and branch are used interchangeably, and do not include the central stem.

For *Carnegiea* at one site, the lateral extension of the arms of each cactus was also categorized into one of three groups; narrow, intermediate, or wide (Figure 1). In the narrow branching form, arms extend vertically adjacent to the central stem. The lateral extension is only that necessitated by the diameter of the branch; 10-20 cm. Wide branches extend horizontally away from the central stem prior to turning upward. The lateral extension is at least 30 cm. *Carnegiea* were classified intermediate when the average lateral extension was borderline between 20-30 cm, and when arm types were combined on the same cactus.

Measurements were taken by one of two techniques. The first involved measurements taken from photographic slides of the cacti with a scale located in the photo next to the plant. The second technique involved measuring the length of the optical image of the cactus on a scale held parallel to the cactus and 1 m from the observer's eye, while standing at a distance 20 m from the observer's eye to the base of the cactus. Heights and arm lengths can thus be calculated using the principle of similar triangles. A plumb attached
Figure 1. Narrow (left) and wide (right) branching forms of *Carnegiea* illustrating the groups used to categorize lateral arm extension at the Cactus Plain site.
to the side of the scale allowed the scale to be aligned parallel to the cactus.

Measurements were made from summer 1989 to summer 1990. Wandering quarter sampling (Krebs 1989) was used. *Carnegiea* greater than 5 m tall were recorded whether branched or not, since 5 m is the minimum height at which branching is usually initiated (Steenburgh and Lowe 1983). At the Sonora sites, all branched *Pachycereus* were recorded. Unlike *Carnegiea*, *Pachycereus* do not show a distinct minimum threshold height for branching. No adult unbranched individuals were encountered in sampling. At the Baja California site, a few unbranched adult *Pachycereus* were present so all *Pachycereus* taller than 1 m were included.

Where real growth form variation exists between populations, one can test for correlation with variation in environmental parameters such as maximum temperatures, minimum temperatures, or precipitation. One can also check for correlation between the variation and the presence of other species. If environmental variation predominates over interspecific competition, populations with similar competitors present will not stand out from patterns of populations without similar competitors.

If the growth form variation is a developmental response to the environment and not an evolutionary adaptation, it will be correlated to environmental variation within individual populations as well as between isolated
populations. Limiting similarity (or other evolutionary divergence) cannot explain variation between subpopulations that are not genetically isolated enough for evolutionary divergence to occur.

Differences in substrate cause great microclimatic differences in the physical environment experienced by columnar cacti. Precipitation penetrates rapidly into flat, sandy substrates. On harder, more compacted surfaces of smaller grain size, penetration is slower and considerable precipitation is lost as runoff. The higher porosity of sandy soils also gives them higher water potentials than soils of smaller grain size and greater clay content. In general, sandy substrates are much more mesic than adjacent harder substrates. Thus, stands of columnar cacti in greatly different physical environments can be separated by as little as a few meters.

For some plant species, little separation may be sufficient to prevent gene flow. This is especially so in species that routinely self pollinate or rely on wind dispersal of seeds and pollen, such as many Composites. However, Carnegiea and Pachycereus are pollinated by wide ranging migratory birds, bats, and flying insects. Cross pollination is essential for fertilization (Alcorn and Kurtz 1959). Their seeds are in fleshy fruits that are also widely dispersed by animals, especially doves (Alcorn et al. 1961, Olin et al. 1989) which have large territories and migrate
seasonally. Thus, it is highly improbable that adjacent stands of *Carnegiea* lack significant gene flow.

Whether variation exists in growth form or just in demographics was evaluated at all of the study sites. The correlation between growth form variation and the physical environment was tested qualitatively at all of the sites. Linear regressions were performed for the five southern Arizona locations. *Pachycereus* and *Carnegiea* existing without similar competitors were compared to those coexisting with *Lemaireocereus* at Puerto Libertad and Organ Pipe Cactus National Monument. Whether growth form variation was genetically derived or is a developmental response to the environment was tested within populations at the Cactus Plain, Valle Montevideo, and Punto Cirio.
STUDY SITES

Southern Arizona

The locations of all the study sites are illustrated in Figure 2. The southern Arizona site is subdivided into five subsites running east to west across southern Arizona. Carnegiea stands with vehicle access near climate recording stations were selected. All were on open bajadas of 5° to 10° slope and similar parent rock material. No flats, valley bottoms, or steep slopes were included. Aridity increases from east to west as elevation decreases. Climate data was derived from Sellers and Hill (1974). Carnegiea is the only columnar cactus present, except at the Ajo Mountains where Carnegiea coexists with Lamaireocereus.

Gila Mountains-

32°41.7'N, 114°19.5'W, elevation 85 m. Climate station: Wellton, AZ, 32°40'N, 114°08'W, elevation 79 m.

Mohawk Mountains-

32°45.2'N, 113°47.0'W, elevation 145 m. Climate station: Mohawk, AZ, 32°44'N, 113°46'W, elevation 164 m.

Casa Grande Mountains-

32°48.6'N, 111°43.2'W, elevation 460 m. Climate station: Casa Grande, AZ, 32°47'N, 111°42'W, elevation 450 m.
Figure 2. Map of the Southwest illustrating the locations of the study sites. 1 - Southern Arizona: a) Gila Mountains; b) Mohawk Mountains; c) Casa Grande Mountains; d) Ajo Mountains; e) Tucson Mountains. 2 - Cactus Plain. 3 - Valle Montevideo. 4 - Punto Cirio. 5 - Puerto Libertad. 6 - Organ Pipe Cactus National Monument.
station: Casa Grande, AZ, 32°53'N, 111°45'W, elevation 428 m.

Ajo Mountains—
31°58.0'N, 112°47.2'W, elevation 520 m. Climate station: Organ Pipe Cactus National Monument, AZ, 31°56'N, 112°47'W, elevation 511 m.

Tucson Mountains—
32°14.9'N, 111°11.8'W, elevation 760 m. Climate station: Arizona-Sonora Desert Museum, AZ, 32°15'N, 111°10'W, elevation 858 m.

Cactus Plain, Arizona

34°00'N, 113°57'W. Stands of Carnegiea on desert pavement and pediments were compared to stands on more mesic sand dunes. At the Cactus Plain, a 5-10 m thick mantle of sand dunes rests on the older alluvial surface. At the edge of the dunes, the older alluvial fans are exposed with a desert pavement surface. The region is relatively flat. Carnegiea density is higher on the dunes. The boundary of the dune sample was 5 km from the nondune sample.

Valle Montevideo, Baja California, Mexico
28°56.5'N, 113°43.6'W. *Pachycereus* on the lower part of a hard 10° bajada slope were compared to those on the sandy valley bottom. The transition between the bajada slope and the sandy valley bottom is abrupt. The boundaries of the slope and bottom samples were separated by only 5-10 m. The centers of the two samples were separated by 0.25 km. *Machaerocereus gummosus* (Engelm.) Britt. & Rose (Pitahaya Agria) was also present at low density in both environments.

**Punto Cirio, Sonora, Mexico**

29°50'N, 112°40'W. *Pachycereus* on coastal sand dunes were compared to those on the nearby hillsides of granite and the alluvial surface at the base of the slopes. The two samples were separated by 1 km. No other columnar cacti were present in the sample sites.

**Puerto Libertad, Sonora, Mexico**

30°00'N, 112°30'W. The *Pachycereus* at Punto Cirio were compared to those coexisting with *Lamaireocereus* at this inland site. The substrate is sandy, though not in dunes.

**Organ Pipe Cactus National Monument, Arizona**

31°58.0'N, 112°47.2'W. *Carnegiea* coexisting with
Lamaireocereus in the Ajo Mountains at Organ Pipe Cactus National Monument were compared with Carnegiea at the other four subsites within the southern Arizona site.
RESULTS AND CONCLUSIONS

Southern Arizona

The allometric relationships between the number of arms (N) and central stem height (H) of *Carnegiea* for the five sites running east to west across southern Arizona are shown in Figures 3-7. N and H are not clearly linearly correlated at all sites. Figure 8 provides comparison of the extremes of the east to west populations. The area to the right of the dashed lines shows that the distribution of points on the graph extends farther to the right in the eastern population in the Tucson Mountains. Thus, the Tucson Mountains population has a higher representation of taller cacti than the Gila Mountains population. However, cacti in the Tucson Mountains do not have more arms than cacti of the same height in the Gila Mountains. In fact, the opposite is true for the shorter cacti in the area left of the dashed lines. 50% of the cacti shorter than 7 m in the Gila Mountains have more than two arms, versus 11% in the Tucson Mountains ($\chi^2=8.48$, df=1, p<.005). Clearly, the systematic differences from east to west are not attributable to growth form differences in arm number. This is opposite the prediction of Steenburgh and Lowe's (1983) adaptation hypothesis.

The sum of arm lengths (ΣL) and H are linearly
Figure 3. Number of branches as a function of height for Carnegiea at the Gila Mountains. $r^2 = 0.016$, $n=52$, $p=0.369$. 
Figure 4. Number of branches as a function of height for Carnegiea at the Mohawk Mountains. $r^2=.059$, $n=50$, $p=.089$. 

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Figure 5. Number of branches as a function of height for *Carnegiea* at the Casa Grande Mountains. $r^2=.021$, n=30, p=.446.
Figure 6. Number of branches as a function of height for *Carnegiea* at the Ajo Mountains. $r^2=.000$, n=50, p=.935.
Figure 7. Number of branches as a function of height for *Carnegiea* at the Tucson Mountains (variance is nonuniform).
Figure 8. Relationships between number of branches and height for *Carnegiea* at the Tucson Mountains (shaded circles) and the Gila Mountains (open circles). Dashed line at right emphasizes the higher proportion of taller *Carnegiea* in the Tucson Mountains. Dashed line at left delineates *Carnegiea* shorter than 7 m.
correlated at all sites. Natural log transformations correct nonuniform variance (Figure 9-13). These height-specific relationships were regressed against the seven different environmental variables shown in Table 1 using a multiple regression model:

\[
\ln (\Sigma L+1) = \beta_0 + \beta_1 \ln H + \beta_2 (\text{environmental variable}).
\]

These variables are measures of the maximum temperatures, minimum temperatures, and precipitation at each site. None of the environmental variables significantly improved the regression model. As with arm number, comparison of the easternmost and westernmost populations (Figure 14) reveals differences in the size structure of the populations, but not in growth form allometry. Differences from east to west are not explained by growth form differences in arm length; rather the large cacti present in the Tucson Mountains merely represent an extension of the same allometric growth form relationship.

The distribution of the first insertion heights \((I_1)\) for each site is shown in Figure 15. This growth form parameter changes systematically from east to west. Variation in \(I_1\) was significantly correlated with indices of aridity (Table 1). For instance, measures of high temperatures account for up to 26% of the variation in \(I_1\). Measures of precipitation can explain 25% of the variation.
Figure 9. Sum of arm lengths as a function of height for *Carnegiea* at the Gila Mountains. $r^2=.204$, $n=52$, $p=.001$, $Y=-2.07+1.68X+e$ (original height data in m).
Figure 10. Sum of arm lengths as a function of height for *Carnegiea* at the Mohawk Mountains. $r^2 = .206$, $n=50$, $p = .001$, $Y = -2.60 + 1.87X + e$ (original data in m).
Figure 11. Sum of arm lengths as a function of height for Carnegiea at the Casa Grande Mountains. $r^2=.350$, $n=30$, $p=.001$, $Y=-3.10 + 2.47X + e$ (original data in m).
Figure 12. Sum of arm lengths as a function of height for *Carnegia* at the Ajo Mountains. $r^2=.082$, $n=50$, $p=.043$, $Y=-1.14+1.05X+e$ (original data in m).
Figure 13. Sum of arm lengths as a function of height for Carnegiea at the Tucson Mountains. \( r^2=.373, n=51, p=.043, 
Y=-3.10+2.18X+e \) (original data in m).
Figure 14. Relationship between the sum of arm lengths and height for *Carnegiea* at the Tucson Mountains (shaded circles) and the Gila Mountains (open circles). Dashed line emphasizes the higher proportion of taller *Carnegiea* in the Tucson Mountains.
Figure 15. Frequency distributions of first insertion heights of *Carnegiea* at the southern Arizona locations.
Table 1. Correlations between environmental variables and ΣL vs. H, and between environmental variables and I1.

<table>
<thead>
<tr>
<th>Environmental Variable</th>
<th>Correlation (r²)</th>
<th>Annual mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ΣL vs. H r²</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I₁/ p-value</td>
<td></td>
</tr>
<tr>
<td></td>
<td>elev. daily</td>
<td></td>
</tr>
<tr>
<td></td>
<td>prec. no.days</td>
<td></td>
</tr>
<tr>
<td></td>
<td>max.T 2.5mm</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;32°C monthly</td>
<td></td>
</tr>
<tr>
<td></td>
<td>min.T daily</td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
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<td></td>
</tr>
<tr>
<td>Annual mean daily max.</td>
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<td>.26/000</td>
</tr>
<tr>
<td>temp.</td>
<td></td>
<td>.70</td>
</tr>
<tr>
<td>Annual mean no. days</td>
<td>.000</td>
<td>.25/000</td>
</tr>
<tr>
<td>temp. &gt; 2.5 mm</td>
<td></td>
<td>.92</td>
</tr>
<tr>
<td>Annual mean precipitation</td>
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<td>.25/000</td>
</tr>
<tr>
<td>Annual mean no. days</td>
<td>.000</td>
<td>.21/000</td>
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<tr>
<td>max. temp. &gt;32°C</td>
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<td>.48</td>
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<tr>
<td>Annual mean monthly</td>
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<td>.14/000</td>
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<tr>
<td>temp.</td>
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<td>.28</td>
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<tr>
<td>Annual mean daily min.</td>
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<td>.03/015</td>
</tr>
<tr>
<td>temp.</td>
<td></td>
<td>.02</td>
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<tr>
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<td>.00/635</td>
</tr>
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<td></td>
<td></td>
<td>.41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.74</td>
</tr>
</tbody>
</table>
As temperature increases and precipitation decreases at sites from east to west, so does the distribution of $I_1$ (Figures 16-17). There was not a significant correlation between temperature minima and $I_1$.

Variables measuring precipitation and temperature regimes cannot be combined in a multiple regression model because they are all highly autocorrelated. Each of these variables is also autocorrelated with elevation. Elevation serves as an index of aridity which combines the effects of heat and precipitation, and provides a slightly better regression model ($r^2$ change=1.3%) than mean daily maximum temperature (Figure 18).

Cactus Plain, Arizona

$N$ and $H$ are significantly correlated for both the dune and nondune subpopulations of *Carnegiea* at the Cactus Plain (Figure 19). The correlation seems stronger here than at the five southern Arizona locations because young and medium sized cacti predominate and few large cacti are present. The allometric relationships between the dune and nondune subpopulations can then be compared by comparison of the regression lines using multiple regression with dummy variables ($Z_{\text{dune}}=0$, $Z_{\text{nondune}}=1$) according to the model:

$$ Y = \beta_0 + \beta_1 X + \beta_2 Z + \beta_3 XZ + e $$
Figure 16. Relationship between first insertion height and mean daily maximum temperature for Carnegiea at the southern Arizona locations. $r^2 = .256$, $p = .000$, $Y = -6.57 + .323X + e$. 
Figure 17. Relationship between first insertion height and mean annual rainfall for Carnegiea at the southern Arizona locations. $r^2=.253$, $p=.000$, $Y=4.33-.00629X+e$. 
Figure 18. Relationship between first insertion height and elevation for *Carnegiea* at the southern Arizona locations. 

$r^2 = .269$, $p = .000$, $Y = 3.84 - .00159X + e$. 
Figure 19. Relationship between number of branches and height for *Carnegiea* on dune (shaded circles) and nondune (open circles) substrates at the Cactus Plain. $Y=-1.64+.759X+3.37Z+.350XZ+e$. Analysis of covariance lines are shown, $Y=-2.70+.972X+1.23Z+e$. 
(Kleinbaum and Kupper 1978). $H_0: \beta_2=\beta_3=0$ was rejected ($F(XZ, Z|X)=4.02, \ .01<p<.025$), therefore the two regression lines are not coincident. $H_0: \beta_3=0$ was not rejected ($t=.81, p=.422$), therefore the lines differ significantly in intercept, but not in slope. Since the regression lines are parallel, the term for interaction can be dropped from the model and an analysis of covariance can be applied. Cacti in the less xeric dune habitat have an average of 1.23 more arms than nondune cacti of the same height ($\text{adj.} \bar{N}_{\text{dune}}=3.22$ arms, $\text{adj.} \bar{N}_{\text{nondune}}=1.99$ arms; $\bar{H}=6.09$ m). This constitutes a small difference in growth form that is apparent only across an extreme aridity gradient, such as sand dunes versus desert pavement substrates. The difference is a developmental response to the physical environment, and not divergent adaptations because the two samples are nearby on level terrain and are unlikely to lack significant gene flow. The growth form variation is more likely due to differences in aridity than to freezing because the subpopulations differ little in elevation and there is little topographic relief in the vicinity of the site. So the subpopulations experience essentially the same freezing temperatures.

Similarly, the height-specific $EL$ is also slightly greater for dune cacti than for the nondune cacti (Figure 20). The regression lines for the two subpopulations were parallel ($H_0: \beta_3=0; \ t= .04, \ p=.967$) but not coincident
Figure 20. Relationship between the sum of arm lengths and height for *Carnegiea* on dune (shaded circles) and nondune (open circles) substrates at the Cactus Plain. 

\[ Y = -4.35 + 3.14X - 0.530Z + 0.039XZ + e \]  

Analysis of covariance lines are shown, \( Y = -4.39 + 3.16X - 0.464Z + e \) (original data in m).
(H₀: β₂=β₃=0; F=4.62, .01<p<.025). Cacti in the less xeric, dune environment averaged 1.39 m greater arm length than nondune cacti of the same height (adj. $\bar{x}_{\text{dune}}=2.74$ m, adj. $\bar{x}_{\text{nondune}}=1.35$ m).

Frequency distributions of $I_1$ for the two subpopulations are compared in Figure 21. The less arid, dune cacti have lower $I_1$'s than the nondune cacti ($t=1.52$, df=45, p=.068). Although the p-value is in the marginal range, the pattern of lower branching in more mesic environments matches that of the five southern Arizona locations, and other sites below. Also note the sample size for nondune cacti is smaller (n=24) than for other sites tested.

Lateral arm extension was also compared at this site. A two-sample test for population proportions (Kvanli 1988) revealed wider lateral arm extension in the more mesic subpopulation. Among the dune cacti, 56% (n=34) were classified as wide branching versus 7% (n=15) of the nondune cacti (Z=3.22, p=.0006). This represents an additional growth form variation that is a developmental response, not divergent adaptation.

**Valle Montevideo, Baja California, Mexico**

The hard bajada slope at Valle Montevideo was relatively dry compared to the sandy valley bottom.
Figure 21. Frequency distributions of first insertion heights of *Carnegiea* on dune and nondune substrates at the Cactus Plain.
Precipitation rapidly runs off the harder 10° slope of the bajada and accumulates in the valley. The time measured for 2.00 cm precipitation (368 ml water in a 15.3 cm diameter enclosed circle) to penetrate on the slope was longer than on the bottom (137 s versus 47 s, t=2.94, df=3, p=.03). The relative dryness of the slope was also apparent by comparing the leafiness of drought-deciduous shrubs. Shrubs on the valley bottom had a much higher ratio of green leaved versus leafless or yellow leaved plants (Figure 22).

For *Pachycereus* at Valle Montevideo, the relationship between N and H shows nonuniform variance that cannot be corrected with natural log transformations. Figure 23 shows that the drier slope environment may have more tall cacti that are unbranched than does the relatively wet valley bottom. On the slope, 54% of the cacti over 6 m tall were branched, versus 86% on the valley bottom ($\chi^2=3.91$, df=1, .025<p<.05). Otherwise, the growth form of cacti did not differ in arm number between the relatively wet and dry subpopulations.

The relationship between $\Sigma L$ and H also was not linearly correlated, and showed nonuniform variance not correctable with natural log transformations. Figure 24 shows no growth form differences in $\Sigma L$ were apparent between the subpopulations.

Distributions of $I_1$ are compared in Figure 25. $I_1$'s on the valley bottom are significantly lower than on the bajada
<table>
<thead>
<tr>
<th>Foliage</th>
<th>Bajada Slope</th>
<th>Valley Bottom</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ocotillo</td>
<td>Ocotillo</td>
</tr>
<tr>
<td>none</td>
<td>2</td>
<td>18</td>
</tr>
<tr>
<td>yellow</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>green</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 22. Foliage status of drought deciduous shrubs (*Fouquieria splendens*, *F. diguetii*, *Bursera microphylla*) on the bajada slope and valley bottom substrates at Valle Montevido.
Figure 23. Relationship between number of branches and height for *Pachycereus* on bajada slope and valley bottom substrates at Valle Montevido. For comparison, the plot for the valley bottom is presented in mirror image to that of the slope. Dashed lines delineate *Pachycereus* 6 m or taller.
Figure 24. Relationship between the sum of arm lengths and height for *Pachycereus* on bajada slope and valley bottom substrates at Valle Montevideo. For comparison, the plot for the valley bottom is presented in mirror image to that of the slope.
Figure 25. Frequency distributions of first insertion heights of *Pachycereus* on bajada slope and valley bottom substrates at Valle Montevideo.
slope \((t=2.43, \ df=28, \ p=.011)\). Once again, \(I_1\) is lower in those populations in less xeric environments. Unlike the southern Arizona and Cactus Plain sites, cold temperatures cannot be ruled out as a cause because the subpopulations differ in elevation, and temperatures have not been recorded. However, the growth form variation does not constitute divergent adaptations.

**Punto Cirio, Sonora, Mexico**

The comparison of dune and nondune subpopulations of *Pachycereus* at Punto Cirio is analogous to the dune versus nondune comparison with *Carnegiea* at the Cactus Plain. \(N\) and \(H\) are not linearly correlated at Punto Cirio. However, comparison of Figures 26 and 27 shows dune cacti are more likely to have numerous branches (>10) than nondune cacti of the same height. Here, the growth form varies considerably in height-specific arm number between relatively wet and dry subpopulations.

The relationships between \(EL\) and \(H\) match those for \(N\) and \(H\). Comparing Figures 28 and 29 shows that dune cacti are more likely to have great arm length (>30 m!) than nondune cacti of the same height.

Distributions of \(I_1\) are compared in Figure 30. Dune cacti have significantly lower \(I_1\)'s than nondune cacti \((t=4.27, \ df=71, \ p<.00005)\).
Figure 26. Number of branches as a function of height for *Pachycereus* on nondune substrate at Punto Cirio. Dashed line delineates the proportion of *Pachycereus* with more than 10 branches.
Figure 27. Number of branches as a function of height for *Pachycereus* on dune substrate at Punto Cirio. Dashed line delineates the proportion of *Pachycereus* with more than 10 branches.
Figure 28. Sum of arm lengths as a function of height for Pachycereus on nondune substrate at Punto Cirio. Dashed line delineates the proportion of Pachycereus with sum arm length greater than 30 m.
Figure 29. Sum of arm lengths as a function of height for *Pachycereus* on dune substrate at Punto Cirio. Dashed line delineates the proportion of *Pachycereus* with sum arm length greater than 30 m.
Figure 30. Frequency distributions of first insertion heights of *Pachycereus* on dune and nondune substrates at Punto Cirio, and at the inland Puerto Libertad site where *Pachycereus* coexist with *Lemaireocereus*. 
The *Pachycereus* population at Punto Cirio can be compared to the inland population in Sonora where *Pachycereus* coexist with *Lemaireocereus* in roughly equivalent densities. Competition theory (e.g. Cody 1984, 1986) predicts that the structural niche of *Pachycereus* coexisting with *Lemaireocereus* will have fewer arms, and will branch higher than *Pachycereus* that do not coexist with other columnar cactus species. In this experiment, the growth forms either did not differ, or the observed pattern was opposite that predicted by the theory of limiting similarity.

Comparing the relationship between N and H for the inland population (coexisting with *Lemaireocereus*) (Figure 31) with the dune population (Figure 27) shows no differences. Comparison of the inland population with the nondune population (Figure 26) shows the *Pachycereus* coexisting with *Lemaireocereus* actually tend to have more branches than the nondune cacti of equal height. Comparing Figure 32 with Figures 28 and 29 shows the height-specific $\Sigma L$ is also actually greater in the inland population with *Lemaireocereus*.

$I_1$'s are actually lower in the inland population than even in the dune population (Figure 30) ($t=2.93$, $df=45$, $p=.0026$). This is also opposite the prediction of limiting
Figure 31. Number of branches as a function of height for Pachycereus at the inland Puerto Libertad site.
Figure 32. Sum of arm lengths as a function of height for *Pachycereus* at the inland Puerto Libertad site.
similarity theory. But it is not unexpected if abiotic responses predominate over interspecific interactions, because the inland site is sandy and higher in elevation. It probably receives considerably greater precipitation than the sites at Punto Cirio.

Organ Pipe Cactus National Monument, Arizona

The *Carnegiea* population at Organ Pipe Cactus NM (where *Carnegiea* coexist with *Lemaireocereus*) can be compared with the other Arizona populations where no other columnar cacti are present. Like the Puerto Libertad experiment for *Pachycereus*, limiting similarity theory predicts that the structural niche of *Carnegiea* coexisting with *Lemaireocereus* will have fewer arms, and higher first insertion heights than *Carnegiea* that do not coexist with other columnar cactus species. Cody (1984, pp214-15 and Fig. 8) reported that *Carnegiea* at Organ Pipe Cactus NM are more branched, and initiate branching around 1.2 m lower on the stem than in the Tucson Mountains. However again, in this experiment, the *Carnegiea* growth forms at Organ Pipe Cactus NM either did not differ from those in the Tucson Mountains, or the pattern was opposite that reported by Cody.

Figure 33 shows no growth form difference in N between sites in the Tucson Mountains and Organ Pipe Cactus NM. Likewise, Figure 34 shows no growth form difference in ΣL.
Figure 33. Relationship between number of branches and height for *Carnegiea* at the Tucson Mountains (shaded circles) and Organ Pipe Cactus National Monument (open circles).
Figure 34. Relationship between the sum of arm lengths and height for *Carnegiea* at the Tucson Mountains (shaded circles) and Organ Pipe Cactus National Monument (open circles).
For $I_1$, Figure 15 shows *Carnegiea* actually branch lower where they coexist with *Lemaireocereus* than in the Tucson Mountains ($t=2.81$, $df=67$, $p=.0033$). This makes the *Carnegiea* at Organ Pipe Cactus NM actually more similar to *Lemaireocereus* than in the Tucson Mountains.

Reexamination of Figures 15 and 18 show that although $I_1$ varies with aridity, the coexistence of *Lemaireocereus* with *Carnegiea* at Organ Pipe Cactus NM does not cause the Ajo Mountains population to deviate from the linear relationship between $I_1$ and aridity.
DISCUSSION

General Conclusions

In general, the influence of the physical environment predominates over biotic interactions in determining the structural niches of *Carnegiea* and *Pachycereus* in the Southwest. I found no evidence of evolutionary divergence among *Carnegiea* or *Pachycereus* populations. Careful measurements showed populations running east to west across southern Arizona differ primarily in size structure, not in growth form. The presence of a small fraction of large cacti can easily bias one's perception when viewing a population. Where growth form differences do exist, they are correlated with variation in measures of aridity. *Carnegiea* and *Pachycereus* in less xeric environments have more branches, greater total branch length, and earlier initiation of branching than those of equal height in more xeric environments. Experiments comparing adjacent stands supported the hypothesis that the growth form variation is a developmental response to the environment, and not an evolutionary adaptation. Also, the presence of a similar competitor was not associated with divergence of *Carnegiea* or *Pachycereus* populations from the growth form of populations without similar competitors.
Other Evidence

In the Arizona Upland subdivision of the Sonoran Desert, several *Carnegiea* sometimes become established under the same *Cercidium microphyllum* (Torr.) Rose & Johnst. (foothill palo verde) nurse tree. McAuliffe and Janzen (1986) compared the growth form of closely crowded *Carnegiea* with that of *Carnegiea* with no near neighbor, within a single population. The closely crowded *Carnegiea* exist in a more xeric microclimate than those without near neighbors because of mutual extraction of water from a limited area. *Carnegiea* in the less xeric microclimates had greater total arm length than those of equal height in the more arid microclimates. There is even less opportunity for genetic isolation between subpopulations in this experiment, because they are interspersed rather than merely being adjacent.

The fossil record can also be examined to assess the relative influence of limiting similarity versus developmental responses to the physical environment. Arid-adapted columnar cacti differentiated from tropically derived species in the late Tertiary, 10-3 mya (Axelrod 1950, 1979 cited in Steenburgh and Lowe 1983). During the Pleistocene, the plant communities have gone through 15-20 glacial periods of 100 000 yr. duration with 15 000 yr. interglacial periods. Communities did not shift latitudinally and elevationally as a unit. Rather, species
responded individualistically to the changing climate (Van Devender and Spaulding 1979, Van Devender 1986, Davis 1986, Graham 1986), so that each glacial cycle has presumably reshuffled the community assemblages. Modern desert community associations didn't begin to assemble until the late Holocene, 8000 yr. ago (Van Devender and Spaulding 1979, Van Devender 1986). Carnegiea have been in Organ Pipe Cactus NM for 10000-11000 yr.; Lemaireocereus arrived only 4000 yr. ago (Van Devender 1987). There has been insufficient time for significant coevolutionary adaptation to occur in populations of columnar cacti with lifespans of 175-200 yr. These species are more likely to be adapted to conditions during the long glacial periods than to conditions of the relatively brief interglacials.

Mechanisms

In models of limiting similarity (as per MacArthur and Levin 1967) morphological variation is used as an index to measure the partitioning of a limiting resource. However, what limiting resource can be partitioned by variation in the aboveground growth form of columnar cacti? Segregation of aboveground growth form could occur as a result of competition for space, or for light in crowded, closed canopy conditions. Root systems of columnar cacti typically extend on the order of 10 m in radius. Columnar cactus
populations are of such low density that interspecific aboveground space preemption or shading is virtually nonexistent. Thus, competition for aboveground space and light are implausible mechanisms for the observed variations.

Plausible mechanisms have been reported for developmental responses to aridity. The allocations of plant resources to branching, rather than central stem growth, increases the surface area:volume ratio of the cactus. Geller and Nobel (1986) have shown this substantially increases PAR interception and whole-plant CO\textsubscript{2} uptake. This effect is mitigated by the corresponding increased rate of evaporative water loss, and the decreased water storage capacity per unit surface area. The optimum degree of branching is a tradeoff between CO\textsubscript{2} uptake and water conservation. This balance shifts with the aridity of the microclimate. \textit{Carnegiea} and \textit{Pachycereus} may increase their rate of branch production as water becomes less limiting.

Implications for Theory

No plausible mechanism exists for competition to explain differences in the aboveground growth form of columnar cacti in the Southwest. Furthermore, the recent fossil history of temperate zone North America shows that communities have been in their present form for only a short
time, and have been under continual change. If anything, species are more likely to be adapted to the mixes of species present during glacial periods. This evidence suggests that the competitive model is inappropriate to explain current patterns. Despite this evidence, competition theory continues to be employed to explain patterns in communities of columnar cacti in the Southwest. Tests of competition and alternative hypotheses reveal no support for evolutionary adaptive causes of differences within the cactus species. Likewise, there is no critical support that differences between species are caused by interspecific interaction. Each species likely evolved different forms under differing environmental conditions, and have only recently been reshuffled into their current assemblages.

Competitive mechanisms have been further invoked to explain patterns of continental species diversity. Cody (1989) attempts to show:

"that growth-form diversity increases with climatic factors associated with the 'severity' of the desert's physical regime...and defend[s] the notion that morphological diversification in desert plants is associated with different modes of moisture utilization and different growth strategies. Such adaptation to and evolution into different 'structural niches' (Cody, 1986a) is, I believe, a major component of a general explanation for species diversity among desert perennials."

However, the MacArthur and Wilson (1967) theory of island biogeography can predict these patterns of diversity without invoking interspecific competition as an additional effect. The relationship between species diversity and area does not
depend on the supposition that interspecific interactions set an upper limit to the number of coexisting species (Wilson 1969). Differences in immigration and extinction rates determine the equilibrium level of species diversity. The noninteractive species equilibrium will change if immigration or extinction rates change in response to the "severity of the desert's physical regime."

The conclusions of several other authors have not been supported by the critical testing of hypotheses employed in this study. Further adherence to the method of multiple working hypotheses in testing other communities can help determine how far these results can be generalized beyond columnar cacti. Desert communities have often been considered ideal for study of community processes because of their low diversity and apparent simplicity. However, understanding plant population dynamics may actually be more difficult in deserts because of the low rates of growth and recruitment, and the high longevity in many dominant species. In the Southwest deserts, even simple parameters such as average lifespan are unknown for many species. The role of history and abiotic factors relative to interspecific interactions may be greater in desert communities than in more mesic communities because of the slower pace of population dynamics.
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