

INTRODUCTION TO
SYSTEMS ECOLOGY

by

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PART I. FOUNDATIONS

CHAPTER 1. AN ORIENTATION TO SYSTEMS

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1.1 What is Systems Ecology?

To define what systems ecology is it is perhaps desirable to say something about what it is not. It is not an organized body of knowledge, and it is not a subdiscipline of ecology which is widely accepted by practicing ecologists. It certainly is not a panacea for all of the world's environmental problems, nor for all of the scientific problems of ecology as currently conceived.

Systems ecology is more of a hope right now than a reality. It is a vision of what ecology could become, should become, or perhaps *must* become if ecological science is to persist into the future as a viable enterprise. For the problems of our age, many of which touch ecology as a conventional academic discipline, are more and more seen to be problems of systems-- "copeless" problems of complexity, bigness, intangibility and unmanageability which do not yield to traditional thinking and methods of descriptive, analytical science.

What ~~systems ecology is~~ is a *way of thinking* whose hallmark is holism. It was Aristotle who first said that a whole is greater than the sum of its parts. Thus, in western science holistic thought predates causal reductionism, the central paradigm now, by several centuries. Systems ecology is part of a broad movement in contemporary science to return to the Aristotelian pursuit of wholes. It decomposes its systems--populations, communities and eco-systems--only to the extent necessary to understand how parts are knit together to create a whole. Systems ecology is interested in focusing on traditional problem areas, but from points of view that are new in relation to the perspectives of analytical science. By altering the frames of reference through which reality is viewed, systems ecology would seek also to generate new classes of problems that take form and have meaning only

within the changed context. So, systems ecology wants to approach old problems in new ways, but at the same time it wants to produce totally new kinds of problems which haven't been thought of yet.

Systems ecology is a *way of doing*. Its methodology, or proposed methodology, comes from areas of mathematics and engineering in contrast to the base of most of modern biology in physics and chemistry. Again, it is interested in analysis of how ecological systems operate, not through detailed examination of the functioning of isolated component parts, but rather through understanding of how parts are synthesized by interactive coupling into wholes. The tools of systems ecology presently are mathematical modeling, simulation, systems analysis and operations research. These named methods, which this book surveys, span a broad and developing spectrum of techniques which reflect systems thinking and which are specifically adapted to the investigation of wholes. The methods are not definitive, however. Quite the contrary. Existing methodology should be thought of as providing a base of knowledge from which new techniques more appropriate to systems of large size and fuzzy definition, which typically confront the ecologist, may be developed. Thus, ~~systems ecology is interested in exploring the applicability of existing systems methods to problems of ecological scale,~~ but also in using this experience to develop new methods of addressing both old problems and new problems.

Finally, in its broadest sense the principal concerns of systems ecology may be said to be theory on the one hand and application on the other. Systems ecology should seek to produce a unified formal theory of ecology and place this within the framework of a consistent general theory of biological organization. At the same time it should derive much of its motivation from real world needs to design, construct and manage large scale natural resource systems that place and maintain man in a proper relationship to nature.

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1.2 Qualitative vs. Quantitative Relationships

PATTERN + PROCESS

The trend in modern ecology has been toward quantification. The science proceeds by making measurements of natural events, analyzing these data, and drawing inferences therefrom. It would seem that systems ecology should be the height of this process, and consequently it will come as a surprise to the mathematically uninitiated that it is not. Systems ecology should not be confused with or equated to quantitative ecology! Much of its procedure is qualitative, involving emphasis on the logical structure of models, and concern with general behavior of classes of models as well as specific behavior of particular models. It is only in the final stages of problem development, usually, that specific models are implemented and verified by measurements. The distinction is much like that between arithmetic and algebra, wherein a quantitative statement like $4 + 3 = 7$ becomes a special case of a more general qualitative relation such as $x + y = z$, or even $x^2 + y = z$ (if $x=2$). The "behavior" of $4 + 3$ is fixed, but the two indicated classes of models ($x + y$ and $x^2 + y$) to which it could belong have quite different mathematical characteristics. It is important, therefore, in addition to obtaining purely quantitative data, to associate this data with appropriate qualitative statements about the natural processes which generated it. This, not mere quantification, is the real challenge of systems ecology. The point can be illustrated further by means of an example.

*Process in Ecology**EX**Example 1.1* Dynamics of Periphyton Growth

Periphyton or "aufwuchs" communities are assemblages of attached organisms which grow on solid surfaces underwater. They consist largely

it can be concluded as a general rule that uniform vertical distributions of periphyton biomass (Fig. 1.1c) do not tend to develop, and that patterns like those of Fig. 1.1b would be more typical of steady state communities. This has been verified by field observations (Neal *et al.* 1967).

In summary, definite conclusions about both the rate of periphyton biomass development and its vertical steady state distribution have been reached without making any quantitative measurements. The problem was so structured that many details of real periphyton communities were omitted, the assumption about a uniform water column being particularly artificial. Simplification of reality and inclusion of only those known empirical facts that are pertinent to a model's objectives are typical of the abstraction process by which models are constructed. If there is no abstraction the model tends to be too unwieldy and complicated mathematically. If abstraction is too severe, the model may bear little resemblance to reality.

Smith

The ~~art~~ **art of modeling** is the art of identifying essential features of a system to be modeled, and placing these in such qualitative relations to one another that the model's quantitative behavior represents reasonably the (pertinent) measured behavior of the real system.

1.3 The Time Line

Behavior is a concept related to time. *Behavior* and *dynamics* may be taken as synonyms. To discuss system dynamics it is necessary to be clear about time, or at least about the notations that will be associated with it. The reader should consult Sections 2.4.1, 2.4.3 and 2.4.6 at this time if unfamiliar with basic concepts of sets, subsets and set notation.

Time will be denoted by the variable t , having range T . For *continuous-time* systems, T will be taken as the real line $(-\infty, \infty)$ unless otherwise specified. For *discrete-time* systems T is usually the integers, $\dots, -1, 0, 1, 2, \dots$. *Time intervals* are subsets of T , with the following combinations for continuous systems from open to closed:

$$\begin{aligned} \text{open: } (t_0, t_1) &= \{t: t \in T \text{ and } t_0 < t < t_1\}, \\ \text{semi-open: } [t_0, t_1) &= \{t: t \in T \text{ and } t_0 \leq t < t_1\}, \\ \text{semi-closed: } (t_0, t_1] &= \{t: t \in T \text{ and } t_0 < t \leq t_1\}, \\ \text{closed: } [t_0, t_1] &= \{t: t \in T \text{ and } t_0 \leq t \leq t_1\}. \end{aligned}$$

1.4 First Concepts of State

The notion of system *state* is of central importance in systems science. In its general form the state concept is intuitive enough that in Section 1.2 terms like "steady state" and "equilibrium" could be used without prior definition. When one considers the behavior of a system, at base is implied something about change of state.

The state of a dynamic system is defined in terms of *state variables*. In Example 1.1, biomass $B(z, t)$ was used as an index of the "condition" of the periphyton system at depth z and time t . However, it was pointed out that other properties such as energy content, proteins, species composition, total nitrogen, nucleic acids, plant pigments, etc. would be useful parameters to monitor in studying the community's growth and development. As a matter of fact, a pretty extensive list of interesting variables could be drawn up. Each item on such a list would constitute a state variable, and the whole

group taken together is a *state set* or a *state vector*, depending upon how it is represented mathematically.

If a system has n state variables which are functions of time,

$$x_1(t), x_2(t), \dots, x_n(t),$$

then the state set can be denoted by $X(t)$,

$$X(t) = \{x_1(t), x_2(t), \dots, x_n(t)\}, \quad (1.4)$$

and the state vector by $\underline{x}(t)$, - *ORDERED*.

$$\underline{x}(t) = (x_1(t), x_2(t), \dots, x_n(t)). \quad (1.5)$$

In either case, the state of the system at time t is defined in terms of the values of the n variables at that time. A "value" does not have to be numerical, either. For example, suppose the state of a small mammal is defined in terms of two state variables, x_1 = body temperature, and x_2 = activity. Three possible states at time t might be

$$\underline{x}(t) = (37^\circ\text{C}, \text{eating}),$$

$$\underline{x}(t) = (37.3^\circ\text{C}, \text{running}),$$

$$\underline{x}(t) = (37^\circ\text{C}, \text{sleeping}).$$

Does not have to be numerical.

The temperature states are expressed numerically, but the activity states are not.

1.4.1 Discrete-Time Systems

1.4.1.1 The state transition operator

If $X(t)$ is the state of a system at time $t \in T$, where T is the set of integers, then the state at the next time, $t + 1$, is $X(t + 1)$. ~~if at least one of the n state variables has changed value in the interval between t and $t + 1$, then $X(t) \neq X(t + 1)$ and the system is said to have undergone a~~

DEF

change of state. This can be conceived as having occurred under the influence of a *state transition operator*, say α , which in some sense represents how the system responds to either external or internal forces exerted upon it. Thus, a discrete change of state can be represented as

→ rule for change

$\alpha = \text{rules for state transition}$

$$\alpha \begin{cases} X(t) \\ \downarrow \\ X(t+1), \end{cases}$$

and repeated operation of α in time generates state behavior:

$$\dots \xrightarrow{\alpha} X(t-2) \xrightarrow{\alpha} X(t-1) \xrightarrow{\alpha} X(t) \xrightarrow{\alpha} X(t+1) \xrightarrow{\alpha} X(t+2) \xrightarrow{\alpha} \dots$$

The system state acted upon at each step in the sequence is called the *operand*, and the resultant state is the *transform*.

NUMB

1.4.1.2 Transient and steady states

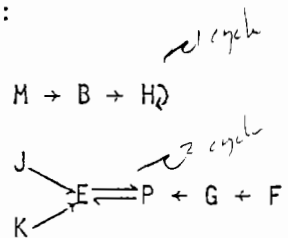
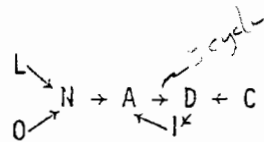
As an example, consider a hypothetical abstract system with 16 possible states: A,B,...,P. Suppose the behavior of the system under the action of an operator α is defined as follows:

$\alpha \downarrow$	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
	D	H	D	I	P	G	P	H	A	E	E	N	B	A	N	E

Permutation matrix

Good Example

If the system is started, say, in state M, then the discrete-time sequence of behavior will be $M \rightarrow B \rightarrow H \rightarrow H$. Once in state H, the system remains there. With other states as starting points, the complete behavior available to the system can be exhibited as follows:



Domains of Behavior or ATTRACTORS

This kind of representation is called a kinematic or behavior graph. The graph shows at a glance that, depending on the initial state, the system will advance to one of three sets of state sequences where it will remain: the self-loop $H \rightarrow H$, the cycle $A \rightarrow D \rightarrow I \rightarrow A \rightarrow \dots$, and the oscillation $E \rightleftharpoons P$.

3 possible end conditions (steady states) dependent upon initial conditions

1.13

These three end conditions comprise the steady state behavior of the system, and the remaining sequences constitute its transient behavior. The transient responses disappear eventually, leaving the system in one of its three steady state sequences.

NOTE: THIS may be true only until the system is disturbed again - Disturbance is an important + recurrent process in ecosystems (at any scale of life)

Example 1.2 Plant Succession on Isle Royale

The scheme just outlined can be used to characterize many different kinds of ecological phenomena where states, state changes and transition operators can be recognized. For example, in his study of the vegetation of Isle Royale in Lake Superior, Cooper (1913) identified 27 different kinds of plant communities (states):

- VALUES
- 1 crustose lichens (*Grimmia*),
 - 2 foliose lichens (*Hedwigia*),
 - 3 *Cladonia* species,
 - 4 heath mat,
 - 5 xerophytic forest,
 - 6 climax forest,
 - 7 crevice herbs,
 - 8 crevice shrubs,
 - 9 tuft mat,
 - 10 shrubs (*Vaccinium*),
 - 11 scattered herbs,
 - 12 low shrubs,
 - 13 tall shrubs,
 - 14 aquatic, bog,
 - 15 sedge mat,
 - 16 bog shrubs,

VALUES for the variables.

- 17 bog shrub - *Sphagnum*,
- 18 bog forest (*Larix*, *Thuja*),
- 19 *Ledum* - *Sphagnum*,
- 20 bog forest (*Larix*, *Picea*),
- 21 aquatic, delta,
- 22 sedge mat,
- 23 grasses,
- 24 shrubs (*Myrica*, *Alnus*),
- 25 swamp forest,
- 26 fireweeds,
- 27 burn forest.

Three significant ecological influences were distinguished:

- α normal succession,
- β burn succession, humus burned,
- γ burn succession, humus unburned.

The action of these factors produced the following state transitions:

Transition State

Alnus P. Penicillium matrix

↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
α	2	3	4	5	6	6	8	4	10	4	12	13	6	15	16,17	18	19	6	20	6	22	23	24	25	6	6,27	6
β	1	1	1	1	-26	7	7	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
γ	1	-	-	-	-26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

The kinematic graph of this succession is shown in Fig. 1.2, with additional information about the different classes of successions as recognized by Cooper. The graph displays to good advantage several sequences of transient behavior which comprise the seral stages of each distinct kind of site. All of these sequences converge toward state 6, the climax community, except when there is fire disturbance in which case the normal

state 6 is the climax community

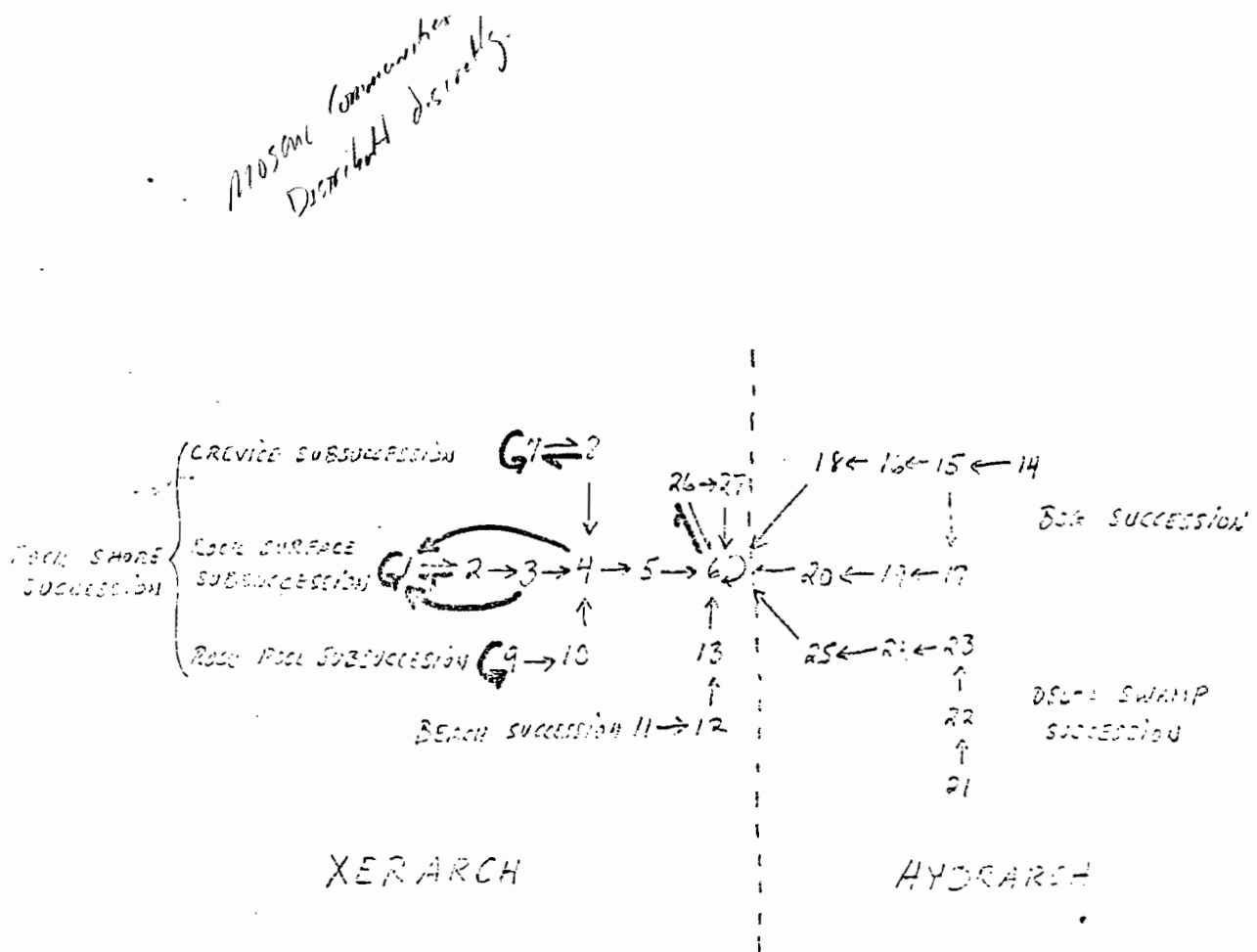


Fig. 1.2 Kinematic graph of plant succession on Isle Royale. Normal successions, α , are indicated by lighter arrows, and fire successions, β and γ , by bolder arrows.

successional processes are reversed. Three fire disclimaxes are indicated by self-loops, 1, 7 and 9. Note that state 15 may transform to either 16 or 17 and 26 to either 6 or 27. These alternatives are determined by particular ecological characteristics of the site in the first case and by whether or not the humus has been burned in the second case.

Example 1.3 The Hydrologic Cycle

Water moves in cyclic patterns around the globe, as described, for example, by Penman (1970). Consider the following states:

- 1 oceans,
- 2 water vapor,
- 3 land-surface water,
- 4 ice caps and glaciers,
- 5 lakes and rivers,
- 6 ground water,
- 7 water in organisms,

and processes:

- α_1 evaporation,
- α_2 sublimation,
- α_3 precipitation,
- α_4 freezing,
- α_5 runoff,
- α_6 percolation,
- α_7 melting

- 5 dry carcass (only skin, cartilage and bones remaining),
- 6 remains (hair, bits of skin, bones and teeth).

•Carriion kept free of insects decomposed and dried very slowly, retaining its form for many months, while 90% of the carcasses exposed to insects disappeared in six days. Insect-free carriion decomposed in five recognizable stages:

- 1 fresh carcass,
- 7 bloating and decomposition,
- 8 flaccidity and dehydration,
- 9 mummy (drying and gradual disappearance of flesh),
- 10 desiccation and disintegration (exposure and disarticulation of remaining tissues).

The agents of decay include a variety of:

- δ_1 bacteria and fungi,
- δ_2 arthropods.

Figure 1.6 depicts the sequences of decay stages. No cycles, loops, or other forms of steady state behavior are indicated. Decomposition is a transient phenomenon, viewed by itself, although actually a part of the cyclic behavior of chemical elements such as described for carbon and nitrogen in Examples 1.4 and 1.5.

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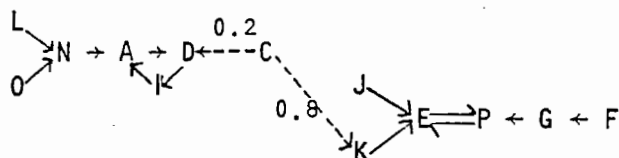
1.4.1.3 Deterministic vs. stochastic systems

The hypothetical 16-state system described before Example 1.2 above, is *deterministic* because given an operand the transform is predictable with

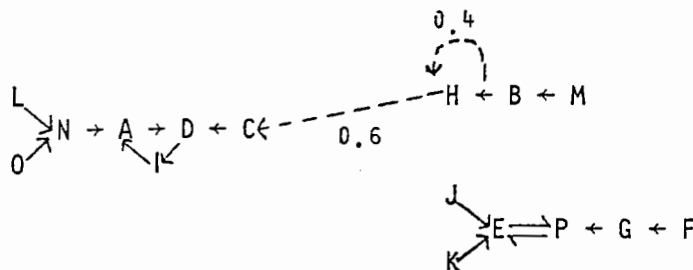
certainty. If state C transformed to D only 20% of the time and to, say, K 80% of the time, then the system would be called *probabilistic*, or *stochastic*. Probability is an element in its behavior, and this is one of the fundamental distinctions in classifying dynamic systems.

In the case cited the system would "resonate" between two different patterns of behavior, conforming to the kinematic graph above 0.2 of the time, and to another configuration 0.8 of the time:

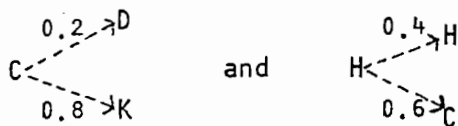
$$M \rightarrow B \rightarrow H \rightarrow$$



In another example, if H changed to itself with a reduced probability of 0.4 and to C with a probability of 0.6, a different "resonant" structure would occur:



Finally, if both



occurred simultaneously, there would be four kinematic graph configurations to consider: (i) the system when $C \rightarrow D$ and $H \rightarrow H$, which has a

Different Classes of Systems Exist

probability of $0.2 \times 0.4 = 0.08$; (ii) the system when $C \rightarrow D$ and $H \rightarrow C$, probability of $0.2 \times 0.6 = 0.12$; (iii) the system when $C \rightarrow K$ and $H \rightarrow H$, probability $0.8 \times 0.4 = 0.32$; and (iv) the system when $C \rightarrow K$ and $H \rightarrow C$, probability $0.8 \times 0.6 = 0.48$. Note that the separate probabilities sum to 1.00, indicating that all possible configurations are accounted for.

It is not hard to imagine other ways of introducing probabilistic behavior into this simple hypothetical system, and when the combinatorial consequences of doing so are considered (e.g., n probabilistic transformations lead to 2^n different behavior graphs), it is easy to see how rich in behavior alternatives stochastic systems can become. This fact makes categorizing the behavior of such systems exceedingly difficult.

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Example 1.7 Zoospore Production in *Protosiphon*

Protosiphon is a genus of green alga which reproduces asexually by means of flagellated spores called zoospores. Zoospore production is related to the nutritional state of the plant. O'Kelley and Deason (1962) provided the following information about the effect of nitrogen sources on zoospore formation in the species *P. botryoides*. Cultures in seven states were treated with six levels of each of three kinds of nitrogen--nitrate, ammonia and urea--and effects on zoospore production observed. The seven states were defined in terms of the percentage of total cells which were zoospores: 1=0-10%, 2=10-20%, 3=20-30%, 4=30-40%, 5=40-50%, 6=50-60%, 7=60-70%. The levels of nitrogen treatment were 0, 0.439, 4.39, 8.78, 21.95 and 43.90 ppm, with treatments v_1, \dots, v_6 in ascending order as nitrate, $\alpha_1, \dots, \alpha_6$ as ammonia, and u_1, \dots, u_6 as urea. Results were as follows:

Ex 1.10 Interspecific Action in Many Intertidal

This example is based on a paper by Paine (1966) dealing with rocky shore intertidal environments in which density space is a limiting factor. Paine's basic idea was that "local species diversity is

1.32

directly related to the efficiency with which predators prevent monopolization of the major environmental factors by one species." He suggested that top predators (starfish, such as *Pisaster* and *Heliaster*) affect community diversity out of proportion to their abundance because they prevent barnacles from monopolizing space. In cage studies comparing predation of starfish versus carnivorous gastropods upon barnacles, J. H. Connell has shown that starfish disrupt barnacles much more than gastropods do since they knock off many dead animals in the act of crawling over the community in search of food. This example will consider results from one of three geographical areas treated in Paine's study, the location at Mukkaw Bay, Washington. The feeding regime there is shown in Fig. 1.9. Of interest is the effect on local species diversity of removing the top carnivore, *Pisaster*, from a mid-intertidal to a low-intertidal strip.

The *Pisaster* was removed in June. By the following September, *Balanus glandula* occupied about 60-80% of the available space. By next June, *Mytilus* and *Mitella* had crowded out the *Balanus*. *Mytilus californianus* typically accumulates in clumps and eventually may be swept away by winter storms. After this happens *Mytilus edulis* and *M. californianus* will compete for the available space. The latter species has stronger byssal threads per unit weight, and hence is favored in wave-swept environments. *Mytilus edulis* exhibits crawl-out behavior when covered by gravel, and this allows this species to survive in calmer silt-laden waters.

Four states of this community may be recognized as follows:

- 1 natural intertidal community (barnacles, limpets, chitons, benthic algae, mussels, sponges, and nudibranchs),

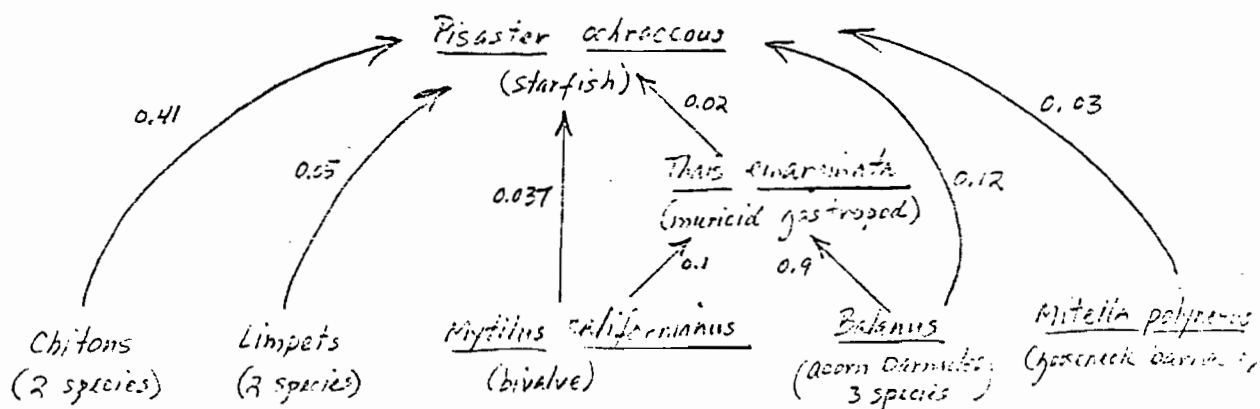


Fig. 1.9 Feeding regime in the intertidal community of Mukkaw Bay.

- 2 60-80% barnacle stage,
- 3 *Mytilus californianus*-*Mitella* stage,
- 4 *Mytilus edulis*-*M. californianus* stage.

The four significant operators on these states are the following:

- α_1 *Pisaster ochraceous* present,
- α_2 *Pisaster ochraceous* absent,
- α_3 winter storms,
- α_4 interspecific competition between mussels (*Mytilus*).

The table of state transitions is as follows:

↓	1	2	3	4
α_1	1	1	1	1
α_2	2	3	-	-
α_3	4	-	4	3
α_4	-	-	-	3

The corresponding kinematic graph is shown in Fig. 1.10. The effect on the community of removing the top predators is shown by the heavier arrows.

Example 1.11 Competition in *Tribolium*

Park (1954) studied competition in two species of flour beetles under different conditions of temperature and humidity. Populations of *Tribolium confusum*, when cultured alone, were able to exist at all six environmental combinations of temperature and humidity presented experimentally. Populations of *T. castaneum*, when cultured alone, were able to

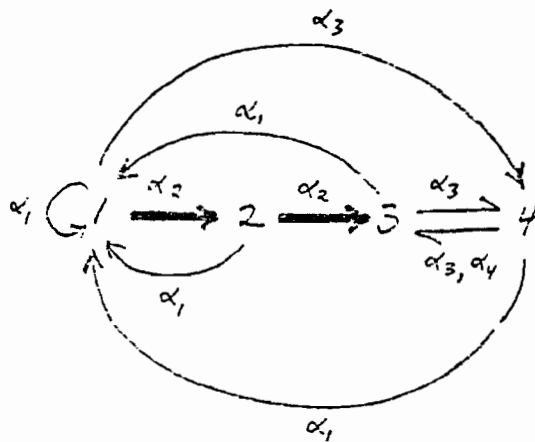


Fig. 1.10 Kinematic graph for the intertidal system discussed in Example 1.10.

exist in only five of the six environments. When cultures were started with equal numbers of both the species, one species was always eliminated after a period of time. Four recognizable states in an experiment were:

- 1 *T. confusum* only present,
- 2 *T. confusum* and *T. castaneum* present,
- 3 *T. castaneum* only present,
- 4 no beetles alive.

The operators, corresponding to experimental conditions, were as follows:

<u>Operator</u>	<u>Temperature</u>	<u>Relative humidity</u>
ϵ_1	34 C	70%
ϵ_2	34	30
ϵ_3	29	70
ϵ_4	29	30
ϵ_5	24	70
ϵ_6	24	30

A kinematic graph of the experimental results is shown in Fig. 1.11. The numbers associated with each operator in the figure are probabilities for the corresponding state transition. The graph shows that this system studied by Park is stochastic since state transitions do not always occur with unit probability.

Example 1.12 Mutualism between a Plant and an Ant

This example is based on a paper by Janzen (1967). Species of *Acacia* are plants that appear in disturbed areas of several community types in Central America. In general, the acacias are poor competitors in the plant community. They are highly limited by shading, and they

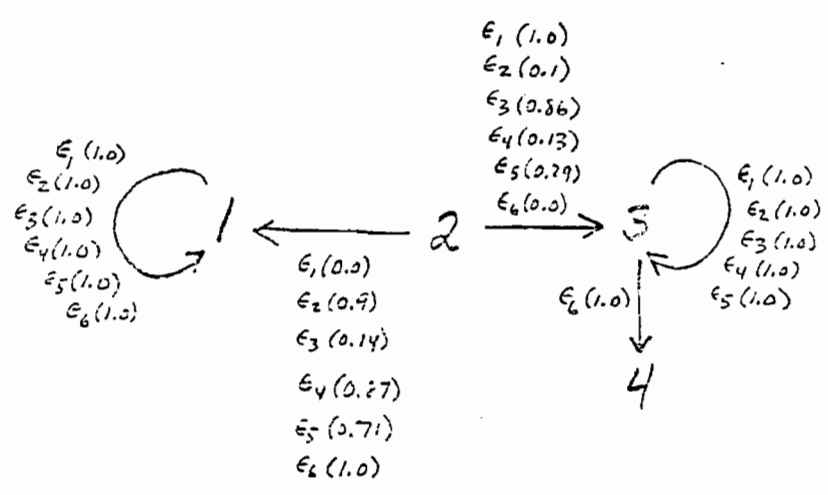


Fig. 1.11 Kinematic graph representing *Tribolium* competition experiments. Numbers in parentheses are probabilities.

Parse : competitions.
 competitive exclusion principle.

produce few deterrents against phytophagous insects and as a result are heavily grazed by these insects. The plant also has a thin bark and a heat sensitive cambium, and is consequently very susceptible to fire damage or destruction. Individual plants are generally eliminated from the community in 2-15 months.

However, a mutualistic relationship between the species of *Acacia* and species of the ant genus *Pseudomyrmex* increases the competitive ability of *Acacia*. The ants form colonies on the *Acacia* plants, and obtain energy by grazing certain parts of the plant's leaflets and by consuming nectar from numerous foliar nectaries. During unfavorable weather conditions the ants seek cover in the enlarged stipular thorns of the acacias.

The ants actively patrol all of the surface parts of the plant and destroy plant material and other insects that come in contact with *Acacia*. This patrolling reduces the shade effects of neighboring plants and also grazing by phytophagous insects. It also has a third important effect, that of reducing the amount of litter around the base of the *Acacia* stems. This reduces the fuel load in an area and in turn reduces the temperatures that could be produced by a fire near the base of the stems.

Acacias associated with an ant colony become viable members of the plant community. However, if the ant colony is destroyed the plant will be rapidly eliminated unless a new colony becomes established.

The states of this system x_i , where i is the number of states, can be described in terms of two state variables, x_1 and x_2 :

$$x_i = (x_1, x_2).$$

$$X_i = (x_1, x_2)$$

$$x_1 = \{0, 1, 2, 3, 4\}$$

$$x_2 = \{0, 1\}$$

x_1 is a measure of size of the *Acacia* plants, and takes on values 1, 2, 3 and 4 corresponding, respectively, to an increase in size from a new shoot to a full grown (greater than 2 m tall) *Acacia*. x_2 describes the condition of the ant colony and assumes the values 0, no colony, and 1, a colony present. In addition, x_1 can take on a value of 0 to indicate that the plants and their ant colonies have been killed by fire. For example, a system in state (0,0) indicates one in which the *Acacia* and its colony have both been killed by fire. The *Acacia* roots will regenerate a new shoot. A system in state (0,1) indicates one in which the plants have been killed by fire but the ant colonies have remained alive. In this instance the colonies will move to a new *Acacia* shoot when regenerated.

Nine states of the system can be recognized:

$x_1 = (1, 0)$	shoot with no ant colony,
x_2	dead plant (both root and shoot),
$x_3 = (1, 1)$	increasing plant growth,
$x_4 = (2, 1)$	
$x_5 = (3, 1)$	
$x_6 = (4, 1)$	
$x_7 = (0, 0)$	fire damage.
$x_8 = (0, 1)$	
$x_9 = (\geq 2, 0)$	

The following operators act on these states:

- α action of ants in maintaining plants,
- ι action of phytophagous insects,
- π shading by other plants,
- ϕ_1 light ground fire,

ϕ_2 hot ground fire,

ϕ_3 canopy fire,

τ elapse of time and absence of ϕ_1 , ϕ_2 , and ϕ_3 .

OTHER
 Rules IN
 Rules
 (ALGORITHMS ?)

Certain constraints exist between the operators and the system states:

- (1) ι and π are not considered to operate if $x_2 = 1$,
- (2) ϕ_1 acts if and only if $x_1 > 3$,
- (3) ϕ_2 operates on x_4 and x_5 to produce variable results; the probabilities of each behavior cannot be determined from data in the original paper except to note that when ϕ_2 operates on x_5 it produces x_7 with a low frequency,
- (4) Since fire in an area reduces the fuel load of that area, it also reduces the probability of a second fire. Therefore, to simplify the model it will be assumed that fire may not act as an operator twice in succession.

The state transitions of this system are summarized below:

\downarrow	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9
α	x_4	-	x_4	x_5	x_6	x_6	-	-	x_5
ι	x_2	-	-	-	-	-	-	-	x_2
π	x_2	-	-	-	-	-	-	-	x_2
ϕ_1	x_7	-	x_7	x_7	-	-	-	-	-
ϕ_2	x_7	-	x_7	x_7	$\left\{ \begin{array}{l} x_7 \\ x_8 \\ x_9 \end{array} \right.$	$\left\{ \begin{array}{l} x_6 \\ x_8 \end{array} \right.$	-	-	-
ϕ_3	x_7	-	x_7	x_7	x_7	x_7	-	-	-
τ	-	-	-	-	-	-	x_1	x_3	-

The corresponding behavior graph is shown in Fig. 1.12. Action of the ants in maintaining the *Acacia* populations is indicated by the heavier arrows.

The foregoing examples are sufficiently varied in substance and notation to illustrate with some generality the concepts of state and change of state as applied to discrete-time ecological systems. The reader should refer to Ashby (1956) for general reference and for further development of this systems approach along similar lines.

Exercise 1.1

Do these patterns occur

(with + in line)

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Final Report*

*Describe
1 transition
↓
Pull out the
Patterns*

1. Prepare kinematic graphs to represent the behavior of several different kinds of ecological systems obtained either through a literature search or from personal experience.
2. What virtues and limitations of this kind of modeling are particularly noticeable?
3. Are alternative ways of modeling these same systems obvious?

1.4.1.4 Change of transition operator

Systems not only undergo *state* transitions, but the rules of such changes may themselves be **subject** to dynamic behavior. In other words, the transition operators may change. Let δ_1 , δ_2 and δ_3 be operators whose behavior is determined by another operator, Δ :

$$\begin{array}{ccc} & \delta_1 & \delta_2 & \delta_3 \\ \Delta \downarrow & & & \\ & \delta_2 & \delta_2 & \delta_1 \end{array}$$

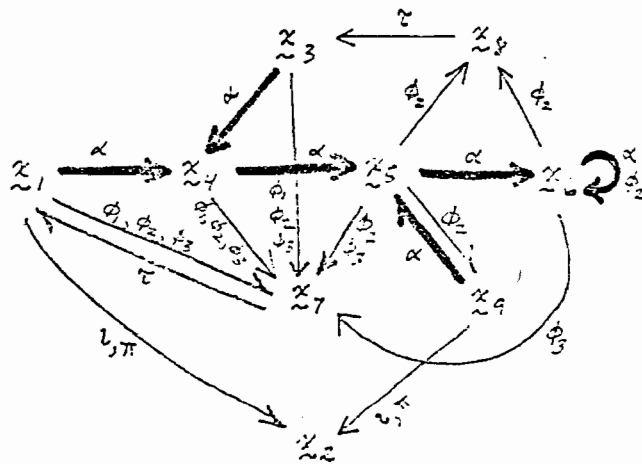


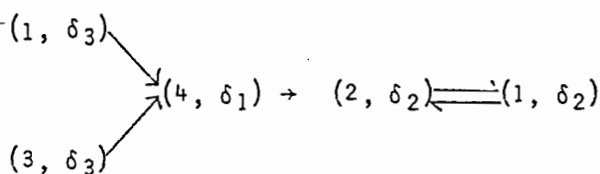
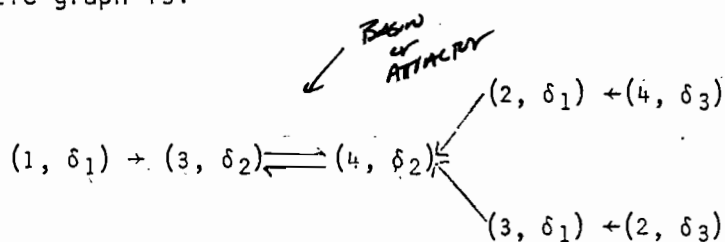
Fig. 1.12 Behavior graph for the *Acacia-Pseudomyrmex* system.

Let the behavior of a system with four possible states 1, 2, 3 and 4 be defined by the following transition matrix:

\downarrow	1	2	3	4
δ_1	3	4	4	2
δ_2	2	1	4	3
δ_3	4	3	4	2

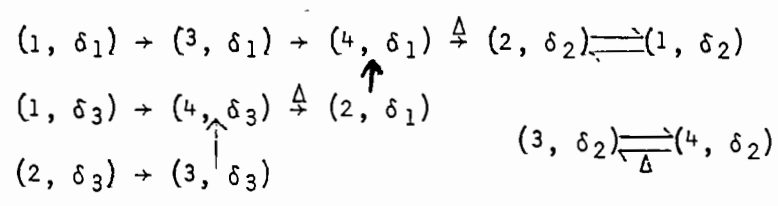
There are numerous ways for this system to behave, depending upon how the operator Δ is read in. Several cases will be sufficient to illustrate.

Suppose Δ operates after each change of state. Then, denoting each system "state" by two arguments, (i, δ_j) , where $i = 1, \dots, 4$ and $j = 1, 2, 3$, the kinematic graph is:



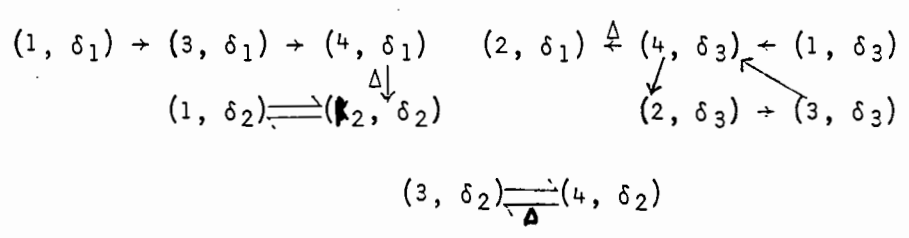
Note that the number of "states" is $i \times j = 4 \times 3 = 12$ in all, and also that there are two steady state sequences.

Now suppose that Δ is state-actuated and operates only when the system is in state 4. Then, although the two steady states are unchanged, the transient behavior is quite different (the points where Δ operates are indicated):



*Strong
steady
states
But Different
Doubt. HMMs*

Again, if Δ were related to the history of the system, and operated only when state 4 was preceded by 3 or ~~4~~ but not ~~1~~^{10/2}, the graph would be:



*Weak steady states
is enough*

The transient and steady state behavior are both different.

The preceding examples illustrate how system behavior may become "self-organized" in the sense of the rules of change becoming themselves state-determined. The main point to be stressed, however, is that different rules for specifying when operators act determine different patterns of system behavior.

1.4.1.5 Generalization of discrete-time behavior

Let $\underline{x}(t)$ be the state vector of a system at time t . In most of the preceding examples system behavior was not observed at unit steps along the time line,

$$\dots \rightarrow \underline{x}(t-2) \rightarrow \underline{x}(t-1) \rightarrow \underline{x}(t) \rightarrow \underline{x}(t+1) \rightarrow \dots,$$

nor at finite but even steps of other than unit length,

$$\dots \rightarrow \underline{x}(t-2\Delta t) \rightarrow \underline{x}(t-\Delta t) \rightarrow \underline{x}(t) \rightarrow \underline{x}(t+\Delta t) \rightarrow \dots,$$

where Δt is a constant finite time interval. System states were noted for convenience at arbitrary times $k_i \Delta t$, where k_i are real numbers. Such behavior is still discrete-time dynamics because the time steps between state

observations are finite, although unequal:

$$\dots \rightarrow \underline{x}(t+k_{-2}\Delta t) \rightarrow \underline{x}(t+k_{-1}\Delta t) \rightarrow \underline{x}(t) \rightarrow \underline{x}(t+k_1\Delta t) \rightarrow \dots,$$

AND INTERVAL
will work

where the k_i ($i = \pm 1, \pm 2, \dots$) are real constants. In the type of systems to be considered next, the time interval between states is infinitesimal.

1.4.2 Continuous-Time Systems

Let Δt be a finite interval of time and dt be an infinitesimal increment; i.e.,

$$dt = \lim_{\Delta t \rightarrow 0} \Delta t .$$

If $\underline{x}(t)$ is the state of a system at $t \in T$, where T is the real line, then the state at the next instant following t is $\underline{x}(t+dt)$. State behavior,

$$\dots \rightarrow \underline{x}(t-2dt) \rightarrow \underline{x}(t-dt) \rightarrow \underline{x}(t) \rightarrow \underline{x}(t+dt) \rightarrow \dots,$$

is *continuous*, and such systems are called continuous-time systems (Section 1.3) if their states are observed continuously. The periphyton system of Example 1.1 was formulated as such a continuous system, as indicated by the fact that a differential equation [Eq.(1.1)] was used to define its state transitions. In ecology, classical models describing growth of populations serve as a good introduction to continuous-time systems.

Models of population growth and development have always been popular in animal ecology. Early concerns in epidemiology and demography generated the basic form of mathematical treatments of population phenomena. Good reviews of this work are to be found in Lotka (1925) and D'Ancona (1954). The basic approach through differential equations carries over into some of the most modern methods of systems analysis, and it is probably fair to say that present-day interest in mathematical and systems ecology is directly related to an early coupling of mathematical modeling and

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