GLEASONIAN PATTERN OF MAMMALIAN DISTRIBUTION AT A MACROGEOGRAPHICAL SCALE IN TEXAS

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Gleasonian assemblages (Gleason, 1926; Whittaker, 1975) are populations of species that chance and environmental conditions have brought together at the same time and place. Biotic exchange among members of such assemblages is facultative rather than obligatory. Membership in a suite of such species may change, as environmental conditions change. The type of community structure predicted by Gleason's thesis may be interpreted as a consequence of the Hutchinsonian n-dimensional niche (Hutchinson, 1958; Brown, 1995), where spatially autocorrelated resource levels and distributional centroids change continuously across the landscape (Brown, 1984). This pattern focuses on the idiosyncratic, individualistic properties of communities (Brown, 1995). It is very pervasive in nature and has been demonstrated over a wide range of scales, in contemporary (Brown and Kurzius, 1987; Gleason, 1926; Grossman et al., 1982; MacArthur, 1972; Whittaker, 1975) and fossil communities, and vertebrate (Wolfe, 1981; Graham, at al., 1996) and invertebrate groups (Buzas and Culver, 1994).

Cements' (1916) concept of community organization is the polar antithesis of Gleason's. Clements' (1916) view focuses on emergent properties, common to the members of a community (Brown, 1995). It holds that biotic assemblages comprise an integrated whole, in which members are significantly interdependent upon each other. Such species occur together necessarily, or at least at a considerably higher frequency than one would expect by chance alone. Clemensian communities, in the same region, may differ from each other because of temporal asynchronies during the early stages of their development. Nevertheless, all pass through a series of changes leading to convergence upon a final state, that has been likened to a super-organism (Clements, 1916; Brown and Lomolino, 1998). Many investigators have challenged the Clemensian view and it has been slowly superceded by Gleason's interpretation (Brown, 1984; Whittaker, 1975).

Both of these views may be applied to patterns of species importance along environmental gradients and lead to testable hypotheses. Clements' view predicts discrete associations of species, separated by relatively short ecotones; Gleason's predicts that species importance values will be distributed along a gradually changing continuum, without sharp steps. Measurements along an environmental gradient should serve to test the hypothesis of Clements versus Gleason. The question is which pattern comes closest to representing nature? As with many strongly opposing models both contain elements of truth. Importantly, the

conclusions to which one is led may be methodology and scale dependent (Brown and Lomolino, 1998).

In this paper I explore patterns of geographical association, within the conceptual framework of the Clemensian and Gleasonian models, of mammalian species on a regional scale. A high degree of geographical separation, into associated groups, of members of a taxon would suggest a Clemensian pattern. A high degree of geographical mixing among the elements of a taxon would suggest a Gleasonian pattern. The area treated is the state of Texas and the mammalian species treated are the class Mammalia n = 141

species, and the orders Chiroptera n = 31, Rodentia n = 62, and Carnivora n = 29.

While there is taxonomic unity within these categories, they embrace great ecological variation. Ecological interactions among populations of some of the species subsumed within these taxonomic categories probably do not occur enough to be significant. This study focuses on the distributional patterns, at a regional scale, that would be predicted by the models of Clements and Gleason. It does not imply species interactions, at a local scale, as an etiological basis for such patterns.

METHODS AND MATERIALS

The state of Texas occupies about 69.2×10^4 km² in the south-central region of the U.S.A. Since the states' size, shape, and orientation were determined by political considerations, it may be considered to be an arbitrary sample for the study of mammalian distributions. I prepared maps of the geographical distributions, within Texas, of 141 species of mammals native to the state. I used all known records of marginal

specimens as a guide to map preparation. All maps consisted of a system of quadrats, each representing 63.9 km on a side (Owen, 1990). I recorded a species as either present or absent within each quadrat. Such maps have often been used as a basis for making inferences about the biology of the distributions of mammalian species (Simpson, 1964; Pagle, et al. 1991). These data are functionally equivalent to a full census.

RESULTS

Distribution of species among quadrats with respect to sympatric species

In this paper, sympatric means geographical sympatry on a regional scale. A necessary and sufficient condition for sympatry, between a given suite of species, is that they occur together in the same quadrat, for at least one quadrat, somewhere within their collective ranges. It does imply close proximity at the local community level, although this may often be the case for many suites of species. This variable is sensitive to the size, shape, and orientation of ranges with respect of each other. Figure 1 shows the number of quadrats, as a function of the number of species per quadrat. This plot represents the correspondence between area and species richness.

I fitted the data to Poisson distributions. These distributions are used as null models that represent the number of quadrats that would be inhabited by different numbers of species, expected on the basis of a random distribution of species among quadrats. The modes of the Poisson curves are located to the right, with respect to the empirical data for Mammalia, Chiroptera, and Rodentia; each of their modal values is low. These taxa have considerably more area allocated to species-poor classes than one would expect on the basis of chance alone. The Poisson curve for Carnivora is located a little to the left of the data; its modal value is very low and the entire curve is relatively flat. Carnivores have much more area allocated to species-rich classes than one would predict on the basis of chance. Not surprisingly, none of the Poisson curves were significant using a chi-square test of goodness-of-fit.
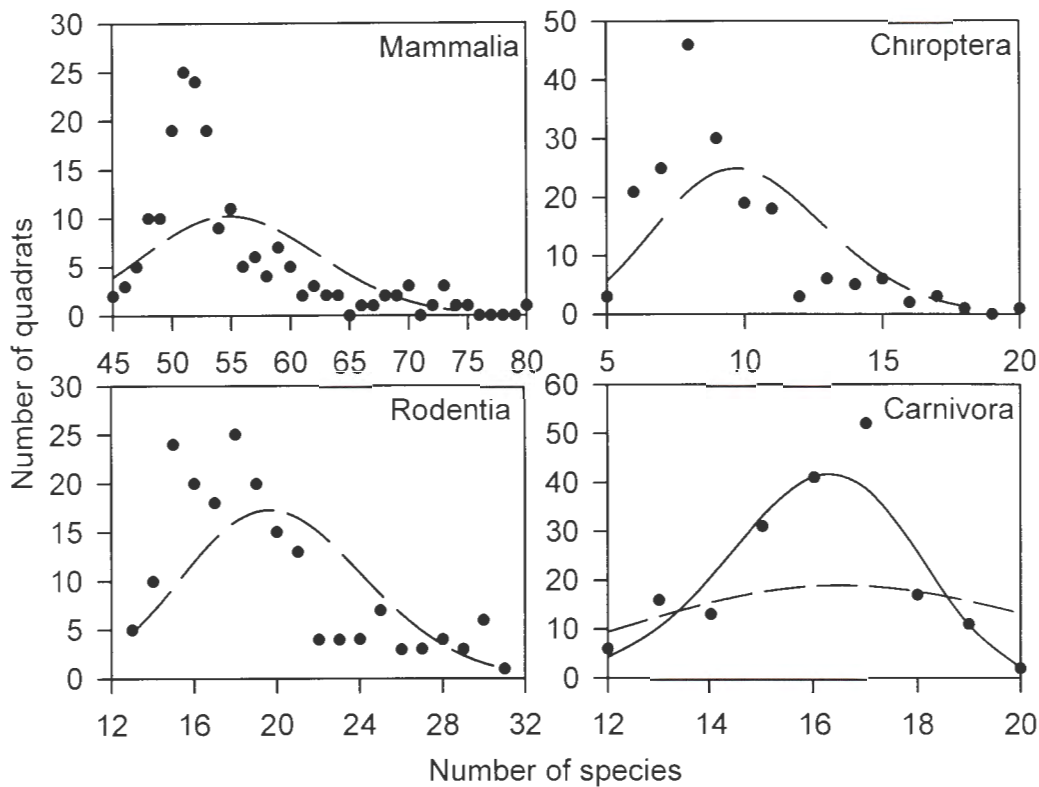
Figure 1. Number of quadrats, as a function of the number of species per quadrat. Dashed curves are Poisson distributions fitted to the data. Solid curve for Carnivora is a positive binomial distribution.

Because the data resemble lognormal distributions, I also fitted this model; none was significant. The empirical data have higher, more peaked modes, than a two-parameter lognormal distribution. The data for Carnivora, but not the other taxa, had a significant fit to a positive binomial distribution $16.22 = \lambda^2_{8, 0.039}$. The fit to a positive binomial suggests that carnivores may have a regular or uniform distribution, a condition that is unusual in field or geographical ecology (Elliott, 1977; Ludwig and Reynolds, 1988)

Figure 2 presents patterns exhibited by the number of species when they are plotted as a function of the number of species, with which they are sympatric. Many species are geographically sympatric with a wide range of other species, varying from few to many. The data have much spread but there is an overall tendency for many species to be geographically sympatric with many other species. The straight lines represent regressions, none of which were significant. The power of these tests was so low as to

give little confidence in failure to reject the hypothesis of a slope equal to zero.

Combinations of geographically sympatric species

I use the word combination to mean the set of species that is present within a given quadrat. Distinct combinations of sympatric species can differ from each other with respect to either the identity of their constituent species or with respect to the number of species of which a combination is comprised, or both. If two combinations differ in size, then they necessarily differ in species composition, but the converse is not necessarily true.

A plot of the number of species against the number of different combinations, with which said species are combination members, is illustrated in figure 3. Each of these regressions was significant ($\underline{P} < 0.05$),
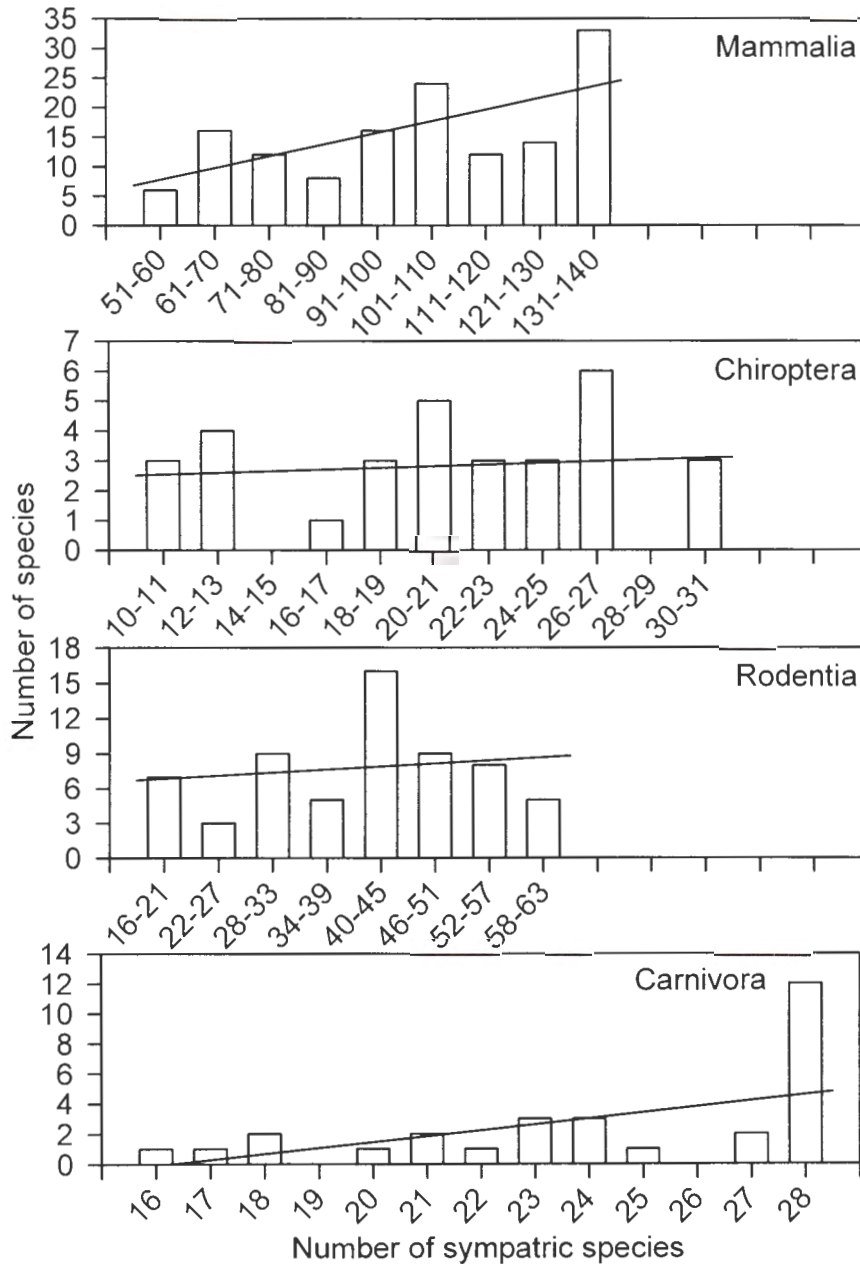
Figure 2. Number of species, as a function of the total number of species with which they are geographically sympatric.

except the one for carnivores. The power was low for each test, except Rodentia. There is a general tendency for species of Mammalia, Chiroptera, and Rodentia to be members of combinations of small size. In the plot for Carnivora there is a slight increase from left to right in the regression line, due to the influence of the large datum on the extreme right. In sum, many

species exist as a part of many different, but often small (except Carnivora), species combinations.

Figure 4 shows the frequency distribution of the number of combinations of species as a function of the number of times each combination occurred. The data for Chiroptera, Rodentia, and Carnivora are fitted
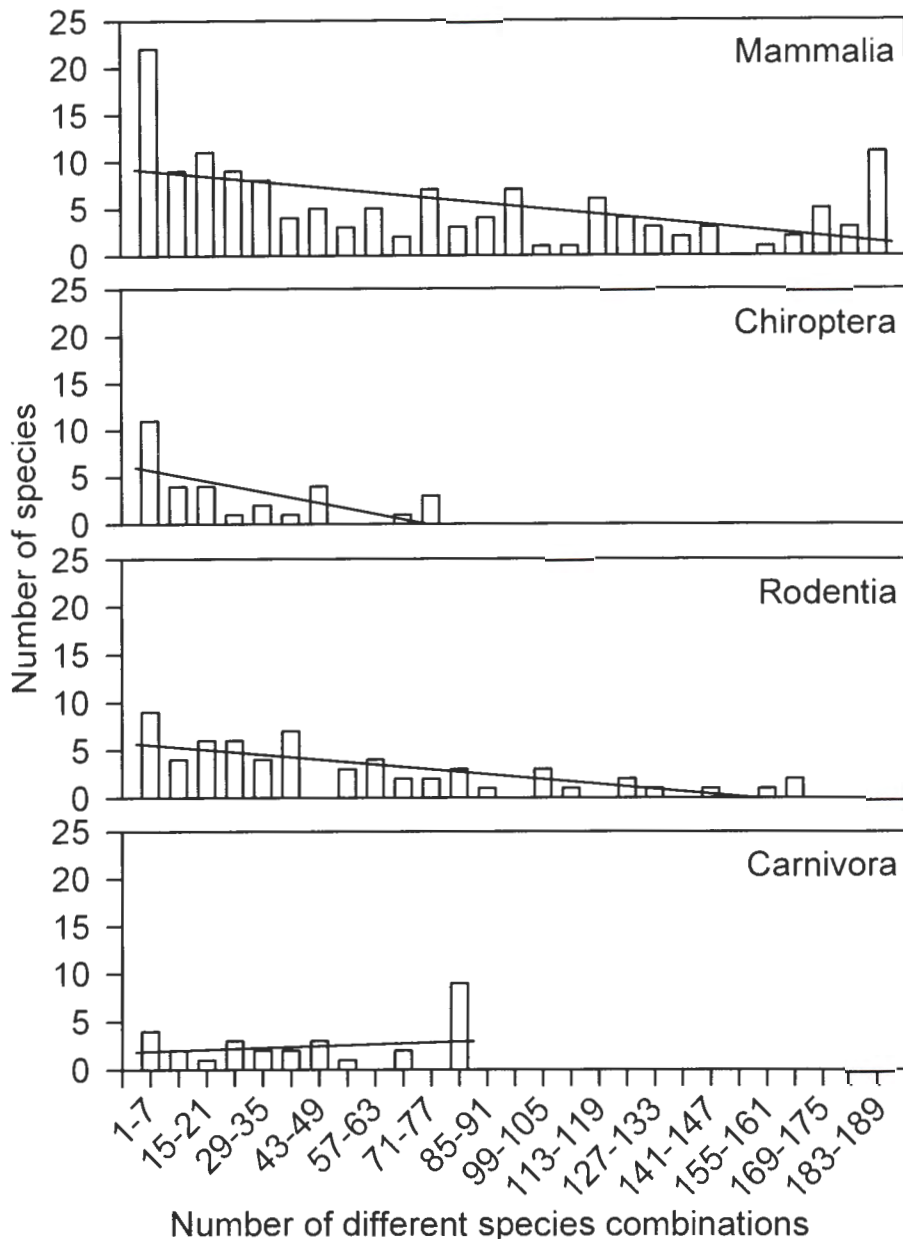
Figure 3. Frequency distribution of the number of species, as a function of the number of different combinations in which they occurred.

to power functions; each curve is highly significant (P < 0.001). The lowest possible value for this variable is one. This value would be the case if all quadrats were completely homogeneous i.e., if every species were sympatric with every other species throughout the entire state. Because each quadrat is characterized by one and only one combination, the maximum possible number of combinations is 189. This value would obtain if each of the quadrats had a unique assemblage.

Mammalia had 184 different combinations, which is not significantly different from the maximum of 189 (binomial test, $\underline{P}$ = 0.72). Ninety seven percent of these combinations were observed only once. Rodents had 164 combinations, which also was not significantly different from the maximum possible value of 189 ($\underline{P}$ = 0.069). Most of these combinations (89.6%) also occurred only once. Bats had 73 combinations. This value was significantly less than the
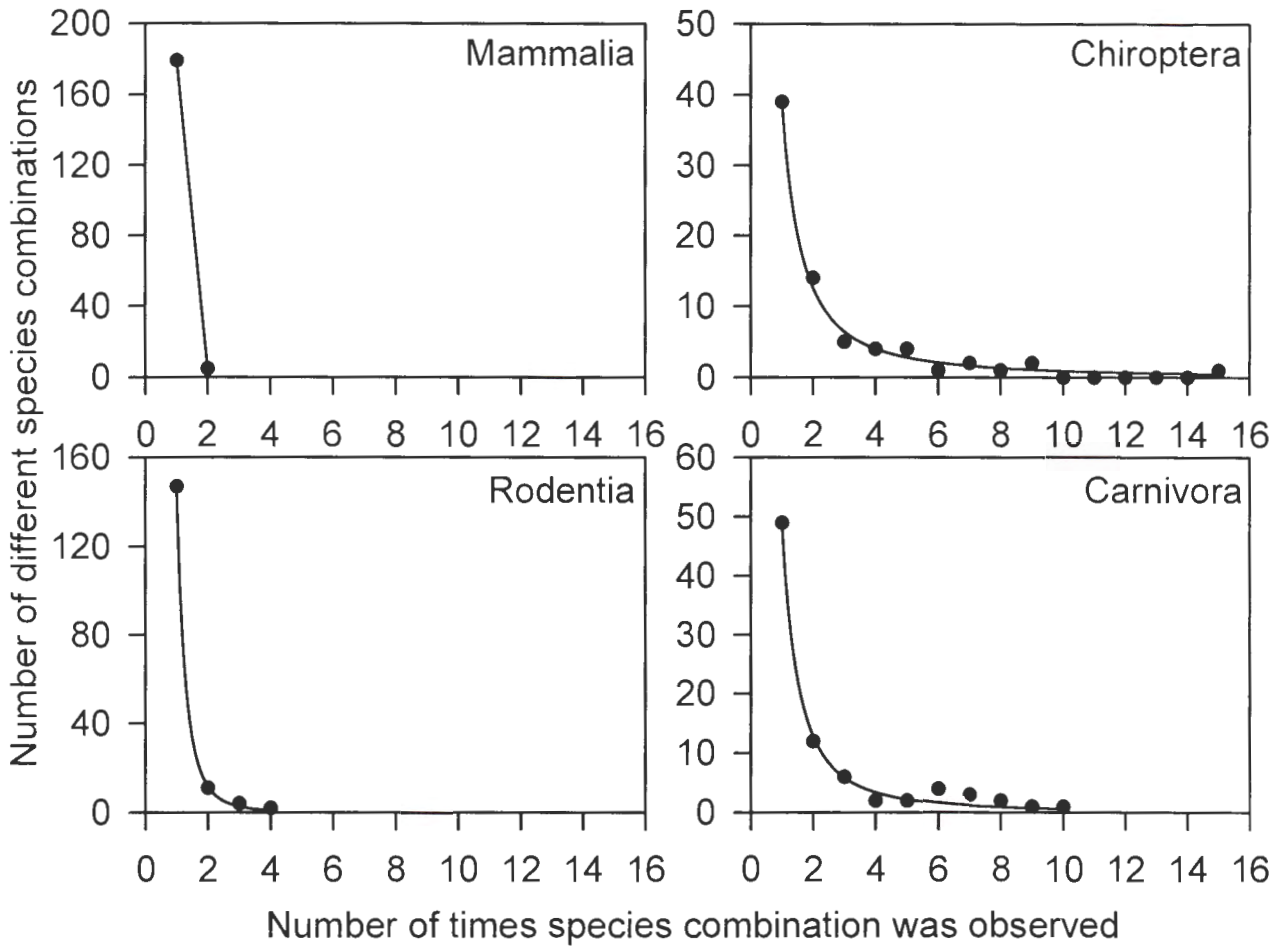
Figure 4. Frequency distribution of the number of combinations of species, as a function of the number of times each combination was observed.

maximum number possible ($P < 0.001$). Of these 53.4% occurred once. Lastly carnivores occurred in 82 species combinations, which also is significantly less than the maximum possible ($P < 0.001$). Of these 59.8% occurred only once. It is noteworthy that bats, which can disperse by flying, had a lower number of combinations than any other taxon. The upshot of this figure is that most combinations of sympatric species occur only once and that most of the others occur only two or three times.

The frequency distribution (Fig. 5) of the number of species belonging to different combinations is

illustrated as a function of the number of species per quadrat. I contrasted these data with a positive binomial distribution having its probability of "success" set equal to $P = 0.5$. This distribution is symmetrical by construction and approaches a normal distribution, as sample size increases without bound. This approach amounts to the null hypothesis that different combinations are equally likely. The procedure includes some combinations that were not observed because one or more of the component species do not have overlapping geographical ranges. This model is neutral in the sense that it assumes that no species interactions or extrinsic factors influence distribution. As such I did
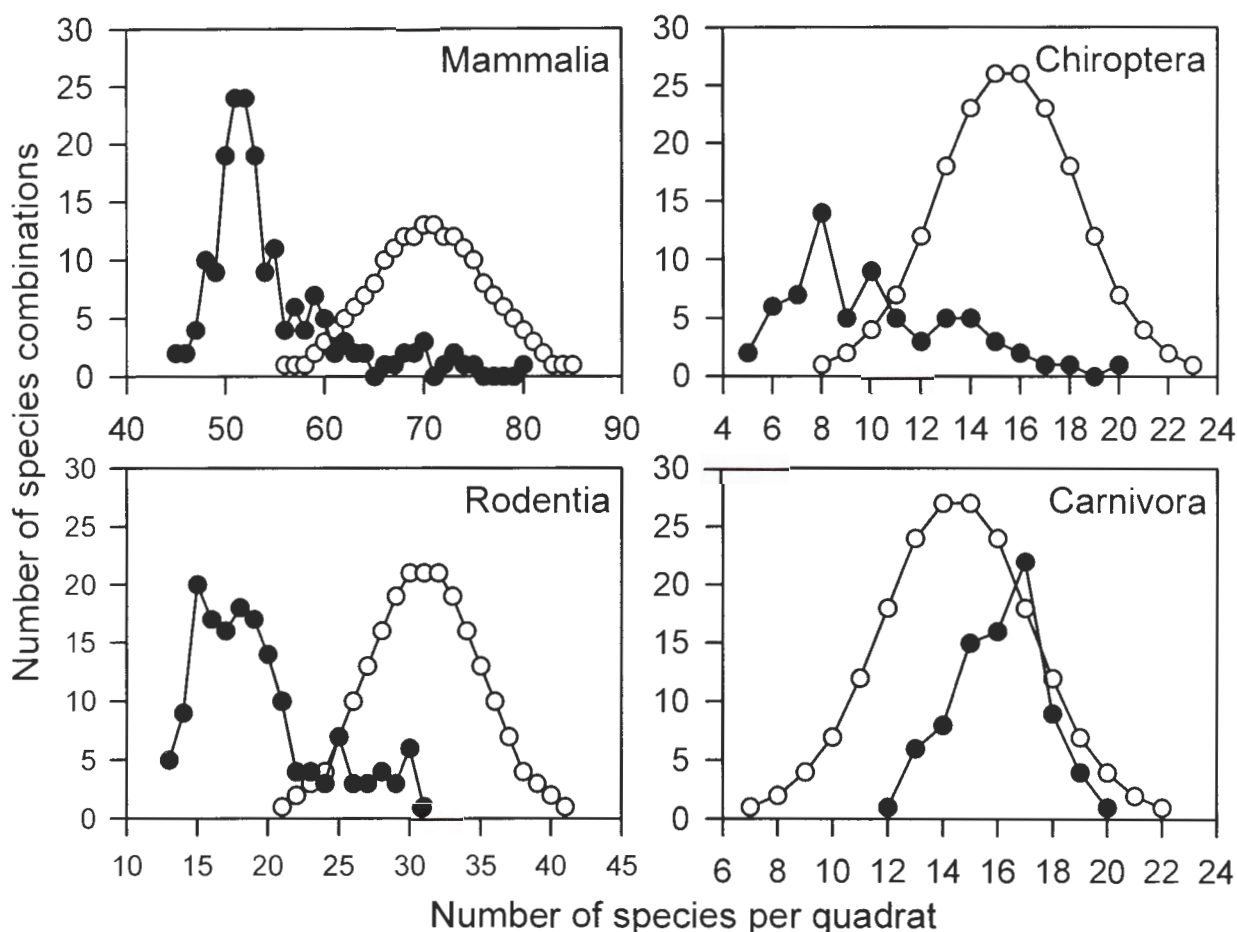
Figure 5. Frequency distribution of the number of species pertaining to different combinations, as a function of the number of species per quadrat (black dots). Circles represent the expected number of species pertaining to different combinations, based on the null hypothesis that each different combination is equally likely.

not expect the data to conform to this model, but rather was interested in the manner and degree in which lack of conformity might be expressed.

I used a two-sided normal approximation to the Mann-Whitney test to assess the null hypothesis that the empirical and theoretical data belong to the same underlying population. The alternative is that they differ in location. This test was highly significant ($P < 0.001$) for each taxon. Lack of fit seems to be attributable to both the locations of the modes and to their degree of skewness. The empirical modes of all mammals, rodents, and bats are strongly shifted to the left

of their corresponding null modes. Their distributions have strong positive skew. They are characterized by an abundance of species-poor classes, i.e. classes that are composed of a relatively low number of species.

Interestingly, the distribution of carnivores differs from the other groups in several ways. Carnivores are not positive skewed but rather seem to be slightly negatively skewed (Fig. 5). They have more area allocated to high species richness classes, with respect to the other three taxa, and more species combinations that are composed of a larger number of species. Overall they are more nearly symmetrical, their

mode is displaced a little to the right of the null mode and, except for a single datum point, the empirical distribution for carnivores is completely enclosed within the density of its corresponding null distribution.

Impressionistically, carnivore assembly seems to be closer to the null model than to that of the other three taxa.

DISCUSSION

The data presented in this paper, together with findings referenced from the literature, suggest that a mosaic-like pattern is characteristic of biotic assemblages across a large range of different taxonomic, temporal, and spatial scales. The spatial scales are known to range from local, homogeneous habitat patches to subcontinental regions. The taxonomic scales range from feeding guilds of mice to an entire class and the temporal scales span millions of years.

Two exceptional patterns are emergent among Carnivora: (1) High species-richness is distributed over a greater area for carnivores than it is for all mammals, rodents, or bats; (2) geographically, carnivores are grouped together in such a way as to produce combinations of species that are species-rich relative to the other taxa. Both of these phenomena may be explained as consequences of the larger geographical ranges of carnivores. Larger geographical ranges should overlap more with each other, yielding numerically higher combinations of species. This effect is reinforced by the presence of high carnivore richness in central Texas (Owen, 1988). The accumulation of carnivore species in central Texas and its gradual decline outwards to the east and west, gives carnivores more opportunity to acquire numerically high combinations, while remaining within the study area. This exceptional pattern for carnivores does not obviate their inclusion within a Gleasonian frame of reference. The same pattern and its explanation would seem probable on a continental scale. North American carnivores have considerably larger ranges than several other orders of North American mammals (Pagle, et al., 1991).

The Gleasonian pattern of spatial association found in this study is not completely antithetical to non-randomness. Two non-random patterns are identified: (1) The lack of fit of the data to Poisson curves

(Fig. 1) and; (2) the lack of fit to binomial curves (Fig. 5). This means that one or more of the basic postulates of these distributions is seriously violated. A two-dimensional Poisson or binomial process assumes, among other things, that each quadrat or sampling unit has equal probability of being inhabited by a given species. In particular, this postulate seems likely to have been violated by the Texas data. The state is not homogeneous with respect to its resource content for mammals. Some areas offer more favorable conditions and so accumulate more species than others. This is consonant with the widely varying qualitative features of different habitat types in Texas (Gould, 1975). Limit relationships between the Poisson and binomial distributions imply that, for large sample sizes, and small probability of success for each species presence-absence event, it makes little practical difference which of the two distributions one uses (Hogg and Craig, 1978; Boswell, et al., 1979).

Each of the patterns in the data, suggests a patchy, mosaic-like geographical assemblage with little internal homogeneity. At a regional scale species number, degree of sympatry, and combinational size, occur in constantly changing spatial configurations. This change is probably produced by responses to environmental conditions that are species-specific, rather than assembly-specific. The pattern corresponds to a Gleasonian interpretation of mammalian distribution in Texas at a statewide scale. Quadrats cannot (except arbitrarily) be organized to form internally cohesive biogeographical assemblages. This is the case in spite of the ease with which certain areas of the state can be superficially distinguished on the basis of their vegetation physiognomy. Knowledge of the species composition of one quadrat does not permit the prediction of the species composition of other quadrats, at the ordinal and class levels of taxonomy.

Fossil faunas have demonstrated great age of conditions that fit the Gleasonian hypothesis of species associations. Buzas and Culver (1994) studied foraminiferal communities, from Cenozoic shelf deposits of the North American Atlantic Coastal Plain. These communities exhibited little unity, during nearly 55 million years of successive oceanic transgressions and regressions. Their results indicated a lack of local community unity. Graham et al., (1996) analyzed fossil mammalian communities at 2,945 localities in the United States. They documented geographical range shifts of individual species, at different times, in different directions, and at different rates, in response to late Quaternary environmental fluctuations. Such abundant data suggest that the pattern is real. Such long expanses of time suggest that the Gleasonian pattern is not an epi-phenomenon, but rather an integral part of the ecological milieu through geological time.

That a mosaic-like pattern holds up for taxa at the class and ordinal level is perhaps to be expected. Members of the same class or order exhibit a wide range of form and function. The rub is that Brown and Kurzius (1987) found that patterns, qualitatively very similar to the ones described in this paper, characterize members of a well defined desert, rodent feeding guild, where perhaps it was not to be expected.

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