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Three Monte Carlo Models
of Faunal Evolution

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ABSTRACT

Monte Carlo models (computer simulations) based on certain assumptions of randomness in evolutionary events provide a fairly good fit with some families of "climbing" curves seen in taxonomic sets of data.

INTRODUCTION

In a paper on patterns of faunal evolution (as expressed in the relative numbers of taxa in different groups, which are a result of faunal evolution, Anderson, In press) a logarithmic frequency distribution was demonstrated and the history of explanations for this distribution was summarized. A number of sets of taxonomic data were examined and found to have distributions of this sort. Explanations were related to an interplay of stochastic and deterministic philosophical concepts.

The paper mentioned above was completed in April, 1973, and revised in February, 1974, principally by shortening it to meet page limitations. Some material was discarded and a brief presentation of the models described here was removed.

Two recent contributions toward explaining faunal diversity that were not dealt with in the above-mentioned article should be commented upon here. These contributions are in the fields of paleontology (Raup et al., 1973, and earlier papers cited there by the same authors) and of evolutionary theory (Van Valen, 1973).

Raup et al., 1973, predicated their work upon the idea that models can usefully render the real world, yield generalizations, and redirect field exploration. The use of equilibrium models is seen as part of a trend in paleontological work from descriptive to predictive, individual to general, idiographic to nomothetic. Their model (1) begins with a single lineage, (2) forms new lineages only by branching from older ones, (3) determines the fate of each line through time by selecting at regular intervals of time from the alternatives (μ, π, or β) of extinction, persistence, or splitting into two lines according to probability values that can be changed from one run to

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another, and within a single run so that changes in probabilities of μ, π, or β are density dependent and tend to maintain a specified equilibrium diversity.

The taxonomic interpretation or classification of the dendrogram resulting from a given run through the program (1) defines the limits of size for a taxon of a given category or hierarchical level and requires that no contained subgroup falls in the same limits; (2) defines size as the sum of the times of existence for contained lineages, not as the number of lineages; (3) requires monophyly; (4) selects the clade with the earliest origin if more than one classification is possible under 1 and 2.

The authors attempted to hold constraints on randomness to a minimum. The models we present below operate with fewer constraints, or at least without the constraint of density dependent probabilities. This is because $\mu=\beta$ in our models. Our models are simpler and also less flexible in testing the effects of changing certain parameters.

In the paleontological model, as in stochastic models generally, two groups under identical constraints usually behave differently. Observed variation does not therefore demand biological differences. Caution is advised in using diversity as the major evidence for assessing evolutionary potential (Raup et al., 1973, p. 534). A similar conclusion was also drawn by Anderson (In press).

Raup et al., 1973, compared major reptilian groups with the clades of the simulation or model and considered in what ways the model resembled and differed from the real data. They judged that the model differed in having (1) no allowance for extremely small or large higher taxa, (2) less frequent occurrence of mass extinctions, (3) less frequent occurrence of mass radiations, and (4) less frequent occurrence of the "coelocanth effect" of a once diverse group reduced to a very few that then persist for a long time. Modifications that are possible in the stochastic model can provide a better approximation of the real data, and the authors indicated their intention to develop such modifications.

Their discussion was lengthy, and we offer only two comments. Their remark that "taxonomists rarely erect higher taxa on the basis of very few species" seems misleading unless "rarely" is defined. The number of monotypic taxa at different hierarchical levels in most groups studied provides a reasonably close match to the numbers derivable in certain stochastic models (Anderson, In press). Their discussion and statement that the taxonomy of real organisms is subject to constraints similar to those used in the simulation would have been clearer if the concept of taxonomy (classification) were distinguished from concepts of the real organisms. This distinction has been discussed by Anderson (1974).

Van Valen (1973) documented a number of cases of fairly constant rates of extinction within different groups of organisms. The rate is different for different groups. He presented this as a new evolutionary law and couched it also in ecological terms such as "the effective environment of the members of any homogeneous group of organisms deteriorates at a stochastically constant rate," or "extinction in any adaptive zone occurs at a stochastically constant rate." The concepts of "effective environment," "homogeneous group," and "adaptive zone" were discussed, but remain somewhat unclear. They are, as Van Valen pointed out, abstractions beyond the evidence. The most significant point, in our opinion, in Van Valen's paper is his demonstration of the existence in one aspect of faunal evolution, namely the extinction rate, of a major pattern that could have resulted from a random or stochastic process and that is not "derivable with confidence from lower-level knowledge of the causes of individual extinctions and the nature of species interactions" (p. 19). Similar conclusions were drawn independently, by considering other aspects of the pattern of faunal evolution, by Anderson (In press).

As a result of discussions on the study by Anderson, we decided that it would be interesting to simulate some simple cases of faunal evolution under several sets of assumptions to see whether frequency distributions seen in nature could be approximated.

THREE MODELS

Our models were programmed and run on electronic computers by C. S. Anderson using terminals at the Northern Valley Regional High

School in Demarest, New Jersey, and at Franklin and Marshall College in Lancaster, Pennsylvania.

In the first model the conditions were: (1) N items initially in G separate groups, N = G = 100; (2) a group was selected randomly (using the random number generator in the computer); (3) an item was either subtracted or added to this group, the decision again being random; (4) the number of such events was tallied; (5) after each 100 events, the numbers of groups containing different numbers of items were tallied and printed.

The average cumulative frequency distribution curves after 100, 500, and 2000 events are plotted in figure 2. The probabilities of the two kinds of events are equal. In this model the probability of an event (in evolutionary terms either a division or an extinction of a species) is equal for each group (genus) rather than for each item (species) so that as a group proliferates the probability that a given species of that group will be hit by an event decreases. The evolutionary action is thus concentrated on the species of smaller genera and the result is a pronounced right hand truncation of the curves, relating to the one-way gate (generic extinction) at the bottom. A set of "climbing" curves such as seen in figure 1 is generated but the shape of the curves is different.
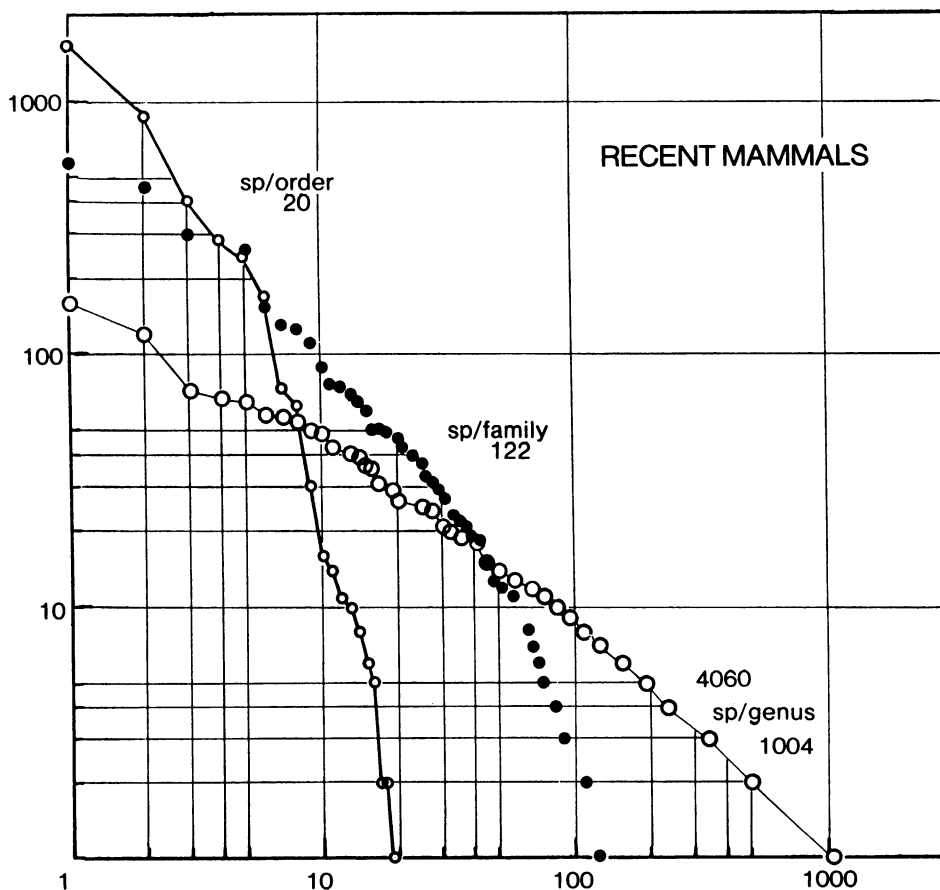
In a second Monte Carlo model the conditions

FIG. 1. Cumulative frequency distributions of species of Recent mammals per taxon at three different categories or levels in the classification. The numbers of species, genera, families, and orders are given. Drawn from Anderson (In press) for comparison with figures 2 and 3.
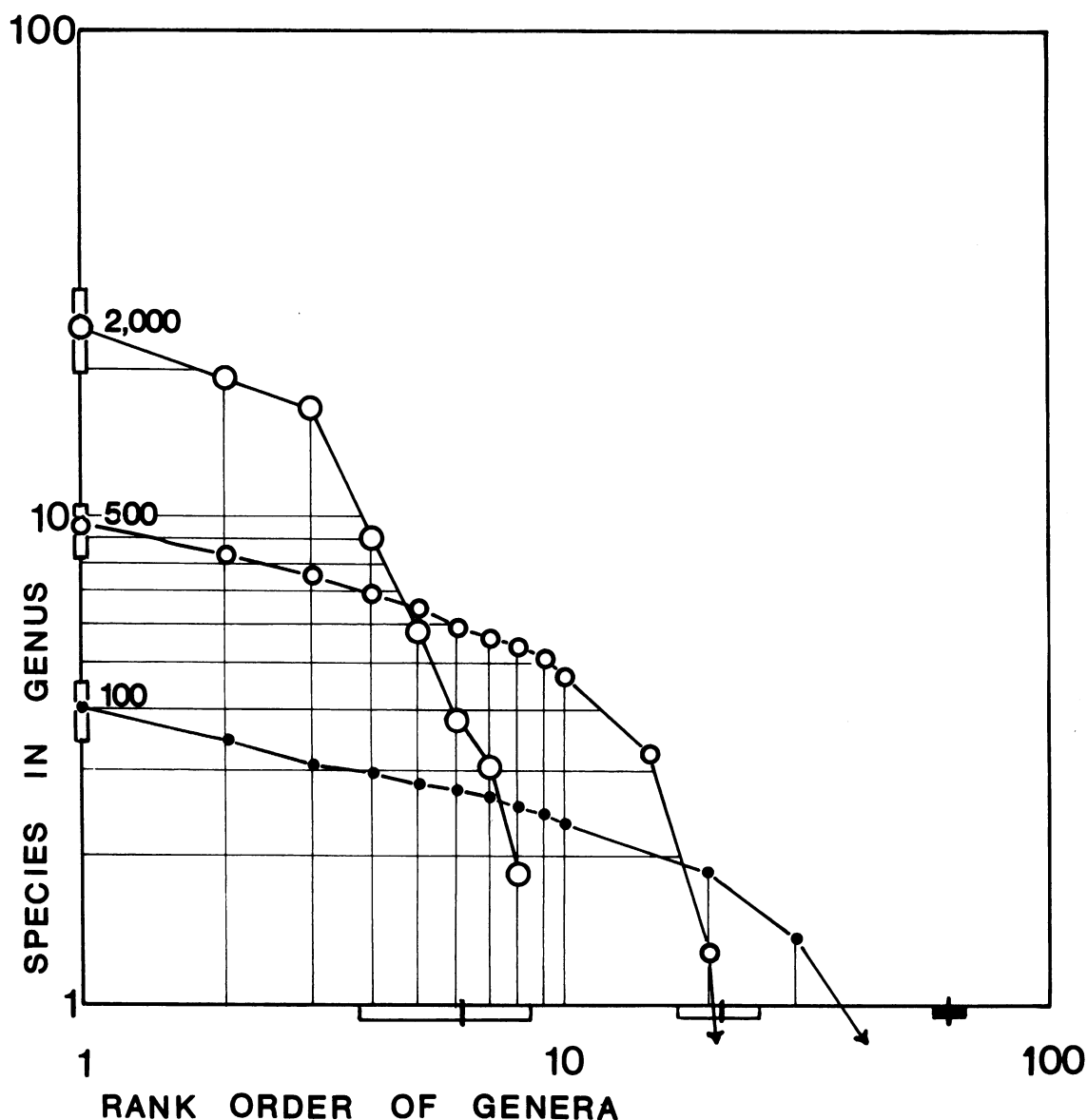
FIG. 2. A set of curves representing the average cumulative frequency distribution for groups (genera) of different size (numbers of species) in the first Monte Carlo model described in text after 100, 500, and 2000 events. In this model the probability of an evolutionary event was equal for all groups. The points are means of 24 runs, and the ranges shown are one standard deviation either side of the mean.

were: (1) N = G = 100 initially; (2) item selected randomly; (3) selected item exterminated or divided into two items, the event randomly determined; (4) the number of events was tallied; (5) after each 100 events the numbers of groups

containing different numbers of items were tallied and printed.

Average curves after 100, 500, and 2000 events are plotted in figure 3. These curves look reasonably like those for real data such as shown
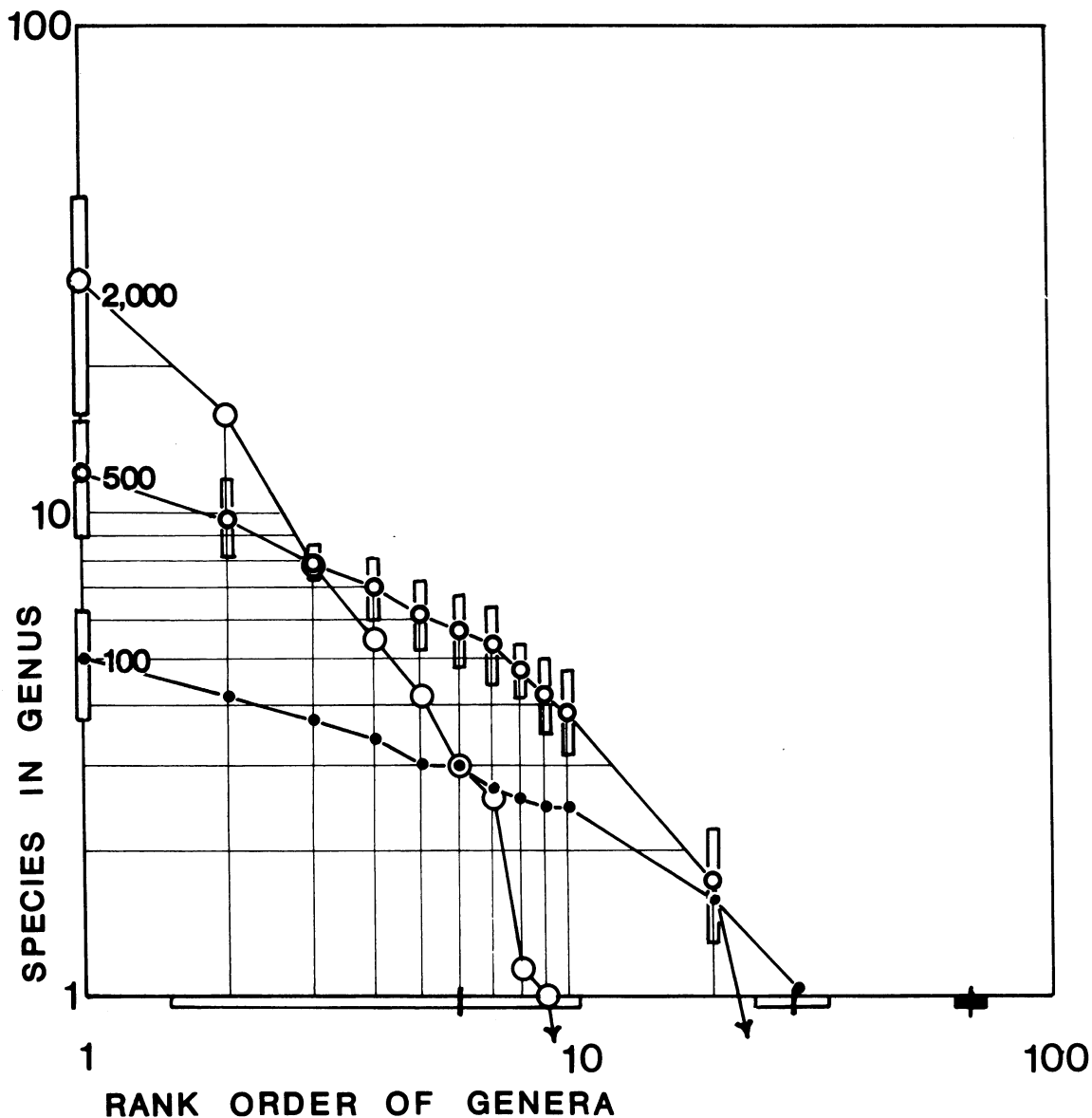
FIG. 3. A set of curves as in figure 2 for a second Monte Carlo model in which the probability of an evolutionary event was equal for all species. Ranges of plus and minus one standard deviation are shown for some points. Points are means of results of 10 computer runs of the simulation.

in figure 1. The "genera" of figure 3 correspond only at about the 500 event level with genera of figure 1. At the 100 event level the "genera" in figure 3 correspond with what would be about subgenera if plotted in figure 1, and the 2000 event correspondence is near the category of family in figure 1.

A third Monte Carlo model was prepared by adding to the operations of the second model a provision for splitting any genus into two genera if it had surviving members of two lineages formed by a split at any selected earlier event. Five computer runs were made through 1500, 1500, 2000, 2500, and 3000 events, requiring

lineages that had been separate for 500 events to be recognized as separate genera. Three computer runs were then made through 1000 events, this time requiring lineages that had been separate for only 100 events to be recognized as separate genera. Curves such as those shown in figure 3 for the second model were drawn. When 500 events was the criterion for recognizing a genus, the curves climbed during 500 events to the position of the curve for 500 events in figure 3, and then remained approximately at that position as long as the run continued. When 100 events was the criterion, the curve climbed during the first 100 events to the position of the curve for 100 events in figure 3, and then remained approximately at that position as long as the run continued.

We have demonstrated a simple random or stochastic model in dynamic equilibrium that fairly well fits certain aspects of observed diversity. This does not prove that the assumptions of the model apply to faunal evolution for there may be other models that fit also. However, this does suggest that caution in drawing conclusions or formulating hypotheses from diversity patterns alone is advisable. A group may become abundant by luck as well as "adaptive superiority." Organisms gamble for survival as well as struggle for survival.

We suggest that Monte Carlo simulations such as ours and those of Raup et al. (1973) provide a productive approach to formulating and testing alternate models for faunal evolution, including more complex models that may in-clude both deterministic and stochastic factors.

We raise the question whether there is any deterministic model that resembles or would give rise to the observed diversity.

The occurrence of seemingly random or stochastic patterns in more than one major aspect of faunal evolution (rates of evolution, Van Valen, 1973; frequency distributions in groups, Anderson, In press) and the fact that these can not be derived from the deterministic models we customarily use at lower levels of evolutionary theorizing suggest that deterministic models are not in themselves adequate to deal with or explain evolutionary events on a broad scale. And, as suggested elsewhere (Anderson, In press), deterministic models also may be deficient in the same way on a very local and short-time scale in ecological processes.

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