

AN ABSTRACT OF THE THESIS OF

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A brief review of some current concepts in the philosophy of science was made. As an elaboration of these concepts three major components of scientific conceptual systems were discussed: pattern recognition, language, and automaticity. The current theoretical status of ecology was evaluated on the basis of these three components. It was found that the theoretical problem of the distribution and abundance of organisms could be profitably interpreted as the problem of constructing a mapping (in the mathematical sense) from a description of the habitat (biotic and abiotic) onto a description of communities. It was further found that a distinction between a theory of the "language" of ecological systems and a theory of the "communication" of ecological systems could be made and applied to the mapping problem. The goal of a theory of the "communication" of ecological systems is to provide an automatic procedure that accounts for the

behavior in physical time or space of some system (e.g., an ecosystem) recognized by the user of the theory. The goal of a theory of the "language" of ecological systems is to provide an automatic procedure that supplies the necessary and sufficient conditions for a particular object to be classed as an ecological system (i.e., biological species, community, or temporal ecocline).

The latter task was an objective of this thesis. It was approached by creating a system of generative, transformational grammars that mapped environmental descriptions onto species lists. The result of such a system was a model that constructed biological species and ecosystems. The system of grammars was composed of three parts. The first part was a generative grammar that constructed the habitat requirements of species on the basis of their activities, such as development, feeding, and reproduction. A second component of the system generated the physical habitat of ecosystems and constructed species lists on the basis of the available habitat features in the environment and the required habitat features of species's activities. This process was termed "species insertion" and was performed by a set of transformation rules. A final component of the system of grammars, another set of transformation rules, altered the available habitat of the ecosystem on the basis of physical processes and the effects of those species that had been previously inserted. This technique produced the effects of one community replacing another in

time. This grammatical process was used to simulate ecological succession.

The system of grammars was discussed in light of its possible improvements, applications, and extensions. The philosophical implications of ecological models like the one proposed here were discussed.

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GENERATIVE GRAMMARS THAT SIMULATE ECOLOGICAL SYSTEMS

I. INTRODUCTION: THE APPLICATION OF CONCEPTUAL SYSTEMS TO ECOLOGY

Ecology, like other sciences, comprises a set of concepts which possess interrelations. Such an arrangement is a system (Bertalanffy, 1968), which I call a "conceptual system" (after Harris, 1970). For a variety of reasons, some of which I explore below, scientists are interested in the representations of their conceptual systems by formal languages. It is the aim of this thesis to attempt a formal representation of a few of the central concepts in ecology. Among these, I will investigate a representative of the mechanisms by which "species" are grouped together into "communities," and by which "communities" can be ordered along a time axis in a process called "succession." I will initiate this investigation by analyzing, in this introduction, the goals of any formal representation of a scientific conceptual system. I will then apply this analysis to the particular conceptual system of ecology. This "foundation" will aid me in choosing which formal language might be best for a representation of certain problems in ecology. Second, in the methods section, I will suggest a linguistic metaphor and methodology to model these concepts. This will restrict the kinds of representations that are adequate within the particular

language I have chosen. Third, the results section will contain one particular model of succession as an illustration. And fourth, I will analyze this model by discussing its potential, possible alterations, relations to other models of ecological systems, and philosophical implications.

The conceptual systems of most sciences can be characterized by a relatively small number of components, and ecology is no exception to this. The generality of these components is such that they may be analyzed quite independently of any statement of the goals or interests of a particular group of scientists, such as ecologists. Rather than recipes for achieving the ends of some scientific pursuit they represent categories by which individuals identify a given activity as "scientific." As a result, this introduction will proceed in the following manner. Three components of conceptual systems will be named and discussed: pattern recognition, language, and automaticity. Following this, ecological concepts will be discussed as instances of these three categories. These ecological concepts will then be used to form the broad and imprecise constraints on a model of succession.

The Components of Conceptual Systems: Pattern Recognition, Language, and Automaticity

Recent studies in the philosophy of science, although by different

authors with different intents and terminologies, have treated conceptual systems as composed of two parts. One is a fund of vague, loosely defined concepts or "Umwelts" and the second (in the more mature sciences) is a collection of precise, well-defined methods of interpreting and manipulating these concepts. Concepts analogous to this distinction have been proposed and named by several authors. For example, in the literature there are: conceptual frameworks and conceptual structures (Gutting, 1973), schemata and theories (Harris, 1970), themata and contingency analyses (Holton, 1973), paradigms and theories (Kuhn, 1962), and research programmes and theories (Lakatos, 1970). Certainly there exist differences between these accounts, but one of the points they hold in common is that the activity of science has some precise aspects and some imprecise aspects.

To debate the fine distinctions and subtle differences that exist between these various philosophical accounts does not seem to be an ecologically applicable or useful undertaking. Instead, I shall try to reveal some of the scientific components that contribute to both the imprecise and precise portions of the scientific activity. Following this I shall apply the analysis to ecology in the hope of achieving an alternative perspective for the modeling of ecological systems.

Pattern Recognition

Pattern recognition involves the recognition of simple order among physical objects and explanations. Scientists do not accept any sequence of utterances as an explanation of some phenomenon or class of phenomena. To be explanations, sequences of sentences must show a certain explicit order, an order that can be subjected to public scrutiny and debate. A common explanatory pattern is the hypothetico-deductive explanation. In this pattern one or more sentences correspond to an hypothesized explanans, one or more sentences correspond to the rules of a deductive calculus, and one or more sentences correspond to some observable phenomenon, the explanandum, that is to be explained (Braithwaite, 1968; Nagel, 1961).

Despite the philosophical problems associated with this type of explanation (cf., Harris, 1970; Scheffler, 1963) the pattern holds relevance for the problem of modeling ecological systems. Since ecologists wish to attribute explanatory power to their models, and since most ecologists subscribe to some form of the hypothetico-deductive pattern of explanation, it follows that satisfactory models are required to be an example of that pattern of explanation. We shall see, I believe, that the models herein proposed adhere to the form of hypothetico-deductive explanations.

In addition to explanatory patterns, scientists recognize patterns of an empirical nature. Principally, these are structural patterns recognized by the organization of sets of objects or relationships. The nature and characteristics of the objects and relationships a scientist perceives, recognizes, and organizes into patterns is one of the major components of the imprecise aspect of the scientific activity. Later I will examine ecology for its important objects and patterns; they will emerge in the form of "species, " "niche, " "competition, " and so on. More generally, if the objects are visual elements such as lines, angles, or shadings, then the organization or pattern is the "gestalt picture" which is the perceived totality. But scientific observation is not merely "seeing"; it is Hanson (1958) who gives the best account of these differences.

Hanson's major point is that observation cannot proceed without an organization of the visual field. Organization, which he calls "pattern, " is not in a picture as are lines, shapes or colors. ["The plot is not another detail of the story, " Hanson (1958, p. 13)] . Pattern arises from the context of the picture; the context is part of the picture (Hanson, 1958, p. 15). The presence or absence of a perceived pattern can have a tremendous impact upon a discourse about the visual field observed. This is why Kepler and Brahe differ in their account of the rising sun: "The elements of their experiences

are identical; but their conceptual organization is vastly different" (Hanson, 1958, p. 18).

The reasons that the patterns perceived by Kepler and Brahe (and hence their discourse) may differ are many and varied. It will depend on the spatial and temporal resolutions chosen by the observers. It will also depend upon the language the observers use.

"Another influence on observations rests in the language or notation used to express what we know, and without which there could be little we could recognize as knowledge" (Hanson, 1958, p. 19). But this linguistic connection is not a result of the fact that language somehow pictures reality for the user. The linguistic component of observation does not arise by virtue of the fact that language might somehow re-draw or graphically re-characterize our pictorial, visual experiences. Language, apparently, does not work in so simple a way. "Seeing is . . . an amalgam of the two--pictures and languages" (Hanson, 1958, p. 25). But scientific observation, for all that, is not seeing. Scientific observation has something to do with gaining knowledge, if only in a sense relative to the individual observer. Scientific observation increases our knowledge of the world and therein lies the significance of language for science; for "knowledge of the world is a system of propositions" (Hanson, 1958, p. 26). And this is just how we use the word "language": a system of propositions glued together

by a common organized pattern, a pattern created in part by the syntactic and semantic rules of grammar for the language.

If observation of the world comprises a system of propositions, then, to the extent that the world is what we know it to be, the world is our propositions. Thus, the study of the world, in a sense, is the study of a system of propositions. Individuals who participate in the scientific observation of a facet of the world also participate in and contribute to a system of propositions. This requires that such individuals acquire the necessary vocabulary, rules of grammar, and "logical out-look" that constitute any linguistic community. The logical out-look that accompanies initiation into a scientific community stimulates and constrains the scientific questions that individuals raise, and, ultimately, the changes a community can undergo. New questions are generated by the manipulation of an implicit grammar that describes an individual's scientific knowledge and is supplemental to the natural language grammar of the scientist. The extent to which an individual's scientific grammar (including both syntax and semantics) overlaps with that of others determines the extent to which that individual participates in the scientific community.

Grammatical manipulations that generate new scientific questions may take several forms. They may be a deduced prediction from a set of differential equations. It may be the creation of a new set of equations from some higher level set of constraints (as

Einstein's constraints on the invariance of physical law). It may also represent problem solving by the manipulation of "goal trees" (Simon, 1966a, b, 1973), internal psychological "structures" that represent the intuition used in the discovery process. Such manipulations may not take the explicit form of questions. But they easily may be converted into this form by testing the results of grammar manipulation against the natural system under study. Thus, we may ask: Does the system behave in this way? Are these equations acceptable descriptions? and so on.

The idea that the activity of science is, in part, the manipulation of a grammar has certain advantages. It suggests that scientists use a set of explicit rules to create and distinguish between acceptable and unacceptable propositions. It also suggests that the basis for the scientific activity is both internal to the individual and shared by a scientific community. Moreover, this fulfills some of the requirements of scientific change (Toulmin, 1972), for whenever scientific change occurs it must occur within individuals and be transmitted through the community. Thus, there must be something that changes in humans, and it must be heterogeneous, for not every scientific change is a complete revision of science. Grammars are heterogeneous in the sense that they are a collection of rules; a change in any one rule may or may not support substantive and radical changes in the class of acceptable propositions. Changing some rules induces

greater alterations than changing others. The output of grammars, further, are sentences or propositions that are testable against the natural systems that scientists study. The manner in which systems are studied allows two large classes of grammars to be created, both of which produce and stimulate new questions. This is a topic of the following section.

Language

The answers to questions stimulated by the manipulation of internal grammars are provided, of course, by the natural systems of interest. This situation is similar to that in linguistics where one important research problem is to produce a grammar for a language of which the linguist is not a native speaker. This requires posing questions to an "informant," a native speaker of the language. However, the observation of conversing humans involves the observation of two separate processes, both of which can be represented by grammars. One process is the use, by the participants, of a particular, natural language that converts the intended meanings of the users into sounds. Both the meanings and the conversions are unique to the individual users; each possess slightly different meanings and rules. But there is, apparently, a sufficiently large amount of overlap between individuals so that understanding is achieved. "Language community," then, is an abstraction in the same way "species

population" is. Both are composed of individuals that have properties such that a coherency is given to the group that does not disappear with the removal of any one of the individuals. In the linguistic case, language is the process that provides this coherency; thus, it is distinct from the second process occurring during conversations. The second process, the exchange of messages, or communication, is one that influences the direction which any given conversation takes. One idea, thought, or sentence follows another in some orderly fashion, which could be subjected to rigorous scientific investigation. But such an ordering or "trajectory" of a conversation is closely connected with the past histories, interests, and psychological states of the participants. Moreover, any particular discourse or conversation ends with the termination of communication between two individuals. Thus, the distinction I want to make here is that when any actual discursive interaction is observed between two or more humans there are two different types of processes occurring; the communication and the language use. The two are obviously connected in some way, but that does not prohibit them from being fruitfully studied by independent means.

This distinction can be applied to other aspects of the natural world if the criterion of application can be generalized. I shall say that the distinction between "language" and "communication" can be applied to any object that comprises a collection of unique systems, the parts of which are elements of classes.

Here the word "system" is being used in the sense of any collection of parts that possess interrelations. The key to this criterion is the uniqueness of systems and the ordering of the elements into an hierarchy of classes. The distinction, thus, applies to almost every "natural system" (sensu Laszlo, 1972, p. 30) provided that the uniqueness of its constitutive systems and their hierarchical organization are maintained. For example, a natural language (I claim) is an object comprising a collection of unique sentences. These are composed of elements (letters, sounds, words) that are hierarchically grouped. Sounds are grouped into words, words into grammatical categories (verbs, nouns, adjectives), grammatical categories into phrases, and phrases into sentences. Similarly, to preview an argument that follows, the class of ecosystems comprises a collection of unique ecosystems. These are composed of environmental features and the utilization of those features by species. The environmental requirements of species can be grouped into the requirements of particular activities, the activities can be grouped into activities at different developmental stages, and the stages can be grouped into species. These two examples show that both the actual use of sentences in conversations (i. e., communication) and the actual existence of ecosystems allow an observer of these phenomena to distinguish "language" and "communication."

Given this distinction, the next step in the analysis is to examine the characteristics of a theory of a "language" and a theory of "communication. " A theory of a "language" is a theory of those elements and their relations required for any arbitrary system of elements and relations to be categorized as an "s-system, " where an s-system is some specified class of systems. An s-system, then, can be such things as "grammatically acceptable English sentence, " "biological species, " "ecosystem, " or "temporal ecocline. " Thus, the definition states that a theory of a "language" provides the necessary and sufficient conditions for an object to be categorized as an s-system. For example, a model of English (Chomsky, 1965) states that it is necessary for a grammatical English sentence to have a "noun phrase" and a "predicate phrase"; the sufficiency conditions are contained in the remaining rules of the grammar. A theory of a "communication" is a theory of the behavior in physical time or space of one or more s-systems. Such a theory must assume the existence of an s-system, assume that it has certain properties, and use these assumptions to explain certain spatial or temporal behavior that the s-system manifests. For example, a model of two humans conversing would assume the existence of two objects that speak grammatical English, assume they have certain properties (e. g., interests, psycho-physiological states, vocabularies, and so on) and that "ideal" conversations obey a particular dynamic law or equation.

These dynamic laws might take the form: "If Smith is of psychological class A and Jones of class B, then the probability that the topic of their conversation will be Q is p." From this the theory would deduce how a particular conversation would proceed, given some initial conditions.

In adopting the distinction between "language" and "communication" I am disregarding the classical distinction of Chomsky (1957, 1965), separating "competence" and "performance." This distinction is intended to reflect the difference between what a native speaker knows (intuitively, perhaps) about acceptable and unacceptable sentences and what that speaker does in actual conversational encounters with other native speakers. There are several justifications for a departure from this fundamental distinction. One of these is that Chomsky's distinction suggests that both competence models and performance models are models of the same thing: a language user. In fact, however, the literature on the nature of language suggests that language is distinct from the user. For instance, Chomsky (1965, p. 9) writes that "a generative grammar is not a model for a speaker or hearer." And this is particularly evident when one examines a grammar for a natural language such as English. Such a grammar has no need for a human actor whatsoever; it comprises nothing more than disembodied instructions, much like a computer program. A further justification is that my interest in any

such distinction is to provide one that may be applied to many different systems. The notion of competence seems particularly difficult to apply to systems not involving humans.

I also reject the notion that a speaker's competence represents an idealization of that speaker's performance. I maintain, instead, that there is a continuum of "language" models and "communication" models extending from those that are highly ideal and abstract to those less so. This conceptualization lends support to my distinction since it is possible to create idealized "communication" models that are not "language" models. An idealization of the former would make such assumptions as: perfect memory, simple psycho-physiological states, and noise-free communication channels. These are assumptions that would appear in no models of "language." The relevance of this distinction to ecology and the idealized models in ecology will be explored later.

To represent symbolically and publicly natural phenomena is to map the structure of facts onto the structure of a language (Wartofsky, 1968, p. 133). Whether or not the phenomena are viewed as "language" or "communication" the fact remains that the public, representing languages are not like a blank, neutral blackboard on which the results of scientific observation may be written. Any language, or system of axioms (Nagel, 1961, p. 91), influences and filters the observations that can be made public. Thus, the question can arise

as to whether or not any particular language or model is adequate to faithfully represent the systems we observe. The primary difficulty in investigating this problem is that, since one's representations are biased by one's language, there is no neutral statement of the observed system that may be used to establish criteria for a "faithful representation." At best, it seems, one may propose alternative linguistic representations and check these, not against the precise conceptual structures (Gutting, 1973) of another linguistic representation, but against the imprecise conceptual framework of the patterns that comprise the science. Once such a comparison is made, however, two broad categories of criteria can be examined; observational adequacy and descriptive adequacy.

Observational adequacy refers to a language's ability to represent the activity of a system which an observer counts as the system's output. Descriptive adequacy refers to a language's ability to mimic the operations and mechanisms of the system in producing the observed output. For example, if the patterns of the science possess a collection of unique individuals, or class of individuals, such as chemical elements or organic species, then the observational adequacy criterion requires that the language represent all of these individuals. The descriptive adequacy criterion requires that the manner in which the language represents the individuals and their interactions be similar to the perceived patterns of the individuals and their

interactions. In this way an observationally adequate language covers the complete range of concepts and a descriptively adequate language reflects the operations and interrelationships of the entities to which the concepts apply. Both these criteria will appear later when the infinite capacity of ecosystems and the activities of species are discussed.

Automaticity

Thus far we have seen "pattern" as a component of what Gutting (1973) refers to as a science's conceptual framework, an imprecise aspect of conceptual systems. Further, I developed the importance of "language" to scientific activity both as its relation to pattern recognition and as a means of providing an imprecise framework encompassing more explicit, and precise structures. The representing language, through its own patterns, structures, and constraints, was presented as a broad, vague model that contained narrower, more precise models. Precision, and its correlated attribute of falsifiability, can be increased by making pattern recognition automatic. That is to say, conceptual frameworks can be given public and precise structure by investing the framework with "automaticity." Automaticity is defined as the tendency among scientists to favor methods or procedures of those processes (observation, explanation, theory) that reduce the role that individual scientists, as humans, play.

Automaticity may operate on all areas and levels of conceptual systems. It reduces a dependency upon human beings to make intuitive and non-explicit decisions that occur (a) during any particular explanation of a particular phenomenon and (b) with respect to questions relating to proposed theoretical and methodological procedures.

There are two separate aspects of automaticity: (a) the automatic categorization of individuals and relations into classes and (b) the acceptance of rules that dictate how such categorizations may be effected and automated. Categorizing individuals and relations can be viewed as a three step process. First, a finite set of measurements is made on some object O. Second, these measurements are classified so that a list of features (which could be just the measurements) is associated with O. For example, the temperature of bath water can be measured with a thermometer and the resulting numerical value classified as either "hot" or "cold." Third, the complete set of features are compared to some categorical framework. That is, categories are defined or specified by lists of features. A particular object O can be placed in a category by (a) matching its set of features with the categorical framework or (b) by using a rule that relates a particular set of features with a category. Since an object is considered to be an abstract entity it need not be composed of elemental units (say, atoms), so it follows that categories may

themselves be categorized and an hierarchical framework results.

Categorization may be made automatic in any of a number of ways. One important means is to provide instruments and machines to take samples and make measurements. For example, measurements of the visual range of electromagnetic radiation can be made by eye (which involves assigning color-names) or by a machine that converts radiation into electron flow. Further automation can be achieved by eliminating the feature classifications such as "hot" or "red." Thus, an observer can automatically measure radiation-induced electron flows and automatically (i. e. , without recourse to a humanly defined framework) categorize these measures as belonging to some category. A third way of automating the categorization process is by providing theories and models that can group either features or measurements according to the structure of the models. For example, if we entertain the Bohr model of the hydrogen atom, then it automatically classifies electrons as an example of those objects that possess elliptical orbits. The model works automatically because, by definition, a model assigns features (or measurements) of one class of objects to another class of objects. A model, like a language, maps one structure onto another structure. And because of the hierarchical nature of the categorization process this model of automated categorization also applies to systems of models and laws, i. e. , theories. The automation also applies to dynamic models such

as those used extensively in ecology and referred to as "ecosystem models." Under my interpretation a dynamic model is said to explain a natural system because the model's output is an automatic response of a particular model structure that supposedly bears a close resemblance to the structure of the natural system. Later I shall discuss the role that dynamic models play in an automatic account of ecological systems and present another class of automatic models that categorize ecological systems.

In addition to categorizing individuals the scientific activity also provides rules for the creation of these automatic categorization procedures. The rules specify conditions that automation must meet and generally exist independently of scientific change. Although the actualization of the rules (i. e., the automations and the categories themselves) clearly change during scientific upheaval, the justification for alternative categorical frameworks must proceed along certain established rules. It is perhaps true that Kepler and Brahe saw (i. e., categorized) the dawn in different ways and it might further be true that their separate categorizations suggested to them different questions, experimental and theoretical techniques, and so on. But this does not force us to conclude that either one or the other of them was any the less of a scientist for the variance of their categories. The fact remains that they could both justify their procedures by appeal to the same rules that guide the formulation of their respective categorical frameworks.

The nature of these rules, or "founding intentions" as Gutting (1973, p. 226) calls them, is difficult to ascertain for they correspond, in part, to the heuristic, intuitive judgments made by scientists. Gutting places among these rules: public languages, precision, and empirical verification. Automaticity seems to be another rule that guides the formation of conceptual systems. The application of technology can be a major source of automation. But this alone is not sufficient for the acceptability of an automation procedure. A clear example of this is the almost universal skepticism that is met by attempts to apply lie-detection technology to plants. In part this skepticism resides in the absence of any reasonable mechanism to account for a plant's supposed perception of visual and verbal signals. And it is not so much that to date there has been proposed no satisfactory mechanisms, but rather that any mechanism of plant perception will violate or contradict already established categorical frameworks of plant mechanisms. To measure plant response to visual stimuli implies a model that categorizes plants into mutually contradictory categories, viz., the class of objects responding to visual stimuli and the class of objects possessing no nervous system.

The resulting picture is a conceptual system that categorizes plants into the class of objects without nervous systems and the class of objects that have mechanistic explanations of their responses to visible clues. This situation is a contradictory one. In order to

alleviate the contradiction either plants must not be classed as (a) responding to visible clues, (b) possessing no nervous system, or (c) having a mechanistic explanation of its responses. Since modern biology makes it very difficult to choose alternatives (b) or (c), the hypothesis that the response of plants to visible clues can be measured with a lie-detector is held to be very weak.

Thus, since theories provide a mechanism for the automation of categorization, many of the constraints placed upon the rules that govern this automation relate to currently held beliefs about the forms that adequate and satisfactory theories and explanations may take. One such belief is the importance attributed to mechanistic or causal explanation, a belief that gained scientific stimulation from Newton and his immediate predecessors (Burt, 1954). The pre-eminence of these beliefs and their application to living systems, as it is reflected in biology's methodological and theoretical procedures, is the primary reason for a categorical framework that excludes the validity of results obtained by applying lie-detectors to plants. It also accounts for the theoretical analysis of ecological systems in terms of the mathematical language of differential or difference equations, for this is essentially the language of physics and, particularly, mechanics. Such an analysis is required not only by the development of ecosystem models (e. g. , Patten, 1971) but also by the theories being created in the name of "evolutionary ecology" (e. g. , Mac Arthur, 1969, 1970;

May and MacArthur, 1972). A difficulty thus arises when a theoretical analysis is espoused in languages other than that of physics, as is the case in the present thesis. This difficulty is so grave that it allows the explanatory power of other languages to be questioned, as occurred in a recent exchange between Chomsky (1970) and Black (1970). Similar objections can be raised in response to the models proposed in this thesis and a certain amount of space in the discussion section must be devoted to meeting those arguments.

Ecological Applications: Pattern, Language, and Automaticity in Ecology

The previous section has provided the philosophical foundations I shall need to undertake a meaningful conceptual analysis of ecology. It has revealed some components of scientific conceptual systems. These components I discussed under the headings: pattern recognition, language, and automaticity. They form the constraints placed upon any attempts to formulate a theory of ecological succession. That is, the construction of a theory of ecological succession requires that the theory take into account the explanatory and empirical patterns perceived by ecologists, the languages they use to model those patterns, and the extent to which the models are automatic. The task now facing us is to perform the conceptual analysis. In order to avoid confusion stemming from semantic ambiguities I will, first, provide definitions of important terms.

When we speak of ecological succession or development we are referring to the development or change in time of an ecological system comprising plants, animals, and an abiotic environment. A problem arises with respect to an appropriate name to call such an ecological system. There is a problem because the expression "the development of x" could mean either of two things. It could mean that there exists a well-defined object x which develops into another well-defined object y. In other words, it could mean that x, y, z, and so on, refer to the developmental stages of an ongoing process, as is the case when we say "the 12-hour chick develops into the 14-hour chick." On the other hand, "the development of x" could mean that x is the abstract object which develops, as when we say "the development of the chicken." Accordingly, both chickens and chicks "develop" and this is a source of confusion when we wish to speak of ecological succession.

Basically, the problem is whether to use "ecosystem" as a concept applying at a point in time analogous to "12-hour chick" or as an abstract concept that refers to all of the stages in the developmental process. Unfortunately, not only is the ecological literature unresolved with respect to this question but certain authors discuss the concept in confusing, ambiguous, and even self-contradictory language. Rather than untangle these semantic webs I will merely define explicitly my terminology.

- community: a set, or listing, of the taxonomic species present in some specified region of space and time, inclusive of both plants and animals. Thus, the concept applies to a point in time, one stage of an ecological succession. The set of species may be represented as an unordered listing, as a two-dimensional listing plus arrows connecting species indicating functional interrelations (with quantification, such as energy units, optional), or as idealized, profile-drawings of plants.
- habitat: a set of physical and chemical factors or conditions (e. g. , temperature, carbon dioxide, mean energy input rate, etc.) present in some specified region of space and time. This concept refers to the abiotic environment of the community, thus, it too applies to one stage in an ecological succession. Habitats are usually represented in the form of data graphs, with the magnitude of the habitat factor (e. g. , temperature) plotted against time or space.
- ecosystem: the union of the representations of the community and the habitat for a common region of space and time, where the "short-run" interactions between the community and the habitat are represented (e. g. , nutrient cycling). 'Ecosystem', then, refers to all biotic and abiotic aspects of one stage in an ecological succession.
- succession: a temporal sequence or series of ecosystems. It can be characterized by a combined alteration of the community and the habitat, that is, by an addition and/or deletion of species and habitat factors, over time.

This choice of definitions is motivated by virtue of the fact that it is consonant, I believe, with an already existing body of literature (e. g. , Clements, 1928; Emlen, 1973; Odum, 1959, 1969; Weaver and Clements, 1929; Whittaker, 1970). The terminology does not explicitly

define any object as being the set of all developmental stages through which the object passes in its development. This is not to say that no such ecological concept exists, but only that none of the above defined terms symbolizes this concept. Whittaker (1970, p. 69) suggests a convenient term when he writes of succession as an "ecocline in time," where an ecocline is a collection of ecosystems arranged continuously along some environmental gradient (e. g., soil moisture). Thus, a succession of ecosystems is a collection of ecosystems arranged continuously along a "time gradient." To distinguish ecoclines in time from other ecoclines I suggest using the term temporal ecocline to symbolize the ecological object that comprises a series of developmental stages. Thus, "temporal ecocline development" means the ecological development of one entity composed of several stages, and is analogous to "chicken development." "Ecosystem development" means the development, or change, of one stage of a temporal ecocline.

In addition to the definition of these ecological "objects" I will require a statement of the fundamental problem that I will attempt to solve. It is not enough to propose a "theory of succession," for this in no way relates to any expressed goals of ecology. I shall assume that the primary goal of ecology is to explain the distribution and abundance of plants and animals (Andrewartha and Birch, 1954; Cody, 1974; Krebs, 1972; Macfadyen, 1963). I acknowledge, however, two

levels from which this problem may be asked. The classical approach is to determine the environmental tolerances and physiological limits of individuals and relate this to the success of the population at a given place and time. A more recent approach attempts to relate the ability of a population to compete at a place and time to its evolved characteristics (Colinvaux, 1973). One approach studies the individual; the other studies populations, although overlap occurs. In both perspectives the goal is to relate features of the environment to the presence and abundance of species. And this is what I take to be the problem of constructing a "theory of succession": providing a mechanism that will map, or relate as does a mathematical function a representation of the environment onto a representation of a species list. In this thesis I will not attempt to further relate a species list (community) to the numbers of individuals in those species, as the problem of abundance demands. Instead, I will be concerned only with the presence or absence of species, where "presence" will have the criterion that the species could survive and reproduce (but may or may not be actually, or developmentally, capable of reproducing at the time a species's presence is noted). The problem of abundance is very difficult and outside the confines of this discussion; its importance, however, should not be disapprobated as a result of this.

Any solution to this problem of mapping environmental features onto species lists must do so in ways that adequately reflect the

conceptual systems of ecologists. I turn now to a discussion of the components of those systems: pattern, language, and automaticity.

Pattern in Ecology

'Species' form one of the most important classes of ecological structural pattern. The term, however, has essentially two different meanings. First is the taxonomic meaning that is applied to populations when they are considered as "operational taxonomic units" (OTUs). This entity is characterized as a class of individuals bearing certain morphological, reproductive, and phylogenetic relationships to one another. All three of these relations are often needed in defining an OTU because often there are important morphological differences between sexes and often many species do not reproduce by interchanging genetic material between individuals. This view differs from a typological conceptualization of species (Mayr, 1963) but nevertheless holds species to be essentially non-active (but not unchanging) physical objects, that do not interact with either other species or a physical environment. In contrast is an ecological approach that conceives of species as an abstraction of living populations. Such populations and their individual members interact with their environment by performing certain activities such as feeding, growth, respiration, reproduction, and so on. Species in the ecological view maintain their distinctiveness by virtue of the difference in

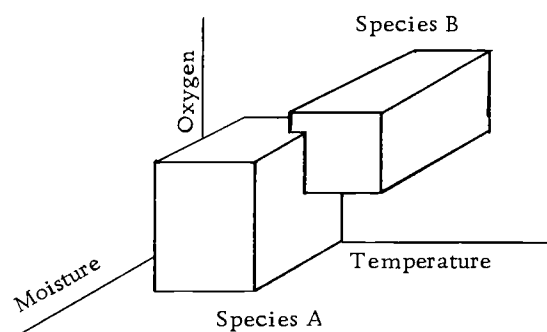
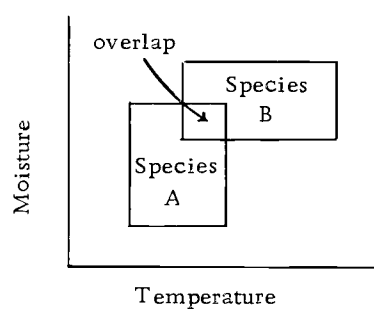
their activities and environments. This meaning of species contains the necessary concepts for an explicit description of how selection acts upon the set of activities and environmental requirements that define a particular species. When a species possesses such a particular set of activities and environments it is said to possess a "strategy." Strategies in species, as in games, either benefit or hinder their players and this has led some biologists (Lewontin, 1961; Slobodkin, 1964) to explicitly present the process of evolution as a problem to be solved by a species's play of an adaptive strategy. The taxonomic and ecological views of species are connected, as the literature relating body size to foraging efficiency or energy conservation or the ability to avoid predators aptly attests. But there is no routine, formal procedure to connect the required activities of a particular adaptive strategy with the morphological features necessary to achieve those activities. This non-automatic shortcoming in the current concept of species is one I hope to rectify.

Closely associated with the ecological notion of species is the concept of niche. Most of what has been recently written on this subject is based on Hutchinson (1958). In this view a fundamental niche is a set of points, each point representing a combination of values of environmental variables (e. g. , temperature, moisture, etc.), such that at each point in the set the species in question can survive and reproduce. Since there can be any number of

environmental variables and each variable is associated with an axis in a cartesian coordinate system, a fundamental niche is a "hyper-volume." Excluded from the set of possible environmental variables are the population densities of the competing species (Hutchinson, 1965, p. 32). When these are taken into consideration the potential for a species to survive and reproduce is diminished. This reduced set of points in the hyper-volume is called the realized niche (Hutchinson, 1958, p. 418; 1965, p. 32). Since any given species may meet many different species of competitors, there exist many different realized niches, all contained within the fundamental niche. Emlen (1973, p. 210 ff) has modified this conceptualization to permit the hyper-volume to include competing species. This he does by defining a continuous measure of success (fitness) at each combination of values of all environmental variables. Emlen's realized niche is defined as a small region of the hyper-volume surrounding the average fitness of a local population. He defines a species's fundamental niche to be the set union of the realized niches for all local populations. Both the Hutchinsonian view and Emlen's modification of it are presented in Figure 1.

The advantages of these conceptualizations are very numerous. By presenting the niche in a geometric setting it becomes easily pictured, at least at low numbers of dimensions. This picturability elicits suggestive and productive theoretical metaphors such as the

(a)



(b)

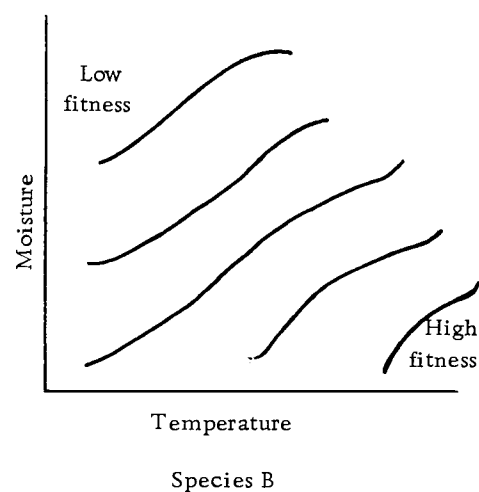
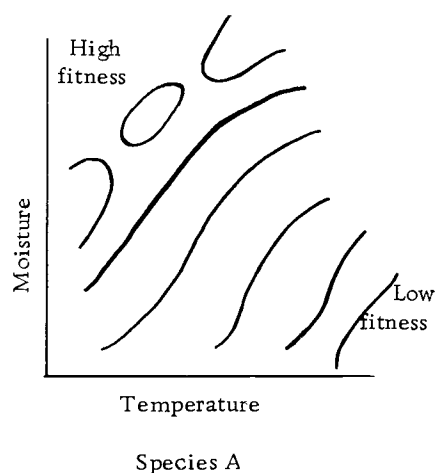


Figure 1. Two current views of the niche. (a) An example of the Hutchinsonian niche in two and three dimensions. The enclosed spaces indicate the values of the environmental variables at which species A and B can survive and reproduce. Niche overlap is shown as areas of intersection. (b) An example, in two dimensions, of Emlen's modification. Since the adaptive surfaces (represented by contours of fitness values) are unique to species, no overlap can occur. Fitness is measured by the relative change in offspring from one generation to its successor. (After Emlen, 1973)

"size" of niches (e. g. , niche width), the "intersection" of niches (e. g. , niche overlap), and the relative "positioning" of many niches (e. g. , niche or species packing).

Despite its productivity, there exist many disadvantages to a geometric representation of the niche. The concept is ambiguous as to whether it applies to individuals, populations, or species; the concept is sometimes applied interchangeably to all three (as in Emlen, 1973, and Maguire, 1973). It also treats only one moment in time, thus excluding a representation of niche changes occurring during the ontogeny of individuals within the species. Moreover, the niche becomes difficult to picture and manipulate mathematically when more than two or three variables are taken into consideration. It also assumes that all of the relevant aspects that define a niche can be represented as linearly independent coordinate axes. Since the aspects of the niche are represented as metric values of a variable, the representation of a species that has requirements spanning very large intervals (of temperature, for example) requires just as much information or specification as a species with small variable requirements. Thus, the geometric view requires as much information to represent an indiscriminant species as a highly selective one. And yet, the intuitive feeling concerning an indiscriminant species is that it must receive much less information from its environment than does a discriminating species in order to make a decision about the

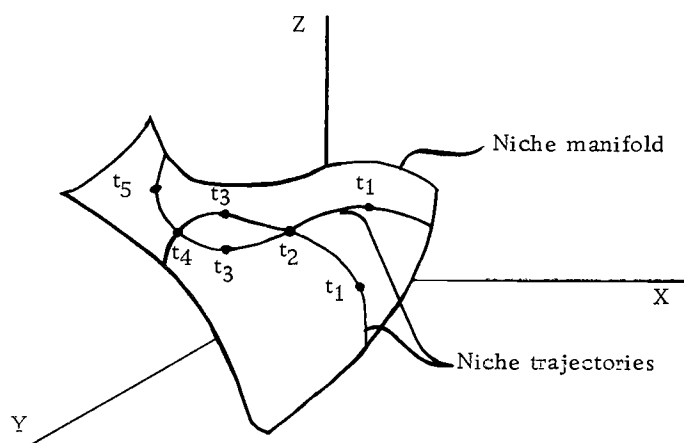
suitability of that environment. Hence, the Hutchinsonian representation of a niche does not incorporate one of the patterns that ecologists perceive in niches. A way to avoid this is to provide a representation of the niche based on an hierarchical decomposition; below I will detail how such a representation might be designed. The geometric niche concept also fails to provide a mechanism whereby the dimensions of the niche are related to the activities of the individuals of the population. Part of the idea that species possess an adaptive strategy is that the performance of a particular activity requires certain environmental features. A species becomes adapted to a particular environment because the strategic activities its individuals perform require, for their completion, the features present in the particular environment. The geometric representation does not indicate this. Furthermore, Emlen's account assumes that each species has one and only one set of success measures (adaptive surfaces, Emlen, 1973, p. 211). This means that either every individual of the species has an identical adaptive surface, or there exists, for each species, an "average" adaptive surface to which all individuals may be related. Both alternatives violate Emlen's earlier (1973, p. 12) definition of fitness.

Because of my need for clarity on these issues I will present a reformulation of the niche concept. What follows is a synthesis of Emlen (1973), Maguire (1973), and Mason and Langenheim (1957).

Assume that the environment of an individual can be represented by some set of features, not necessarily described as a coordinate system. I define an individual's niche trajectory as the locus of environmental features that are required by that individual in order to develop, survive at each developmental stage, and reproduce (including some quantitative measure of reproduction, e.g., number of offspring). Since individuals possess plasticity with respect to their requirements (e.g., alternative developmental stages, different temperature ranges, optional behavior, etc.) an individual may possess more than one trajectory. Therefore, I further define an individual's niche manifold as the bounded set of niche trajectories, for that specified individual. In Figure 2a, a niche manifold and two niche trajectories on that manifold are represented as a continuous surface and two continuous, intersecting lines. This pictorial representation is not a requirement of the definitions; later I will give a radically different method of description from linguistics. The set of all niche manifolds of a population of individuals is the niche of the population; it is given in Figure 2b.

At every instant in time every individual in the population is "on" a niche trajectory. Different trajectories correspond to different sequential sets of environmental features. As these features change in time (due to random fluctuation, perhaps) individuals "follow" these changes by "moving" over their niche manifolds. This

(a)



(b)

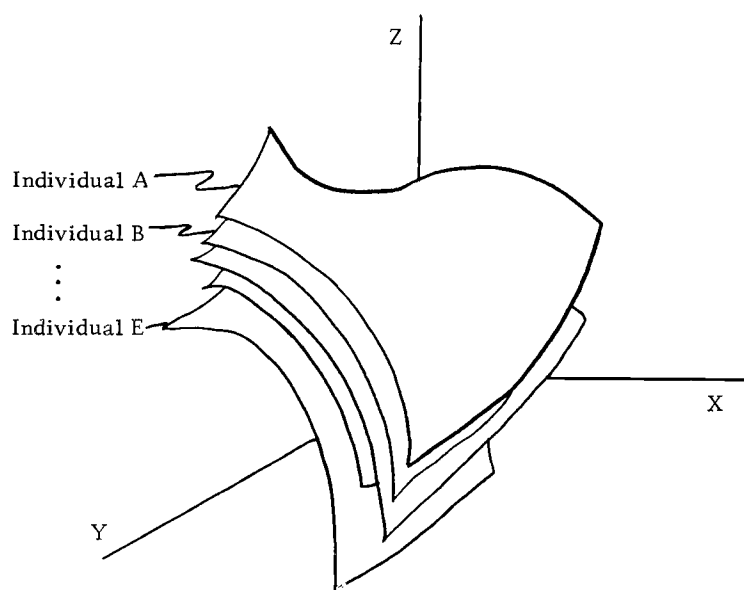


Figure 2. A reformulation of the geometric representation of the niche. (a) The niche manifold of an individual composed of all possible niche trajectories, with two particular trajectories indicated. Arbitrary time designations are specified by labeled points along the trajectories. Environmental features X, Y, and Z are arbitrary. (b) The collected niche manifolds of a population of five individuals representing the niche of the population.

process defines their trajectories. If the environmental features change to a "point" not on an individual manifold, then the trajectory ends and the individual is no longer a member of the reproducing population. If one were to follow a trajectory through time its "shape" would depend upon the niche manifold (i. e. , upon the individual's genome) and upon the fluctuations of the environmental features that the trajectory followed. Environmental features may be both biotic and abiotic factors, including competitors as well as non-competitors. Thus, niche manifolds are defined over all environmental features including a description of competitors. Considered as a coordinate system the manifold is defined over (say) the density of a competing population, just as it is for temperature; at some density of competitors the manifold of an individual ends. If the environment of an individual changes such that the density of competitors increases beyond the edge of the manifold, then that individual has failed to survive and reproduce because of competition (ceteris paribus). If the niche of the population (i. e. , the set of all niche manifolds) is such that an increase in competitors extends beyond all manifolds, then the population is said to be "out competed" by its competitors.

In this reformulation there is no such thing as a "realized niche." There is only a collection of "potential environmental features" (i. e. , a collection of niche manifolds), and a set of particular trajectories on those manifolds. If the set of all local

populations are grouped together as a "species," then it is possible to define the "fundamental niche" as a "collection of a collection of niche manifolds." But this latter concept is of little utility, since most of the interesting problems in ecology concern either the structure of individual manifolds, or the evolution of this structure. Indeed, one of the major problems of this thesis is to provide a representation of this structure which can interface with a procedure that maps environmental features onto species lists. This requires, however, that I assume that every niche manifold in a population is identical, i. e., that there are no genetic differences among individuals. My purpose in criticizing the geometric view of 'niche' is to illustrate that it presents inadequate structure to solve the "mapping" problem I have defined. An adequate representation must show how particular environmental features restrict the manifold. This requires a procedure that relates environmental features to niche trajectories. In other words, I require a procedure that specifies the structure of the idealized manifold by defining the possible niche trajectories of an idealized individual of a species.

Although Hutchinson's view of the niche fails to incorporate certain kinds of organismic and ecological information, this is not to say that such information is completely missing from the patterns ecologists perceive. The concept of "structure," both organizational and physical, subsumes some of this remaining information.

Organizational structure refers to the usual levels of biological organization, i. e. , organism, population, community, and biosphere. These elements are levels of organization because they form a whole/part relationship with one another. Even though Mesarovic, Macko, and Takahara (1970) have produced an abstract, formal treatment of hierarchical systems there still remains substantial difficulties in the construction of particular hierarchical systems such as ecosystems. Since succession has been characterized earlier as a sequence of ecosystems the difficulties of construction must be considered explicitly.

Another structural pattern that has an important impact on modern empirical and theoretical accounts in ecology is physical structure. Physical structure is a concept that applies to all levels of biological organization. As a result, a general definition that may have several interpretations will be most useful. Thus, I define physical structure to be the arrangement of certain elementary or atomistic physical units into observable patterns. On the level of the individual organism, physical structure is morphology. A particular morphology is a particular arrangement of such elementary units as tissues, appendages, leaves, and so on. Chemical compounds that are produced by many plants and animals also constitute an aspect of physical structure. Furthermore, size, when measured on a fixed scale, is an elementary characteristic that is relevant to

morphological structure. On higher levels of biological organization, such as populations and communities, physical structure is referred to as "physiognomy." Physiognomy is the patterned arrangement of elementary units constituting canopy height, cover density, number and characteristics of vegetative layers, and so on. Although physiognomy is not conceptually restricted to either plant or animal populations or communities, it has historically been applied almost exclusively to vegetation. The only possible exception to this is the use of 'density' with respect to animal populations, but this is not used in the same way that 'percent cover' or other similar vegetative physiognomic descriptions are used.

There is an ecological interest not only in the description of particular structures but also in the placement of particular elementary units over some area of space or duration of time. That is, it is often of interest to know, for example, how frequently a certain vegetative layer occurs in time or space. When this is done the problem is said to center around the "patchiness" of some specified elementary unit. Patches, although rarely defined exactly, are thought to be physically recognizable objects composed of either one or more elementary units. They have the property of being either coarse-grained or fine-grained, which is defined relative to the use such a patch receives from a particular species. By the definition of MacArthur and Levins (1964), a coarse-grained use of a patch occurs

when that patch is selected from several possible patches and a fine-grained use is one in which the patches are not discriminately selected, but only used as they are encountered in the environment. Although the importance of this distinction and the general concept of structure cannot be denied, at present there is no formal way of representing a niche as either coarse-grained or fine-grained in terms of the actual elementary units themselves. Nor is there a formal procedure that represents an environment of a species in a way consonant with the notion of physical structure, patches, and relative patch use.

Besides the previous set of patterns based on static objects or "elements" there are also patterns that emerge from an analysis of relations between elements. These relational patterns are mainly concerned with (a) the biotic-biotic interrelationships, and (b) the biotic-abiotic interrelationships. Relational patterns emerging from the interaction of two biological systems are exemplified by competition, predation, symbiosis, and the creation of niches by the use of environmental factors. Niches can be created or elaborated (Whittaker and Woodwell, 1972) by the vegetational structure that plants must produce in order to fill the niches that they do. Vegetation provides not only a food source but also other aspects of a niche such as nesting sites, burrowing sites, and so on. Similar remarks can be extended to animals as well; thus, in part, to fill a niche is to

create a niche. Competition effects also comprise important biotic-biotic patterns. They are typified by species packing (MacArthur, 1972), the Paine conjecture (Paine, 1966), and niche shifts (Diamond, 1973). In brief, they are those effects on species that are a result of other species being present (or absent) in the environment. Predation is another relational pattern that has not only the subtle effects of altering competitive outcomes (Paine, 1966), but also the obvious effect of utilizing a niche that has been created by some other species. Predation will be used in this discussion in the broad usage that includes uptake of light and nutrients, herbivory, carnivory, and saprotrophy. A final biotic-biotic relation of importance is symbiosis. A definition that will be important to this discussion is that a symbiotic relation is one in which habitat requirements are a two-way relation between two species. That is, the niche created by both species forms the niche requirements for both species, unlike, for example, predation, which is a one-way relation.

There are, however, relational patterns arising from the interaction of a biological system and an abiotic system. One of these patterns I have already mentioned. The view is that a species fills a niche; a niche being "empty," in some sense, until a species "occupies" those functions and habitat features already present in the environment. Recently, Darlington (1972) has questioned this position by suggesting that merely because an ecologist can successfully

introduce or extend the range of a species does not imply that previously those factors of the niche of the introduced species were unused. They could easily have been used by microorganisms, Darlington claims, their use having merely escaped the observer. The final relational pattern of interest to us concerns the effect of occupying a niche on the abiotic system. A classical example of this is shading by vegetation, which affects light, temperature, moisture, and so on, near the plant. These types of relationships are very important to the problem of succession, in part because they are important in mediating the outcomes of competitive interactions.

I have tried briefly to outline and define some of the major patterns or conceptualizations predominant in ecology today. Those that I have chosen to enunciate are by no means exhaustive of all of those available. Still, much of ecological research can be reduced to an analysis of the problems raised by one or more of these patterns. As I explained earlier, I have excluded all explicit mention of the effects of population numbers or density on any of these patterns, with the exception of physiognomy. I have, in addition, omitted any reference to the genetic constitution of a population. Thus, I have excluded any reference to such topics as polymorphisms, genetic variability, fitness sets, or any other subject of population genetics. The questions of population genetics and the broader questions concerning the evolution and creation of species are also outside the

scope of this discussion. This is so not merely because of the complexities that those questions raise, but also because they center around issues beyond the range of applicability of the evaluation criterion of descriptive adequacy. The problems associated with the genetic structure of a population and its congenors relate to a much more powerful criterion for the evaluation of models which I call "explanatory adequacy" (after Chomsky, 1965), and discuss briefly in the Discussion section. In any event, the claim is made that with the exception of these two areas of research, plus perhaps a few others, the patterns that I have sketched provide a broad delineation of the task facing any descriptively adequate model of ecological succession. But in order for a model to be scientifically satisfying it must be presented in a publicly intelligible language. The character of such a language will be influenced by whether or not the pattern of the science is viewed as "language" or "communication." Furthermore, the utility of the language and its models will be determined by both its observational and descriptive adequacy. These topics will be discussed below.

Language in Ecology

Most current theoretical and empirical treatments of ecological phenomena seem to be undertaken from the perspective that such phenomena represent "communication," and not "language," resulting

from the interaction of ecological systems. The basis for this evaluation stems from a consideration of the natures of a theory of a "language" and a theory of "communication," in an abstract sense.

Difficulties of the two approaches are that a theory of "languages" cannot, without external boundary conditions, describe the spatial or temporal behavior of those systems that use the "language" and a theory of "communication" cannot guarantee that its assumptions about its s-system contain the necessary and sufficient conditions. This situation holds in ecology. For example, ecosystem compartment models are clearly an example of a theory of "communication." A set of compartments is assumed, the compartments are assumed to have certain transfer properties which are represented by differential equations, and the temporal behavior of these s-systems is deduced by numerical solution. Another example of the study of "communication" is from competition theory, particularly that analysis espoused by MacArthur (1972). Here, the s-system is a system of biological species competing for limiting resources. The species are assumed to have certain abilities to utilize the resource and the models examine the temporal behavior of the system of species at equilibrium to determine which can co-exist. A similar example of a theory of "communication" in ecology is the theory of island biogeography (MacArthur and Wilson, 1967). There does not, however, appear to be in ecology a formalized theory of "languages" and

the development of such a theory is a major concern of this thesis. Such a theory will attempt to approach the problem of supplying necessary and sufficient conditions for "species, " "ecosystem, " and "temporal ecoclines. "

Whether or not one approaches ecology as "language" or "communication, " the representation of the systems must be embedded in some language and this language can be evaluated in terms of its observational and descriptive adequacy with respect to the patterns of ecology. The languages chosen by most ecologists rest largely on the fact that their concern is with "communication. " Thus, differential equations that are functions of time or space are used very frequently. This reliance on differential (or difference) equations places constraints on the observational adequacy of the models. Most systems of differential equations map the value of a "state-variable" (e. g., plant biomass) onto a time axis. Thus, the models can only "discuss" those objects representable by time varying measurements and can only discuss them in the detail provided by the model. Accordingly, models embedded in the language of physics, as are differential equations, can only abstract the systems of study by simplifying the models. This is done by assuming linear equations, ignoring unimportant factors, and so on. This process guarantees that any particular model will not be adequate to completely represent a system. But clearly this is not to say that such languages and

models will prove to be fruitless, non-explanatory, and non-predictive. The fulfillment of criteria for these characteristics is a separate methodological issue. Nevertheless, the fact that this approach has been successfully adopted by physics does not repudiate the possibility that other languages modeling the "language" aspect of ecological interactions, analogous to theoretical linguistics, will also prove to be fruitful. The evaluation of the models embedded in languages of this sort must and can explicitly approach the problem of adequacy (Chomsky, 1965, p. 24). This criterion includes not only the ability to represent the unique individuals of the science (observational adequacy), but also the ability to mimic their operation and interrelationships (descriptive adequacy). Thus, representation of unique individuals is the goal of languages that model the "language" aspect of natural interactions. And this is a goal that is not recognized as interesting, either by those that construct ecosystem compartment models or those that construct models of particular ecological interactions, for example, competition or foraging models.

A problem related to the considerations of the adequacy of a representing language is the extent to which the operations of the language mimic the behavior or operations of the s-system. For example, ecosystem compartment models that are evaluated on an analogue computer, where energy flow is analogous to electron flow, are descriptively adequate because of the similarities between the two

kinds of flows. But the language of electron flows restricts the class of problems that can be modeled. Thus, the ability of compartment models to mimic the process of the specification of a species's niche, or the way in which species are added to ecosystems, or the way temporal ecoclines develop is very low, since the ecological patterns of these processes do not suggest an analogy with the flow of any measurable quantity. But when these latter processes are viewed from the perspective of a "language," then models analogous to those of linguistics do allow a high degree of mimicry, as I shall try to demonstrate in later sections of this thesis.

Automaticity in Ecology

There is one remaining pattern of ecological s-system behavior that I wish to discuss and this is the obvious fact that such systems come into existence and operate without any need for human intervention. This is to say that the operation of systems like species or ecosystems is automatic. As a result, the operations of languages intended to represent these systems, if they are to mimic the behavior, must be automatic as well.

Earlier I stated that the perception of organized pattern was like speaking a language and I provided a discussion of the steps necessary to categorize observations. At that time I claimed that the mechanization of measuring was one way to automate this

categorization of organization. In ecology there has been no dearth of such mechanizations with the advent of remote sensing, or instruments to measure caloric values, and so on. But this has not pervaded all types of ecological observation. In particular, there is no automatic procedure for the user of the Zurich-Montpellier vegetation analysis to define "homogeneous stands." This lack of automation is one of the issues that separates this school from that of gradient analysis; the latter claiming that statistical bias enters if one tries to study homogeneous vegetation (Krebs, 1972; Shimwell, 1971). But, even gradient analysis requires a non-automatic choice of which gradients to measure; one does not attempt to correlate vegetation with every ecological factor.

Another method for automating categorization, I claimed, was the construction of models and theories. And this approach, as I have already indicated, is used extensively in modern ecology. There are several ways in which these models fail to be automatic. For example, in ecosystem compartment models the structure of the system is assumed. There are provided no automatic procedures to restrict which state variables must be modeled. There is a reliance on human intuition that any particular system of trophic levels, or functional units (McIntire, 1972), with any particular system of interaction functions, represents or corresponds to a natural ecosystem. This is reflected in the dissatisfaction that results from model validation by

the comparison of model outputs with empirical data. There exists no exterior checking procedures for validating the original, intuitively-derived model structure. This situation prompts students of these methodologies such as McIntire (1972) to write with regard to the construction of functional units in model ecosystems: ". . . the proper partitioning of these groups. . . is a difficult and messy problem." Or, in a different context, Vandermeer (1972, p. 110) has said: "What a 'natural' community is, how one recognizes one, etc., is difficult to say." Much of the lack of automaticity in these analyses stems from the absence of any automatic procedure for specifying the niches of species and how these species interact to form communities.

A final aspect of automaticity, I said above, was the specification of rules that govern the automation of categorization. The rules that now exist in ecology have resulted from a commitment to explanations couched in mechanistic or causal terms. This is due to the present emphasis placed in ecology on the analysis of "communication" and the success physics has achieved by discovering mechanistic equations of motion (Burt, 1954). Thus, compartment models attempt to account for the dynamic behavior of ecosystems by defining compartments whose contents are mechanistically related to the contents and dynamic equations of other compartments. Models of competition, based on the Hutchinsonian niche, try to relate the number of species present to the causal effects their mutual presence

has on the values of the parameters in an equation defining the growth of the populations. My belief is that these mechanistic rules for the deployment of ecological theories must be supplemented by similar rules that apply to the automatic analysis of ecological "language."

In summary, this analysis of the philosophical criteria of a fruitful ecological theory allows us to state more explicit criteria for an analysis of the "language" of ecological systems. The discussion of ecological automaticity revealed that the analysis must provide an automatic method, mechanical procedure, or algorithm that will create, build, or generate, in some sense, the ecosystems that constitute temporal ecoclines. Moreover, it must do this in ways that accurately reflect the patterns that ecologists perceive in temporal ecoclines.

A theory with these aims must be a finite device with infinite capacity. For the device to be finite means that it can complete a description of species and ecosystems by using a finite number of steps in a finite period of time. There are basically two reasons for this requirement. First, if the device is to be descriptively adequate is must represent the fact that organisms accomplish their activities, whatever they may be, in a finite period of time. Regardless of how long an 'organism's developmental sequence is, it never requires an infinite amount of time. Any organism requiring an infinite amount of time to complete a reproductive act will produce very few offspring.

The insertion of species into an ecosystem must also require only a finite period of time, otherwise it will never be possible to identify an ecosystem as a complete entity. The second reason for the device to be finite is because of the finite limitations of the users of such a device or theory. If a theory is to be understood by humans, then they must be capable of representing it, in some way, in a brain of finite extent.

The device must also have an infinite capacity. This means, in the present case, that the device has the capability to describe all species that have any finite number of developmental stages, and all ecosystems that are composed of any finite number of species. This assertion is maintained knowing there is a very high probability that every past, present, or future ecosystem on Earth has no more than (say) 100 million species. The point is that (a) this observation does not constitute an a priori argument, (b) there is no reason why the applicability of the method should be restricted to Earth, in which case the validity of empirical arguments are weakened, and (c) the empirical verification of the observation would be very difficult. The ability to compose ecosystems of any arbitrary, finite number of species is the meaning of "infinite capacity." The final constraint that we might want to place on any such automatic method is "universality." For any arbitrary method to be completely automatic it must work for every ecosystem, so that there is no intuition

required in deciding which method to apply to which ecosystem. If no such single method can be derived, then a secondary procedure must be designed which specifies which method to use. Thus, universality is a desirable goal for any automatic method or model of ecological succession.

In addition to generating finite lists of species, the automatic method must mimic the methods by which these lists are naturally produced. Species must be listed together either because they create niches for each other, or they cannot competitively exclude each other, or they are not excluded by the character of the physical habitat. More specifically, the discussion showed that one part of the device must represent species in some natural way that will allow them to be inserted into an ecosystem on the basis of their habitat requirements and competitive abilities. In accordance with the niche creation aspects of species, the device must also represent the morphological and behavioral properties of species. Both the habitat requirements and morphology of the species must be stored by the device under a unique characterization (e. g. , the Latin binomial) so that the species will be available to that part of the device that generates the ecosystem. This latter portion of the device must represent the "structure" of the ecosystem by representing the habitats that are available to be utilized by species. Thus, the ecosystem representation must relate to the species representation

in such a way that insertions can be made. Following the initial insertion the results of competitive interactions must be made, either as the deletion of some species or the alteration of the species involved by a process of niche shifts. Once all of these processes have been carried out a final portion of the device must alter the original habitat description on the basis of the effects those inserted species have on the environment. This procedure, when iterated a sufficient number of times, will effectively force the temporal ecocline through its component successional stages.

A device that has the above characteristics is to be considered as a calculus that can with rigor and precision examine and deduce the consequences of certain hypotheses about the nature of ecological systems. These hypotheses will be contained in the structure or mechanisms that are required of a device that will produce series of species lists. The hypotheses can be tested against the real world by comparing the output of the device with the species list of real ecosystems and by examining the mechanisms of the device to see to what extent they reflect or mimic such actual processes as niche specification, species insertion, and niche alteration.

II. METHODS FOR A LINGUISTIC ANALYSIS

Unfortunately, specifying the constraints that philosophy places upon a scientific theory does not uniquely specify the form that the theory must take in order for it to be scientifically satisfying. Philosophical constraints are too broad for this purpose, and further specification is needed. The first step I will take in this direction is, frankly, a metaphorical (and metaphysical) leap. The hypothesis is made that a device meeting the constraints stated in the Introduction can be constructed if ecological systems are treated as if they constituted a language. This hypothesis as stated is testable, of course, by simply displaying a device that meets those constraints. However, the ontological stance that ecological systems are languages is no more testable by any set of empirical data than is the similar stance that species are geometric volumes in an n -dimensional space. The problem is not one of truth or falsity, but the criteria: pattern, language, and automaticity. The fundamental claim being made here is that a language metaphor of ecological systems meets these criteria.

If we adopt this position, then the problem of constructing a theory of ecological succession will be related to the problem of constructing a theory of a language having the particular properties I have enunciated as constraints. A theory of a particular language

comprises a grammar of that language (Chomsky, 1957, p. 49), unlike an abstract theory of all natural languages. As such, an ecological grammar may constitute only a model of ecological succession and not a complete theory. Certainly the grammar will not be a completely abstract calculus; it will contain interpreted elements, just as the English grammar of Chomsky contains the interpreted elements "noun phrase" and "predicate phrase." To relegate such a grammar to the status of a "model" or a "theory" requires a commitment to a particular position concerning the philosophical status of these concepts. The tradition of the logical empiricists would favor regarding particular grammars as models of both theories of English and language in general (Braithwaite, 1968; Nagel, 1961). But there exist arguments favoring the opposite view (Campbell, 1957; Hesse, 1966; Wartofsky, 1968). I will adopt the more modest position and refer to an ecological grammar as a model.

The ecological models that are suggested below will be interpreted examples of abstract grammars that do not possess defined or interpreted elements. It is the purpose of this Methods section to examine these abstract grammars to assess their adequacy for simulating ecological phenomena. This assessment will depend both on the characteristics of the abstract grammars and the requirements created by the conceptual framework of ecology. The exposition of this subject will proceed in that order. First, I will discuss the

nature of abstract grammars, their ability to produce various types of sentences and their relation to English. Second, I will discuss the adequacy of abstract grammars for ecological modeling.

The Nature of a Generative Grammar

As I indicated in the summary of the Introduction, one of the constraints on the ecological models is that they be an automatic procedure that produces species lists. Within the class of objects known as grammars one that fulfills this automaticity constraint is called a "generative grammar." I will restrict the discussion to this type of grammar.

A generative grammar is a set of rules that produces a set of objects (or constituents) in a particular order. When the objects are symbols (e. g. , words or letters) the grammar is said to produce a string, which can be read from left to right. If the elements of the string are constituents, or examples of classes of elements (words, letters), then the grammar can produce a string by decomposing or analyzing a set of classes into their elements. Thus, in order to operate, a generative grammar requires a set of elements that can be grouped into classes and a procedure that explicitly decomposes the classes. Such a procedure is called a re-write rule. This procedure directs or commands any device obeying such a rule to "re-write" (replace, analyze, decompose, etc.) one set of symbols with another

set of symbols. It is represented as a right-pointing, single-stemmed arrow occurring between two sets of symbols: $A \longrightarrow B$. This translates as "the set of symbols called 'A' is re-written as the set of symbols called 'B'." When A or B is a string, the order of the elements is indicated by concatenation symbols, denoted "+." Thus, the string A is written: $a_1 + a_2 + a_3 \dots + a_n$. If no confusion results, the concatenation symbols can be dropped: $a_1 a_2 a_3 \dots a_n$. This can be further shortened to " a^n ," if no distinction is drawn between the elements of A, as might occur in discussions of abstract languages.

Because generative grammars produce strings by re-writing one set of symbolic constituents (A) with another set of symbolic constituents (B), it follows that the symbols of A do not appear in the final or terminal string. The symbols of A may be necessary for the production of the terminal string (for example, $b_1 + b_2 + b_3 + \dots + b_n$), but they are not present. They have been erased and replaced by the elements of B; A is a "resting station" on the path to produce B. It is possible, therefore, to call the symbols of A non-terminal vocabulary items and the symbols of B terminal vocabulary items.

An important property of generative grammars is that they are composed of a finite number of rules and, yet, can produce an infinite number of sentences or strings. They achieve this infinite capacity by special rules known as recursive rules. A recursive rule is a

re-write rule that has the form: $A \longrightarrow B + A$. Since A is non-terminal in this example, the A that occurs on the right of the arrow can again be re-written as $B + A$. This can continue for any finite number of iterations. This process must cease, however, after some number of iterations, and so the grammar requires at least one additional rule that will analyze A into a set of terminal vocabulary items. Such a rule might be simply: $A \longrightarrow B$. Figure 3a, Rule 1, illustrates this property of recursion.

This example also indicates that the order of re-write rules affects the strings that can be produced. If Rule 2 had been strictly ordered before Rule 1, then the grammar would not be recursive. The terminal string, in that case, would be one iteration of Rule 2, and one iteration of Rule 3. Rule 1, as ordered in Figure 3, is optional.

As Figure 3a further indicates, a grammar may have choices to make in re-writing a particular symbol as its constituents. This is illustrated by the decomposition of "B" into one of its terminal vocabulary items, or by the number of iterations occurring in a recursive grammar. As a result, different strings can be produced by the same grammar and the path by which each string is generated is apparent by recording the history of the grammar from the time it starts (Rule 1 in Figure 3a) to the time all non-terminals have been re-written as terminals (Rule 3). Such a history can be represented

- (a)
1. $A \longrightarrow B + A$
 2. $A \longrightarrow B$
 3. $B \longrightarrow \{b_1, b_2, b_3, b_4\}$

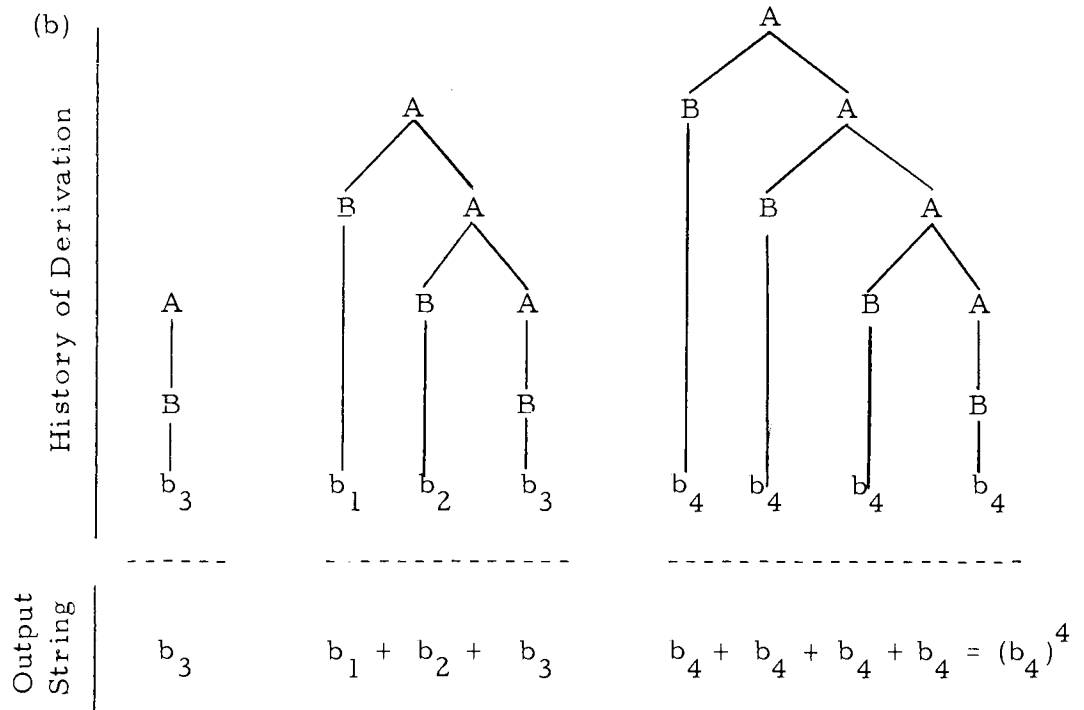


Figure 3. An illustration of generative grammars. (a) A generative grammar with infinite capacity is a set of re-write rules, at least one of which is recursive, as is Rule 1. Upper case letters are non-terminal vocabulary items; lower case letters are terminal items. The parentheses indicate that any one of the items may be chosen by the grammar. (b) The tree diagrams of three strings. The terminal strings, with concatenation symbols inserted, are presented below each tree.

by a tree diagram; a sample of this is presented in Figure 3b. A tree diagram does not define a complete grammar, but only one particular "action, " or "production" of that grammar.

A Hierarchy of Generative Grammars: Regular,
Context-Free, Context-Sensitive,
and Transformational

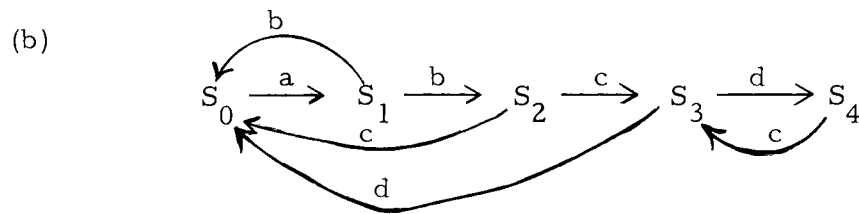
By using the previously introduced notation and terminology we can proceed to a more specific discussion of four families of grammars. Since each of these four families are candidates for a model of succession, they must all be examined to determine which, if any, are inadequate to generate strings that represent species and ecological systems. In particular, I will briefly discuss the "Chomsky hierarchy." This hierarchical ordering of grammars is based on the number of different types of sentences that each grammar can generate. The grammar highest in the hierarchy is the most general; it can generate the greatest number of sentence types. In what follows I will define and exemplify the four major types of grammars that comprise the Chomsky hierarchy. These are: regular grammars, context-free grammars, context-sensitive grammars, and transformational grammars. Each of these will be defined in the above order, followed by an analysis of the adequacy of each. The results of this analysis will substantially constrain the kind of grammar (and, therefore, theory) that can be used to model ecological succession.

Regular Grammars

A regular grammar (RG) is the weakest grammar that I will consider; it generates the fewest different kinds of sentences. It is defined as any grammar that has only the rules of the following kind: $A \rightarrow aB$ or $A \rightarrow a$. A device with this grammar is directed, every time A is on the left of a re-write arrow, to print the terminal symbol "a" and either go to the next non-terminal "B" (which is then re-written) or to stop after having printed just "a. " These are the only kinds of rules allowed in an RG, but they permit recursive rules and, therefore, possess an infinite capacity. It can be shown (Kain, 1972) that every RG is equivalent to what is known as a "finite automaton. "

These are abstract machines that are defined by a finite number of states, any one of which may be "active" at any one point in time. These machines also possess a rule that sequentially activates the states, that is, a rule that sends the machine from state to state. In going from one state to another, a finite automaton may be made to produce, or output, a symbol. A complete set of states and transition rules produces a linearly-ordered set of symbols, i.e., a string. These machines can be represented as state diagrams, as in Figure 4b, where the S_i are states, lower case letters are the output symbols, and arrows represent the transition rules. Figure 4

- (a)
1. $A \longrightarrow a + B$
 2. $B \longrightarrow b$
 3. $B \longrightarrow b + c$
 4. $C \longrightarrow c + D$
 5. $C \longrightarrow c$
 6. $D \longrightarrow d + E$
 7. $E \longrightarrow c + D$
 8. $D \longrightarrow d$



- (c)
- $$L = \{ab, abc, abcd, abcdcd, abcdcdcd, \dots ab(cd)^n\}$$

Figure 4. An illustration of a regular grammar, a finite automaton, and the language they generate. (a) A regular grammar. Upper case letters are non-terminal vocabulary items; lower case letters are terminal items. (b) The state diagram of the associated finite automaton. S_i represent the states of the machines; lower case letters are outputs; arrows are transition functions. The machine stops, and one production is complete, when it returns to S_0 . (c) The language, or set of strings, generated by the RG or the finite automaton. The concatenation symbols have been deleted.

indicates that finite automata permit recursive "loops" and so have infinite capacity. Two common examples of a finite state automaton are combination padlocks and digital computers. The connection between RGs and finite automata is important because most abstract definitions of general systems are in terms of finite automata (cf., Klir, 1969, p. 283 ff.; Cornacchio, 1972). Thus the adequacy of RGs for the representation of ecological phenomena will reflect on the adequacy of general systems theory.

It is now generally accepted (Chomsky, 1957; Grinder and Elgin, 1973; Kimball, 1973; but see Daly, 1972) that RGs are not adequate (i. e. , are too weak) to produce all of the sentences in a natural language such as English. Without going into details that may be found in the above references, the type of sentences that an RG cannot generate are those that have any number of nested dependencies. An example of this in English is (after Chomsky, 1957): "If P, then Q, " where P and Q are sentences that have the same "if-then" form. Therefore, we could have "if, if R, then S, then, if T, then U, " and this nesting or embedding of sentences within sentences could, theoretically, be expanded to any number of nestings. The "if-then" form of the sentence requires that there always be precisely as many symbols following "then" as there are following "if. " Greatly simplified, an "if-then" sentence with n nestings is a string of the type $a^n b^n$ (i. e. , $\{a+b, a+a+b+b, a+a+a+b+b+b, \dots\}$),

where "a" represents the "if" portion and "b" the "then" portion. An RG cannot generate strings of the $a^n b^n$ type, for any unlimited (but finite) value of n . Since examples of these types of strings are within the capacity of English grammar, RGs are not adequate to represent English.

Context-Free Grammar

Context-free grammars (CFG), however, can generate sentences of the $a^n b^n$ type. They do this by allowing rules that can print more than one terminal or non-terminal at one time. For example, the language $a^n b^n$ can be produced by the following CFG:

- (i) $A \rightarrow aB$
- (ii) $B \rightarrow aBb$
- (iii) $B \rightarrow b$

In this example "B" functions to achieve the nested character of the language. That rule (ii) has both "a" and "b" appearing together ensures that no matter how many iterations or cycles of the rules are used there will always be exactly as many b's as a's. In this sense the number of occurrences of "b" is dependent on the number of occurrences of "a." But the dependency is not of the type that "b" must be associated with "a"; any letter other than "b" could have been used. There are however, many examples in natural languages where only certain terminals, and not others, may occur together. An easy instance of this is the requirement in English for the subject

and the verb to agree in number. Thus, "the man runs" is acceptable, but "the man run" is not. A context-free re-write rule does not take into account any of the outputs of any other rules of the grammar. Context-free rules are insensitive to the context or environment of their operation. As a result, they produce both the grammatical as well as ungrammatical forms of subject-verb number agreement. Thus, CFGs are not adequate for English.

Context-Sensitive Grammar

Grammars whose output is produced by at least one rule that is dependent upon the output of some other rule are called context-sensitive grammars (CSG). Context-sensitive rules have the form $X + A + Y \longrightarrow X + B + Y$, which states that A is replaced by B whenever A is in the context $X + _ + Y$. Either X or Y or both may be null or not present in the rule. If X and Y are both null, then the context of A plays no role in the operation of the rule and the rule is, in that case, context-free. As a result, CFGs are a special case of CSGs, and it follows that every language that can be produced by a CFG can also be produced by a CSG, but not the reverse (Kain, 1972). CSGs are then said to have a stronger generative capacity than CFGs, just as CFGs are stronger than RGs. Ginder and Elgin (1973) provide a fragment of an English grammar that demonstrates how a CSG can ensure the agreement in number of a subject and a verb. Roughly,

their example is:

- (i) $\text{Noun} \longrightarrow \left\{ \begin{array}{l} \text{Noun-singular} \\ \text{Noun-plural} \end{array} \right\}$
- (ii) $\text{Noun-singular} + \text{Verb} \longrightarrow \text{Noun-singular} + \text{Verb-singular}$
- (iii) $\text{Noun-plural} + \text{Verb} \longrightarrow \text{Noun-plural} + \text{Verb-plural}$

where $Q \rightarrow \left\{ \begin{array}{l} A \\ B \end{array} \right\}$ means either A or B, but not both, may be produced by the rule.

Transformational Grammar

Although CSGs are very powerful devices there exist arguments in the linguistic literature (Chomsky, 1957) that illustrate a number of shortcomings. Many of these are technical and specific to linguistic analysis, *viz.*, the relation between pronominal nouns and particles (Grinder and Elgin, 1973, p. 62), sentence conjunction (Chomsky, 1957), and the nature of auxilliary verbs (Chomsky, 1957), to name only three. But a more general and intuitively appealing reason for arguing against CSGs as adequate for English lies in the fact that certain sentences are commonly judged by native speakers to be intimately related to one another. Examples of this relation are the relationships (a) between the active and passive form of a sentence, (b) between a question and its answer, and (c) between the active and imperative forms of a sentence. It is currently held that CSGs are inadequate to represent this particular pattern of language. Since

Chomsky (1957), it is believed by linguists that to embed this pattern into the generative grammar requires that the grammar has the capability to transform one sentence into another.

Transformational grammars are grammars that have in them rules which, rather than re-write symbols, change one tree diagram into another. This is done by a rule that is sufficiently unlike re-write rules that it merits a novel symbol: \Rightarrow . The action of this rule is to change the history of a derivation, as illustrated, for an abstract example, in Figure 5. There are many ways of doing this. One way is to change the left to right order of the input string; this is a way of changing an active form into a passive form. Another way is to delete part of the input string and combine other parts of that string; this procedure can be used to form questions from their declarative answers. A third way is to add symbols to the input string; this can be used to form the negative of an active sentence. In general, a transformation rule requires an ordered input string and an ordered output string. An abstract example is the following:

	X_1	X_2	X_3	X_4	X_5
SD:	1	2	3	4	5
SC:	$1+X_6$	2	\emptyset	5	4

where, SD = "structural description, "

SC = "structural change, " and

X_i = symbolic constituents (e. g. , non-terminal items).

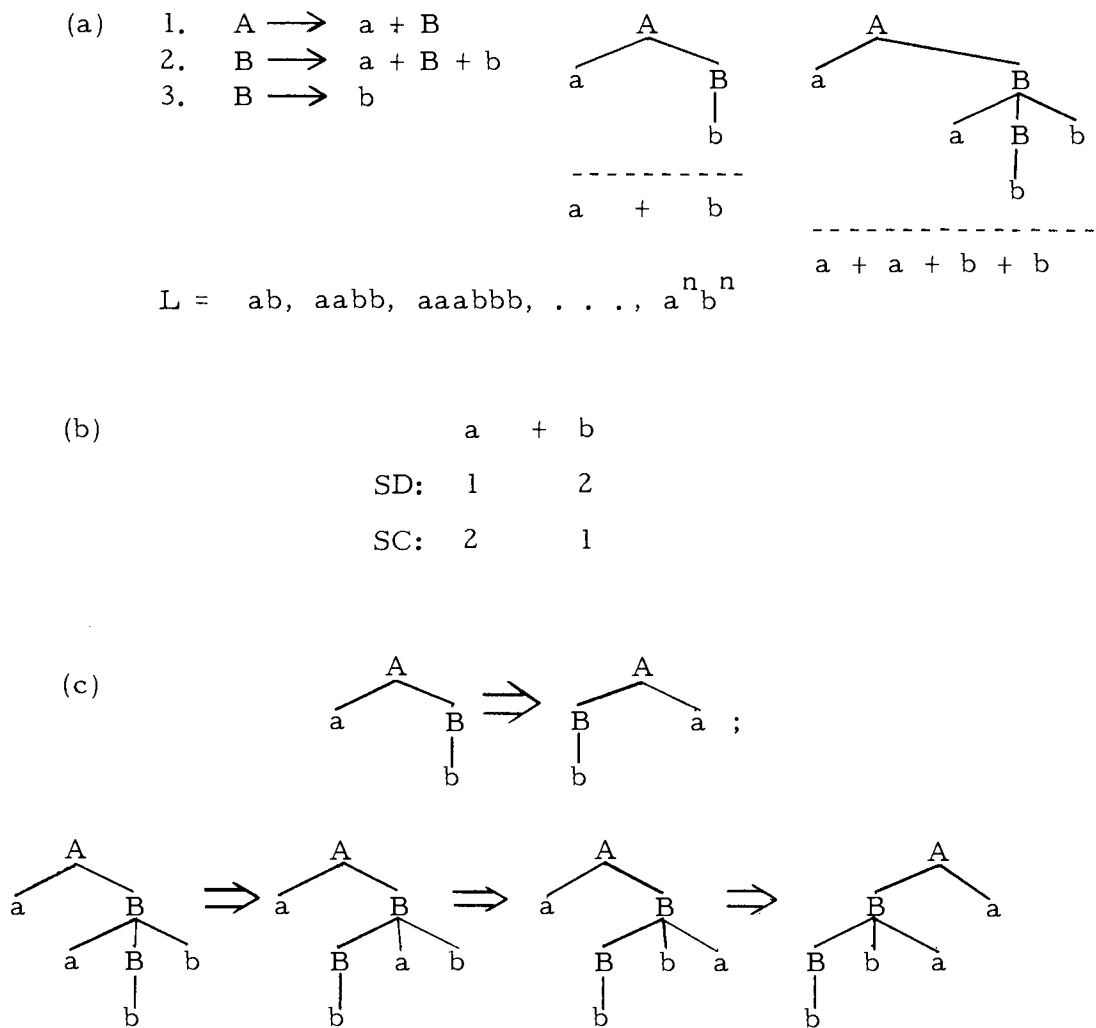


Figure 5. The effects of appending a transformational rule to a CFG. (a) A context-free grammar, its language, and two examples of its derivations. (b) A transformation rule applying to the grammar in Figure 5a. Its effect is to permute a and b . (c) The action of the transformation rule in Figure 5b on the histories of two derivations of the re-write rules in 5a.

This particular example uses many of the possible changes that I mentioned above. Transformational grammars are considered to be the most powerful class of grammars presently available and they are believed to be adequate to satisfactorily describe a natural language such as English (Grinder and Elgin, 1973).

Applications to Ecology

Given these remarks describing the Chomsky hierarchy, the problem now is to investigate the generative capacity required of a grammar that will produce strings of symbols representing species, ecosystems, and temporal ecoclines. To make this application to ecological systems we will need to recall some basic assumptions about species and ecosystems. A species, I indicated earlier, can be represented by both the activities its individuals perform and the morphological characteristics necessary to perform these activities. This relationship is such that every activity must have at least one morphological structure that performs or helps to perform the activity. Moreover, the activities performed by individuals of species can be arranged in an hierarchical pattern. Tinbergen (1951) provides a clear and explicit treatment of the hierarchical activities of the reproductive instinct in sticklebacks. Reproduction, in this case, is an activity that requires both the performance of a number of sub-activities ("fighting, " "nest-building, " "mating, " etc.) and

certain morphological characteristics (e. g. , a central nervous system) to perform those activities. "Mating, " for example, is also composed of sub-activities ("zig-zag dance, " "fertilizing eggs, " etc.) and morphological requirements (muscles, eyes, etc.). Further, the zig-zag dance is also composed of sub-activities with morphological requirements. The assumption we make when we wish to model the "language" aspect of species is that there is no limit to the finite number of activity decompositions that could be performed by some species. This does not say that every species could perform any number of decompositions; obviously, this is false. It does say, however, that there are no valid reasons for limiting the number of decompositions that a model of species is capable of performing.

A similar idealization occurs in the modeling of ecosystems. In a simple way, ecosystems can be represented by resources and utilizers of resources. Regardless of the distribution of species in relation to resources, every utilizer in an ecosystem must be associated with at least one resource. So, in the simplest form, the number of utilizers must not exceed the number of resources in an ecosystem. Moreover, as the discussion of niche creation illustrated, the utilization of a resource (and the associated morphological structures required) create resources for other utilizers. This can be represented as a hierarchy of utilizers and resources. For example, plants require a certain resource, and the morphology of

the plant forms a resource for herbivores, which, in turn, form a resource for carnivores, and so on. The basic assumption of the "language" aspect of ecosystems is that there is no limit to the finite number of resources that can be created by the utilization of some other resource. In the case of trophic resources, this assumption does not claim that the efficiency of transfer from trophic level to trophic level is perfect. Instead, it claims that there is no reason for limiting that finite efficiency to some upper limit.

These discussions of species and ecosystems now allow us to apply the results of the Chomsky hierarchy to ecological systems.

Regular Grammars

As I have already indicated, an RG meets the basic requirement of an infinite capacity that a species's activity and morphology decomposition demands. But an RG fails because of the dependency of activities on morphology. To relate this to the previous linguistic example, the relation of an activity to its required morphology can be indicated by an "if A, then M" type of string. If a species performs activity A, then it must have morphology M. Since A can be decomposed, strings describing the activities and morphologies can have the form: "if, if A_2 , then M_2 , then M_1 ." An example taken from Tinbergen's description of the mating behavior of the sticklebacks will help clarify this situation.

In order to reproduce, a male stickleback must mate; for mating to occur, the male must attract a female by performing a zig-zag dance. Suppose this dance is performed by swimming towards the surface of the water in a zig-zag manner. I can illustrate the relation of this hierarchy of activities to strings of the "if-then" form by progressively substituting activities, as below.

1. "if activity, then morphology"
2. "if mating, then gametes present"
3. "if, if dancing, then muscles, then gametes present"
4. "if, if, if swimming up, then gravity detection, then muscles, then gametes"

This substitution could, conceivably, be extended to include muscular movements and enzymatic reactions. It could also be extended in the opposite direction to describe reproduction as a sub-activity of another activity, and so on. The result is an arbitrary number of "nested dependencies," nested due to the hierarchical decomposition of activities and dependent due to the relation between activities and morphology. In general, this has the form: $A^n M^n$. Strings of this form, as we have seen, cannot be produced by an RG.

Regular grammars also fail to produce ecosystems because of the nested dependencies existing between utilization and resources. As with activities and morphology, utilization and resources can be related to an "if-then" string. "If U, then R" means: if a utilizer is

present, then a resource must be present. Moreover, if the utilizer constitutes a resource, and thereby creates a niche, then there exists an "if-then" relation embedded in the original utilizer. The assumption I have made is that this embedding can occur any finite number of times. For example, the niche creation process of plants is illustrated below:

1. "if U, then R"
2. "if tree, then soil"
3. "if, if insect, then bark, then soil"
4. "if, if, if bird, then insect, then bark, then soil"

Because there are no a priori reasons for limiting the number of species in an ecosystem or for limiting the number of divisions that may be made of an arbitrary, unspecified resource, it follows that U may be replaced by any number of species and that R must be replaced by exactly the same number of divisions. Evidently this condition shows that any grammar of ecosystems must be able to generate languages of the sort $U^n R^n$. Since regular grammars cannot do this we may exclude them from consideration.

Context-Free Grammar

This result raises the next possibility: context-free grammars. Although they have the capability of meeting the shortcomings of RGs they are also inadequate to describe succession largely for the same

reason that they fail to describe natural languages. Consider the case of species first. There are a number of instances where "concord" plays an important part in life histories. For instance, species require an agreement between their feeding activities (plus habitat requirements) and the morphological structures they possess to perform those activities. Most ecologists would recognize as ill-formed an organism whose feeding activity description was "pursue by flight" and whose morphology description corresponded to "wingless." Thus, we can, by using CFGs, generate strings that are clearly inappropriate and unfeasible as viable species, if the morphological description is insensitive to the activity description. Indeed, this sort of concord we have been discussing is just what ecologists mean when they make reference to an adaptive morphological trait. It is also possible to suggest the existence of concord relating two separate activities, such as predator avoidance and feeding, within one developmental stage. There are instances when the agreement is surprisingly loose as with the case of birds that might be feeding on the ground or water one moment and escaping terrestrial predators by flight the next. Even so, there are limits; plants cannot avoid predators by running away. A third concordance requirement is between developmental stages. Here, too, there is an amazing amount of context insensitivity, as exemplified by insects. By metamorphosing insects can change from benthic, carnivorous crawlers to flying

herbivores. Nor is there need for concord between their reproductive activities and their development, since social insects are well known for their arrested development. But even so, no insect metamorphoses into a plant or a giraffe into a fish; thus, early development stages place constraints on later ones. This is a form of between-stage concord and is, at one level, an example of canalized metamorphosis (Waddington, 1966). Therefore, CFGs cannot be used for a theory of species life history.

A similar result obtains for ecosystems. Here, there is an obvious need for concord between the available resource and the characteristics of the utilizers. One does not find living trees floating around in the middle of the ocean, nor does one find fish swimming in air. Thus, the insertion of species into ecosystems cannot be done without regard for the context of utilization. Nor can the actual structure of the habitat be specified without regard to what other elements are present. If features or structures are selected by the grammar that describes a terrestrial grassland, the next chosen feature cannot pertain to a mountain stream. Similarly, the layering of tropical forests requires context sensitivity, since higher layers affect lower layers by altering sunlight, wind velocities, humidity, and so on. Thus, I conclude from this and the previous paragraph that context-free grammars cannot provide a sufficiently powerful theory of ecological succession.

Context-Sensitive and Transformational Grammars

We know, then, that any model of succession must possess at least a context-sensitive grammar. It is a much more difficult question, however, to ascertain the adequacy of CSGs. Earlier I emphasized the relationship between sentences as an important consideration used in linguistics to eliminate from consideration CSGs, the view being that sentences related by transformations have meanings that are identical in some sense. We can evaluate CSGs as models for species by discussing a fragment of a grammar which will be more fully presented later.

In the Introduction I objected to current conceptualizations of the niche on the grounds that they did not provide a means of representing the "invariance" of species through changes in a species's niche (i. e. , idealized niche trajectory). That is, current niche theory fails to represent the fact that the bacterium E. coli is called E. coli regardless of whether it is feeding on sucrose or dextrose, or whether it is reproducing by fission or conjugation, for example. The same remarks apply in the case that a niche changes from its fundamental to its realized form. To say that the realized niche results from the "shrinkage" of the fundamental niche, an implicit metaphor in the geometric view, is not a sufficiently precise formulation. In the following fragment of a grammar I will represent the invariance of

species by subsuming optional descriptions (labeled " Σ ") of a species under one Latin binomial ("LB"). Thus, the Latin binomial "E. coli" must dominate or appear in a tree diagram at a higher node than the nodes that describe the optional behavior of the species (dextrose or sucrose, fission or conjugation) in order that such a representation satisfy my interpretation of "species invariance." Figure 6a illustrates this condition. The grammatical problem is to provide a set of re-write rules that produce this set (and only this set) of options in a satisfying way. In what follows I will present three possible sets of rules and evaluate their abilities to represent species invariance.

The first, and simplest, possibility is a context-free grammar represented by the following rules:

- (1) $LB \longrightarrow \Sigma (\Sigma)$
- (2) $\Sigma \longrightarrow \text{Feeding} + \text{Reproduction}$
- (3) $\text{Feeding} \longrightarrow \{ \text{dextrose}, \text{sucrose} \}$
- (4) $\text{Reproduction} \longrightarrow \{ \text{fission}, \text{conjugation} \}$

Rule (1) means: re-write the Latin binomial as a species (Σ) plus an optional Σ . Thus, there can be any finite number of Σ 's dominated by LB (see Figures 6b and 6c). Rule (2) decomposes each Σ of Rule (1) as the two activities "Feeding" plus "Reproduction." Rule (3) means: re-write "Feeding" as either "dextrose" or "sucrose," but not both. And Rule (4) means: re-write "Reproduction" as "fission" or "conjugation," but not both.

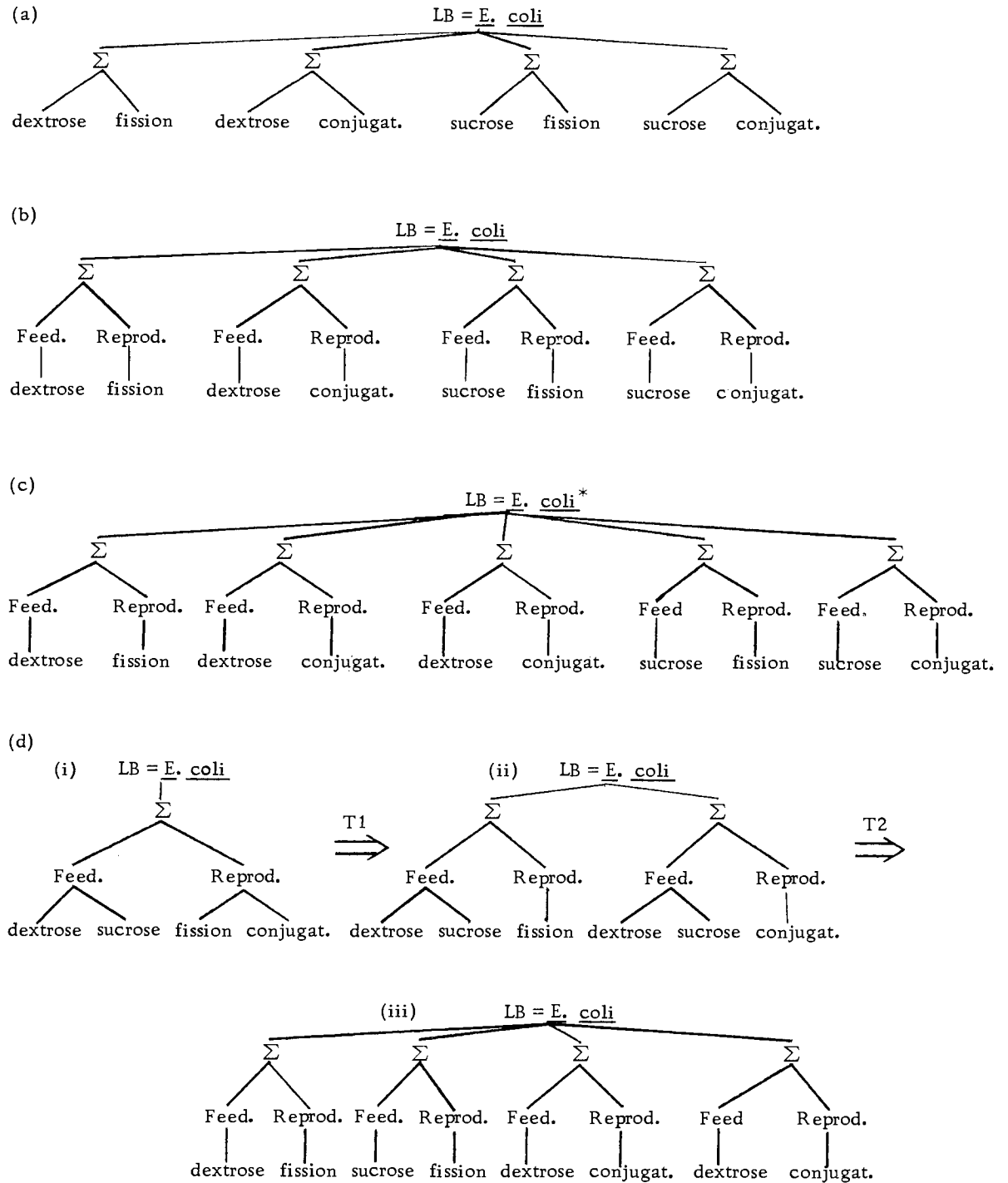


Figure 6. Hypothetical tree diagrams illustrating the necessity of transformational grammars. (a) A tree diagram representing an hypothetical species called E. coli. (b) The history of a production from a context-free grammar that produces E. coli. (c) Another tree diagram from the grammar in (b) showing the redundancy that results from this CFG. (d) The transformations of tree diagrams from a transformational grammar that produces E. coli.

As Figures 6b and 6c indicate this grammar cannot restrict the number of Σ categories that it generates on the basis of the number of options available to the species. In this example, E. coli has only four distinct options, yet the grammar can generate any finite number of Σ categories. Thus, there must be repetitions in those trees that possess more than four Σ 's (e. g. , Figure 6c). But this violates the meaning of an "optional form of species. " By dominating two (or more) identical representations under different Σ nodes the grammar asserts that a tree with no duplications, as in Figure 6b, is distinct from another tree (representing another Latin binomial) that differs only in that it has two duplications (E. coli* in Figure 6c). This is an extremely artificial distinction, one resting solely on the manner of representation. Moreover, any model of the insertion of species into ecosystems based only on a species's required habitat (sucrose, dextrose, etc.) has no basis for separating E. coli from E. coli*. Indeed, since, because of the possibility of duplication, both E. coli and E. coli* are assumed to be taxonomically distinct species, and since they have identical activities and habitat requirements, there can be no way of associating the productions of the grammar with the action of evolution. The two species have identical niches but different representations. So, this grammar is inadequate to produce trees of the form in Figure 6a in a satisfying and unproblematical manner.

The second possibility that produces Figure 6a is a context-sensitive grammar with the following rules.

- (1)
- $$LB \rightarrow \begin{cases} \Sigma \\ \Sigma + \Sigma \\ \Sigma + \Sigma + \Sigma \\ \Sigma + \Sigma + \Sigma + \Sigma \end{cases}$$
- (2)
- $$\Sigma \rightarrow \begin{cases} \text{dextrose} + \text{fission}/Q-P, \text{ where } Q \& P \neq \text{dextrose} + \text{fission} \\ \text{dextrose} + \text{conjugation}/Q-P, \text{ where } Q \& P \neq \text{dextrose} \\ \quad + \text{conjugation} \\ \text{sucrose} + \text{fission}/Q-P, \text{ where } Q \& P \neq \text{sucrose} + \text{fission} \\ \text{sucrose} + \text{conjugation}/Q-P, \text{ where } Q \& P \neq \text{sucrose} \\ \quad + \text{conjugation} \end{cases}$$

Rule (1) means: re-write LB as any number of Σ 's up to four. Rule (2) means: re-write Σ as any one of the four combinations of food or reproduction mode whenever the particular combination has not been previously chosen.

Although this grammar avoids the shortcomings of the CFG and includes E. coli (as in Figure 6a) as one of its productions, it is clear that this grammar cannot specify the general case. Other species may have more than four options, but they could not be generated by this grammar. Indeed, if species may have any finite number of developmental stages, and if each stage has four options, then there is no grammar like the second possibility that can generate them all with a finite number of rule. So, this grammar is judged to be inadequate also.

The third possibility that overcomes the inadequacies of the

previous two is a transformational grammar with the following rules.

- (1) $LB \longrightarrow \Sigma$
- (2) $\Sigma \longrightarrow \text{Feeding} + \text{Reproduction}$
- (3) $\text{Feeding} \longrightarrow [(\text{dextrose}) (\text{sucrose})]$
- (4) $\text{Reproduction} \longrightarrow [(\text{fission}) (\text{conjugation})]$

$$T1. \quad \begin{array}{ccccccc} [X & + & \text{fission} & + & \text{conjugation}] \\ \Sigma & & & & \Sigma \end{array}$$

$$SD: \quad 1 \qquad \qquad 2 \qquad \qquad 3 \qquad 4$$

$$SC: \quad (1 + 2 + 4) \quad (1 + 3 + 4)$$

$$T2. \quad \begin{array}{c} [\text{dextrose} + \text{sucrose} + \left\{ \begin{array}{c} \text{fission} \\ \text{conjugation} \end{array} \right\}] \\ \Sigma \qquad \qquad \qquad \Sigma \end{array}$$

$$SD: \quad 1 \quad 2 \qquad \qquad 3 \qquad \qquad 4$$

$$SC: \quad (1 + 2 + 4) \quad (1 + 3 + 4)$$

Rules (1) and (2) are previously defined. Rules (3) and (4) indicate that either one or both of the choices to the right of the arrow may be generated by the grammar. The first transformation rule (T1) creates an additional Σ node, as Figure 6d(ii) indicates; each of the two Σ nodes dominates a reproduction node. Rule T2 also creates another Σ node that dominates each food source. Curved brackets around "fission" and "conjugation" mean either one may be present. T2 has been applied twice in Figure 6a, once for fission and once for conjugation.

Not only does this third possibility never create more nodes than there are options (as the CFG did) but it can state the general case when any number of developmental stages are present (as the CSG failed to do). This it does by iterating the transformation rules for each developmental stage where options are present. Thus, transformational grammars appear to be the only satisfying type of grammar that represents a fundamental property of species.

A similar problem arises when one tries to write a CSG for species insertion. A CSG can give no general method for incorporating niche creation while ensuring that the ecosystem grammar produces no greater number of utilizers than can be defined by some finite set of species. For examples, one possibility suggests itself:

- (1) Ecosystem \longrightarrow Habitat + Utilizer (Utilizer)
- (2) Habitat $\longrightarrow \{+dextrose, +sucrose, \dots, \pm \text{other habitat features}\}$
- (3)
$$U + U + \dots + U \longrightarrow \begin{bmatrix} \text{Morph.} \\ \text{feat.} \end{bmatrix}_{\substack{\text{E. coli} \\ \text{E. coli}}} + U + \dots + U / +sucrose \text{ } ______.$$
- (4)
$$\begin{bmatrix} \text{Morph.} \\ \text{feat.} \end{bmatrix}_{\substack{\text{E. coli} \\ \text{E. coli}}} + U + \dots + U \longrightarrow$$

$$\begin{bmatrix} \text{Morph.} \\ \text{feat.} \end{bmatrix}_{\substack{\text{E. coli} \\ \text{E. coli}}} + \begin{bmatrix} \text{Morph.} \\ \text{feat.} \end{bmatrix}_{\text{LB}_2} + \dots + U / +sucrose \begin{bmatrix} \text{Morph.} \\ \text{feat.} \end{bmatrix}_{\substack{\text{E. coli} \\ \text{E. coli}}} \text{ } ______.$$

The rules continue in this way until all remaining U categories have been re-written as some set of species. There is no guarantee,

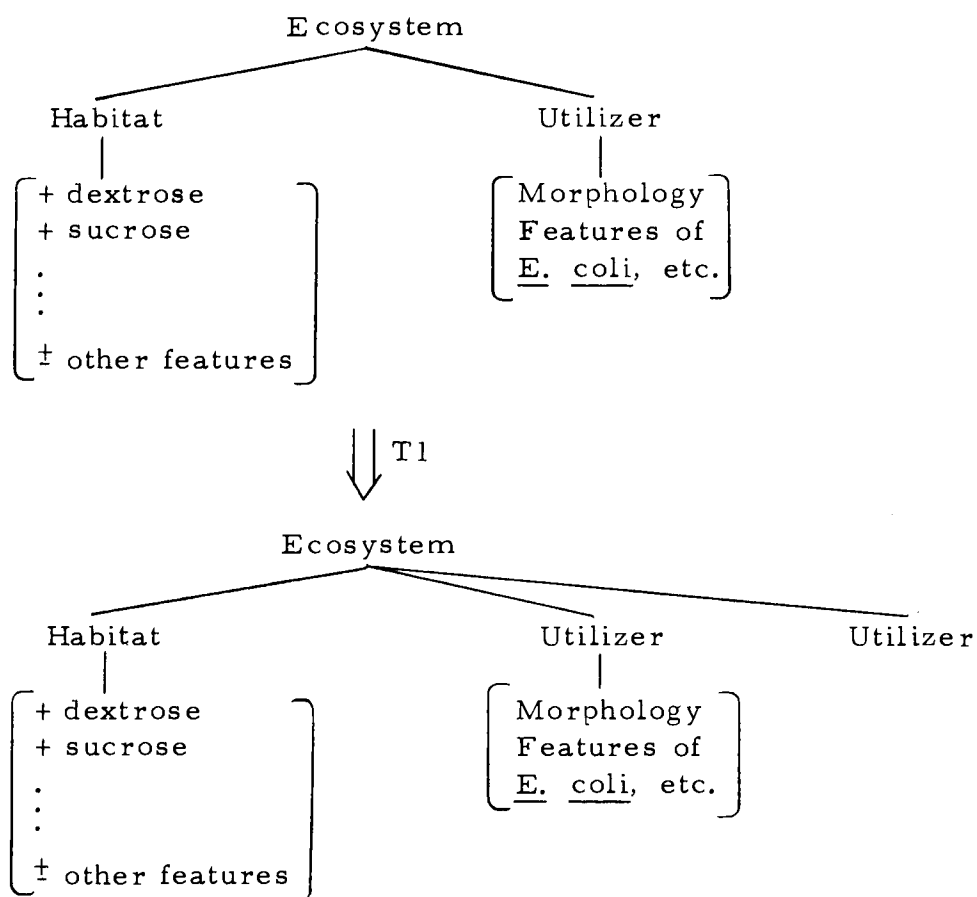


Figure 7. The action of T1 on the derived tree diagram.

The preceding arguments are intended to show that legitimate reasons exist for judging regular, context-free, and context-sensitive grammars inadequate to represent species's niches and the process of inserting species into ecosystems. I maintain, therefore, that any system of generative grammars that satisfactorily simulates ecological systems must possess transformation rules. I turn now to an explicit discussion of some of these grammars.

III. RESULTS: CONTOURS OF A SIMULATION ALGORITHM

It is the purpose of this section to specify a particular model of ecological succession by stating the rules of a system of generative grammars. As I have already indicated the final output of such a system is to be a series of species lists (i. e., communities) that corresponds to the succession of communities within a temporal ecocline. The tactic that I shall employ in writing such a system of grammars will be to divide the system into three major components. The first component will be a generative grammar that describes the habitat requirements of species. A particular set of species generated by this grammar will constitute a "lexicon." The lexicon will correspond to the pool of species that is capable of occupying an ecosystem. The second component will be a generative grammar that describes the habitat features available in a particular ecosystem and will insert species from the lexicon on the basis of their requirements. The third component will not be a distinct grammar, but will be an explicit procedure for altering the habitat availabilities of an ecosystem based on the effects that a community has on its habitat. The alteration of the environment by the communities present will result in a series of habitats and communities that follow one another in time. This will create temporal ecoclines. A "flow diagram" of the complete system of grammars is available in Figure 32, p. 158.

I will begin the discussion of this system of grammars with a consideration of the species component.

Species

The species component will have three parts: (1) a context-sensitive, "base" grammar, (2) a context-sensitive grammar that specifies morphology, and (3) a set of transformation rules. The "base" grammar will be described first, but before this I will describe the special terminology and notation that will appear in the model.

Re-write rules have been previously introduced, but recall that their general form is $X + A + Y \longrightarrow X + B + Y$ where A, B, X, and Y are elements of the vocabulary of the grammar. This vocabulary may be either terminal or non-terminal, "A" is non-terminal by definition. The function of the rules in the base grammar will be to decompose a species into its developmental stages (its life history) and the activities that a species must perform during each of its stages. Since every activity must be performed in some habitat, the rules describing a species must also specify or describe the habitat requirements of those activities.

The non-terminal vocabulary of the activities will be represented either by common English words or their abbreviations, selected for maximum mnemonic and heuristic value. Some of the

activities and all of the habitat descriptions will be represented by what are called "distinctive features." Distinctive features will again be represented by words or their abbreviations, but in addition they will be prefaced by either a "+" or a "-." A "+" preface indicates that the species being represented possesses the feature in question. For example, "+ sub" might mean that the species requires the presence of the substrate (or soil) in order to, for example, forage; "- sub" might mean that the substrate is not required. Or, an activity may be described as "+ evade" meaning physical evasion is used as a predatory escape mechanism. Clearly a large number of these distinctive features are required to completely describe any given species, and a complete list of them will not be presented here. Two comments, however, can be made in defense of this fragmentation: (a) the list is assumed finite in length so that in principle nothing stands in the way of providing a completed list in the future and (b) many interesting things can be said on the basis of a partial list.

One further remark is in order here because it may be argued that the attributes of biological species cannot be reduced to such qualitative expressions as "+" or "-." There are, for example, many habitat requirements, such as temperature, that act as continua and restrain and limit the niches of species. To avoid this criticism it is necessary to indicate how such a scheme can be "quantified."

Observe that every quantifiable habitat feature that can be named (temperature, pH, salinity, etc.) has an upper and lower bound of biological relevance. That is, there is some lower and upper temperature (pH, salinity, etc.) beyond which no species can survive. If no other temperature limitations are known then at least -273°C and the vaporization temperature of hydrogen will serve as bounds, but some limits must exist. As a result, we can divide up the continua into a finite number of regions. For example, temperature can be divided up into three regions: I = -10°C to 0°C , II = 0°C to 100°C , and III = 100°C to 200°C . Since there will be a finite number of intervals, they can be ordinally ranked. The unique ranking numbers can replace "+" and "-", and they represent the range of temperatures over which the species can perform its activity. For instance, if a bacterium can survive temperatures from 0°C to 200°C , we can represent this as "II temp + III temp." If it is further argued that this scheme still fails to denote continua and can never be sufficiently resolved, then two remarks can be made. First, it is not obvious that organisms respond to infinitesimally divided continua and not to relatively broad classes of continuous factors. Relatedly, our measurements of both species's responses and characteristics (e. g., body size) are statistical and, thus, have associated with them confidence intervals or intervals of standard error, and not unique, specific points. Second, since each individual region (e. g., "II temp") spans

a finite interval of temperatures it can, itself, be more finely divided by providing re-write rules such as: $II \text{ temp} \rightarrow II_1 \text{ temp} + II_2 \text{ temp} + II_3 \text{ temp}$. And this process can be carried on indefinitely, since each sub-division is bounded and can be further divided itself. Therefore, a procedure exists to quantify the description and a detailed example of this process will be provided later.

A CSG for Life History

We can now specify a grammar that is a description of a species's habitat requirements based on its life history and activities. In what follows, I will first present a set of rules and then a verbal translation of those rules plus definitions of the notation. After this, I will present some simple examples. The rules themselves are to be found in Figure 8; the order may not be changed. An hypothetical example is given in Figures 9, 11, and 13. Below is the translation and explanation of the rules in sequential order.

Rule 1: "re-write the category Lexicon as LB (Latin binomial, i. e., a unique name) plus an optional LB." The notational use of the parentheses gives the grammar the choice of incorporating or not another LB category. An operation of this grammar that does not make use of this option generates a lexicon with one species. The number of species in the lexicon equals the number of LB categories. Any finite number of iterations of this rule may be made by the grammar.

1. $\text{Lexicon} \longrightarrow \text{LB}(\text{LB})$
2. $\text{LB} \longrightarrow \Sigma$
3. $\Sigma \longrightarrow \text{I} + \text{R}$
4. $\text{R} \longrightarrow \text{Main} [(\text{RepSex})(\text{RepAsex})] (\Sigma)$
5. $\text{I} \longrightarrow \begin{cases} \text{ISex} / \text{---} + \text{Main} + \text{RepSex} \\ \text{IAsex} / \text{---} + \text{Main} + \text{RepAsex} \\ \text{ISex} + \text{IAsex} / \text{---} + \text{Main} + \text{RepSex} + \text{RepAsex} \end{cases}$
6. $\text{ISex} \longrightarrow \text{Main} + \#\text{Morph}\# (\text{ISex})$
7. $\text{IAsex} \longrightarrow \text{Main} + \#\text{Morph}\# (\text{IAsex})$
8. $\text{RepSex} \longrightarrow \begin{cases} \text{site}(\text{care}(\text{species}(\text{care}))) \\ \text{pollination}(\text{fruit}(\text{species})) \end{cases}$
9. $\text{site} \longrightarrow \text{place} + \text{temp} + \text{light} + \text{osmo}$
10. $\text{pollination} \longrightarrow [(\text{cross} + \text{carrier}) (\text{self})]$
11. $\text{cross} \longrightarrow \text{temp} + \text{light} + \text{osmo}$
12. $\text{self} \longrightarrow \text{temp} + \text{light} + \text{osmo}$
13. $\text{fruit} \longrightarrow \#\text{fMorph}\#$
14. $\text{care} \longrightarrow [(\text{nest}) (\text{feed})]$
15. $\text{RepAsex} \longrightarrow \text{place} + \text{temp} + \text{osmo}(\text{light})$
16. $\text{Main} \longrightarrow \text{Per}(\text{PA})\text{F}$
17. $\text{Per} \longrightarrow \text{place} + \text{temp} + \text{osmo}(\text{current})(\text{light})$
18. $\text{PA} \longrightarrow \begin{cases} \text{crypsis} \\ [(\text{burrow})(\text{climb})(\text{maneuver})] \\ [(\text{passive})(\text{chem})(\text{weapon})] \end{cases}$
19. $\text{F} \longrightarrow \text{F}(\text{F})$
20. $\text{F} \longrightarrow (\text{search}) ((\text{pursue})\text{attack})\text{consume}$

Figure 8. A context-sensitive, ordered base grammar used for the description of species activities and habitat requirements.

Rule 2: "re-write each LB as the abstract category Σ ("species")." The need for this rule can be made most clear following a discussion of the transformation rules. Its major purpose, however, is to state that every object possessing a unique Latin binomial is also a species (the characteristics of which are elaborated in the following rules). A separate Σ category is necessary because optional habitat requirements will be represented as optional Σ categories, dominated by the same LB.

Rule 3: "re-write the category marked Σ as two sub-activities: I ("initiation") plus R ("reproduction")." This rule forces the grammar to ensure that every species reproduces and that each species begins the life cycle in some initial state (I). Rule 3 states that the activity categories R and I are necessary conditions for an object to be classed as a species.

Rule 4: "re-write R as the sub-activities Main ("maintenance") plus either RepSex ("sexual reproduction") or RepAsex ("asexual reproduction"), or both, plus an optional Σ ("species")." This rule continues the activity decomposition by further decomposing the activities of R. There are, however, two notational devices that need explication. The first is a notation that takes the general form: $A \longrightarrow [(B)(C)]$, which means "re-write A as either B alone, C alone, or B + C." It is understood that the square bracket may contain strings of any finite length. Rule 4, by allowing "RepSex +

RepAsex' as a valid string, states that there are some species that can perform both sexual and asexual reproduction. There are many instances of this in plants, e. g., strawberries. The second notational device noted in Rule 1, has the general form $A \longrightarrow B(C)$ and gives the grammar the choice of incorporating or not incorporating category C into the derivation. Thus, there are two possibilities: "B" or "B + C." In the specific case of Rule 4, it must be understood that " Σ " is an option of the grammar, but is not an option of the species. Once the device has chosen to write Σ in Rule 4 that symbol becomes a part of the description of the species. So, not every optional rule of the grammar specifies an option, such as sexual or asexual reproduction, of the species. The distinction between options of the grammar and options of the species will become clearer following a discussion of certain of the transformation rules. The need for an optional category in Rule 4 stems from the existence of certain plants, metazoans, and parasites that possess alternating generations that are separated by a "reproductive act." By "reproductive act," I mean either a fusion of genetic material (as with egg-sperm fusion), budding-off, splitting, or any other mode of reproduction, excluding, by this, radical changes in development due to metamorphosis or birth. Finally, note that, for simplicity, the parenthesis notation replaces the usual concatenation symbol.

Rule 5: "re-write I as ISex if Rule 4 chooses RepSex, IAsex if Rule 4 chooses RepAsex, or ISex + IAsex if Rule 4 chooses RepSex + RepAsex." This context-sensitive rule forces the grammar to match different development sequences with the correct method of reproduction.

Rule 6: "re-write ISex as Main ("maintenance") plus #Morph# plus an optional (recursive) ISex." "Maintenance" represents the category of activities that an organism must perform at every developmental stage in its life cycle, if it is to survive and develop further. The category #Morph# represents a category that describes the morphology of the developmental stage that maintains itself in the specified way and reproduces sexually. The # symbols on either side of "Morph" are required in order to separate features that describe the morphology of the species from those features that describe the habitat requirements of the species.

Rule 7: "re-write IAsex as Main plus #Morph# plus (optionally) IAsex." This rule is identical to Rule 6 except that the markers denote the development of an asexually reproducing life cycle.

Figure 9 gives an hypothetical example of the rules illustrating the major structural characteristics of the first seven rules. The tree diagram of this figure represents the history of one operation of the base rules of the grammar. Triangles in the figure denote portions of the tree not represented by this figure.

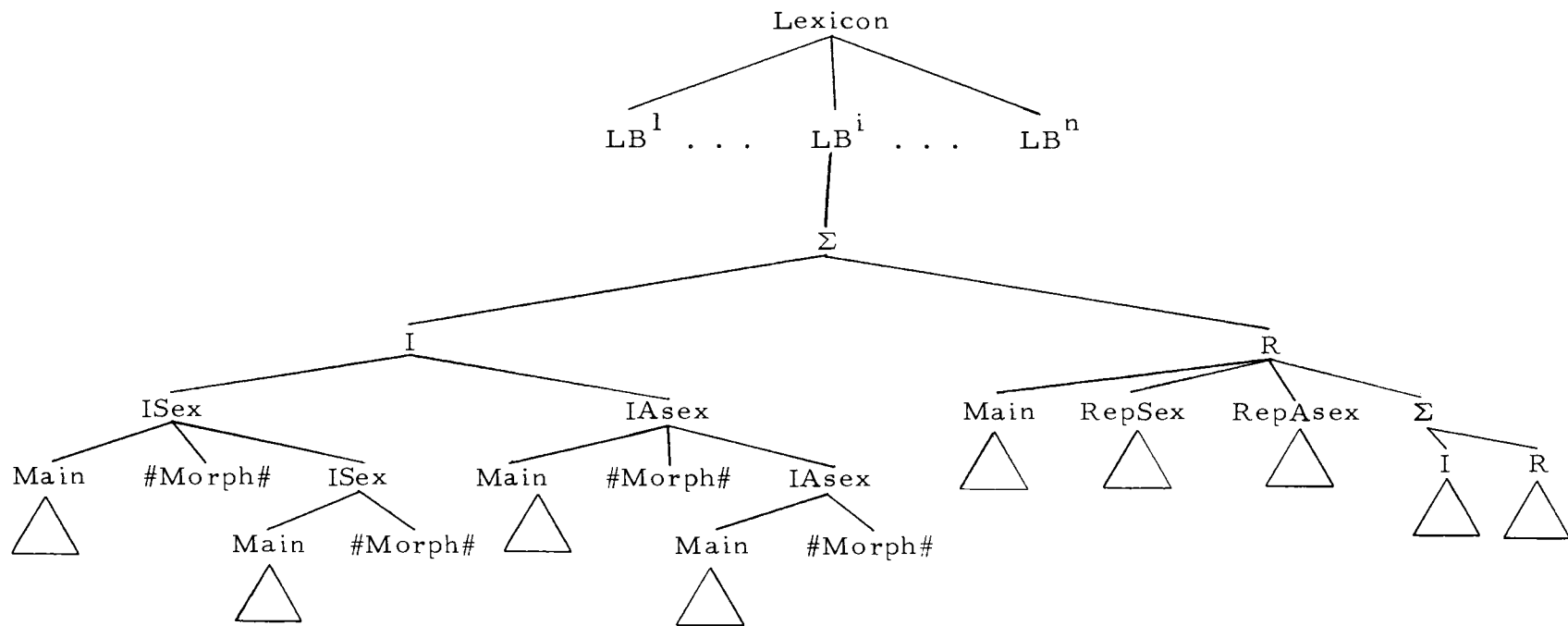


Figure 9. One history of the operation of the species base rules illustrating the basic structure of multiple developmental stages, alternating generations, and optional modes of reproduction. Triangles indicate portions of trees not included here.

Rule 8: "re-write RepSex as either one of the following two sets of alternatives: (1) 'site' plus (optionally) 'care' plus (optionally and contingent upon 'care') 'species' plus (optionally and contingent upon 'species') 'care', or (2) 'pollination' plus (optionally) 'fruit' plus (optionally and contingent upon 'fruit') 'species'." The embedded parentheses are a notational device that ensures that "site + species" will never occur without "care" and that "pollination + species" will never occur without "fruit." This rule states that if a species reproduces sexually, then it must do so either at some location or by pollination. If it does not need to be pollinated, then in addition to reproducing at some site (i. e. , at some site with some feature specifications) a species may be described as caring for its young. If it does care for its young, then there is the option open to the grammar to describe the species as using other species in its reproductive act. This situation is fairly common among birds, such as cowbirds, that are brood parasites. The rule also allows those species that have the option of being parasites or caring for their own young, as happens in redhead ducks (Aythya americana). If a species requires pollination, then it may be described as producing fruit. Here "fruit" indicates the material covering a seed, the flowers, and any nectar-like material that may be produced by a pollinating species. If fruit is produced, then the grammar may

describe the species as requiring another species, such as an insect, to complete the pollination.

Rule 9: "re-write 'site' as 'place' plus 'temp' plus 'light' plus 'osmo' (osmotic pressures: salinity, moisture, etc.)." This rule describes the physical habitat necessary for non-pollinated, sexual reproduction to occur. These non-terminal vocabulary items will be rewritten with a set of distinctive features.

Rule 10: "re-write 'pollination' as either 'cross + carrier' or 'self' (or both)." The purpose of this rule is to allow species that can reproduce by both cross- or self-pollination. "Carriers" refers to the medium by which pollination occurs.

Rule 11: "re-write 'cross' as 'temp' plus 'light' plus 'osmo'." This rule, like Rule 9, gives the physical habitat necessary for cross-pollination.

Rule 12: "re-write 'self' as 'temp' plus 'light' plus 'osmo'." This rule also describes the physical habitat for self-pollination. Since self-pollination is frequently a "back-up" method of reproduction, it often occurs later in the season than cross-pollination. Thus, its (physical) habitat requirements are different.

Rule 13: "re-write 'fruit' as '#fMorph#'. " This rule describes the morphology of the fruit that may serve as a food source for other species.

Rule 14: "re-write 'care' as either 'nest', 'feed', or 'nest + feed'." This is to say, care, as a component of some sexual reproduction, is composed of building a nest and/or the feeding of young. The habitat requirements of these two activities will be provided below.

Rule 15: "re-write RepAsex as 'place' plus 'temp' plus 'osmo' plus (optionally) 'light'." This rule describes the physical habitat necessary for asexual reproduction.

Rule 16. "re-write Main as the sub-activities Per (persistence) plus (optionally) PA (predator avoidance) plus F (feeding)." This rule states that at every developmental stage a species must be able to perform the activities of maintenance, and this requires, at the minimum, persistence and feeding. Predator avoidance is considered optional because there are some species of phytoplankton that have adopted a life style that precludes intricate avoidance responses. There are also some species such as hawks that have adopted a feeding regime that excludes the possibility of their suffering predation (at least for part of their life history). At this point in the operation of the grammar there is no requirement that any of the developmental stages agree with one another. A species may have PA at one stage of its development and not at some later stage.

Rule 17: "re-write Per as 'place' plus 'temp' plus 'osmo' plus (optionally) 'current' plus (optionally) 'light'." With this rule the grammar begins to specify the physical habitat in which the species

can persist (at one developmental stage). It does this by specifying certain aspects of the environment to which every species (and every developmental stage) must adapt: place, temperature, and osmoregulatory problems. "Place" refers to the species's requirements for substrates (soil), medium (air or water, or both) or its dependency on other species. "Temperature" specifies the range of temperatures that a given developmental stage can withstand. Such a specification corresponds roughly to the upper and lower incipient lethal levels as defined by Fry (1947). "Osmosis" refers to any problem faced by the species that pertains to its ionic balance. Thus, it specifies not only salinity ranges, but also the amount of water that a species can tolerate or must have in order to persist. It could also be used to specify acceptable levels of toxicants or pollutants that a species could tolerate, but, for the moment, these considerations will not enter into the discussion. The optional category "current" refers to the fact that some species are adapted to environments that possess strong physical currents such as occur in streams and intertidal areas. "Light" is optional since temperature is considered by the grammar to be a distinct factor and since not all species are limited by a particular range of light conditions.

Rule 18: "re-write PA as either (1) 'crypsis', (2) any combination of 'burrow', 'climb', or 'maneuver', or (3) any combination of 'passive', 'chem', or 'weapon'." This rule basically divides up the

category Predator Avoidance into three major sub-divisions:

(1) cryptic behavior or coloration, (2) evasive tactics of avoidance, and (3) avoidance tactics making use of external protection. In the case of (2) "burrowing, " "climbing, " and "maneuvering" are all clear examples of active escape either by utilizing a physical dimension to which the predator is not adapted (burrowing, climbing) or by relying on speed or quickness of reflexes. "Crypsis, " however, meaning avoidance by morphological or behavioral structures that impede the ability of a predator to detect the prey, is something of a passive activity and, thus, might be more accurately placed with the third group of options. But since cryptic coloration and other morphological adaptations of that sort are often very specific to the background or habitat, it is a category that can be used to specify habitat requirements, unlike the third group of options. The necessity of including (3) as a strategy stems from the morphological structures upon which those options rely. Although these morphological characters do not aid in the problem of inserting into an ecosystem those species which rely upon them to avoid predators, it will aid in deciding which predators to include or exclude from consideration. The category "passive" indicates any armour that a species adopts, including both the thorns, spines, and burrs of plants and the chitinous or leathery plates of animals. Chemical defenses include not only poisons but also the terpenes that plants and some insects employ.

"Weapons" indicates morphological structures that a species can actively use to inflict injury upon a predator. In large carnivores, for example, these structures will be identical, for the most part, with the morphological structures used for feeding.

Rule 19: "re-write F (feeding) as F plus (optionally) F." The sole purpose of this rule is to provide the grammar a means of specifying alternate feeding behaviors that are available to some species. This is deemed necessary since, for example, some species may act either as herbivores or carnivores or detritivores. Since these feeding modes utilize vastly different search, pursuit, and attack strategies, the grammar must have some means of specifying these alternatives.

Rule 20: "re-write F as the optional sub-activities 'search', or 'pursue', and/or 'attack' plus an obligatory 'consume'." The result of this rule is that some species only consume their food source, they do not search for it, pursue it, or attack it, examples being non-carnivorous plants. Thus, in this sense, "attack" requires that the prey be alive, prohibiting detritivores from using an attack mode. "Search" and "pursuit" require that the predator possess some directed mobility. The rules also indicate that there exist some species that can search and attack without pursuit (viz., herbivores) but that no species will search and pursue, but not attack. Finally,

many scavengers such as vultures are capable of searching for prey but do not need to pursue or attack.

These rules, as they are stated and described, constitute the "base" of the grammar, and are restricted to the order outlined above. They are not the complete grammar, for, as I have indicated earlier, it is still necessary to supply a morphological description of the species. Before an outline of this procedure can be given, however, it is necessary to provide descriptions of a number of categories of activities that have been utilized in the base rules. These are non-terminal vocabulary words such as: place, temp, osmo, crypsis, maneuver, search, attack, and so on. Their description necessitates providing the grammar with a rule somewhat different than the re-write rule used earlier. The meaning of this new rule, which I shall symbolize as $\vdash\rightarrow$, is approximately "store and re-write as." Thus, the expression " $A \vdash\rightarrow B + C$ " is read as "duplicate A in a memory and re-write it as B + C." A sequence or chain of these rules ($A \vdash\rightarrow B, B \vdash\rightarrow C, C \vdash\rightarrow D, \dots$), then, gradually builds up in a memory a list of symbols (A, B, C, D, \dots). It is by these means that I will describe the undefined non-terminals that the base rules have produced. This "store and re-write" rule is equivalent to the earlier, simple re-write rule, if recursion is not defined. That is, if " $A \rightarrow A + B$ " is not interpreted as a recursive rule (i. e., does not produce sentences of the form: " $A + B^n$ "), then

the sequence " $A \mapsto B, B \mapsto C, C \mapsto D, \dots$ " is equivalent to " $A \longrightarrow A + B, B \longrightarrow B + C, C \longrightarrow C + D, \dots$ " Figure 10 lists, in one place, all of the residual non-terminals and a partial description of a few of them. The "+" or "-" characterizations serve to define the habitat requirements of the species. It is on the basis of these lists, that are unique to species, that any given species is inserted into an ecosystem. An "n" that replaces a "+" or a "-" refers to a range of a quantitative trait. For example, "n temp" means "a range of temperatures denoted by n." In this, and later instances, an unspecified set of features that are used to describe a category (e. g., habitat requirements, morphology, etc.) but are not explicitly discussed will be represented by $\begin{bmatrix} \alpha F_1 \\ \nu F_n \end{bmatrix}$. In this notation, the Greek letters refer to an unspecified prefix (e. g., +, -, or a numerical prefix) and F_i stands for " i^{th} feature." If two different sets are being used, I may emphasize this difference by using different letters for each of the different sets.

Figure 11 is a more detailed representation of the hypothetical species illustrated in Figure 9. Figure 11 shows the feature descriptions of the habitat requirement for the activities performed by the fictitious species.

Morphological Description

Once these descriptions have been completed it is possible to

place \rightarrow \pm sub* \pm med* \pm org* \pm surface
 \pm org* \pm surface --- \pm vertical* \pm smooth* \pm bark* \pm thin
 temp \rightarrow n range* m maximum* k variance
 osmo \rightarrow \pm ion* \pm water* \pm periodic
 \pm ion \mapsto \pm chlorine* . . .
 \pm periodic \mapsto n range
 current
 light \rightarrow n range* m max* \pm periodic
 nest \rightarrow n physiog* m density* \pm construct* \pm hole* . . .
 \pm construct* - hole \rightarrow - hole* \pm grass
 - grass \rightarrow m twig size
 \pm grass \mapsto m length
 feed \rightarrow \pm self
 \pm self \rightarrow \pm same
 \pm same \rightarrow $\begin{bmatrix} \alpha & F & 1 \\ v & F & n \end{bmatrix} / X + \begin{bmatrix} \alpha & F & 1 \\ v & F & n \end{bmatrix} + Y \text{---}$
 - self \rightarrow "features of another species"
 maneuver \rightarrow \pm aquatic* n physio layer* n density of layer* . . .
 climb \rightarrow \pm vegetation
 \pm vegetation \rightarrow "morphological features"
 chem \rightarrow \pm leaves* \pm fruit* \pm fatal
 crypsis \rightarrow \pm change* \pm pattern* \pm ornament
 - pattern \rightarrow n background color
 \pm pattern \rightarrow n background pattern
 \pm ornament \rightarrow \pm living* \pm vegetative matter
 search \rightarrow place + temp + light
 pursue \rightarrow place + temp + light
 attack \rightarrow place + temp + light
 consume
 passive
 weapon
 burrow
 carrier

Figure 10. Some rules for the description of the residual non-terminal items of the species base grammar.

describe the morphology of each species. It is imperative to note the precise reason for describing the morphological structure of a species, for this will greatly limit the detail to which we must go in making the description. We must specify the morphology of every species for the same reason we must specify the "morphology" of the abiotic habitat: some species's morphologies describe, in part, the environmental requirements of certain other species. Morphological structures are, in my view, context-sensitive; in fact, they are completely so. This position adopts an essentially teleological stance. First, we specify the activities (goals), then we specify the habitats required for the completion of those goals, and finally we specify the morphological features necessary to perform these activities.

The primary objects that must be included in a description of morphology are the exterior of the species, its size, any chemical substances it may emit, and its active defenses that are used to avoid predators. The morphological exterior of a species includes a description of important parts of the species (legs, leaves, etc.) and a description of the composition of the exterior (woody, fleshy, spiny, etc.). The descriptions of these objects will proceed primarily in the same way as the non-terminals such as "place," "temp," and so on, by means of the "store and re-write" rule: $\vdash \rightarrow$. There will, however, be a few context-free rules. An example of the morphological descriptions is provided in Figure 12. An application of these

1. Morph \rightarrow size + parts
2. size \mapsto n vertical* n max length* n max width
3. parts $\mapsto \left\{ \begin{array}{l} - \text{body}* + \text{exterior} / \text{"size = small"} \\ + \text{body}* \pm \text{legs}* \pm \text{wings}* \pm \text{tail} / \text{search attack} \# \text{size} __ \# \\ \pm \text{roots}* \pm \text{stem}* \pm \text{branches}* \pm \text{leaves} / \text{consume} __ \# \\ \hspace{10em} \# \text{size} __ \# \end{array} \right.$
4. $\left[\begin{array}{c} - \text{body} \\ + \text{exterior} \end{array} \right] \mapsto \begin{array}{l} \pm \text{spines}* \pm \text{cilia} \\ + \text{spine} \rightarrow \text{n length* . . .} \end{array}$
5. + roots $\mapsto \begin{array}{l} \pm \text{branching} \\ + \text{branching} \mapsto \text{n depth* n width* n ave diameter} \\ - \text{branching} \mapsto \pm \text{tap root* n diameter} \end{array}$
6. + stem $\mapsto \begin{array}{l} \pm \text{woody} \\ + \text{woody} \mapsto \pm \text{smooth* n bark depth} \\ - \text{smooth} \mapsto \pm \text{scaly}* \pm \text{thorns* . . .} \end{array}$
7. + branch $\mapsto \text{n size* } \pm \text{similar* n between distance}$

$+ \text{similar} \mapsto \left\{ \begin{array}{ll} + \text{woody} / \left[\begin{array}{c} \pm \text{stem} \\ \pm \text{woody} \end{array} \right] & __ \\ - \text{woody} / \begin{array}{c} \pm \text{stem} \\ - \text{woody} \end{array} & __ \\ - \text{similar} \mapsto - \text{woody} / \begin{array}{c} + \text{stem} \\ + \text{woody} \end{array} & __ \end{array} \right.$
8. + leaves $\mapsto \begin{array}{l} \pm \text{needles} \\ - \text{needles} \mapsto \pm \text{succulent}* \pm \text{hairy}* \pm \text{serrated edges}* \\ \hspace{10em} \pm \text{oriented* . . .} \end{array}$
9. + body $\mapsto \begin{array}{l} \pm \text{distinct head}* \pm \text{streamlined}* \pm \text{scales* n size} \\ - \text{scales} \mapsto \pm \text{hair} \\ - \text{hair} \mapsto \pm \text{chitin} \end{array}$
10. + legs $\mapsto \text{n number* n size}$
11. + wings $\mapsto \text{n number* n size}$

Figure 12. Some rules for the description of the morphology of a species.

descriptions to the earlier hypothetical species is given in Figure 13.

Two aspects of these rules that are not evident from Figure 12 are that the actual choice of +, or -, or a particular numerical prefix is context-sensitive, and the order in which the #Morph# categories for each developmental stage is re-written must be specified. The context-sensitivity of the prefacing symbols will be a function of activities and required habitats. They must be specified in any complete grammar of morphological characters, but I will not provide these CS rules.

Because earlier developmental stages influence the morphology of later stages, the specification of the #Morph# categories must be ordered. This ordering is provided by context-sensitive rules of the following form.

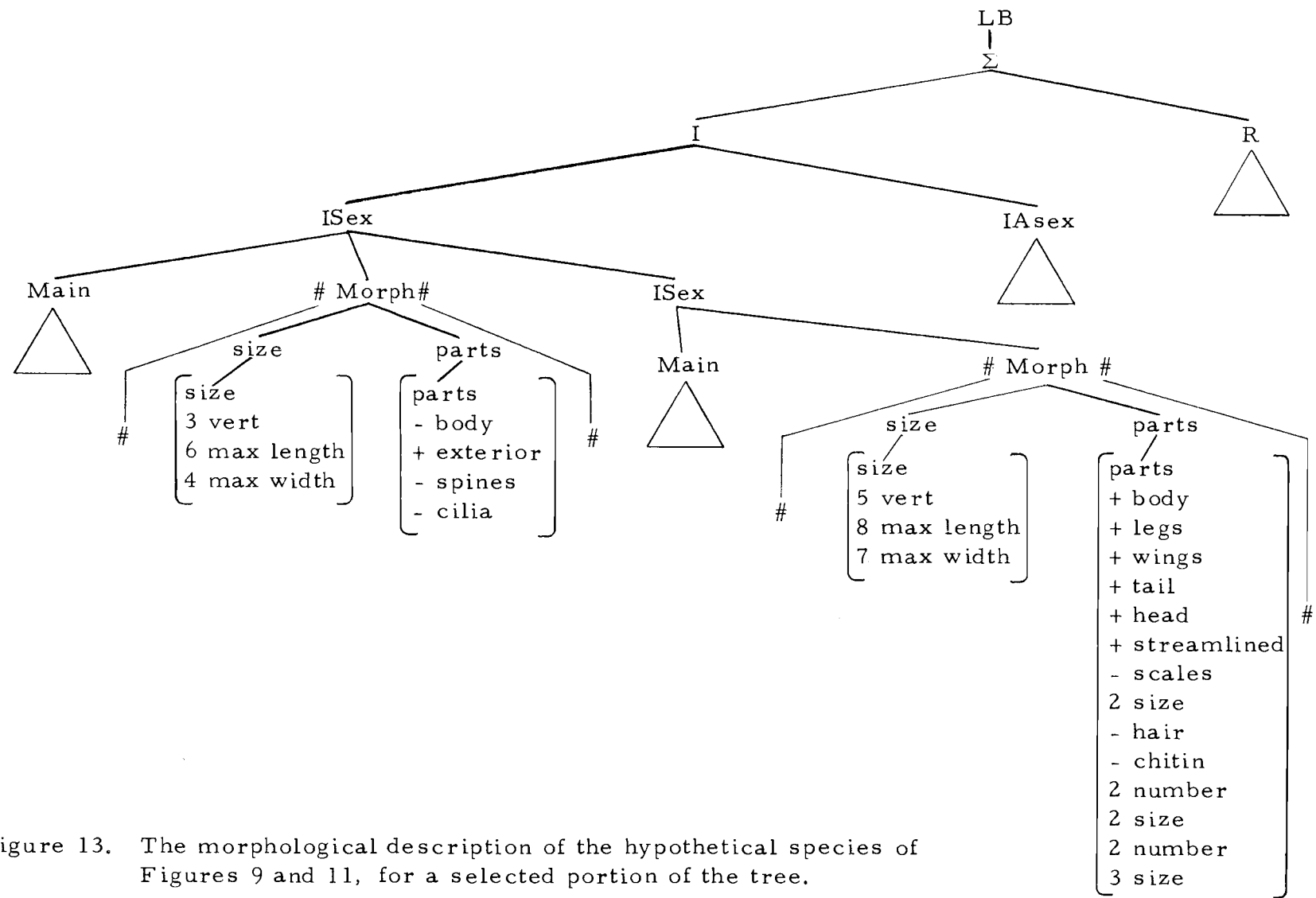
$$1. \quad V + \#Morph\# + W + \#Morph\# + X \dots Y + \#Morph\# + Z \longrightarrow$$

$$V + \# \begin{bmatrix} \alpha \vdots F_i \\ \nu \vdots F_n \end{bmatrix} \# + W + \#Morph\# + X \dots Y + \#Morph\# + Z$$

$$2. \quad V + \# \begin{bmatrix} \alpha \vdots F_i \\ \nu \vdots F_n \end{bmatrix} \# + W + \#Morph\# + X \dots Y + \#Morph\# + Z \longrightarrow$$

$$V + \# \begin{bmatrix} \alpha \vdots F_i \\ \nu \vdots F_n \end{bmatrix} \# + W + \# \begin{bmatrix} \alpha \vdots F_i \\ \nu \vdots F_n \end{bmatrix} \# + X \dots Y + \#Morph\# + Z$$

This is continued until all #Morph# categories have been re-written. In this way the path of morphological development is contingent upon both previous stages and the activities of the present stage.



The morphological description of the optional "fruit" proceeds in essentially the same way except there is less context-sensitivity on the activity structure of the species. The sensitivity that does exist is mainly dependent on the species morphology, which implies that fruit description must follow species description. Thus, the color of the leaves could influence the color of the fruit, and the size of the plant limits (but does not determine) the size of the fruit. A brief example of the fruit morphology rules is given in Figure 14.

A Transformational Grammar

An additional topic relating to a grammar of species is the justification and description of the transformation rules that are required. In the Introduction I reformulated the concept of niche, and, by the assumption of genetic homogeneity, related the problem of its representation to the problem of specifying the set of all possible trajectories that constitute an idealized niche manifold. The operational criterion (theoretically, at least) for including any given trajectory among those possible for a particular species is that the trajectory corresponds to a set of environmental features that are a subset of the requirements of the activities of the individuals of the species. That is, if it can be shown that a set of environmental features are a subset of those features dominated by a particular LB in a tree diagram, then the set of features are part of the niche

1. $\text{fMorph} \rightarrow [(\text{flower}(\text{liquid}))(\text{solid})]$
2. $\text{flower} \mapsto \begin{array}{l} \pm \text{compound} * \pm \text{single color} * \pm \text{rough texture} \\ + \text{compound} \mapsto \text{n diameter} * \text{n height} * + \text{individual} \\ + \text{individual} \mapsto \text{n diameter} * \text{n height} \\ - \text{compound} \mapsto \text{n diameter} * \text{n height} \end{array}$
3. $\text{solid} \mapsto \begin{array}{l} \pm \text{coat} * \pm \text{sweet} \\ + \text{coat} \mapsto \text{n thickness} * \pm \text{hairy} \end{array}$
4. $\text{liquid} \mapsto \text{n amount}$

Figure 14. Some rules for the description of the morphology of the "fruit" (including: flower, nectar, and fruit) of a species.

manifold of an idealized individual that represents the entire, homogeneous species. Since this idealized individual can perform different activities at different times that require different features, it follows that the structure of the idealized niche manifold must comprise a composite of those different activities. Niche invariance is a name I give to the phenomenon that different activities performed by the same idealized individual ("species") alter the set of niche trajectories without altering the name (i. e. , LB) of the species. I shall use transformation rules to provide an explicit procedure that changes niche trajectories without changing species names.

The transformation rules perform two major tasks. The first task is to alter the base descriptions that gave to the species optional habitat requirements. For example, it was possible for the grammar to generate a species that could reproduce by both sexual and asexual means. But the criterion of inserting species into a habitat is made on the test that the environment meets all of the demands of the species. The base grammar of a species possessing optional behavior states that the environment must provide not one or the other of the options, but rather the requirements of both options. Thus, one of the functions of the transformation rules is to alter the base grammar output so that the same species can be represented by both of its options. Thus, after the transformation rules operate, a species with options is represented as having two or more sets of

requirements, any one of which is sufficient for insertion. The second major task of transformation rules is to alter the description of those species that do not perform certain activities that the base rules generate as required. For example, salmon do not feed during a portion of their life; to eliminate this activity requires a special transformation.

Figure 15 contains a list of some relevant transformations. These rules consist of a structural description (SD) that describes which structures must be present in the derivation in order for the rule to apply. They also possess a structural change (SC), which describes what changes in the history are produced by the rule. The labeled brackets in the rules indicate that the string contained within the brackets are all dominated by (or decomposed from) a node in a tree diagram that has the same label as the labeled bracket. Thus, $\begin{matrix} [B + C + D] \\ A \qquad A \end{matrix}$ represents a portion of a tree derived from the history of the rules: (1) $A \rightarrow Q$, (2) $Q \rightarrow B + C + D$, where A may or may not be directly above, or dominating, the string "B + C + D."

Undefined non-terminal items in these rules, such as W, X, Y, Z, represent variables that may be filled by any set of defined non-terminal items. The variables are merely notational devices that indicate that the transformation rule will still apply regardless of what string the base rules have generated for the variable. Figure 16 shows the effects these transformation rules have on the tree diagrams.

$\Sigma T1$: (optional)

$$[W + [X + F + \text{site} + Y] + Z]$$

	$\underbrace{\text{LB}}$	$\underbrace{\text{R}}$		$\underbrace{\text{R}}$	$\underbrace{\text{LB}}$
SD:	1	2	3	4	5
SC:	1	2	\emptyset	4	5

$\Sigma T2$: (obligatory)

$$[W + [X + F_1 + F_2 + Y] + Z]$$

	$\underbrace{\text{LB}}$	$\underbrace{\Sigma}$		$\underbrace{\Sigma}$	$\underbrace{\text{LB}}$
SD:	1	2	3	4	5
SC:	1	(2+3+5)		(2+4+5)	6

$\Sigma T3$: (obligatory)

$$[X + [\text{ISex} + \text{IAsex} + \text{Main} + \text{RepSex} + \text{RepAsex} + Y] + Z]$$

	$\underbrace{\text{LB}}$	$\underbrace{\Sigma}$					$\underbrace{\Sigma}$	$\underbrace{\text{LB}}$
SD:	1	2	3	4	5	6	7	8
SC:	1	(2+3+5+6+8)			(2+4+5+7+8)			9

$\Sigma T4$: (obligatory)

$$[W + [X + \text{cross} + \text{carrier} + \text{self} + Y] + Z]$$

	$\underbrace{\text{LB}}$	$\underbrace{\Sigma}$		$\underbrace{\Sigma}$	$\underbrace{\text{LB}}$
SD:	1	2	3	4	5
SC:	1	(2+3+5)		(2+4+5)	

$\Sigma T5$: (obligatory)

$$[X + [Y + \text{care} + \text{species} + \text{care}] + Z]$$

	$\underbrace{\text{LB}}$	$\underbrace{\Sigma}$			$\underbrace{\Sigma}$	$\underbrace{\text{LB}}$
SD:	1	2	3	4	5	6
SC:	1	(2+3+4+6)			(2+5+6)	

Figure 15. Some transformation rules of a species grammar.

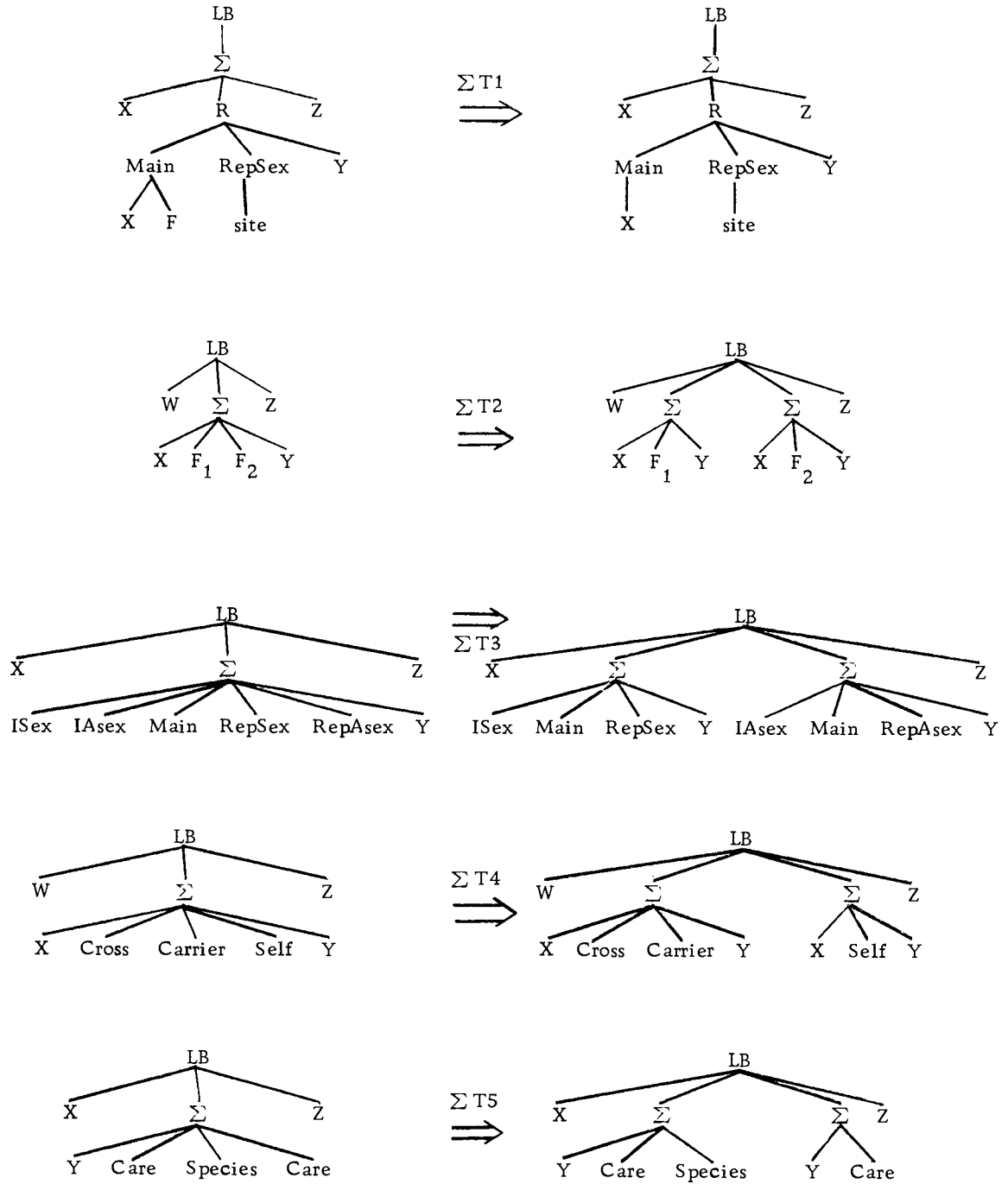


Figure 16. The effects of the species transformation rules on the tree diagram.

Transformational rules numbered $\Sigma T2$ through $\Sigma T5$ are all examples of rules that convert a "species" with options into a set of "species" that all go by the same Latin binomial. That is, the transformations create new species that are dominated by the same LB node. For example, $\Sigma T3$ converts a species with an option between sexual and asexual reproduction into a species that may reproduce either sexually or asexually. This rule is obligatory in the sense it must be applied every time the SD conditions are met. Similar remarks apply to $\Sigma T2$, $\Sigma T4$, and $\Sigma T5$. Transformation $\Sigma T1$ is a rule of the type that accounts for certain special cases; as a result, $\Sigma T1$ is optional. This rule allows some species to reproduce without feeding during their reproductive mode. Salmon are an example of this behavior.

Ecosystems

The next major topic to be considered is the nature of the rules that generate a species list that could be called a stage in an ecological succession. One of the important obstacles in the way of defining a grammar for an ecosystem stems from the arbitrariness involved in defining any particular system. Laszlo (1972, p. 30), following James G. Miller, defines a natural system as ". . . a region of physical space-time. . . organized into coacting interrelated subsystems or components." Such a definition entails, and was intended

to entail, a wide variety of interpretations. Nor is there, among ecologists that claim to be students of ecosystems, an agreed upon set of physical or biological features that every ecosystem must possess in order for it to be classed as an ecosystem. Thus, there have been studies of "ecosystems" that are no bigger than a laboratory flask, no more complicated than a single species, that have no other habitats than a column of water or a portion of soil. Dale (1970) defines ecosystem as any system with at least one living thing in it. Odum (1959) requires that an ecosystem have both autotrophs and heterotrophs. Evidently, the concept is intended to apply to any collection of organisms living under more or less natural conditions. This requires that the concept apply to terrestrial and aquatic, marine and freshwater, as well as lotic and lentic systems.

A CSG for Resource Utilization

The rules I will use to generate a description of the ecosystem will resemble for the most part the rules used for species. Both re-write (\rightarrow) and storage (\mapsto) rules will be used. There will, as well, be transformation rules, but these will have a slightly different use than previous transformations. The process of generating a species list corresponding to some ecosystem is based on an iterative process, which will be explained and described below. Figures 17 and 18 provide an example of the ecosystem grammar; Figure 17a

(a)

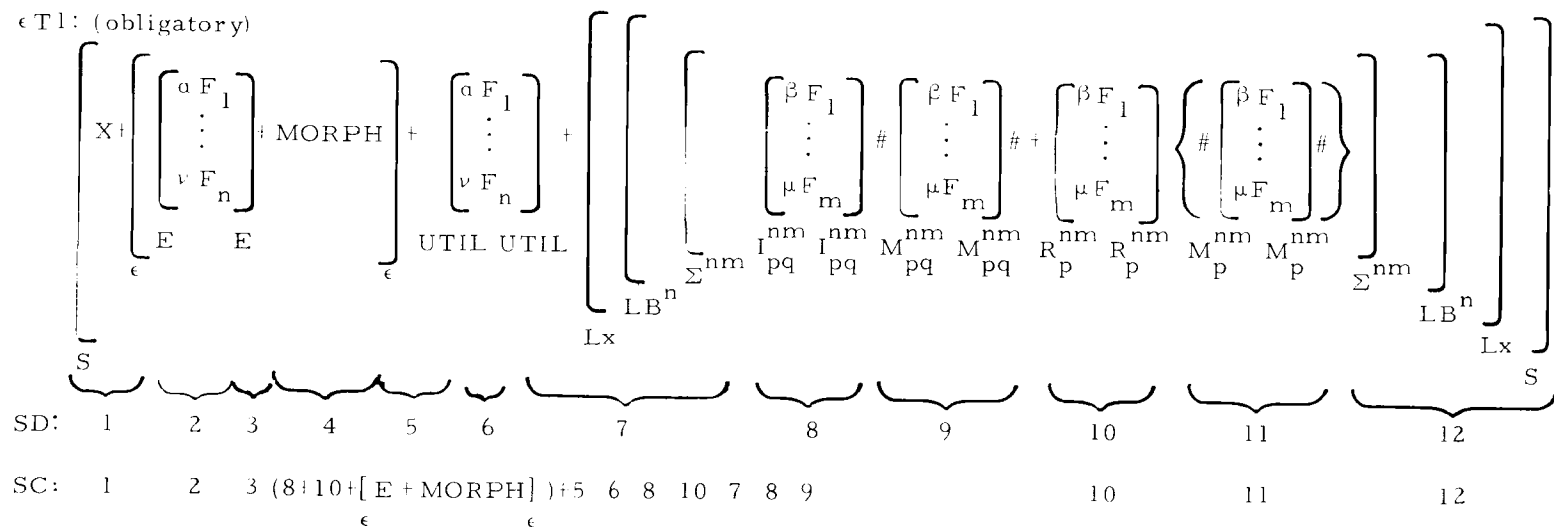
1. $S \longrightarrow \epsilon + \text{UTIL} + \text{Lexicon}$
2. $\epsilon \longrightarrow E(E)\text{MORPH}$
3. $E \longrightarrow (\text{Air}) [(\text{Water})(\text{Soil})] (E)$
4. $\text{Air} \longrightarrow \text{radiant} + \text{temp} + \text{moist}(\text{current})\text{physiog}(\text{Air})$
5. $\text{Water} \longrightarrow \text{radiant} + \text{temp} + \text{nut} + \text{osmo}(\text{current})\text{physiog}(\text{Water})$
6. $\text{Soil} \longrightarrow \text{temp} + \text{moist} + \text{nut} + \text{osmo} + \text{physiog}(\text{Soil})$

(b)

$\text{physiog} \longrightarrow n \text{ height} * m \text{ density} * p \% \text{ cover} * q \text{ stem width} * . . .$
 $\text{temp} \longmapsto \pm \text{seasonal} * n \text{ range} * n \text{ average}$
 $\text{osmo} \longrightarrow \pm \text{saline} * \pm \text{CO}_2 * \pm \text{O}_2$
 $\text{radiant} \longmapsto \pm \text{seasonal} * n \text{ range} * n \text{ average}$
 $\text{nut} \longmapsto \pm \text{NO}_3 * \pm \text{PO}_3$
 $\quad \quad \quad + \text{NO}_3 \longmapsto n \text{ amount}$

Figure 17. The base grammar and distinctive features for describing ecosystems. (a) The base grammar. (b) The distinctive features of some residual non-terminal items.

εT1: (obligatory)



Conditions:

- (i) $\forall n \forall m [\bigcup_{i=1}^p \bigcup_{j=1}^q (I_{ij}^{nm} \subseteq 2) \wedge \bigcup_{i=1}^p (R_i^{nm} \subseteq 2)]$; where $I_{ij}^{nm} \subseteq 2$ means $\{ [\beta F_1, \dots, \mu F_m] \} \subseteq \{ [\alpha F_1, \dots, \nu F_n] \}$
 $I_{pq}^{nm} \subseteq 2$ means $\{ [\beta F_1, \dots, \mu F_m] \} \subseteq \{ [\alpha F_1, \dots, \nu F_n] \}$
 $R_p^{nm} \subseteq 2$ means $\{ [\beta F_1, \dots, \mu F_m] \} \subseteq \{ [\alpha F_1, \dots, \nu F_n] \}$
- (ii) $\forall n \forall m [\bigcup_{i=1}^p \bigcup_{j=1}^q (I_{ij}^{nm} \not\subseteq 6) \wedge \bigcup_{i=1}^p (R_i^{nm} \not\subseteq 6)]$
- (iii) $\forall M_{pq}^{nm} \exists [n \text{ height }]_{\text{phys}} ([n \text{ height }]_{\text{phys}} \in 2 \wedge \# [n \text{ size }]_{\text{phys}} \leq [n \text{ height }]_{\text{phys}})$, $q = \{0, 1, 2, \dots\}$

Figure 18. The first ecosystem transformation, εT1, giving the three conditions for species insertion.
Lx = Lexicon.

corresponds to the base grammar; Figure 17b describes some of the non-terminals as terminal distinctive features, and Figure 18 provides a mechanism for the insertion process. In what follows I will provide a translation of the rules.

Rule 1: "re-write S (state) as ϵ (ecosystem) plus UTIL (utilization) plus Lexicon." This rule decomposes a state (S) of a temporal ecocline into an ecosystem plus a list of species which utilize a portion of the ecosystem plus a pool of species, the Lexicon, from which the utilizers are drawn. The category ecosystem will, after a complete operation of the grammar, comprise a set of habitat features plus a set of morphology features. To avoid terminological difficulties I will refer to habitat features as the abiotic aspects of the ecosystem, morphological features as those aspects of the ecosystem that derive from the morphology of an organism, and environmental features as the set union of the above two.

Rule 2: "re-write ϵ as E (environment) plus (optionally) E plus MORPH." The following rules will specify the particular environmental features that E may dominate. The optional E provides the grammar a means of describing patchy environments. That is, by choosing the optional E the grammar may describe an ecosystem that possesses both aquatic and terrestrial types of habitats. It may also describe terrestrial habitats that differ in their distinctive features, but exist in close proximity to one another, such as forests and woodland meadows.

(optionally) 'Air'. " This rule describes the set of characters that define the physical habitat of one layer of air. More categories of habitat features than I have enumerated may be needed, of course. In choosing the optional Air, the grammar maps the left-to-right order of the layer descriptions onto the top-to-bottom vertical order of the real vegetative layers.

Rule 5: "re-write Water as radiant plus 'nut' (nutrients) plus 'osmo' (osmotic forces) plus 'temp' plus (optionally) 'current' plus 'physiog' plus (optionally) 'water'. " This rule is identical in form to Rule 4 above, except that it describes the water component of a physical habitat.

Rule 6: "re-write Soil as 'osmo' plus 'moist' plus 'nut' plus 'temp' plus 'physiog' plus (optionally) 'Soil'. " This rule is identical in form to Rules 4 and 5 above, except that Rule 6 describes the soil component of a physical habitat.

In the second part of the grammar, Figure 17b, the distinctive features of the non-terminals generated by the ecosystem base rules are provided. These features define the abiotic plus physiognomic features of the ecosystem. There are several systems of features that have been proposed in previous literature. Wiens (1969) offers a succinct review of some of these systems plus a detailed system that he applied to grassland bird communities. Schoener (1974) reviews the literature of many independent studies and provides a

table (Table 1, p. 30-31) of features that separate a wide variety of taxonomic groups. Knight and Loucks (1969) provide a system of functional and morphological features that they applied to Wisconsin vegetation. Other systems of physiognomy can be found in Shimwell (1971). The actual specification of the non-terminals is by means of the storage rule and the basic format is similar to the analogous species rules that I have enumerated. Layers are defined according to some system of physiognomic classification. Any suitable system must, however, reflect the use of vertical space by animals, as well as the vertical distribution of vegetation. The order, however, which each layer (within "Air," for example) is specified must be defined, since there is a strong context dependency among the features of the various layers. Within the habitat "Air" the procedure is to first describe the physiognomy of the vegetative layer that lies closest to the interface of the next habitat (either "Water" or "Soil"). Next, the physiognomy of the vegetative layer that lies immediately above this lowest layer is described. This process is continued until the physiognomies of all the vegetative layers enumerated by one particular action of the grammar have been described. Finally, the distinctive features of the habitat are described by means of the storage rules. This procedure is done in the reverse order of the physiognomies, i. e., from the highest vegetative layer to the lowest. An abstract example of this procedure is provided below; let HD be the

category of habitat descriptions. The specification of a two-layered system is as follows.

- $$\begin{aligned}
 (1) \quad & \text{HD} + \text{physiog} + \text{MORPH} + \text{HD} + \text{physiog} + \text{MORPH} \longrightarrow \\
 & \text{HD} + \text{physiog} + \text{MORPH} + \text{HD} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH}. \\
 (2) \quad & \text{HD} + \text{physiog} + \text{MORPH} + \text{HD} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} \longrightarrow \\
 & \text{HD} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} + \text{HD} + \begin{bmatrix} \beta : F_1 \\ \mu : F_m \end{bmatrix} + \text{MORPH}. \\
 (3) \quad & \text{HD} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} + \text{HD} + \begin{bmatrix} \beta : F_1 \\ \mu : F_m \end{bmatrix} + \text{MORPH} \longrightarrow \\
 & \begin{bmatrix} \gamma : F_1 \\ \lambda : F_l \end{bmatrix} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} + \text{HD} + \begin{bmatrix} \beta : F_1 \\ \mu : F_m \end{bmatrix} + \text{MORPH}. \\
 (4) \quad & \begin{bmatrix} \gamma : F_1 \\ \lambda : F_l \end{bmatrix} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} + \text{HD} + \begin{bmatrix} \beta : F_1 \\ \mu : F_m \end{bmatrix} + \text{MORPH} \longrightarrow \\
 & \begin{bmatrix} \gamma : F_1 \\ \lambda : F_l \end{bmatrix} + \begin{bmatrix} \alpha : F_1 \\ \nu : F_n \end{bmatrix} + \text{MORPH} + \begin{bmatrix} \gamma : F_1 \\ k : F_k \end{bmatrix} + \begin{bmatrix} \beta : F_1 \\ \mu : F_m \end{bmatrix} + \text{MORPH}.
 \end{aligned}$$

This ordering is required if the grammar, after defining some x number of layers, began with the highest layer and described it with features appropriate to, for example, a layer of moss, then there would be $x-1$ layers remaining for which there would be no feature specifications. By beginning with that layer closest to the ground, however, even if the grammar described it in terms of a very high canopy, there is still "room" for more layers above the first

described. On the other hand, once the physiognomy has been specified, the descriptions of the habitat features (temperature, sunlight, etc.) can be made. This ordering is justified because of the impact that physiognomy has on the physical habitat. Increased vegetation decreases light intensity, decreases temperatures, decreases evaporation, and so forth. Moreover, since the input of radiant energy is almost exclusively unidirectional from above, the upper layers of vegetation influence the lower ones. As a result, in order for a grammar to correctly match habitat features with vegetative layers, the physiognomy of the layers must be known to the grammar prior to the habitat description. In addition, since higher layers influence lower layers, the habitat description of higher layers must be known prior to that of the lower layers, for the latter are embedded in the "context" of the former. Therefore, physiognomic descriptions must precede that of lower layers.

A Transformational Grammar

The third part of the ecosystem grammar (Figure 18) provides a mechanism for the insertion of species and ensures that the ecosystem never generates utilization of an environment (biotic or abiotic) for which there are no species in the lexicon. Species insertion is, in other words, controlled and limited by the lexicon. The first step in species insertion is to provide utilizers, in the form of

species names, of the physical habitat that the base grammar has generated. Selecting which species have the necessary habitat requirements for insertion is done by some physical device that knows the particular habitat generated and can scan the lexicon for those species which require the available habitat. Once such a device has discovered a species, it notes the name and replaces "MORPH" with a list of features that correspond to the morphology of the species as it is stated in the lexicon. The device then scans the lexicon a second time until it discovers another species which requires some subset of the abiotic environment that the ecosystem rules have generated. The morphology of this second species is appended to the list of features for the first species. The scanning device proceeds in this fashion until no more species in the lexicon can be inserted. Figure 22 shows the transformational effects on the trees generated by the S base grammar.

This procedure has been denoted by a transformational rule, $\epsilon T1$. Since the notation is complex, I will describe this rule in detail. Structural description index number 1 represents a variable X. This variable can be filled by any set of categories that have been generated to the left of the category " ϵ " being considered. X is empty (\emptyset) during the first use of this transformation. $\epsilon T1$, however, is a rule that may apply more than once during the entire species insertion process. Hence, on the second and subsequent applications, X is

non-null; basically it represents the morphology of previously inserted species. SD2 represents the set of environmental features generated by the base grammar. SD3 is a special category that is to be filled by the morphology of the inserted species. SD4 is the utilization category; this will be filled by the habitat requirements of the inserted species. It is a list of habitats that are being used in the ecosystem. The remaining SD index numbers represent the entries of the Lexicon. As Figure 19 shows, each Latin binomial is given a number from one to n , each species type is given a number from one to m , each generation is given a number from one to p , and each developmental stage is given a number from one to q . This system corresponds to the actual lexical contents as illustrated in the bottom of Figure 19. SD 5 represents the habitat features required by the q^{th} developmental stage of the p^{th} generation of the m^{th} species type of the n^{th} Latin binomial; SD6 represents the corresponding morphological description. SD7 represents the habitat requirements of the reproductive stage of the p^{th} generation of the m^{th} species type of the n^{th} Latin binomial; SD8 represents the corresponding morphological description (optionally present).

The structural changes that occur as a result of ϵ T1 are dependent upon fulfilling certain conditions, which I shall describe

(b)

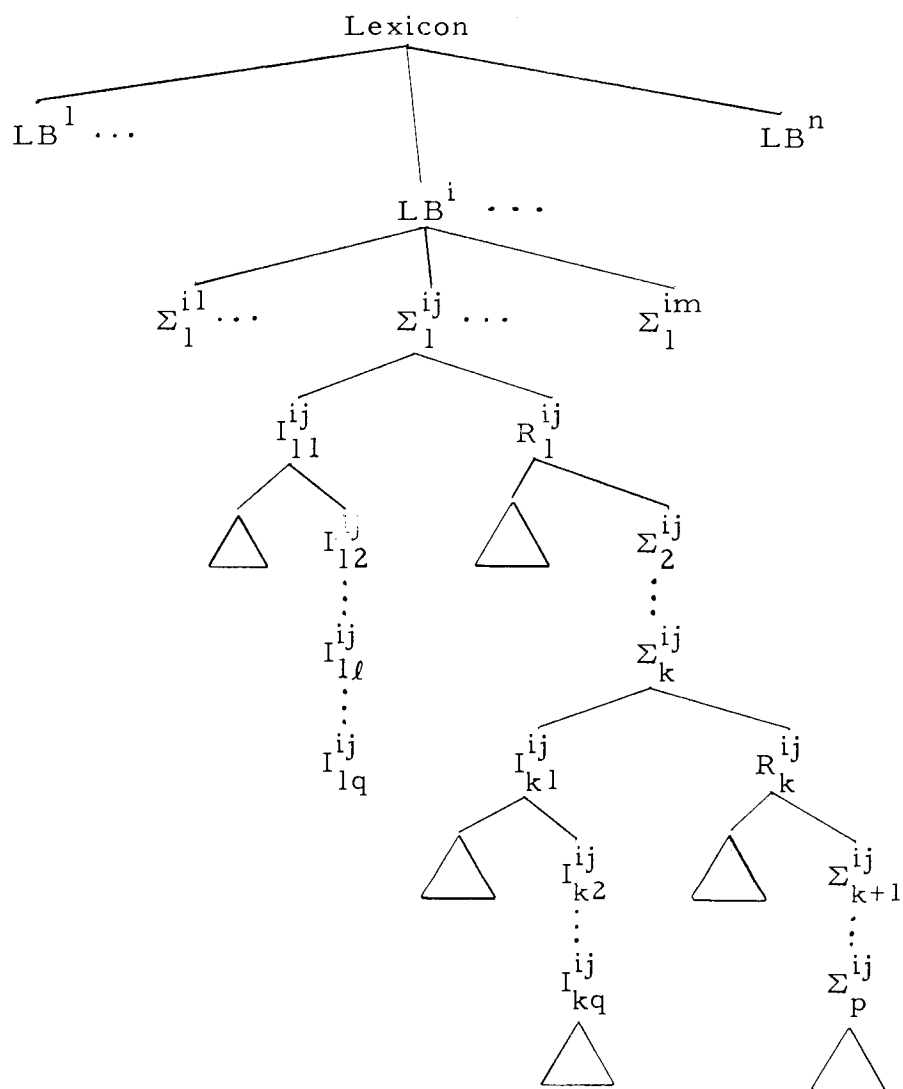


Figure 19. Continued.

presently. There are basically two changes that occur. First, MORPH is replaced by the morphology of the species that can utilize the available habitat of SD2 plus the E (environment) and MORPH categories of another ϵ (ecosystem). This latter addition is the mechanism whereby the niche creation pattern discussed earlier is incorporated into the grammar. The second change is to add to the list of utilized habitats in SD4 by adding to those already present the list of habitats required by new species. It is understood that there may be no features present in SD4 prior to the application of the structural change. $\epsilon T1$ does not affect the lexicon in any way.

The conditions that are placed on the application of $\epsilon T1$ (other than the SD conditions) can be rigorously stated in set notation. Condition (i) merely states that any species type of any Latin binomial may be inserted into the ecosystem provided that the habitat requirements of all generations and stages are available in the environment. Condition (ii) must also be met; it requires that the species types being inserted have not been previously inserted. Condition (iii) governs the morphological characters that are inserted; not every morphological feature of every developmental stage need be inserted even though the available habitat (SD2) allows it, as condition (i) requires. This is important in the case of large vegetation, such as trees, invading uncolonized areas. Young non-reproducing trees establish themselves first, even though a mature tree could reproduce there if it were present.

The niche creation process that was begun in $\epsilon T1$ is completed in $\epsilon T2$ (Figure 20). In the second transformation new environmental features are added to the unspecified E of $\epsilon T1$. These features are merely those features generated by the base grammar (SD2 in $\epsilon T2$) plus the morphological features of those species inserted by $\epsilon T1$. Thus, SD4 in $\epsilon T2$ is replaced by SD2 and SD3, all other SD index numbers remain unchanged. Once $\epsilon T2$ has applied, the structural conditions are met for $\epsilon T1$, so the lexicon scanner once again attempts to insert species into the ecosystem. If it succeeds during this second cycle, then it applies $\epsilon T2$ again. If the scanner fails to find a species that requires the set of habitat features, then it meets both the structural and set theoretical conditions of $T3$. Application of $\epsilon T3$ completes the species insertion cycle, by deleting the unused environment, illustrated in Figure 21.

In summary, the system of grammars has accomplished the following. By using the Σ (species) rules (i. e., base rules plus storage rules plus transformation rules) a lexicon has been created that specifies the habitat requirements plus some morphological characteristics of each species in the lexicon. Second, by using the ϵ (ecosystem) rules a list of species is derived that corresponds to a set of generated habitats (both biotic and abiotic). Now, although there is lack of complete agreement in the literature, there is some evidence that habitat requirements of species can overlap, creating

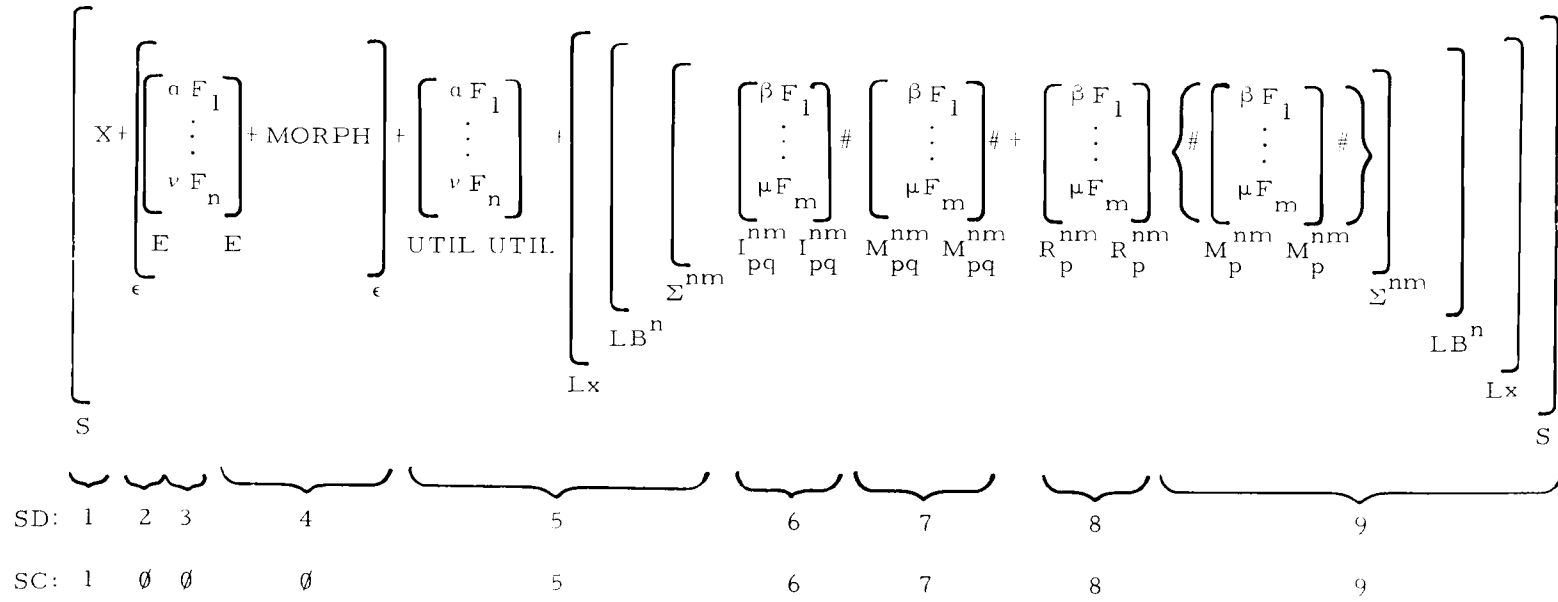
εT2: (obligatory)

$$\begin{array}{c}
 X + \left[\begin{array}{c} \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \\ E \end{array} \right] \\ E \end{array} \right] + \# \left[\begin{array}{c} \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \\ \# \end{array} \right] + \left[\begin{array}{c} E + \text{MORPH} \\ \epsilon \end{array} \right] + Y \\
 \epsilon \qquad \qquad \qquad \epsilon \qquad \qquad \qquad \epsilon \qquad \qquad \qquad \epsilon
 \end{array}$$

$$\begin{array}{ccccccc}
 \text{SD:} & \underbrace{1} & \underbrace{2} & \underbrace{3} & \underbrace{4} & \underbrace{5} & \underbrace{6} & 7 \\
 & & & & & & & \\
 \text{SC:} & 1 & 2 & 3 & 4 & 5 & [2+4] & 7 \\
 & & & & & E & E &
 \end{array}$$

Figure 20. The second ecosystem transformation, εT2. Shows how the morphology of inserted species becomes part of the environmental description of the ecosystem.

εT3: (obligatory)



Condition:

$$\forall n \forall m \left[\bigcup_{i=1}^p \bigcup_{j=1}^q (I_{ij}^{nm} \neq 5) \wedge \exists I_{ij}^{nm} (I_{ij}^{nm} \neq 3) \vee \bigcup_{i=1}^p (R_i^{nm} \neq 5) \wedge \exists R_i^{nm} (R_i^{nm} \neq 3) \right]$$

Figure 21. The third ecosystem transformation, εT3, giving the condition for the termination of species insertion.

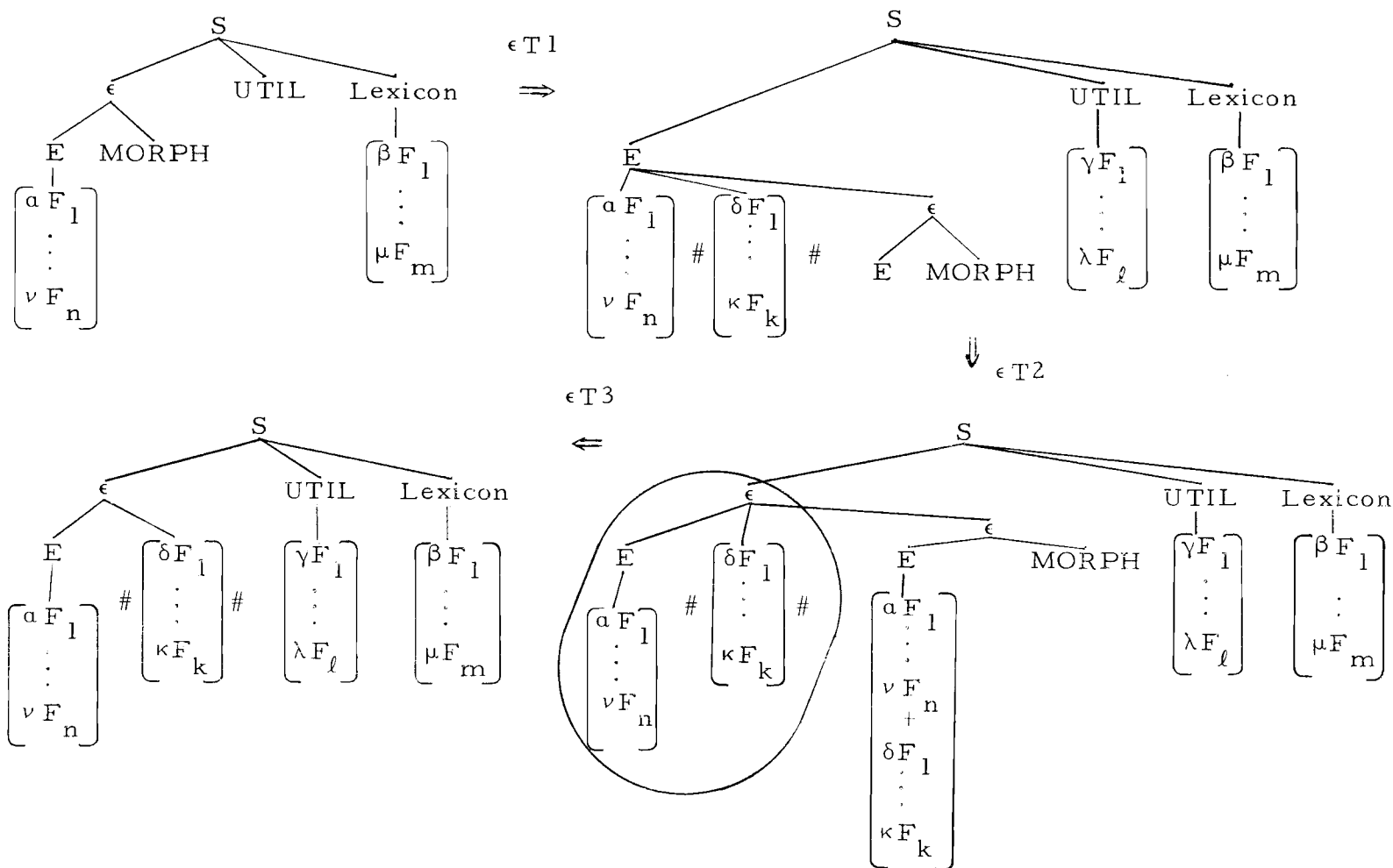


Figure 22. The action of the ecosystem transformation rules on the derived tree structure; shown here is one state of a temporal ecocline that possesses a lexicon with no species that utilize those that require only abiotic features (i.e., vegetation). Had the lexicon comprised users of vegetation it would have cycled back to $\epsilon T1$. The circled region in the third tree is the X category in the formal statements of $\epsilon T1$, $\epsilon T2$, and $\epsilon T3$.

the possibility of competition and, thus, the possibility that one of the competing species will not persist in the habitat. As examples we can cite barnacles (Connell, 1961), "island" birds (Diamond, 1972), and aquatic grasses (McNaughton and Wolfe, 1970). In these cases, and many others, removal of one or the other of the two species resulted in the expansion of the area exploited by one of the two species. The grammars described thus far would be insensitive to such phenomena and consequently would tend to generate ecosystems that are overpopulated with respect to species numbers. As a result, the grammar requires a procedure either to alter the niches of species that compete, or to remove all but one of the competing species from the ecosystem as a means of representing competitive exclusion. This procedure is the topic of the following section.

Species Interactions

There exist several avenues for providing a mechanism that will mimic and describe competitive interactions. In illustrating one such mechanism I will be dealing with three different sorts of competitive interaction. The first, and perhaps simplest, interaction will be between two competitors in the absence of predators. A special case emerges, as Hutchinson (1957) and Miller (1967) note, when one of the niches of two competitors is a proper subset of the other niche, and is "included" in the niche of the competitor. Miller (1967) argues

that niche inclusion can help explain competitive co-existence because a species, by restricting itself to a narrower (included) niche, has specialized to some extent and is, therefore, more efficient at exploitation of that niche. Consequently, it can devote more energy to reproduction, and thereby out-compete a broad-niched competitor.

In Figure 23a, a habitat and three species are listed as a set of distinctive features. Species A has the same habitat requirements as species B, except A has "+f," whereas B has no such requirement. Assume that "+f" is some feature in the environment that indicates that A is more narrowly adapted to the habitat. The feature "f" may be a narrower specification of a continuous variable like salinity, or an additional independent feature of the habitat. If the rule is obeyed that narrower habitat requirements imply greater specialization and increased ability to compete in that habitat, then Figure 23b indicates how the grammar can account for competitive interactions of this type. Refer to Figure 26 for a more general treatment, particularly condition (ii).

The condition on Figure 23b is necessary because frequency dependent predation can alter the outcome of competition between A and B. The rule that can be applied in this case (and it can be modified and restricted by stating additional characteristics of the prey and predator) is that competitors, in the presence of a predator that

(a) HABITAT	SPECIES A		SPECIES B		PREDATOR	
+a	Habitat		Habitat		Habitat	
-b	<u>Requirements</u>	<u>Morphology</u>	<u>Requirements</u>	<u>Morphology</u>	<u>Requirements</u>	<u>Morphology</u>
-c	+a, -b, -c,	-q, +r, +s,	+a, -b, -c,	-q, +r, +s,	-q, +r, +s,	+x, -y, +z
+d	+d, +e, +f	+t, -u, +v	+d, +e	+t, -u, +w	+t, -u, +v,	
+e					+w	
+f						

$$\begin{array}{c}
 \text{(b)} \left[\begin{array}{c} \left[\begin{array}{c} +a, -b, -c, +d, \\ +e, +f, -q, +r, \\ +s, +t, -u, +v, \\ +w, +x, -y, +z \end{array} \right]_{\epsilon} + \left[\begin{array}{c} X \\ \left[\begin{array}{c} +a, -b, -c, \\ +d, +e, +f \end{array} \right]_{\epsilon} \end{array} \right]_{\Sigma^A} + \left[\begin{array}{c} +a, -b, -c, \\ +d, +e \end{array} \right]_{\Sigma^B} + \left[\begin{array}{c} -q, +r, +s, +t, \\ -u, +v, +w \end{array} \right]_{\Sigma^B} + Y \end{array} \right]_{\Sigma^B} + \text{Lexicon} \Bigg]_S \\
 \underbrace{\hspace{1.5cm}}_1 \quad \underbrace{\hspace{1.5cm}}_2 \quad \underbrace{\hspace{1.5cm}}_3 \quad \underbrace{\hspace{1.5cm}}_4 \quad \underbrace{\hspace{1.5cm}}_5 \quad \underbrace{\hspace{1.5cm}}_6 \\
 \text{SD:} \quad \quad \quad 1 \quad \quad \quad 2 \quad \quad \quad 3 \quad \quad \quad 4 \quad \quad \quad 5 \quad \quad \quad 6 \\
 \text{SC:} \quad \quad \quad 1 \quad \quad \quad 2 \quad \quad \quad 3 \quad \quad \quad \emptyset \quad \quad \quad 5 \quad \quad \quad 6
 \end{array}$$

Condition: Predation is not frequency dependent. If predation is frequency dependent, then neither prey species excludes the other.

Figure 23. Simple competitive interactions, (a) shows the distinctive features of three hypothetical species, (b) shows the transformation rule for competitive exclusion.

feeds on all competitors according to their frequency, may co-exist.

There are, however, a great many instances where the outcomes of competition are indeterminant. Miller (1967) reviews some laboratory experiments the outcome of which depend on the initial conditions and, apparently, random events. In the presence of a predator that specializes on the previous winner, species A, the result of the competition between A and B is indeterminant. Thus, specialization alone is insufficient to determine if the predation on A is enough to give B the competitive advantage. As a result, the grammar cannot choose the winner and must do so either by random lot or by including more information in its rules. For the present, I leave this matter unresolved.

A final competitive interaction involves what has been termed "niche shifts" by Diamond (1972). These interactions involve niche alterations that are occasioned by the presence of another species. These alterations can be modeled as transformations of the original species derivations, much like the species transformation rules $\Sigma T1$ or $\Sigma T2$, except in the case of niche shifts the presence of another species is a condition for the applicability of the transformation.

The literature on niche shifts reveals that quite often a species, when in the presence of another species, will adopt a niche that is narrower than one which that species would occupy in the absence of other species. Now, it may be recalled that the grammar specifies

habitat requirements by generating a list of distinctive features. Since some of these features are optional and since some of the features can be used to describe ranges of habitat factors (e. g., temperature, salinity, etc.) it is possible that the presence of a competing species may alter the derivational history of another species. This can be done by adding features that more narrowly define the requirements of the species. It may also be done by providing necessary conditions for a transformation to choose alternative strategies (as, for example, $\Sigma T2$ did).

An example of the first possibility is due to Connell (1961). Here the situation is that a particular barnacle (Chthamalus) has a range of dessication that is broad in the absence of Balanus (another barnacle), but restricted in the presence of Balanus to the upper levels of the intertidal zone. Thus, the region of submergence that Chthamalus can tolerate is reduced in the presence of Balanus. This situation can be represented as a transformation rule, as illustrated in Figure 24. In Figure 24a, I have represented the amount of time that a species can tolerate submersion as an hierarchical decomposition similar to that proposed earlier on p. 88. Thus, the feature "+2.2 duration" denotes a submersion toleration of from 5 to 24 hours; "+4.2 duration" represents a submersion toleration of from 5 to 8 hours, and so on. In Figure 24b a partial feature description is presented for Chthamalus and Balanus, when they are isolated from

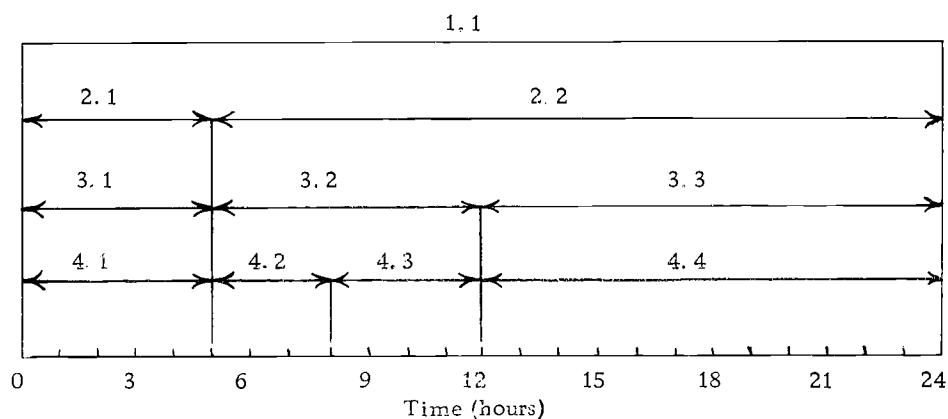


Figure 24a An hypothetical, hierarchical decomposition of desiccation time for marine organisms. For example, "3.3" duration" means the organism can sustain being desiccated for 12-24 hours.

<u>Chthamalus</u>	<u>Balanus</u>
place \rightarrow - sub* + med* + surface* - org	place \rightarrow - sub* + med* + surface* - org
osmo \rightarrow + ion* + water* + periodic	osmo \rightarrow + ion* + water* + periodic
+ ion \rightarrow + saline	+ ion \rightarrow + saline
+ water* + periodic \rightarrow 3.2 duration	+ water* + periodic \rightarrow 4.3 duration* 4.4 duration

Figure 24b. A partial feature description for two marine barnacles.

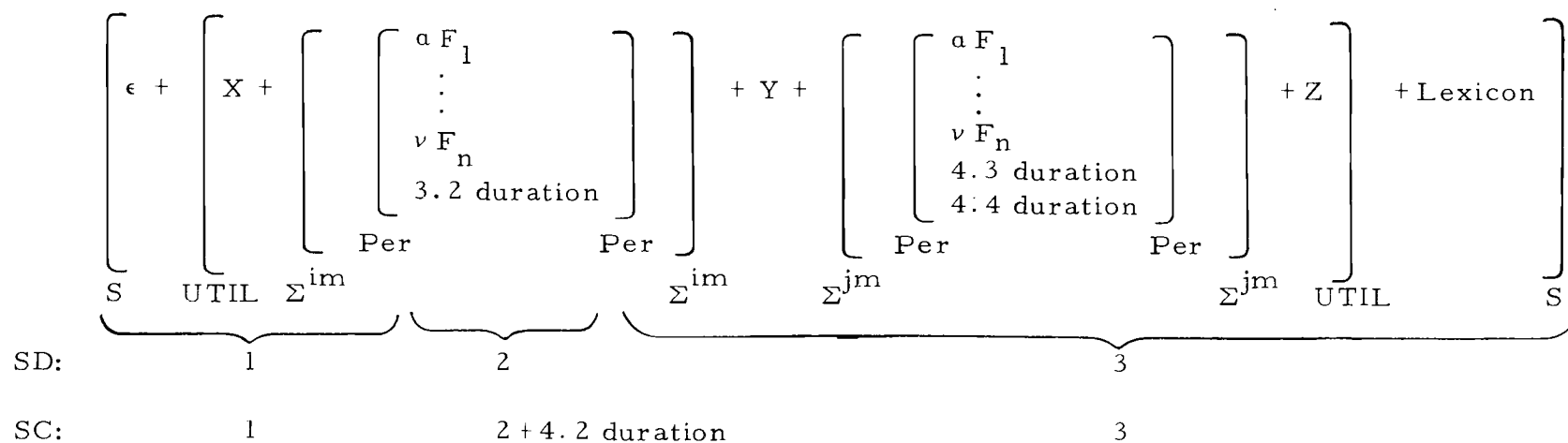


Figure 24c. A quantitative niche shift by Chthamalus (Σ^{im}) in the presence of Balanus (Σ^{jm}).

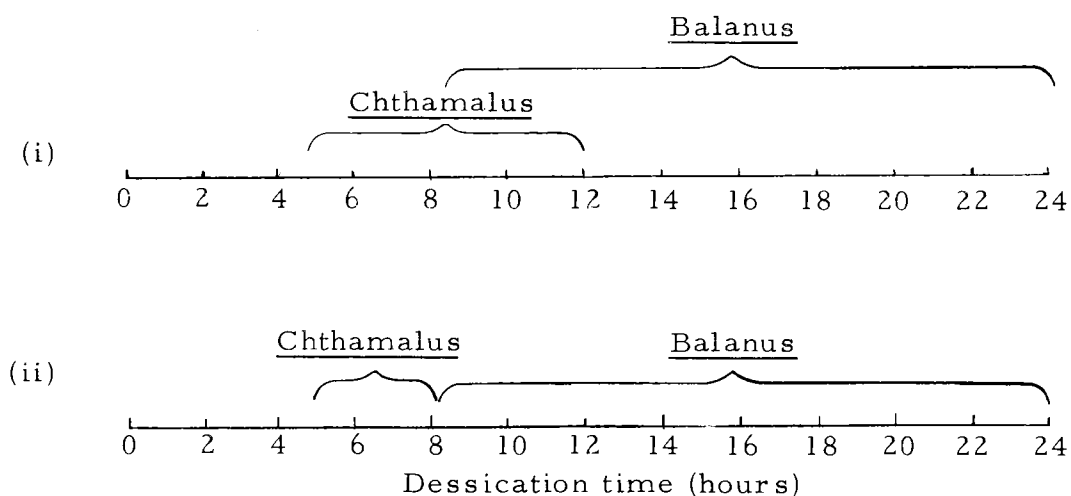


Figure 24d. The effects of the niche shift, (i) before and (ii) after.

one another. Figure 24c shows how the niche alteration of Chthamalus occurs in the presence of Balanus by the addition of the feature "+4.2 duration." Any one of the two representations shown in Figure 24c could be used to express the niche shifts. The effects of this transformation are schematically represented in Figure 24d. Notice, however, that this rule does not tell us that Chthamalus will be located higher in the intertidal zone than Balanus. It only states that, where they co-occur, Chthamalus will be located in any areas that receive only 5 to 8 hours of submergence, and Balanus in those areas that receive 8 to 24 hours of submergence. It is true, as a matter of physical fact, that reduced times of submergence are correlated with regions higher in the intertidal zone, but this is a fact that is secondary to the problem of accounting for the relative niche shifts of Balanus and Chthamalus.

The second representation of niche alteration applies to changes that do not occur across a continuous variable such as time of exposure to dessication. There are habitats or patches that have qualitatively different features and these may represent options available to a species, as asexual or sexual reproduction may be options. A situation of this sort could arise with respect to any of the major activities (Per, PA, or F) associated with "maintenance," but since the previous example was taken from Per, the following one will relate to F.

Consider the case of a species of bird with two foraging options: on the trunks of trees and in the air. The problem is to describe the grammatical mechanisms that will alleviate competition between this species and another that specializes on aerial foraging. Figure 25 gives the history of the applied rules plus the corresponding tree diagrams. I will assume that the aerial specialist's foraging behavior is identical to F_1 . One possible rule for predicting the outcome of competition in this example is that the specialist (being more efficient due to its specialization) outcompetes the generalist. The problem is to state general conditions for the case where one species is more specialized relative to another species. These conditions are stated in Figure 26, where the general case of competitive exclusion is given as a transformation rule. Condition (i) states that a species is more specialized if it can optionally forage in fewer habitats than some other species. In other words, one species has a smaller niche manifold than another. Since optional foraging habitats are denoted by species types (Σ^{nm}), simply counting the number of species types specifies the number of alternative habitats that a given species can inhabit. The more specialized can be determined by comparing these numbers between two species (Latin binomials). An alternative condition (ii) may also satisfy the requirements of $\epsilon T4$. In this condition, if the number of alternative habitats does not indicate the specialist, then the "within-habitat" specialization can be determined

$$F \rightarrow F_1 + F_2$$

$$F_1 \rightarrow \text{search} + \text{pursue} + \text{attack} + \text{consume}$$

$$\text{search} \rightarrow \text{place} + \text{temp} + \text{light}$$

$$\text{place} \rightarrow -\text{sub}^* + \text{med}^* + \text{surface}^* + \text{org}$$

$$+ \text{surface}^* + \text{org} \mapsto + \text{vertical}^* - \text{smooth}^* \\ + \text{bark}^* - \text{thin}$$

$$\text{pursue} \rightarrow \text{place} + \text{temp} + \text{light}$$

$$\text{place} \rightarrow -\text{sub}^* + \text{med}^* - \text{surface}^* - \text{org}$$

$$+ \text{med} \mapsto + \text{air}$$

$$\text{attack} \rightarrow \text{place} + \text{temp} + \text{light}$$

$$\text{place} \rightarrow -\text{sub}^* + \text{med}^* - \text{surface}^* - \text{org}$$

$$+ \text{med} \mapsto + \text{air}$$

$$F_2 \rightarrow \text{search} + \text{attack} + \text{consume}$$

$$\text{search} \rightarrow \text{place} + \text{temp} + \text{light}$$

$$\text{place} \rightarrow -\text{sub}^* + \text{med}^* + \text{surface}^* + \text{org}$$

$$+ \text{surface}^* + \text{org} \mapsto + \text{vertical}^* - \text{smooth}^* \\ + \text{bark}^* - \text{thin}$$

$$\text{attack} \rightarrow \text{place} + \text{temp} + \text{light}$$

$$\text{place} \rightarrow -\text{sub}^* + \text{med}^* + \text{surface}^* + \text{org}$$

$$+ \text{surface}^* + \text{org} \mapsto + \text{vertical}^* - \text{smooth}^* \\ + \text{bark}^* - \text{thin}$$

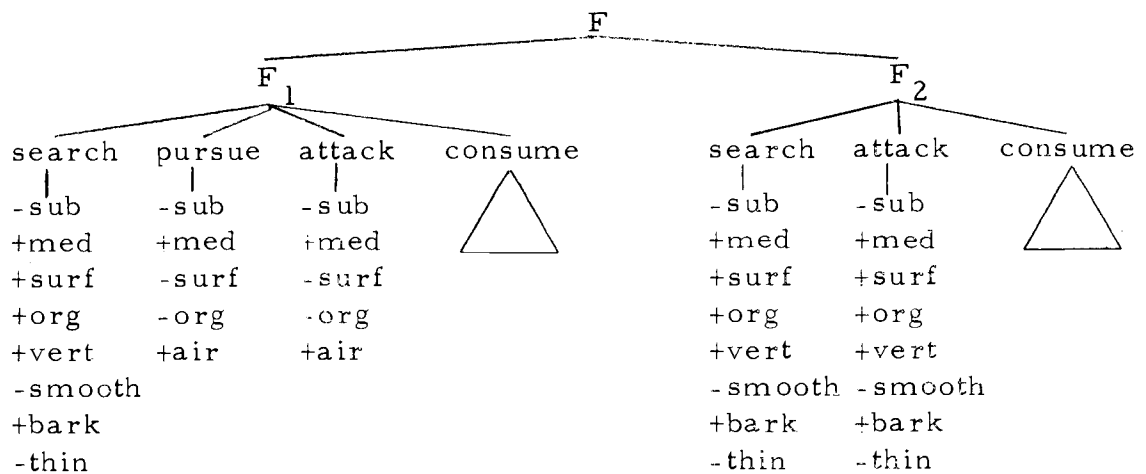
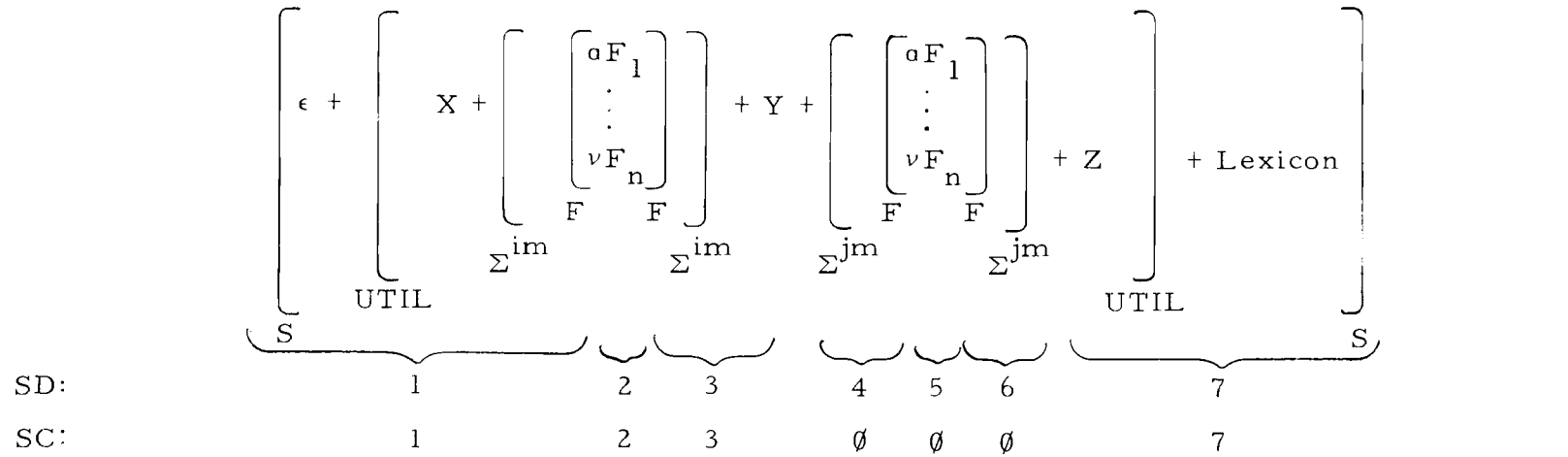


Figure 25. An hypothetical bird species and its two foraging tactics. F_1 is a tactic of searching from a perch and pursuing and attacking while in flight. F_2 is a tactic of foraging among the bark of a tree.

εT4: (obligatory)



Conditions: (i) let $2 \cap 5 = \psi$ for Σ^{im} and Σ^{jm} , $i \neq j$; let m_θ be an index for all $[\Sigma^{nm}]$ such that $\psi \subseteq \{\beta F_1, \dots, \mu F_m\}$ and $\begin{bmatrix} \beta F_1 \\ \vdots \\ \mu F_m \end{bmatrix}_{\Sigma^{nm}_\theta}$. εT4 applies whenever $\frac{|\Sigma^{im_\theta}|}{|\Sigma^{im}|} > \frac{|\Sigma^{jm_\theta}|}{|\Sigma^{jm}|}$;

where $|\cdot|$ equals the number of Σ indexed with either m or m_θ , for a given i, j . (Thus, $|\Sigma^{im}|$ equals the number of species types, or niche trajectories, dominated by LB^i .)

or (ii) if $\frac{|\Sigma^{im_\theta}|}{|\Sigma^{im}|} = \frac{|\Sigma^{jm_\theta}|}{|\Sigma^{jm}|}$, then $\frac{\|2\|}{\|1\|} > \frac{\|5\|}{\|1\|}$. Where $\|N\|$ is a measure defined over the sets denoted by structural description indices. $\|N\|$ may be a simple counting function, equal to the number of elements in each set.

Figure 26. A generalized transformation showing the conditions for competitive exclusion by increased specialization on a food resource.

by examining each species for greater specification of habitat requirements. This is possible because the storage rule ($\vdash \rightarrow$) used to specify requirements (and availabilities) does so by adding features or constraints. The greater the number of required features, the greater the specialization. This is the statement of condition (ii). In short, condition (ii) requires that Σ^{im} require more of the available environment than Σ^{jm} .

Application of $\epsilon T4$ to the hypothetical bird species is straightforward, as Figure 27 shows. In this case, condition (i) applies and the generalist is outcompeted by the aerial specialist.

The analysis so far has been restricted to two cases of "exclusion." I have discussed "exclusion" by the non-insertion of a species based on the absence of some necessary habitat that this species requires. I have also discussed "exclusion" as a niche shift, either as a quantitative or qualitative change in habitat requirements. In both cases of exclusion a species may be absent from an ecosystem. In the latter case this is possible if (for example) there is not present in the ecosystem the necessary substrate that corresponds to a dessication time of 5 to 8 hours. In such a case the grammar would first insert Balanus and Chthamalus (assuming dessication time of 8 to 24 hours), then would separate them by a niche shift in Chthamalus's activity structure and finally would reject Chthamalus due to the absence of substrate in those areas that have an exposure of 5 to 8

$$\begin{array}{l}
\left[\begin{array}{c} \epsilon + \left[\begin{array}{c} X + \left[\begin{array}{c} \left[\begin{array}{c} aF_1 \\ \vdots \\ vF_n \end{array} \right] \\ F_1 \quad F_1 \end{array} \right]_{\Sigma^{11}} + \left[\begin{array}{c} \left[\begin{array}{c} aF_1 \\ \vdots \\ vF_n \end{array} \right] \\ F_2 \quad F_2 \end{array} \right]_{\Sigma^{12}} + \left[\begin{array}{c} \left[\begin{array}{c} aF_1 \\ \vdots \\ vF_n \end{array} \right] \\ F_1 \quad F_1 \end{array} \right]_{\Sigma^{21}} + Y \end{array} \right]_{\text{UTIL}} + \text{Lexicon} \end{array} \right]_S \\
\text{SD:} \quad \underbrace{\hspace{1.5cm}}_1 \quad \underbrace{\hspace{1.5cm}}_2 \quad \underbrace{\hspace{1.5cm}}_3 \quad \underbrace{\hspace{1.5cm}}_4 \quad \underbrace{\hspace{1.5cm}}_5 \\
\text{SC:} \quad \quad \quad 1 \quad \quad \quad 2 \quad \quad \quad 3 \quad \quad \quad 4 \quad \quad \quad 5
\end{array}$$

where (by assumption) $\frac{|\Sigma^{2m_\theta}|}{|\Sigma^{2m}|} = 1$ and $\frac{|\Sigma^{1m_\theta}|}{|\Sigma^{1m}|} = \frac{1}{2}$.

Figure 27. An example of the results of competitive interactions between the two hypothetical bird species of Figure 25, showing the effects of condition (i) of $\epsilon T4$ in Figure 26.

hours. This can be done for all species in the ecosystem by making some finite number of "passes" in the way just described. It may be that the number of passes required to make all the necessary alterations and/or eliminations can be reduced by analyzing the species in some order. If so, what that order might be (e. g. , beginning with the primary producers, or with the top carnivores) is not clear.

There is a third sort of exclusion that I have yet to consider, exclusion resulting from experimentally placing two very similar species together (for example, two species of Drosophila, or Tribolium) in a highly homogeneous environment. Is it possible to describe this sort of "dynamic" exclusion, given the formulation I have presented? The answer, it seems to me, is that there is no way of describing the kind of exclusion that results merely from one population increasing fast enough to effectively remove some feature of the habitat from the environment of another species but not from its own environment. Except for instances when one of the two species actively interferes with the other (a fact that can be represented in the original description of the species), there does not seem to be any means by which the competitive outcome can be predicted when both species have identical habitat requirements in a homogeneous environment. A small consolation is that there are no other theories that can predict competitive outcomes of this sort without doing empirical studies in each and every case. To develop such a theory

seems, at the very least, to require an ability to formulate a dynamic aspect to ecosystems. This is also a necessary property of any model of succession, so a discussion of ecosystem development seems now to be appropriate.

Temporal Ecoclines: Ecosystem Alteration

The foremost problem associated with succession is that it implies a dynamic system when the devices that I have considered up to this point have all been static, or synchronic. This is to say that the problem of ecosystem construction has been construed as a problem of generating a discrete and temporally bounded structure. Succession, on the other hand, requires a "diachronic" description, a description of the processes and mechanisms that force the structure to change in time. These kinds of problems are not unique to ecology for they arise in linguistics where the terminology originated; they also occur in discussions of the philosophy and history of science, where the problems of accounting for a rational substitution of scientific allegiance and commitment from one scientific theory to another predominates.

This difficulty is involved with the problem of distinguishing between the grammatical construction of an ecosystem and the development of the ecosystem. As the discussion of the model for ecosystem construction showed the process is a sequential one: first the

vegetation is added to the ecosystem, then the utilizers of the vegetation, and so on. In fact, this process mimics, to a certain extent, the developmental sequence that actually occurs during succession, especially the earliest stages of development as exemplified by those immediately following a fire or period of glaciation. Thus, it is necessary to distinguish between the construction and development of any particular ecosystem.

One of the criteria required to make this distinction is to distinguish between direct and indirect utilization. Direct utilization of another species, for example, is that utilization that requires the morphology and, perhaps, the physiognomy of the utilized species. Thus, direct utilization may be for food, shelter, reproductive sites, or whatever, but it pertains to structure that is available in the environment. Indirect utilization of another species is utilization of the effects that species has on the environment. For example, a species of plant may, by its particular morphological configuration, cast shadows and thereby create shade. If a species uses (or requires) this shade, then that species is an indirect utilizer of the species that created the shade. As a result, given two species that use a third species, one directly and the other indirectly, the direct utilizer will be inserted during ecosystem construction and the indirect utilizer will not. The indirect utilizer will have to wait for insertion following a rule that alters the environment as a result of action of

the utilized species (e. g. , alteration from "sunlight" to "shade"). This result is consonant with the basic activity of the ϵ -grammar since, in those rules the procedure is to transfer the original physical habitat to the environment of all utilizers, vegetative as well as others. So there is no procedure within the ϵ -grammar to alter the environment on the basis of the insertion process. This requires another mechanism.

As an example of this mechanism I will consider the procedure that adds a lower layer to the vertical structure generated by the ϵ -base rules. These base rules generate a finite, specified number of layers. The base rules have no constraints on inclusion or exclusion of any layers. Thus they have the potential to generate both natural rain forests and well-manicured city parks. One successional change that can occur is the insertion of species with physiognomies corresponding to a layer below the lowest previously generated. (The opposite situation can also occur and I will discuss this case shortly.)

The mechanism that will do this is two transformation rules; one adds the new, lower layer, and the other inserts the habitat features of the new layer. The general statement of the rules is given in Figure 28. The feature insertion transformation, ϵT_6 , is actually just a statement of a context-sensitive, re-write rule. An hypothetical example of these context-sensitive rules is provided in Figure 29. The output of this transformation fulfills the structural

€T5: (optional)

$$\begin{array}{c}
 \left[\begin{array}{c} X + [\text{radiant} + \text{temp} + \text{moist} \{ \text{current} \} \text{physiog}] + Y \\ \text{Air} \qquad \qquad \qquad \text{Air} \end{array} \right] \\
 \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \\
 \text{SD: } 1 \quad 2 \quad 3 \quad 4 \quad 5 \\
 \text{SC: } 1 \quad 2 \quad 3 \quad (2+3+4) \quad 4 \quad 5
 \end{array}$$

€T6: (obligatory, contingent on €T5), generalized format

$$\begin{array}{c}
 X + \left[\begin{array}{c} \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] + \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] + \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] \left\{ \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] \right\} \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] \\ \text{rad rad temp temp moist moist curr curr phys phys} \end{array} \right] + [\text{radiant} + \text{temp} + \text{moist} \{ \text{current} \} \text{physiog}] + Y \\
 \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \quad \underbrace{\hspace{1.5cm}} \\
 \text{SD: } \quad \quad \quad 1 \quad 2 \quad 3 \quad 4 \quad 5 \quad 6 \quad 7 \quad 8 \quad 9 \\
 \text{SC: } \quad \quad \quad 1 \quad 2 \quad \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \left\{ \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \right\} \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \quad 8 \quad 9 \\
 \text{rad rad temp temp moist moist curr curr phys phys}
 \end{array}$$

Figure 28. Two transformation rules showing the addition of a vegetative layer below another.

$$\begin{array}{c}
 \left[\begin{array}{c} X + \left[\begin{array}{c} + \text{seasonal} \\ 8 \text{ range} \\ 6 \text{ average} \\ 5 \text{ max} \end{array} \right]_{\text{rad}} + \left[\begin{array}{c} + \text{seasonal} \\ 8 \text{ range} \\ 6 \text{ average} \\ 5 \text{ max} \end{array} \right]_{\text{rad temp}} + \left[\begin{array}{c} + \text{seasonal} \\ 8 \text{ range} \\ 7 \text{ average} \end{array} \right]_{\text{moist moist}} + \left[\begin{array}{c} 4 \text{ height} \\ 6 \text{ density} \\ 4\% \text{ cover} \\ 2 \text{ stem width} \end{array} \right]_{\text{physiog}} + \left[\begin{array}{c} \text{radiant} + \text{temp} + \text{moist} + \text{physiog} \end{array} \right]_{\text{Air}} + Y \end{array} \right]_S \\
 \underbrace{\hspace{15em}}_{\text{SD:}} \quad \underbrace{\hspace{1em}}_1 \quad \underbrace{\hspace{1em}}_2 \quad \underbrace{\hspace{1em}}_3 \quad \underbrace{\hspace{1em}}_4 \quad \underbrace{\hspace{1em}}_5 \quad \underbrace{\hspace{1em}}_6 \quad \underbrace{\hspace{1em}}_7 \quad \underbrace{\hspace{1em}}_8
 \end{array}$$

$$\begin{array}{c}
 \text{SC:} \quad \quad \quad 1 \quad \quad \quad 2 \quad \left[\begin{array}{c} + \text{seasonal} \\ 7 \text{ range} \\ 3 \text{ average} \\ 2 \text{ max} \end{array} \right]_{\text{rad}} + \left[\begin{array}{c} + \text{seasonal} \\ 7 \text{ range} \\ 3 \text{ average} \\ 2 \text{ max} \end{array} \right]_{\text{rad temp}} + \left[\begin{array}{c} + \text{seasonal} \\ 7 \text{ range} \\ 5 \text{ average} \end{array} \right]_{\text{moist moist}} + \left[\begin{array}{c} 2 \text{ height} \\ n \text{ density} \\ m \% \\ 0.5 \text{ stem width} \end{array} \right]_{\text{physiog}} + 7 + 8
 \end{array}$$

Figure 29. A particular example of €T6 (generalized format) showing how an hypothetical terrestrial vegetative layer is added below another plus the concomitant alterations in habitat features.

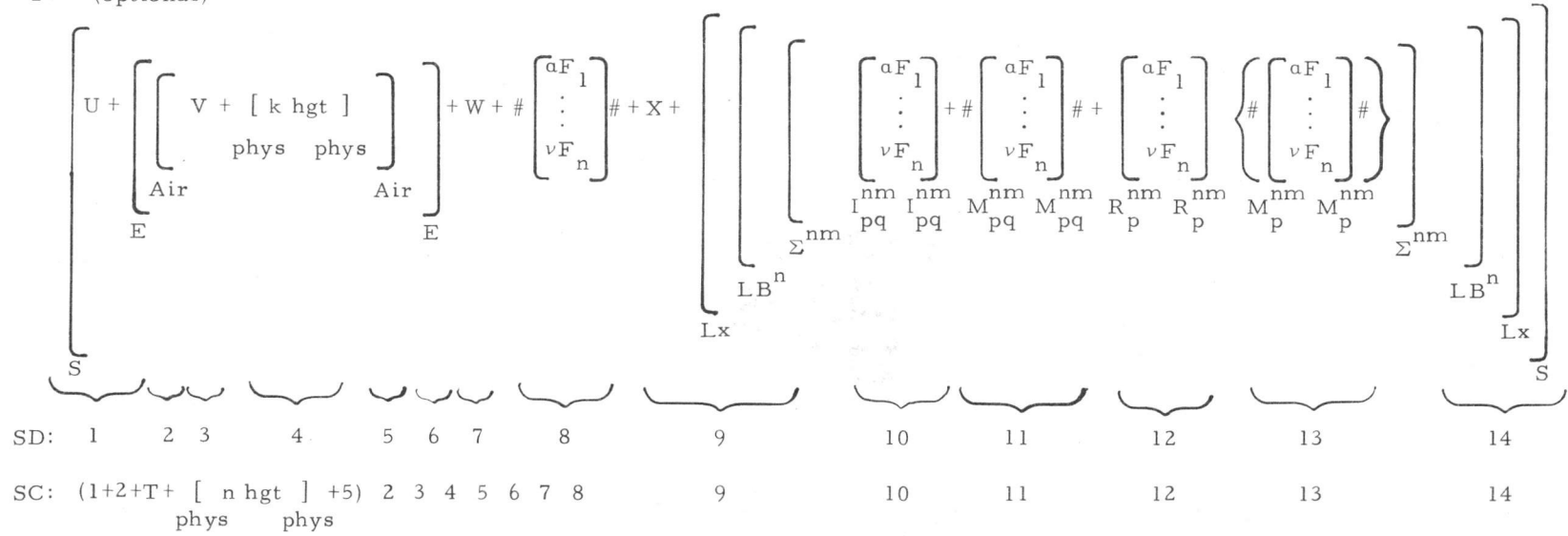
description conditions for $\epsilon T1$, so this latter, obligatory rule is applied after $\epsilon T6$. The point of these rules is that indirect users are forced to be inserted after the direct users, and this can only occur if inserted species affect the set of features describing habitat availabilities. The creation of layers below others is one such effect. Another important effect is the addition of layers above others already present.

Succession that occurs by the addition of taller vegetative layers is due to the growth of individuals previously present in a lower layer. Individuals of this sort must not only possess habitat requirements that allow them to be inserted initially (into the lower layer), but must also possess a morphological description that allows them to grow above the lower layer. Both these conditions are met by the ecosystem grammar: species present have been inserted because of available habitat and their complete morphological description (of all developmental stages) is available to the grammar. The morphological specification for any particular ecosystem, however, is layer by layer. Therefore, the addition of layers by growth must scan the morphological description of the species present in order to determine which have the capacity to grow into a new layer. If at least one such species is present, then the ecosystem can develop by adding a layer. If no such species is present, then development by the addition of layers must wait until such a species is present. This can be

represented as in Figure 30. The specification of the conditions of this rule is a delicate matter and must be examined with care. The addition of a layer above another not only fulfills the conditions of $\epsilon T1$ (as $\epsilon T6$ did), but also creates the possibility, after the insertion of direct users, of indirect utilization. Thus $\epsilon T2$ may be followed by $\epsilon T5$, and the process continues in this way.

An important effect that organisms have that allows indirect utilization is the production of organic wastes. Since wastes appear to be a necessary by-product of every species, another obligatory transformation rule like $\epsilon T6$ is needed to allow the insertion of decomposers. Several other structural changes that occur during succession can be described in a manner similar to the addition of higher and lower layers. For example, alterations of the physiognomy within a layer can result from the growth of plant populations present in the layer. This growth will have further influences on the abiotic factors in the soil, air, or water components. Rules that describe these changes are transformation rules, not unlike $\epsilon T6$. Since they involve context-sensitive alterations of particular environmental features they can only be stated in terms of a particular, complete set of habitat features. I will leave the specific statements of these rules to another time. Similar remarks apply to alterations of habitat features that are not the result of biological processes. An example of this situation is the deposition of sediment in aquatic

εT7: (optional)



Conditions:

- (i) $\forall n \forall m (\exists i \exists j (M_{ij}^{nm} \subseteq 8) \wedge (\exists r \exists s (\begin{bmatrix} aF_1 \\ \vdots \\ vF_n \end{bmatrix} \subseteq M_{pq}^{nm}) \wedge (4 < \begin{bmatrix} m \text{ hgt} \end{bmatrix} \leq \begin{bmatrix} n \text{ hgt} \end{bmatrix})))$
- (ii) $(\begin{bmatrix} + \text{ light} \end{bmatrix} \in I_{ij}^{nm} \wedge \begin{bmatrix} + \text{ light} \end{bmatrix} \in I_{i+r, j+s}^{nm}) \vee (\begin{bmatrix} + \text{ light} \end{bmatrix} \in R_i^{nm} \wedge \begin{bmatrix} + \text{ light} \end{bmatrix} \in R_{i+r}^{nm})$

where: $j, q = \{0, 1, 2, \dots, u\}$; $r, s = \{1, 2, \dots, t\}$, and T is a structural variable.

Figure 30. An ecosystem transformation rule describing the insertion of vegetative layers by the growth of individuals in lower layers.

systems by run-off and river inflow (Walker, 1970; Whittaker, 1970).

I will summarize this section by discussing a few residual aspects of this model of temporal ecoclines. First, when events occur in nature they occur at some particular point in time; thus, there is not only a sequence of events, but a spacing of events in time as well. The grammar that I have displayed is an attempt to mimic the sequence, and not the temporal spacing of events. The grammar does not describe "when" things happen, but only in what order they occur. Moreover, since I have not attempted a mechanistic account, there is no easy way of translating the time scale of the grammar into the time scale of some natural system. Second, although my discourse has been concerned primarily with species insertion, there is a complementary process of species removal. This process will operate after each change in either the habitat features or the morphology features in the ecosystem. It is stated as an obligatory transformation rule in Figure 31. This rule operates by comparing the list of environmental features with the list of features dominated by "UTIL. " Whenever there are requirements under UTIL for which there are no environmental features, both the morphology features and UTIL features for that species (Σ^{nm}) are deleted. Finally, Figure 32 gives a schematic view of the complete set of grammars that generate species lists. In this figure, five-sided boxes represent

εT8: (obligatory)

$$\begin{array}{c}
 \left[\begin{array}{c} \left[\begin{array}{c} \alpha F_1 \\ \vdots \\ \nu F_n \end{array} \right] \\ E \end{array} \right] + \left[\begin{array}{c} \# \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \# \\ \Sigma^{nm} \begin{array}{cc} M_{pq}^{nm} & M_{pq}^{nm} \end{array} \end{array} \right] + \left\{ \# \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \# \right\} \\ \Sigma^{nm} \begin{array}{cc} M_{pq}^{nm} & M_{pq}^{nm} \end{array} \end{array} \right] + \left[\begin{array}{c} \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] + \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \\ \Sigma^{nm} \begin{array}{cc} I_{pq}^{nm} & I_{pq}^{nm} \end{array} \quad \Sigma^{nm} \begin{array}{cc} R_p^{nm} & R_p^{nm} \end{array} \end{array} \right] + \text{Lexicon} \\
 \underbrace{\hspace{1.5cm}}_S \quad \underbrace{\hspace{10cm}}_2 \quad \underbrace{\hspace{10cm}}_3 \quad \underbrace{\hspace{1.5cm}}_S
 \end{array}$$

SD: 1 2 3 4

SC: 1 ∅ ∅ 4

Condition:

$$\exists p \exists q ((\left[\begin{array}{c} \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \\ I_{pq}^{nm} \quad I_{pq}^{nm} \end{array} \right] \not\subseteq 1) \vee (\left[\begin{array}{c} \left[\begin{array}{c} \beta F_1 \\ \vdots \\ \mu F_m \end{array} \right] \\ R_p^{nm} \quad R_p^{nm} \end{array} \right] \not\subseteq 1)) .$$

UTIL UTIL UTIL UTIL

Figure 31. An ecosystem rule for the deletion of species.

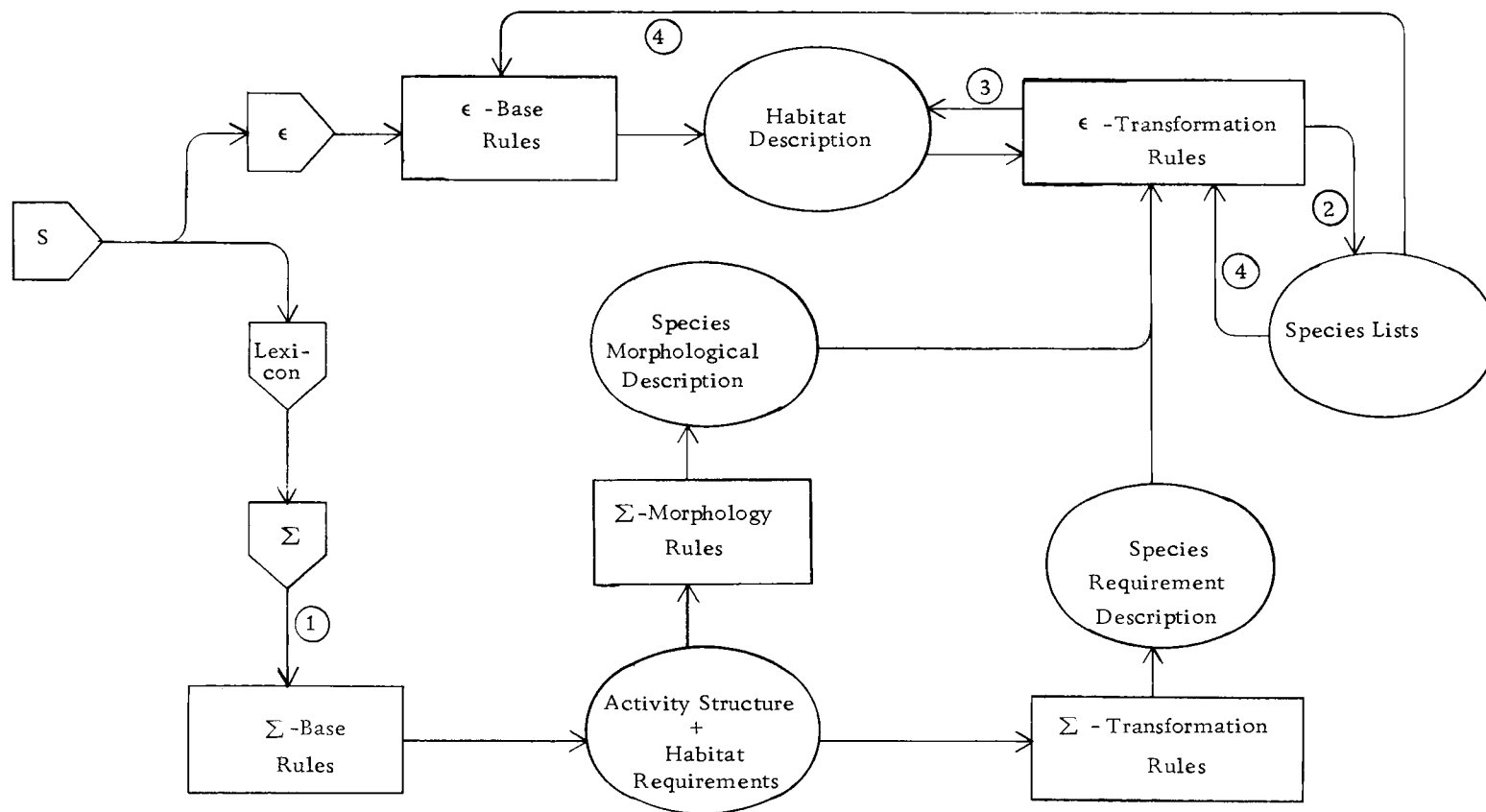


Figure 32. A flow diagram of the complete system of grammars. Five-sided boxes represent "start" symbols, four-sided boxes represent grammar rules, and ovals represent outputs. Numbers indicate functional interrelationships, as defined in the text.

"start" symbols. These symbols are either initial categories (e. g., S), or categories of particular importance that are useful for denoting different components of the grammars (e. g., Σ , Lexicon, and ϵ). The category LB is not included in this figure. Four-sided boxes represent the rules of the grammars, both base and transformational. The output of these rules is represented by ovals. Only ovals or start symbols may serve as inputs to rules. The numbers indicate the functions of some of the interrelationships among the components of the grammars. The arrow labeled (1) is the activity decomposition of species, (2) is species insertion, (3) is the effects of species morphology on the environment, and the arrows labeled (4) are indirect and successional relationships.

IV. DISCUSSION

The preceding section has stated the rules of an algorithm that attempts to formally and with maximum generality map a set of environmental features onto a set of species. It attempts to do this by a procedure that constructs temporal ecoclines. This requires further discussion, which may be conveniently approached in three ways. First, grammars of the type I have proposed require empirical knowledge in order to evaluate their usefulness and validity. This problem of evaluation is common to all representations of systems such as ecological systems; I discuss this under the topic of "model validation" below. Second, the particular algorithm that has been proposed is only one of many possibilities. Some alternatives possess characteristics that make them worthy of serious consideration and discussion. And third, the method I have chosen by which to solve the "mapping" problem of ecological systems is a novel application, not only to ecology but also to other natural systems outside the domain of linguistics. As a result, the philosophical position on which such an application is based possesses certain implications for the philosophy of science. I will also explore these implications in this section.

Model Validation: Observational, Descriptive,
and Explanatory Adequacy

Whatever else they may be, models are representations of objects or natural systems. Because models are representations, it is never valid to suppose that the conclusions of the model are the behavior of the object. It is necessary to "validate" a model by comparing the results of the model with empirical data. This need is particularly acute in consideration of grammars, due to their abstract character. Models of this sort do not make hypotheses or assumptions concerning the distributions of either environments or species in physical space or time. Any natural system, however, with which one may wish to compare the grammar output, does possess some unique distribution. Thus, one cannot compare every output of the grammar with any given natural system. The validation of a grammar by the comparison of species lists, therefore, is a non-trivial undertaking and requires further discussion.

Observational Adequacy

The evaluation of a grammar for its observational adequacy requires a comparison of an output of the grammar with species lists observed from some actual ecosystem or temporal ecocline. Since a grammar produces a large number of different ecosystems, it is necessary to compare only certain grammar outputs with certain

natural systems. To effect this constraint, two types of boundary conditions are necessary. The first type of boundary condition requires that the physical habitat of the actual system matches a derivation of the ϵ -grammar. That is, the generated environmental features from which a grammar attempts to map a species list must be identical to the habitat of the natural system in order for a meaningful comparison to be made. Naturally, if no such habitat derivation is among the set of possible derivations, then the grammar fails to be observationally adequate without requiring a comparison of species lists. The second type of boundary condition must specify the set of species in the lexicon and available for insertion into the ecosystem generated by the grammar. This specification must be comparable to the species pool that is capable of migrating into the area of the ecosystem. Moreover, it is not sufficient to provide a lexicon that is too large (say, all living species on earth). A grammar that used such a strategy would attempt to insert North American organisms into Australian habitats. This approach violates the view that the species pools of the two areas are distinct, owing to their separate geological and evolutionary histories. But the grammar that I have presented takes no cognizance of this fact, and so a non-automatic procedure, the specification of boundary conditions, is required. The determination of the mechanisms and description of the limitation of species pools over the surface of the Earth is an important problem, to which I shall return in a discussion of explanatory adequacy.

In order to "falsify" or invalidate any grammar by list comparison, it is necessary to completely specify these two boundary conditions: comparable habitats and species pools. They are not, however, sufficient for invalidation. This is so because the empirical determination of a species list is the outcome of a procedure subject to statistical error. For example, it is a well known fact that sample size influences the number of species observed (Pielou, 1969). Moreover, most studies do not even attempt to reveal all the species present. Studies of species present are usually restricted either to a particular taxonomic group (e. g. , birds) or to a particular part of the ecosystem (e. g. , the species associated with the soil, or the canopy of trees, etc.). As a result, certain additional constraints on the validation of a grammar by list comparison are required. These must concern themselves with the practicalities of field collection and the problems of falsifying hypotheses with statistically variable data. Because of these difficulties and the difficulties of satisfying the required boundary conditions, evaluating the observation adequacy of the grammar by list comparison appears to be an inefficient and inconclusive procedure. An alternative to the evaluation of observational adequacy would greatly increase the power of a grammar.

Descriptive Adequacy

One such alternative is to evaluate the descriptive adequacy of

the grammar, which I defined earlier as the ability of the grammar to "mimic" the operation of the systems that are described by the grammar. In evaluating this criterion difficulties arise in determining not only which characteristics of the system are to be mimicked but also the measure by which a grammar's success in fulfilling this criterion is to be evaluated. The characteristics of a natural system's operation that we require a grammar to mimic are contained in the conceptual framework of the scientists that study the system. In the Introduction I listed a tentative and incomplete set of some of the elements in the framework of ecologists. This set possessed such characteristics as: the infinite capacity of ecological systems, the habitat requirements of species's activities, and so on. Since different ecologists could produce contradicting frameworks, the evaluation of a grammar on the basis of this criterion will be difficult. But it is not obvious that contradicting frameworks will always characterize a science; so, the difficulty of evaluation may not be permanent. Moreover, a legitimate argument can be made for the observation that widely diverging or contradictory frameworks are held only by scientists pursuing different scientific fields, using different technical methodologies, and subscribing to different explanatory ideals. Thus, a grammar of ecological systems that fails to meet the framework criteria of biochemists is not necessarily descriptively inadequate for ecologists. The problem, then, does not so much revolve

around the characterization of the conceptual framework as it revolves around measures used to separate grammars already acknowledged as descriptively adequate within a particular scientific community. The definition of such a measure seems, to me, to be remote at the present time. Any two grammars may account for the same elements of a conceptual framework in markedly different ways; so, merely counting the framework elements that each model mimics is not an adequate approach. It is likely that such a measure of descriptive adequacy will rely on criteria such as elegance, simplicity, generality, or automaticity which are, as yet, formally intractable (Goodman, 1958; Popper, 1968).

The point, however, is not to belabor the difficulty of agreeing upon any particular measure of descriptive adequacy, but rather to recognize the existence of this evaluation criterion and the desirability of producing ecological models that are empirically distinguishable on this basis. This, it seems, has not been a goal recognized by many ecologists currently engaged in modeling. In fact, since Levins (1966) first introduced the concept of robustness, there has been a move towards the deliberate production of independent models whose empirically verifiable results are indistinguishable (Cody, 1974; May, 1972). I am arguing that this position issues from a view (perhaps borrowed from physics) that the operation of the model is (or ought to be) irrelevant to the operation of the system

being modeled. Once such a view is superseded a statement of the descriptive adequacy of models becomes possible and relevant.

Explanatory Adequacy

A third, and final, evaluation criterion is "explanatory adequacy." This criterion is much more powerful and difficult to fulfill than any of the others, but when, or if, it can be met it will provide the most automatic class of grammars achievable. A grammar will be said to have met the criterion of explanatory adequacy when it provides a procedure to unambiguously limit the lexicon from which a set of species may be inserted. Such a procedure will reflect current theories about continental drift, colonization, the role of particular environmental features on speciation, the effect of the genetic constitution of a population on its speciation, gene flow, random genetic drift, and many other topics. The primary problem of such a procedure is to assign to a set of environmental features a history of speciation and colonization. This history would then, in some way, specify a subset of the set of strings produced by the species grammar.

In short, a grammar that meets the criterion of explanatory adequacy must be based on a theory of the evolution of the lexicon. The lexicon is not a passive "container" of species, as the expression "species pool" might suggest. It is a dynamic, evolving system. I

have chosen to model this system by creating a grammar that has the capacity to produce all possible species plus a secondary device (i. e., a theory) that restricts this set of species to a particular subset. By taking into account the above topics, such a restriction on the set of all species can be stated in detail. But these problems have not been approached in this thesis. Thus, it is not possible at this time to evaluate my model with regard to its explanatory adequacy.

Extensions of the Model: Improvements, Applications, and Innovations

The model that I have presented is, quite clearly, incomplete. It will be useful to specify the areas in which the model is incomplete and how it might be extended both in its applications and its contents.

Improvements

One important way that the current grammar may be improved is by a fuller specification of the distinctive features that constitute the terminal vocabulary of both the Σ -grammar and the ϵ -grammar. Qualitative and quantitative features need to be more precisely defined. A problem of importance is whether or not it is possible to discover one, hierarchical decomposition of a quantitative trait, such as temperature, that suffices for all organisms, or if a number of different decompositions are required. The difficulty arises because,

in order to meet one of the conditions of descriptive adequacy, the grammar must decompose quantitative variables in a way such that indiscriminant species require less decomposition than discriminant ones.

An additional avenue of improvement is the further study of both species and ecosystem transformations. This can involve additional species transformations describing more adequately the options of species. It can also involve the use of transformations to handle special cases such as $\Sigma T1$ does. My feeling is, after investigating this grammar to the extent that I have, that there are many more transformations capable of giving additional insight that can be written. An area requiring emphasis pertains to the evolutionary constraints placed on life history strategies. I have placed essentially no restraints on the order of developmental stages that the suggested grammar may generate. Nor does this grammar limit the complexity of life history that a species may possess. Some of these difficulties may be most appropriately treated by context-sensitive rules, but others may require the greater generality of transformation rules.

A final area of improvement pertains to certain classes of organisms recognized as separate taxonomic species but having a dependence on one another to such an extent as to be obligatory symbionts. This situation creates a difficulty for the present grammar because neither species in an obligate symbiont pair can be

inserted into an ecosystem unless the other has already been inserted. Facultative symbionts, of course, offer no such problem. A possible solution is to provide the grammar a transformation that subsumes two distinct LB classes into one LB class; thus, the habitat requirements of the transformed LB are the sum of those of the two symbionts. Such a transformation would have to delete those requirements of each species that correspond to the morphology of the other member of the symbiosis. The statement of the conditions of such a transformation do not appear to be trivial.

Applications

Besides improvements, the grammar may be extended by a number of applications that are derived from the production of species lists. One important application is the construction of species maps. As it stands now, the grammar is indifferent to any particular physical distribution of environmental features, as I have previously asserted. If, however, a particular distribution of features is generated by the grammar and this distribution also relates to a particular geographical region, then the species lists that are generated will correlate to the distribution of species over that geographical region. This has applications to the design of national parks and wildlife refuges. It will specify not only what size of region is required for a particular number of species (Diamond, 1972, 1973),

but also what size and shape are required for a particular distribution of specified species. And this is exactly what one would expect from any procedure that maps environmental features onto species lists.

Another obvious application is to allow the lexicon to contain Homo sapiens and its effects on environmental features. Toxicants are one form of environmental perturbation that can be conveniently discussed. The grammar cannot predict what effect any particular toxicant will have on a particular species. But if this information is known and incorporated into the grammatical description of those species involved, then the grammar can predict what changes in the species list will occur as a result of toxicant dispersal. In short, the grammar treats any human by-product as any other element of the environment; if it is present at certain quantities, then it alters the species list in certain ways. The larger question of incorporating man into the lexicon in a rigorous way is a difficult matter. This is because of the versatility of human behavior and the wide variety of options that this allows the species. Virtually every environment is inhabitable by humans and it is largely cultural and economic considerations that determine their presence or absence. To create a grammar that considers these aspects seems to be an immense task.

The grammar that I have proposed can also be applied to questions concerning the behavior of macro-scale measures over

time and space. Much of the ecological literature has been devoted to the questions of how measures of species diversity vary over time and space, and how ratios of community biomass to community production (B/P) and production to respiration (P/R) vary during succession. These problems all turn upon the numbers of individuals present in each species, a topic I have not approached. If numbers of individuals were incorporated into the grammar, then the problem of diversity gradients would be amenable to analysis on the basis of the history of the grammar that produced a particular series of species lists. Similarly, if the contribution of individual species to the community B/P and P/R ratios were known and the relative numerical contribution of each species were known, then one should be able to assign B/P and P/R ratios to each ecosystem. As the species composition of the community changes during succession so will the B/P and P/R ratios. These can be studied, perhaps by simulation, and related to environmental features and successional effects. Similar remarks also apply to the changes that occur to the relative contribution of r - and K -strategists over the course of succession.

Innovations

A final tactic for extending the grammar is to construct grammars radically different from the type I have used. Such alterations may imply a new theory of the operation of ecological systems, but

the distinction between models and theories is particularly obscure in this case. I will cite several approaches that I think are sufficiently different so as to warrant consideration as alternate theories. The first example will concern the procedure for specifying the developmental stages of species.

The model that I proposed generated the developmental structure "all at once" by first specifying the number of stages and only afterwards specifying the content of those individual stages. This procedure raises the problem, as I mentioned earlier, of creating a grammar that does not generate bizarre and improbable combinations of stages (e. g., trees into fish). An alternative grammar that avoids this difficulty is one based on an iterative procedure similar to the one used for species insertion. Such a procedure would ensure that each successive developmental stage met certain constraints set by earlier stages. Moreover, the number of stages could be made dependent upon the features of previous stages. It is moot as to whether or not a grammar based on this iteration technique is a mere notational variant of the grammar that I have proposed. A context-sensitive procedure for describing the features in this latter model closely resembles an iteration technique, thus suggesting a fundamental similarity between the two approaches. On the other hand, the intuitive feeling of some scientists concerning the developmental process is that it is "pre-programmed" to a considerable extent and,

thus, does not possess the "contingent" quality of iterative procedures. Whether or not the grammar that I have proposed adequately reflects this notion of "canalized development" (Waddington, 1966) is a point, I believe, that can be rationally debated. Issues and debates of this nature constitute evaluations based on the descriptive adequacy of grammars.

A second type of extension that also entails the creation of a new grammar is to map environmental descriptions onto, not species lists, but rather some broad classification of species. For example, instead of species, the lexical units might be functional units (McIntire, 1972) such as feeding types: filter feeders, shredders, scrapers, scavengers, pursuers, and so on. There are several disadvantages to such an extension. Categories based on functional units are not as well-defined as species. Although this could be remedied to a certain extent by the specification of necessary features for classification, such a specification would face all of the difficulties of classifying individuals into species on the basis of phenotypic characters. Moreover, a functional unit would not possess the operational test of reproductive compatibility that exists for at least some species. Further, an argument can be made, on the basis of descriptive adequacy, for a grammar whose lexical entries correspond to the basic units of evolution (which is not to say that natural selection acts predominantly on populations and not individuals). Because of

this, if functional units are used as lexical entries, then there does not seem any possibility of creating a grammar with explanatory adequacy (as I have defined that evaluation criterion). There is, finally, the problem that functional units of the types that I have listed are not uniquely associated with species. That is, at different stages in development, or at different times in any given developmental stage, a species may possess characteristics that class it into two different functional units. This is a problem that has always plagued analyses of this sort, but a possible solution is to create functional units on the basis of sequences of developmental stages, or reproductive activities. Perhaps continued studies of generative grammars will suggest more adequate classifications of functional units.

A final approach for alternative generative grammars concerns the organization of communities. The model that I discussed gives to the ecosystem no biological categories, such as trophic levels, above species. A decomposition based on trophic levels suffers from many of the same problems as classifying species into functional units. Root (1973), however, has proposed that communities in a specified geographical location be viewed as a collection of "component communities": an assemblage of species that have co-evolved in some microhabitat. His paper concerns an assemblage of herbivorous arthropods and their associated parasite community that have co-evolved on a particular species of plant. This conceptualization can

be incorporated into a grammar by a suitable classification of the lexicon and a set of ecosystem base rules that specify conditions (in terms of habitat features) for the insertion of groups of species. Because of the restrictions that such a grammar would place on the lexicon, this approach is attractive for its potential of achieving explanatory adequacy. It could also greatly reduce the complexity of the insertion process.

Philosophical Implications: Explanation,
the Language-Communication Distinction,
and a Speculation

In justifying the use of generative grammars that simulate ecological systems I have asserted philosophical positions and distinctions, many of which have not as yet been applied to fields of enquiry such as ecology. Part of the evaluation of the procedure that I advocate must rest upon an evaluation of these applications. This requires a knowledge of the philosophical implications that are associated with adoption of a "linguistic metaphor."

Explanation

One of the first philosophical problems that arises regards the explanatory status of mappings of the sort produced by a grammar. To what extent do these mappings constitute a causal explanation? As Nagel (1961, p. 323) puts it, causal explanations are those that

logically determine the future states of a system, given its initial state. Under this view, then, virtually every explanation in the natural sciences strives to be causal. And this applies in ecology to such diverse fields as population genetics, ecosystem modeling, and evolutionary ecology. Grammars, however, do not proceed by assuming the existence of a system with a certain structure and state description. The aim of grammars, as I stated earlier, is to specify the necessary and sufficient conditions for the existence of a system by the construction of the system. This is a fundamental difference: causal explanations assume (or hypothesize), as a boundary condition, the structural existence of a system and grammatical explanations (if you will) prove the structural existence by construction. I will return to this dichotomy in the conclusion of this section.

To say, however, that grammatical explanations are not causal explanations is not to reject or deny the relevancy or utility of causal explanations. Indeed, simulating ecological systems by generative grammars presupposes the possibility (if not availability) of causal explanations in terms of physiological, developmental, and evolutionary processes. But these simulations do not make direct use of these processes. To draw a crude analogy, causal explanations of biological mechanisms explain the hardware necessary for the application of the grammatical software. A similar situation occurs in linguistics. A causal explanation of vocal chords and systems of neurons may or

may not be available, but they are not stated or assumed known (or knowable) by the grammar.

A second philosophical problem concerns the relation of automaticity to various evaluation criteria of theories, such as causality, generality, and simplicity. Causality, according to Nagel (1961, p. 323 f), is the objective of science to achieve explanations that deduce from initial conditions the unique states of a system for any other time. Thus, causality is an enjoiner to formulate explanations in a certain way. There seems to me to be a problem in explaining why this form of deductive explanation is held to be psychologically persuasive. One justification of this form is that it embodies "laws" of nature, and, thus, relates the fundamental working principles of nature to the observed states of a system. Even if this is, in fact, the case there still remains the problem of explaining why humans should find such explanatory forms attractive. Moreover, there are some sciences, notably theoretical linguistics, the objectives of which are not easily stated in the dynamic language that Nagel's account implies. Since there does not appear to be any strong reasons for denying linguistics the status of a science, it appears that an objective of science more general than causality is required. I have attempted to suggest that "automaticity" is one such objective that not only subsumes causality, but also accounts for the directions that linguistics and this thesis have taken.

Certainly every proposed objective of science must embody a commitment to the goal of "accounting for the facts. " And this must be considerably more than mere observation and description. Mere descriptions of a system, with no automatic account, exist (as they are perceived) because humans are present to observe. It is as if automatic, including causal, explanations are necessary in order to justify the reality of observation, to prevent a solipsistic theory of knowledge. If a believable account of a phenomenon can be given that "forces" the system to produce the observation, then the system will produce the observation regardless of the presence of human observers. Accounts that involve the "machinery" of the system, in either automatic or causal terms, are accounts that produce "facts" that are not dependent on the presence of a human observer. How real are "ecological communities" based on no other account except that Braun-Blanquet has a method of classification? How much more real do they become when we understand the mechanisms of co-evolution, competition, and succession? To provide an account, any account, that "forces" an object to produce an effect not only reifies the dubious existence of an external reality, but also justifies the methodological procedures of scientific observation. We might call this "boot-strap epistemology. "

There are two other scientific ideals that are also related to automaticity: generality and simplicity. One explanation or theory is

judged to be of greater generality than another if the number of natural systems to which one applies is larger than the other (Popper, 1968, p. 121 ff). Also, one explanation is simpler than another if the ease of finding a falsifying case is greater in the one than in the other (Popper, 1968, p. 140 ff). An hypothesis of a linear relation between two variables is simpler because there are fewer parameters to test for falsification in a linear than in a curvilinear relation.

Both increased generality and increased simplicity are examples of increased automaticity because both reduce the roles of humans in the explanation process. Explanations are one human's answer to another human's question. To give an answer by citing a theory, or law, requires that a decision be made regarding which theory or law applies in the case raised by the question. Increasing the generality of a theory increases the automaticity of the explanation process. Explanations are not explanations unless they are delivered in public. Therefore, the ideals of science must include not only the justification of particular observations, as causal explanations do, and the static statement of theories (generality in the form of laws), but also the process of explanatory communication. This process can be made more automatic if there exist fewer laws or theories to use as explanations. It is much easier for an ignorant carpenter's apprentice to choose the correct tool if there are fewer tools to choose from. The point is that explanation is a process of the scientific activity

every bit as much as the collection of data, and the ideal of automaticity applies here as well.

A similar argument holds for simplicity. An explanation can be made more automatic if the rule is followed to always use the simplest form. There are many ways to provide a complicated answer, but only one way (of those known) to give the simplest. In other words, there are many forms of the equations for curved lines, but only one for a straight line. Simplicity and generality in our devices of explanations (theories and models) automate the process of explanation by reducing the number of human decisions.

The Language-Communication Distinction

To produce a grammar of a language requires, obviously the existence of a language. I have argued that one may write grammars of species and ecosystems because these two systems both meet the conditions I specified for the application of the distinction between communication and language. These conditions, briefly, were that a set of unique systems exist and that they be structured by an hierarchical arrangement of parts. An important implication of this is that many other areas of scientific enquiry other than ecology and linguistics also fulfill these conditions. Almost all social systems are in this category, primitive societies, as well as those that are more technically advanced. Certain subsystems in society, such as

corporations, meet the conditions as do some domains of the physical sciences. For example, geological structures are the result of complex interactions of well-defined parts. Moreover, geological structures are unique and not every combination of mineral type or rock formation can be found together in nature. As a result, these parts (minerals, formations) may be classed hierarchically. Similar remarks may apply to chemical compounds, and insofar as organisms are composed of chemical compounds, a grammar of bio-chemistry could be integrated with the ecological grammar that I have proposed. On another level, astronomical systems such as solar systems and galaxies, in addition to obeying the causal laws of mechanics, are certainly an unique and restricted collection of elements and relations. So they too may possess a language that can be usefully modeled.

To state, however, that a class of systems constitutes a language in no way restricts the form that a grammar of that language may possess. Nor does such a statement guarantee that the theoretical pursuit of a grammar will prove to be fruitful. The rewards of a grammar depend upon criteria imposed upon a theory quite apart from its empirical accuracy. The aspirations and demands not only of the scientific community in question but also of the society at large must ultimately evaluate questions of utility.

A final implication of the distinction between languages and communication is that it seems to be the meaning of Polanyi (1968),

when he argues for the "irreducibility" of machines (including biological systems) to the laws of physics and chemistry. He does this by asserting that the creation of machines requires the imposition of "boundary conditions" which are not constituents of any currently recognized theory of physics or chemistry. Boundary conditions of the type that Polanyi envisages are exemplified by the strategy involved in a winning game of chess, structural constraints in the design of a machine (e. g., a watch), or stylistic considerations in the composition of writing. Polanyi goes on to make a number of points of a rather more extreme nature with which Causey (1969) and Simon (1971) adequately deal.

The point I should like to make here is that, aside from the extreme positions on biological reductionism that Polanyi adopts, his distinction is a valid one. And one, I believe, that is accepted by his critics. But because Polanyi failed to state the general conditions necessary to distinguish the study of "inanimate nature" from the study of the "imposition of boundary conditions upon the laws of physics and chemistry," he failed to see that he was suggesting a distinction between what I have called "language" and "communication." This is all the more amazing since 'language use' is an example he uses repeatedly. As a result, he failed to realize that a theory of "boundary condition imposition" (for a specified field of knowledge) is a grammar that generates the structures in question. The precise

form of the grammar determines the principles by which the structures are created. But Polanyi does recognize the existence of boundary conditions in the domains of geology, geography, and astronomy. These areas, however, are under the constraints only of their own structural history ("test tube-type boundary conditions") and not under the additional constraint of a design strategy ("machine-type boundary conditions") that characterize man-designed machines and evolving, living systems. If he had recognized the language-communication distinction that he was, in fact, using, then he might have made the further suggestion that theories of systems with machine-type boundary conditions require structural description in terms of the functional roles such structures play in the working of the machine. This, of course, is the strategy that I have employed in designing a grammar of ecological systems.

A Speculation

From this discussion it is possible to conclude with three observations which create further areas of speculation that cannot be pursued here. The first observation is that there are two fundamental strategies to be used in the proofs of mathematical theorems (Wilder, 1967). One of these is a "constructive proof" which proves the existence of a mathematical object or procedure by providing (and using) a well-defined method to construct the object or procedure.

The second strategy is an "existence proof" which proves the existence of an object or procedure by showing that no contradictions result from its existence. The second observation I want to make is that theories of languages using generative grammars prove the structural existence of an object or system by constructing that object or system, and theories of communication prove the "empirical possibility" (Causey, 1969) of objects or systems by showing that the object or system does not violate causal laws (i. e., by showing that the values of parameters and state variables describing the object are among those predicted by the laws). Finally, the third observation I should like to make is that expressed by Gregory Bateson (1967, p. 30):

Cyberneticians have specialized in those explanations which simulate [the mathematical proofs] reductio ad absurdum and 'mapping'. There are perhaps whole realms of explanations awaiting discovery by some mathematician who will recognize, in the informational aspects of nature, sequences which simulate other types of proofs.

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