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**Proceedings of a Joint U.S.-Japan
Seminar in the Environmental
Sciences**

Organized and Edited by
Donald L. DeAngelis and Ei Teramoto
with assistance from
Daryl A. Neergaard

Environmental Sciences Division
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PROCEEDINGS OF A JOINT U.S.-JAPAN SEMINAR
IN THE ENVIRONMENTAL SCIENCES

April 24-30, 1988
East-West Center, Honolulu, Hawaii

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ABSTRACT

The Joint U.S.-Japan Seminar in the Environmental Sciences was based on the premises that questions remain concerning the factors that control many of the regularities observed in ecological communities and that increased collaboration between researchers in the United States and Japan can contribute to answering these questions. The papers included in this report resulted from the Seminar. These papers as well as workshop discussions summarized here outline the main issues that face theoretical ecology today. The papers cover four different areas of theoretical ecology: (1) individual species adaptations, (2) ecological community-food web interactions, (3) food web theory, and (4) concepts related to the ecosystem.

REPORT ON A JOINT U.S.-JAPAN SEMINAR IN THE ENVIRONMENTAL SCIENCES

BACKGROUND OF SEMINAR

The idea of a joint U.S.-Japan Seminar in the environmental sciences was based on the following premise. Despite recent progress in understanding ecosystem behavior, questions remain concerning the factors that control many of the regularities observed in ecosystems.

Fascinating general patterns have been noted, for example, in community structure (e.g., Cohen 1977, 1978; Pimm 1980a,b; Rejmanek and Sary 1979; Briand 1983; Briand and Cohen 1984), but there is as yet no general theory that can explain the observed patterns. Theoretical ecologists have been sharply divided in their views on what the basic factors are that control the structure of ecological communities. Despite the recent publication of several edited volumes devoted to this subject (e.g., DeAngelis et al. 1983; Price et al. 1984; Strong et al. 1984; Kikkawa and Anderson 1986), gaps between competing viewpoints seem little closer to being resolved.

A new approach is needed to attain a generally accepted body of theory of ecological communities (and more generally of ecosystems as well, since abiotic factors and flows of energy and matter must be part of any general body of theory). We believed that a Joint United States - Japan Seminar, structured along the lines described below, could be the beginning of a cooperative effort to achieve a synthesis of alternative views.

The general theme of the workshop revolved around the following questions. Are there regularities in ecosystem structure and, if so, do these regularities reflect constraints related to dynamic stability, energy, or other factors on the ecosystem? How do ecosystem properties and the characteristics of individual species change during succession and/or evolution? Finally, and most importantly, can theoretical ecologists who approach the study of ecosystems from different viewpoints achieve a unified theoretical perspective that will stimulate greater progress in understanding and prediction? Some areas where a unified perspective would be particularly useful in resolving different viewpoints are briefly described below.

A variety of regularities has been noted in the vertical and horizontal structure of trophic webs (Pimm and Lawton 1977, 1978; Cohen 1977, 1978; Sugihara 1982; Briand 1983) and in the numbers and types of connections between species (Rejmanek and Sary 1979; Pimm 1980a,b; Briand 1983; Briand and Cohen 1984). However, interpretations of the causes of these patterns have been divided. The observed consistently short lengths (usually three or four links at most) of trophic chains in communities have been attributed variously to energy limitation (Yodzis 1980, 1981), interspecific population dynamics (Pimm and Lawton 1977, 1978; Pimm 1982), and (in part, at least) probabilistic considerations (Auerbach 1984). A wide variety of hypotheses has also been offered for the fact, observed by Cohen (1978), that niche overlaps of species competing for resources can be represented on a one-dimensional niche space (Yodzis 1982; Critchlow and Stearns 1982; Sugihara 1982; Cohen 1983). A synthesis is needed either to decide among alternative causal explanations or to show that there is a synergistic interaction among the different proposed causal factors. Other equally puzzling patterns include the "species scaling law" (Briand and Cohen 1984), stating that the mean proportion of numbers of basal, intermediate, and top species remain invariant at approximately 0.19, 0.53, and

0.29, and the "linked-species scaling law" (Briand and Cohen 1984), stating that the ratio of mean trophic links to species remains invariant at approximately two over a whole range of variation of numbers of species in food webs.

Another main area where regularities have actively been sought is in the phenomenon of successional and evolutionary changes in ecological communities. Both Drake (1983) and Post and Pimm (1983) studied the assembly of food webs by species invasions through time using computer simulations of Lotka-Volterra systems. Drake showed that only a small subset of species is capable of invading these food webs, while Post and Pimm showed that the rate of species turnover declined with time. These results are only computer simulation results; a deep understanding of how species composition should change through time may require mathematical analysis.

Other theoretical ecologists, studying ecological systems from the point of view of energy and material flows rather than species composition, have proposed that deterministic trends should occur in a number of energy, nutrient, and information relationships during the course of succession or evolution. Some of the hypothesized trends are the following: (a) biomass and the amount of biomass maintained per unit of energy input should increase (Odum 1969), (b) nutrient cycles should become tighter through time (Odum 1969), (c) utilization of energy in the ecosystem should become more efficient through time (Margalef 1963), (d) ecosystems should evolve so as to maximize the power (Odum and Pinkerton 1955), and (e) ecosystems should evolve to maximize the information theory index called "ascendancy" (Ulanowicz 1986). Some of these generalizations have been questioned (e.g., Drury and Nisbet 1973) and some may not be completely consistent with others. These hypotheses should be examined systematically along with the hypotheses for changes in species composition, using both computer simulations of the sort used by Drake (1983) and Post and Pimm (1983), and more general mathematical analyses.

The above brief overview shows that there are many unresolved problems in the subject area of ecological communities, concerning both their structural properties and successional or evolutionary changes. An active search for new perspectives to help in attaining a deeper theoretical understanding of community structure and dynamics has led to a diversity of modeling approaches. For example, Abrams (1982, 1984) has attempted to relate community dynamics to optimal foraging strategies of consumers. Cohen and Newman (1985) proposed a simple neutral model, the "cascade" model, of food webs that requires only a knowledge of the numbers of functional species and links, plus the assumption that species are ordered in a cascade-type hierarchy, to predict other empirically observed food web characteristics. Ulanowicz (1986) developed an approach to ecological communities based on mathematical matrices of nutrient and energy flows. Patten and his colleagues (e.g., Higashi et al., 1989; Patten 1985; Patten and Auble 1981) have proposed a general theory of ecosystems as hierarchically organized networks in which indirect effects play a major role. Pimm's (1979a,b, 1980a,b, 1982) hypotheses concerning food web structure and resilience are based on computer simulations of sets of Lotka-Volterra equations. The approaches have all been useful, but a more unified perspective would clearly help in relating these approaches to each other.

The above outline of mathematical approaches mentions primarily U.S. scientists. However, at the same time, Japanese theoreticians have developed a great body of mathematical theory. This work appears to be relevant both to developing a unified mathematical framework and to helping

resolve some of the questions concerning ecological communities listed earlier. This body of mathematical theory is not generally known in the United States, which was an important reason for bringing together Japanese and U.S. scientists.

At the center of the Japanese contributions to mathematical ecology has been the work of Professor Ei Teramoto of Kyoto University and a group of colleagues (H. Ashida, H. Nakajima, N. Shigesada, K. Kawasaki, and N. Yamamura), known to many through their collective nom de plume as "Mumay Tansky" (Tansky 1976, 1978). The basic objectives of this group have been to study dynamic stability of food webs as a function of energy flow and trophic structure and to develop the mathematics to describe successional processes in food webs. What is particularly important about this work is that it is, in general, applicable to highly complex systems. For example, recent work by Shigesada enables one to consider N species interacting through interference competition and to determine which subset of these species will be eliminated and which will persist in equilibrium. Nakajima has been able to predict mathematically what sort of community will develop through successional (or evolutionary) time if new species having different characteristics continue to invade. He found that a particular quantity, resource utilization, increases with successional change in such models. The techniques used by these theorists and other mathematical ecologists in Japan are original and powerful. They have not in general been used to address the major questions that are being confronted by U.S. ecologists.

In addition, Japanese empirical ecologists have developed their own conceptual theories, emphasizing a holistic and phenomenological view of natural communities and ecosystems. A major focus has been placed on life-style differentiation within communities.

Professor Teramoto had the original idea of holding this meeting to initiate a start towards resolving the issues discussed above and to develop a unified perspective. He asked D. L. DeAngelis to write a proposal to the International Program Section of NSF to secure funding for several theoretical ecologists from the U.S. and Japan. The plan was for the seminar to have a workshop format. Funding was granted and the meeting was arranged to be held at the East-West Center in Honolulu. Appendix A lists the participants of the meeting and Appendix B lists the papers presented. The papers and workshop discussions met the desired goal of outlining the main issues that face theoretical ecology today.

SCIENTIFIC REPORTS AND DISCUSSION

An important aspect of the reports presented at the Seminar, besides their scientific contents, were their relationships with one another. Do they relate as components of a unified perspective?

At the highest level one can divide approaches that center on a population dynamics point of view from those centered around the flows of energy and matter. According to the traditional "population dynamics" point of view, there is a hierarchy that extends from the smallest units, the individual organisms, to single-species populations, then to single-trophic level communities made up of populations, and finally to food webs made up of several trophic levels. Constraints due to natural selection at the individual level affect all of these levels. Each of these topics has traditionally been a field of study in its own right.

The task of attaining a unified perspective requires understanding the interfaces of these fields; for example, understanding how the characteristics of individual organisms affects dynamics at the population or food web level.

According to the "systems ecology" point of view, flows of energy and matter are of great importance. These flows must obey physical constraints, such as the laws of thermodynamics. The area where ecological theory is most in need of unification, or at least of more intense work is the interface between population dynamics and the systems ecology of flow of energy and matter. This should most naturally occur at the food web level, since it is only there that all the organisms of an ecosystem are present for a complete cycle of nutrients through the biota.

Ideally, one should study all of the aspects of the ecosystem discussed above together. However, in a practical sense progress is often best made by approaching the whole problem by looking at only a few pieces at a time. The papers presented at the Seminar can be classified to fall into four general categories.

1. The influence of individual adaptive strategies of individual species (as evolved through natural selection) on population, community, food web, and ecosystem dynamics.
2. Community level theory, especially as it relates to the community as part of the larger structure of the ecosystem. ("Community" is here taken to mean a set of species that occupy a single trophic level and potentially compete.)
3. Food web theory.
4. Ecosystem theory, emphasizing energy and material flows and macroscopic indices of the system derived from information theory and thermodynamics.

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Individual Adaptations: Effects on Multispecies Systems

One of the clearest trends towards unification of different areas of ecological theory is the attempt to build individual adaptive strategies of species, which have evolved through natural selection, into models of populations, communities, and food webs.

REPRESENTING BIOLOGICAL COMMUNITIES CONTAINING OPTIMALLY FORAGING HERBIVORES: IMPLICATIONS OF ADAPTIVE BEHAVIOR FOR COMMUNITY STRUCTURE

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INTRODUCTION

Pimm's (1979, 1980, 1982) pioneering work on food webs adopted a simple Lotka-Volterra representation for between-species interactions. This type of community modelling derives from earlier representations of large communities using Lotka-Volterra equations beginning with MacArthur and Levins. Similar models characterize many studies of food webs up until the present time (e.g., Post and Pimm 1983, Yodzis 1982, Drake 1988). When very little is known of the details of biological interactions, it seems reasonable to assume linear per capita effects on the growth rates of species that eat or are eaten by a given species. However, we all know that the world is a very nonlinear place, and are left with the nagging worry that conclusions based on Lotka-Volterra models may be misleading us in important ways. The question of linearity is especially worrying when considering theories that explain the lack of certain types of communities or food webs based on the dynamical instability of corresponding models with linear per capita effects.

One important source of nonlinearities is adaptive behavior on the part of the species in the community. The processes of finding food and avoiding being eaten both generally involve costs and benefits, and a variety of organisms have been shown to adjust their behavior based on those costs and benefits (e.g., Stephens and Krebs 1986, Kerfoot and Sih 1987). This has been shown to have two types of effects in models of adaptive organisms: (i) interspecific effects of population density on per capita growth rate tend to become nonlinear (if they are not already so), and (ii) a variety of interactions (which are themselves generally nonlinear) arise between species that do not eat or are not eaten by each other. Adaptive behavior by a species on one trophic level is likely to affect the population growth rates of other species on the same trophic level which share predators or parasites (Holt 1984, 1987; Holt and Kotler 1987; Abrams 1987c). This includes higher order interactions, in which one species affects the interaction of two others. Adaptive behavior by either predators or prey affects the stability of the predator-prey interaction (Abrams 1982, 1984; Sih 1984; Ives and Dobson 1987; Hassell and May 1985). Adaptive behavior by a species on one trophic level may result in interactions between the species on higher and lower trophic levels (Abrams 1984, Mittelbach and Chesson 1987). In spite of this diversity of effects, the influence of adaptive behavior on interactions within communities has received relatively little theoretical, and even less empirical attention.

It is perhaps not surprising that the interactions produced by adaptive behavior are absent from general models. In the case of higher-order interactions, for example, there has been considerable documentation that such interactions exist in various communities, but there is no body of theory predicting what sorts of higher order interactions will occur in what circumstances. If one begins with a community description that includes only direct trophic relationships, one has no guidance about what higher order actions will usually occur. By beginning with a model that assumes

adaptive behavior, the higher order interactions arise as a natural consequence of adaptation, and no special body of "higher order interaction theory" is required.

Rather than present a general survey of the effects of adaptive behavior in food web models, I will concentrate on such behavior in a specific group of organisms that is present in most real and model food webs: herbivores. Herbivores have traditionally received less attention from most theoretical community ecologists than have other functional groups. In particular, very little is known about the implications that adaptive foraging by herbivores has for the form of plant-herbivore population models. In the majority of food web models, and the majority of review articles on plant-herbivore models, herbivores are indistinguishable from carnivores except by their location in the food web, and perhaps by their lower trophic efficiency. Because all non-detritus-based food webs contain plants and herbivores, and because these two groups often comprise the vast majority of the community's biomass, understanding plant-herbivore interactions is often essential for understanding community structure and dynamics.

A variety of models of plant-herbivore interactions have been discussed in recent reviews of plant-herbivore dynamics (Caughley and Lawton 1981; Crawley 1983). A notable feature of these models is that the form of the herbivore species' functional response(s) has been similar to those used in traditional predator-prey models. At the same time, the authors of these and other articles stress that herbivores often face a very different set of foraging decisions than do carnivores, and this would lead one to expect different functional responses, if herbivores forage adaptively. For many, if not most, herbivores, edible items are abundant, but much of the potential food is undesirable due to: (1) lack of specific nutrients or improper balance of different limiting nutrients; (2) low concentrations of all nutrients; and (3) the presence of toxins or inhibitors of the digestive process. Low nutrient concentrations constitute a problem because the size of the digestive system and the passage rate through it are both limited. Some analyses of optimal diet in herbivores have considered how an individual herbivore should behave when faced with these foraging problems (reviewed in Stephens and Krebs 1986, Chapter 5). However, this work has not been extended in models of plant-herbivore population dynamics. The purpose of the present article is to provide a foundation for that extension by describing the functional responses that would be predicted for an adaptive herbivore species faced with one or more of the above foraging problems. In addition, I will consider, although in a less systematic manner, the implications that such functional responses have for the form of plant-herbivore population dynamics. Because most of the models include 2 or more plant species, and some include more than one herbivore, they may be viewed as simple food webs. Each of the three foraging problems is treated in turn in the following analysis.

THE PROBLEM OF NUTRITIONALLY INCOMPLETE FOODS

Early in the history of optimal foraging theory, Westoby (1974) pointed out that many generalist herbivores must consume more than a single plant type in order to obtain a diet that supports survival and/or reproduction. Theory related to the optimal use of such nutritionally complementary foods has been discussed by Covich (1972), Pulliam (1975), Leon and Tumpson (1975), Rapport (1980), Tilman (1980, 1982), and Abrams (1987a,b). The problem of nutritionally incomplete

resources is, of course, not restricted to herbivores, and is an important consideration in adaptive resource exploitation by plants.

An extreme form of complementarity occurs when an individual's fitness is solely a function of the resource whose intake is lowest relative to requirements. This case serves to show especially clearly the types of effects that can arise with less extreme forms of complementarity. Such nonsubstitutable resources should usually be exploited in such a way that a constant ratio of intake rates of the two forms is maintained (Abrams 1987a,b). The case in which there are two nonsubstitutable resources and there exists a tradeoff between abilities to consume each type, has been analyzed in detail (Abrams 1987a,b); if the functional response on each resource is given by $C_i R_i$, the optimum values of C_1 and C_2 are those that maximize $C_1 R_1$ subject to the constraint that $C_1 R_1 = B C_2 R_2$, where B is the desired ratio of intake rates. If the maximum possible C_2 is a linearly decreasing function of C_1 , $k_1 C_1 + k_2 C_2 = 1$, then equal intake rates imply the following functional response forms:

$$\frac{B R_1 R_2}{k_2 R_1 + B k_1 R_2} \text{ for resource 1, } \frac{R_1 R_2}{k_2 R_1' + B k_1 R_2} \text{ for resource 2} \quad (1)$$

These response differ from those used in most predator-prey or food web models in that they imply negatively frequency dependent consumption. More effort must be devoted to obtaining a resource as its availability declines in order to maintain a constant ratio of intake rates. Christopher Kitting, who observed such constant ratio foraging by an intertidal limpet feeding on two algal species (1980), suggested that such foraging should be destabilizing if the herbivore had a significant impact on the population densities of the plants. However, until recently, there has been no theoretical analysis of simple food webs in which the herbivores pursued such a strategy. Abrams and Shen (1989) have recently examined the dynamics of one consumer-two resource, and two consumer-two resource models in which resources are self-reproducing populations, and the consumers pursue a constant ratio strategy of resource intake, with functional responses given by the above formulas. If the resources are logistic and the functional responses are as given above, a one-consumer version of such a model has the following form:

$$\begin{aligned} \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1} \right) - \frac{B R_1 R_2 N}{K_2 R_1 + B k_1 R_2} \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2} \right) - \frac{R_1 R_2 N}{k_2 R_1 + B k_1 R_2} \end{aligned} \quad (2)$$

$$\frac{dN}{dt} = bN \left(\frac{B R_1 R_2}{k_2 R_1 + B k_1 R_2} - D \right)$$

The dynamics of both one and two consumer species systems is surprisingly complex. Some of the more notable features of these population dynamics are summarized below:

- (1) Single-consumer systems are characterized by a single stable equilibrium at low rates of resource exploitation, but have three equilibria at sufficiently high rates of exploitation ("high exploitation rates" means that a small resource intake rate is required for zero consumer population growth).
- (2) Depending on parameter values, when three equilibria exist in a one-consumer system, there may be either one or two attractors; if there are two attractors, there may be either two locally stable points, or a stable point and a limit cycle. If there is a time delay in the consumer's numerical response to altered resource densities, there may be two alternative limit cycles.
- (3) Two-consumer systems have a single equilibrium point, which is unstable when the resource densities at that point are sufficiently low. Thus, high exploitation rates result in oscillatory population dynamics. The correlations between the population densities of the competing consumers are usually negative at moderate exploitation rates, but positive at high exploitation rates. Figure 1 illustrates the range of dynamics that occur in a simple, symmetrical case when the consumer's resource requirement for zero population growth is varied.

These and other related results are presented in greater detail in Abrams and Shen (1989).

Some less extreme forms of nutritional complementarity result in constant-ratio strategies of resource exploitation (Abrams 1987b), and therefore can result in the same functional responses and the same range of population dynamics described above. Any type of nutritional complementarity will cause negatively frequency dependent predation to be adaptive in most circumstances.

Speculation about the form of many-species models leads to a number of possible differences between models based on the above framework, and those with "Lotka-Volterra" herbivores. One of the results that can be derived from Eqs. (2) is that increasing the herbivore's (consumer's) D value by increasing its death rate can, depending on the attractor at which the system is located, result in an increase in equilibrium or average herbivore population density (Abrams and Shen 1989). It is possible that, in many-species models, an increase in total carnivore population or an evolutionary increase in carnivore hunting efficiency might increase total herbivore population density. If the plant species in a community can be separated into a small number of nutritionally complimentary groups, then there will be mutualistic interactions between the plants within a group, as the result of their effects on the herbivore's functional response. An increase in one plant species will result in reduced effort by the herbivore to consume all plant species in its nutritional group. At the same time, there are negative interactions between plants in different nutritional categories. If these nutritionally different plants also compete directly for resources, the indirect interaction arising from the herbivore's functional responses could affect conditions for coexistence, often making coexistence less likely.

Omnivores are perhaps even more likely than herbivores to consume nutritionally complimentary foods. The functional responses predicted for omnivores that feed on both animal and plant food are especially likely to involve complementarity (example in Rapport 1980), and the

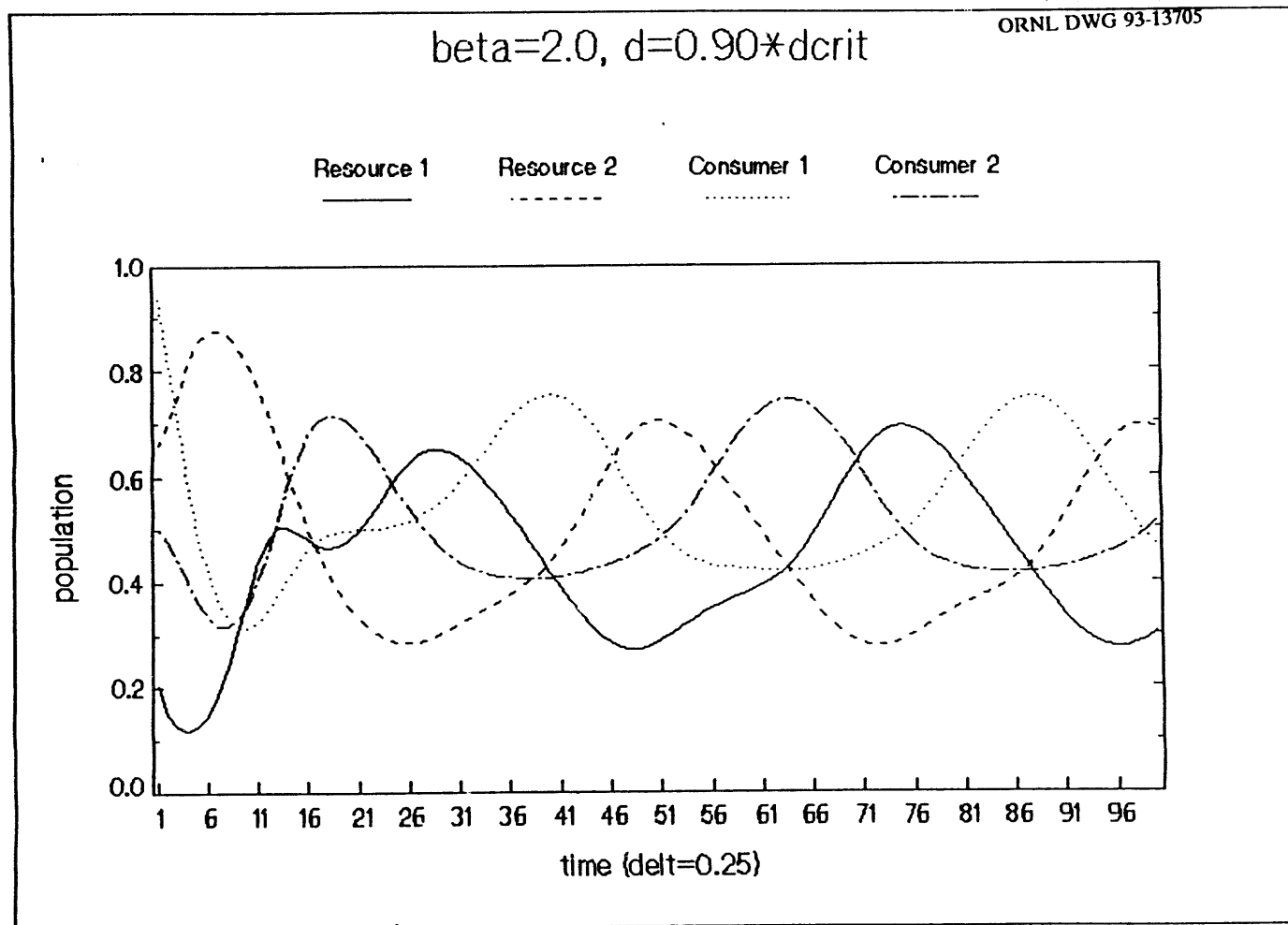


Figure 1a

Figure 1. Four examples of limit cycle dynamics in a two-consumer model analogous to the one-consumer model given by equations (2) in

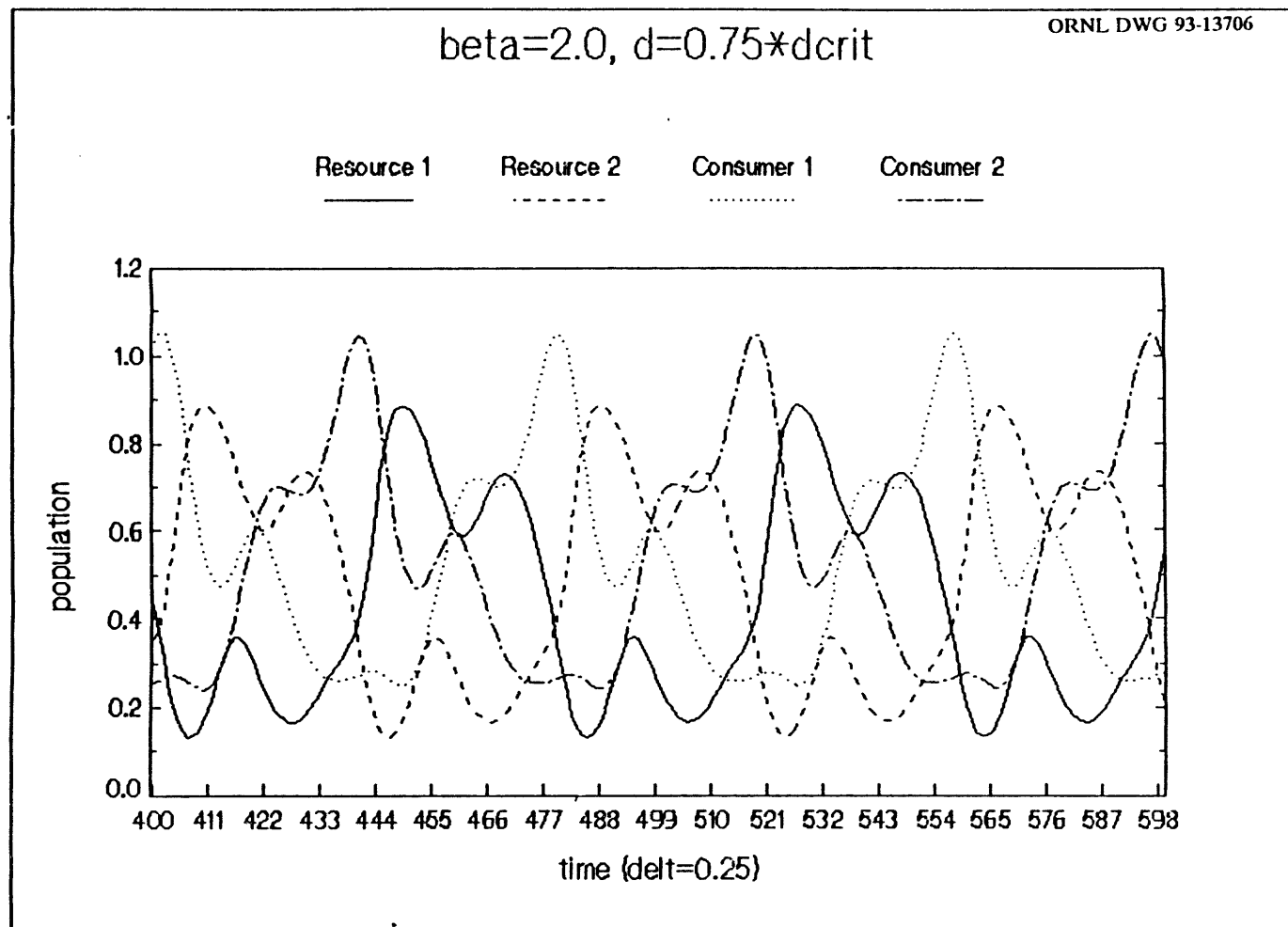


Figure 1b

the text. The model is symmetrical; the resources have identical logistic growth parameters, and the required ratio of resource

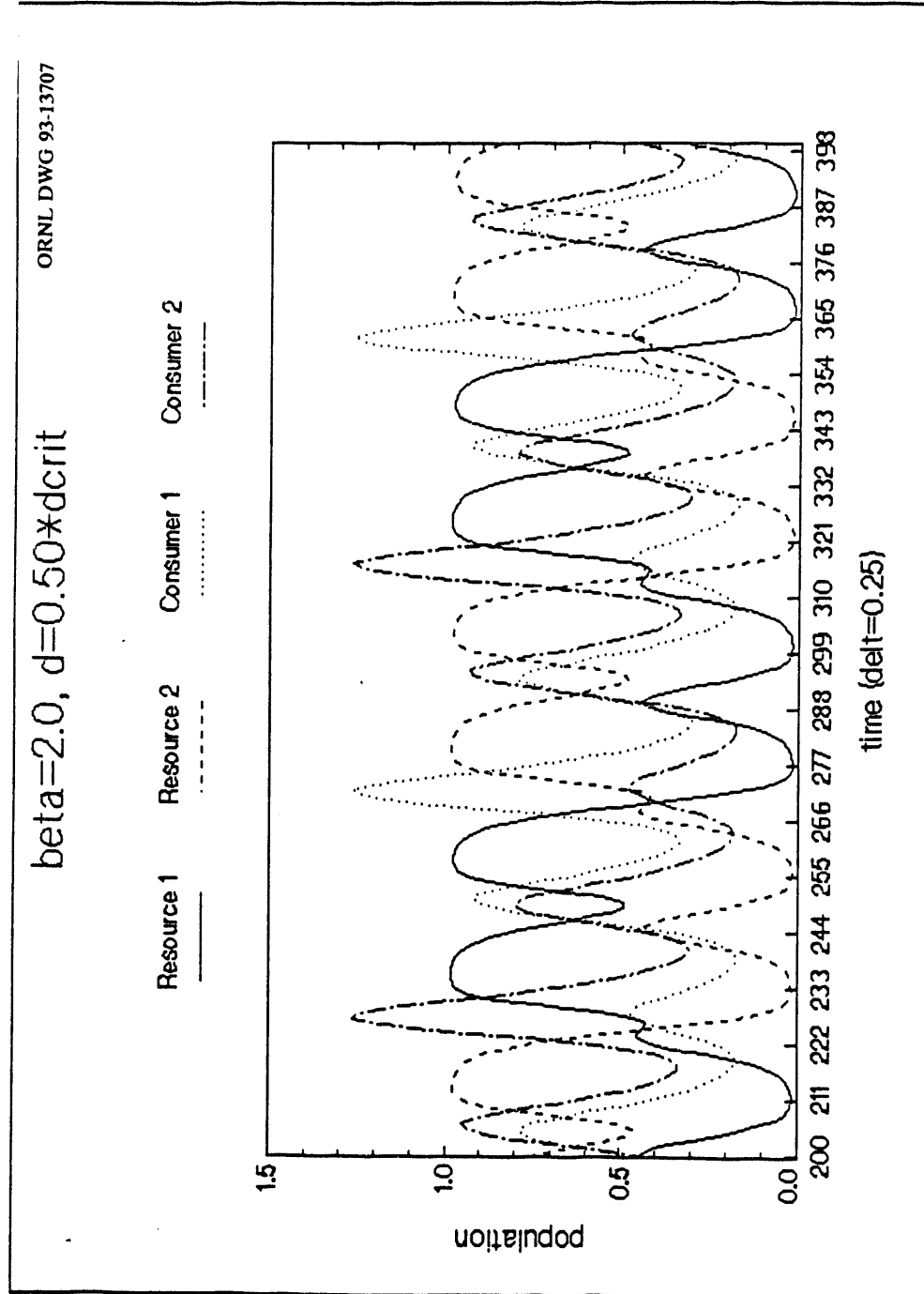


Figure 1c

intakes of one consumer (B) is the reciprocal of the ratio required by the other consumer species (the B (Beta) values in the examples are 2 and .5). The four examples differ in the consumers resource

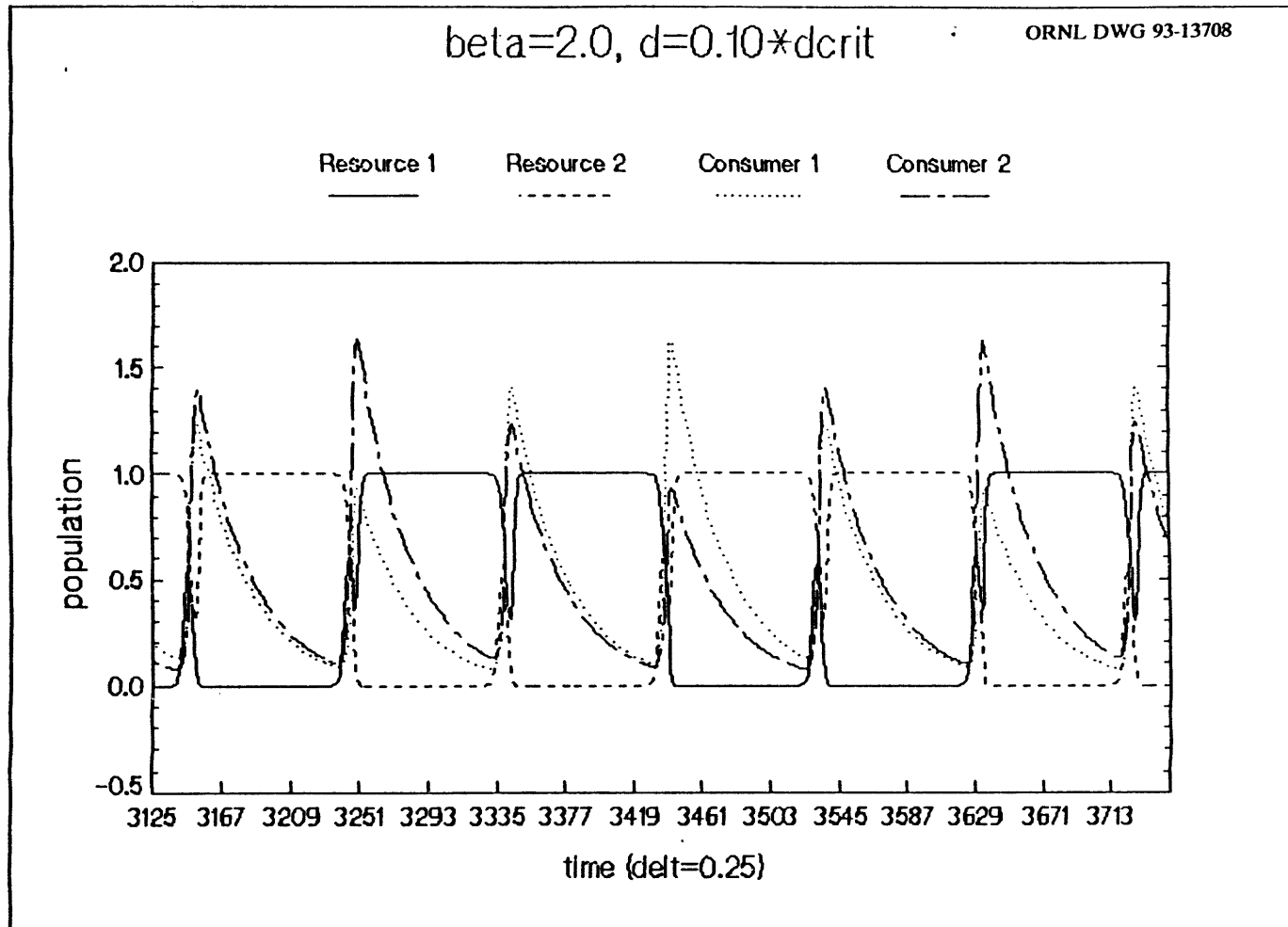


Figure 1d

requirement, d_{crit} in the figures refers to the d value at which the system becomes unstable (0.3137). (Other parameters in the examples are $r_i = 1$; $K_i = 1$; $b = 1$; $k_i = 1$).

adaptive responses may be similar in form to those discussed here. Preliminary analyses of 3-species models in which an omnivore feeds on both a predator and its prey, suggests that dynamic instability and large amplitude population cycles are very common when Eqs. (1) specify the omnivore's functional responses. If there are unusually few omnivores (Pimm 1982), and if dynamic instability has something to do with this fact (Pimm 1982), it may be because of the particular effects of functional responses like those given by Eqs. (1).

THE PROBLEM OF LIMITED GUT CAPACITY

There is considerable evidence suggesting that many herbivores are limited by the quality of the available food, rather than the quantity. If they are not able to digest sufficient amounts of low quality food, herbivores may still be food limited while the world is green. Belovsky (1978, 1986a,b) has amassed considerable evidence suggesting that many generalist herbivores are constrained in their diet both by the limited time available for foraging and by their limited rate of processing low quality food. The diet of many mammalian herbivores may be classified into high and low quality components (often forbs and grasses respectively), and a large part of the optimal diet problem consists of adjusting the relative amounts of each type consumed (Belovsky 1986a,b). The optimal diet problem may then be posed as follows: The herbivore has a maximum consumption rate D , determined by its gut capacity and the passage rate of material through the gut. R_1 and R_2 are the densities of nutritionally low and high quality foods respectively, and A_1 and A_2 are the nutrient contents per unit volume for these two types. (It is assumed that there are no nutritional interactions between the foods; there is only one limiting resource, but it may be calories, nitrogen, or something else.) C_1 and C_2 are the consumption rate constants for the two food types, so that $C_i R_i$ is the volume of food ingested per unit time while searching for food i . The C_i are scaled in time units relative to the length of the maximum foraging period. If the two food types are not consumed simultaneously, the foraging strategy is defined by the amount of time spent foraging for resources i , t_i . The optimum diet is the solution to the linear programming problem, maximize $t_1 A_1 C_1 R_1 + t_2 A_2 C_2 R_2$, subject to the constraints: (i) $t_1 \geq 0$; (ii) $t_2 \geq 0$; (iii) $t_1 + t_2 \leq 1$; (iv) $C_1 R_1 + C_2 R_2 \leq D$. The complete solution of the problem is given in Eqs. (5) below (see Abrams 1989a). Of interest here is the case in which both foods are consumed in the optimal diet. This implies that constraints (iii) and (iv) are binding and that the time allocations for foraging for each type of food are

$$t_1 = \frac{D - C_2 R_2}{C_1 R_1 - C_2 R_2} \quad t_2 = \frac{C_1 R_1 - D}{C_1 R_1 - C_2 R_2} \quad (3)$$

The functional responses are given by $t_i C_i R_i$, which yields

$$t_1 C_1 R_1 = \frac{C_1 R_1 (D - C_2 R_2)}{C_1 R_1 - C_2 R_2} \quad t_2 C_2 R_2 = \frac{C_2 R_2 (C_1 R_1 - D)}{C_1 R_1 - C_2 R_2} \quad (4)$$

These functional responses are unusual in that (i) the amount consumed of resource 1 (less nutritious) decreases as the amount available increases, and (ii) the relative time spent consuming the two resources cannot be described as either positive or negative frequency dependence; increases in R_2 decrease time spent consuming R_1 , and increases in R_1 increase the amount of time spent consuming R_2 . Because of the decreasing functional response on the less nutritious resource, when the responses given by Eqs. (4) are incorporated in consumer-resource population models, limit cycles are a frequent occurrence. Because extreme values of the resource densities result in consumption of a single resource type being optimal, the functional response formulas given by (4) are only valid within a certain range of resource densities. If the full set of optimal responses are incorporated into a simulation model of a one consumer-two logistic resource system, the model has the following form:

$$\begin{aligned}\frac{dN}{dt} &= bN(A_1C_1t_1R_1 + A_2C_2t_2R_2 - D) \\ \frac{dR_1}{dt} &= r_1R_1\left(1 - \frac{R_1}{K_1}\right) - C_1t_1R_1N \\ \frac{dR_2}{dt} &= r_2R_2\left(1 - \frac{R_2}{K_2}\right) - C_2t_2R_2N\end{aligned}\tag{5}$$

where $t_1 = 0$ if $A_2C_2R_2 > A_1C_1R_1$ or if $C_2R_2 > 0$

$$\begin{aligned}t_1 &= 1 \text{ if } A_1C_1R_1 > A_2C_2R_2 \text{ and } C_1R_1 < D \\ t_1 &= (D - C_2R_2)/(C_1R_1 - C_2R_2) \text{ if } A_1C_1R_1 > A_2C_2R_2 \text{ and } C_2R_2 \\ &\quad < D < C_1R_1 \\ t_2 &= D/C_2R_2 \text{ if } C_2R_2 > D \\ t_2 &= 1 \text{ if } A_2C_2R_2 > A_1C_1R_1 \text{ and } C_2R_2 < D \\ t_2 &= (C_1R_1 - D)/(C_1R_1 - C_2R_2) \text{ if } A_1C_1R_1 > A_2C_2R_2 \text{ and } C_1R_1 > D > C_2R_2\end{aligned}$$

There is considerable work left to do before we have an adequate understanding of the dynamic effects of all of the parameters in this model. Nevertheless, it is clear that this type of community model differs from Lotka-Volterra food web models in many important ways. The functional responses of the herbivores set up indirect interactions between resources that usually involve positive effects of nutritious resources on less nutritious ones, and negative effects of poor quality resources on better quality ones. Because of the decreasing functional response of adaptive herbivores on poorer quality foods (when both foods are consumed), weak self-regulation of the populations that constitute the poor quality food will generally result in oscillatory population dynamics.

There are several unrealistic simplifications in the "linear programming" view of herbivore foraging. There is no single inflexible limit on the amount of food that a given organism can process; instead, the probability of mortality increases drastically as the amount consumed increases beyond

some threshold density. There is also likely to be some flexibility in foraging time for any species that does not spend 24.0 hours per day in foraging activities. In a more realistic model, increasing the amount eaten would have some positive and some negative fitness effects, the latter depending on the bulk of the food. As a result, the foraging problem becomes equivalent to the case of foods containing a common set of toxins; the negative effects of too much food may be modelled using a common framework whether the negative effects are due to toxins or simply to excess volume. Such models are treated in the following section.

THE PROBLEM OF FOODS CONTAINING TOXINS

ONLY ONE FOOD TYPE AVAILABLE

A herbivore that consumes a single (homogeneous) food containing toxins or digestion inhibitors must balance the positive effects of energy and calories against the negative effects of the toxins. An individual's intake depends on the amount of time or effort (denoted t) spent in obtaining food (whose availability in the environment is denoted R). The rate at which food is ingested is given by $f(R)t$, where f is the ingestion rate per unit energy or time expended on foraging, and is an increasing function of R . The functional response of the species is given by $f(R)t$. Both the positive and negative effects of ingestion are functions of $f(R)t$. The optimum t is found by setting the derivative of the expression for fitness with respect to t equal to zero, and solving for t . Because t enters into the expression for fitness only as the product $f(R)t$, the solution (assuming there is an admissible value of t that satisfies the equation and is a maximum) has the form $f(R)t = \text{constant}$. This implies that the functional response is a constant. It is also possible that the optimum value of t is its maximum or minimum value, the latter generally being zero. For example, if t represents proportion of available time spent foraging, $t=1$ may represent the optimum foraging strategy at low food abundances, resulting in a functional response having the form $f(R)$. However, for a large range of food densities, the optimum t lies between its extreme values, and the functional response will be a constant. Functional responses that are constant except at low resource densities would also be expected in the case of an organism with an inflexible gut capacity (as in the previous section) that consumed a single food type.

It is straightforward to determine the local stability of a consumer-food model of the usual differential equation form (May 1973, Rosenzweig 1971, Armstrong 1976) in which the consumer species has a constant functional response at the equilibrium point. If the consumer is completely food limited, the equilibrium will be unstable if and only if the equilibrium food density is lower than the food density resulting in maximum food population growth (e.g., $K/2$ in the case of logistic food population growth). Stability would be less likely than if the consumer had a Holling type 1, 2, or 3 functional response.

ONE TOXIC AND ONE NONTOXIC FOOD

In this and the following analyses of systems with two food types, it will again be assumed that the two foods cannot be consumed simultaneously. This assumption applies if the two foods occur

in different habitats or are consumed using different foraging methods, or if food handling (e.g. chewing) consumes most foraging time, so that any additional time devoted to consuming one food reduces by that amount the time used consuming the other. One or the other of these alternatives seems to apply to most generalist herbivores. The modelled herbivore adapts by adjusting the amounts of time and/or effort devoted to obtaining each of the two food types. To simplify the discussion, I will refer to t as the proportion of available foraging time devoted to consuming food type number 1. An individual's functional response on food type 1 will therefore be $tC_1(R_1)$, where C_1 is an increasing function of R_1 , and denotes the intake rate per unit time (or effort) devoted to the first food type. (Note the difference in the meaning of C in this section and the previous one; here it denotes a function rather than a constant.) Similarly, the functional response on the second food type is given by $(1-t)C_2(R_2)$. C_2 is an increasing function of R_2 . Type 1 will be assumed to contain a toxic or digestion-inhibiting substance. In a more general model in which both resources were toxic, it would be necessary to include two time allocation variables, because it might be suboptimal to spend all available time foraging. Because resource 2 is completely nontoxic in the present case, unused time can always be profitably spent foraging for that resource.

The positive effects of food consumption may be expressed as an increasing function of a weighted sum of the two functional responses. If the nutrient or caloric value per unit mass of food type i is A_i , the fitness-enhancing effects of food consumption will be some increasing function f of the quantity,

$$tA_1C_1(R_1) + (1-t)A_2C_2(R_2) \quad (6)$$

The negative effects will be expressed as an increasing function g of the ingestion rate of resource 1 (the toxic food type). If the negative effects do not depend on total caloric intake, individual fitness may be expressed as the difference between f and g . If the negative effect is a reduction in digestive efficiency, this effect may be described by a decreasing function h of toxin intake, and fitness is more appropriately expressed as the product of f and h . Both of these alternatives are considered below.

The optimum value of t may be found by differentiating the expression for individual fitness with respect to t , setting equal to zero, and solving for t . It is also necessary that the second derivative of fitness with respect to t be negative. In the additive model, fitness is $(f - g)$, and the optimum t is determined by

$$(A_1C_1 - A_2C_2)f' = C_1g' \quad (7)$$

subject to

$$(A_1C_1 - A_2C_2)^2 f'' - C_1^2 g'' < 0 \quad (8)$$

It is clear that unless the toxic resource yields a higher nutritional return (i.e. $A_1C_1 > A_2C_2$), Eq. (7) will have no solution, and resource 1 should not be included in the diet (recall that f and g are increasing functions). In the multiplicative model, t is adjusted to maximize fh ; the optimum t is therefore determined by

$$fh'C_1 + hf'(A_1C_1 - A_2C_2) = 0 \quad (9)$$

subject to

$$2[f'(A_1C_1 - A_2C_2)h'C_1] + fh''C_1^2 + hf''(A_1C_1 - A_2C_2) < 0 \quad (10)$$

In either case, it should be clear that the optimum t will generally depend on both resource densities, and consequently, both functional responses will be functions of both resource densities. It is possible to reach a number of conclusions about the nature of the functional responses without making any assumptions about the specific forms of the functions C_1 , C_2 , f , and g or h .

The following analysis examines the following questions from a general standpoint for the additive model: (1) how does the optimum t change with a change in the density of each resource?, and (2) how do the two functional responses incorporating the optimum t change as a function of the density of each resource?

Formulas for $\partial t_0 / \partial R_1$ and $\partial t_0 / \partial R_2$ may be derived by implicit differentiation of expression (8), yielding

$$\frac{t_0}{R_1} = \frac{C_1' \{g''C_1t + g' - A_1f' - (A_1C_1 - A_2C_2)A_1f''\}}{(A_1C_1 - A_2C_2)^2f'' - C_1^2g''} \quad (11)$$

$$\frac{\partial t_0}{\partial R_2} = \frac{A_2C_2' \{f' + (1-t)(A_1C_1 - A_2C_2)f''\}}{(A_1C_1 - A_2C_2)^2f'' - C_1^2g''} \quad (12)$$

It is possible for either of these expressions to be either positive or negative; they may have the same sign or opposite signs. Biological considerations and consideration (8) suggest that g'' is more likely to be positive (than negative), and f'' is more likely to be negative. Both of these conditions favor, but do not insure, a negative $\partial t_0 / \partial R_1$ and a positive $\partial t_0 / \partial R_2$.

Of somewhat greater interest is the form of the functional responses, which are given by t_0C_1 and $(1-t_0)C_2$. The sign of the derivatives of the functional responses with respect to the two resource densities may be determined using expressions (11) and (12). For resource 1, this yields

$$\frac{\partial}{\partial R_1}(t_0C_1) = \frac{A_2C_2C_1' - f' - t(A_1C_1 - A_2C_2)f''}{(A_1C_1 - A_2C_2)^2f'' - C_1^2g''} \quad (13)$$

$$\frac{\partial}{\partial R_2}(t_0C_1) = \frac{A_2C_1C_2' \{f' + (1-t)(A_1C_1 - A_2C_2)f''\}}{(A_1C_1 - A_2C_2)^2f'' - C_1^2g''} \quad (14)$$

It is possible for the functional response on the toxic food (R_1) to decrease as R_1 increases; Eq. (13) implies that this occurs if and only if

$$f' = t(A_1C_1 - A_2C_2)f'' < 0 \quad (15)$$

Thus, if the positive effects of increased nutrient intake are rising slowly, at a decreasing rate, it is possible for increases in the toxic food type to result in a decrease in its consumption rate. The functional response on the toxic resource must increase with its density if the benefit function f is increasing in an accelerating manner ($f'' > 0$).

Increasing the density of the nontoxic resource may either increase or decrease the functional response on the toxic resource, as shown by expression (14). The two terms in the numerator (14) have signs opposite of the two terms in the numerator of (13). Therefore, under a wide range of conditions, the effect of the nontoxic resource density on the toxic resource functional response is opposite to the effect of toxic resource density.

The expressions analogous to (13) and (14) for the functional responses on resource 2 are:

$$\frac{\partial((1-t)C_2)}{\partial R_2} = \frac{C_2'[-A_2C_2f' - C_1^2g''(1-t) + A_1C_1(1-t)(A_1C_1 - A_2C_2)f'']}{(A_1C_1 - A_2C_2)^2f'' C_1^2g''} \quad (16)$$

$$\frac{\partial((1-t)C_2)}{\partial R_1} = \frac{-C_2C_1'[g' - A_1f' + C_1tg'' - A_1t(A_1C_1 - A_2C_2)f'']}{(A_1C_1 - A_2C_2)^2f'' - C_1^2g''} \quad (17)$$

It is again possible for each of these derivatives to be either positive or negative. The biologically more plausible functions (positive g'' and negative f'') favor a response on resource 2 that increases with its own density, and with the density of the toxic resource. Nevertheless, exceptions to both of these predictions are quite possible.

Although this analysis has not produced any general rules about the signs of the derivatives of the functional responses, biologically reasonable forms for f and g seem much more likely to result in a decreasing functional response on the toxin-containing food than on the nontoxic one. Decreasing functional responses are also possible under the multiplicative model, and the signs of the second derivatives of f and h that favor such responses are the same as the signs of f'' and g'' that favor similar responses in the additive model.

TWO OR MORE TOXIC FOODS

It is simple to extend the above framework to the case of two toxic foods. As above, a function f describes the positive fitness effects of resource consumption, and a function g describes the negative effects. The model differs from that in the preceding section only in that g is an increasing function of the intake rates of both resources. The argument of g may not be a simple

weighted sum of the intake rates of both foods if the different foods contain different toxins. It is clear that the range of possible functional response forms is even greater than in the case of a single toxic resource. Because the single toxic resource model is a limiting case of this more general situation, it is also clear that decreasing functional responses may occur with this two-toxic resource model also. The two-toxic resource case is treated in greater detail in Abrams (1989a). If f has the same form as in the additive model of the previous section, g is a function of a weighted sum of the intake rates of the two resources ($B_1C_1t_1 + B_2C_2(1-t_1)$), and resource 1 has the greater reward rate ($A_1C_1 > A_2C_2$), then the functional response on resource 1 decreases with its own density provided that an intermediate optimum t_1 exists, and

(18)

$$\frac{\partial(t_1C_1)}{\partial R_1} = \frac{C_1(g'B_1 - f'A_1) + C_2t_1[g''B_2(B_1C_1 - B_2C_2) - f''A_2(A_1C_1 - A_2C_2)]}{(A_1C_1 - A_2C_2^2f'' - (B_1C_1 - B_2C_2)^2g'')} < 0$$

(where the second derivative condition for t_1 to maximize fitness ensures that the denominator will be negative.) This condition links the discussion of bulky resources in section II with the discussion of toxic resources in the present section. Bulk can be thought of as a form of toxin that leads to a cost function whose second derivative, g'' , is very large (and positive) when intake rate fills the gut completely. Expression (18) shows that this will favor a decreasing functional response on the resource that yields a greater nutrient intake rate per unit time, as was true for the specific case of the model considered in section II.

The population dynamics of models that explicitly incorporate adaptive foraging on toxic foods have yet to be explored. The possibility of decreasing functional responses suggests that oscillatory population dynamics will also occur frequently in these models. Almost any possible form of indirect interactions between resources may be created by the consumers' (herbivores') functional responses.

CONCLUSIONS

ADAPTIVE FUNCTIONAL RESPONSES OF CARNIVORES

Plant-herbivore community models that incorporate the functional responses described above will clearly differ from Lotka-Volterra type models. However, because most community models do not incorporate adaptive behavior of any kind, it may not be apparent that the functional responses described above differ from the functional responses of adaptive carnivores. Most carnivores consume nutritionally substitutable foods (many spiders may be exceptions; see Greenstone 1979). Abrams (1987b) discusses adaptive variation in functional responses that may occur with nutritionally substitutable resources; in general, such variation can be described as positive frequency dependence. Carnivores should concentrate their searching efforts on the most available prey (unless the (energy content)/(handling time) is too low.) This results in switching behavior, which has been incorporated into some very simple community models (e.g. Murdoch and Oaten 1975, Matsuda et al. 1986). In

general, switching stabilizes population dynamics. The short term effects between different food species that arise because of the predator's functional response are mutualistic (Abrams 1987c).

SUMMARY

The three foraging problems commonly faced by generalist herbivores all result in functional responses that differ markedly from any that are frequently used in carnivore-prey models. It is common for the amount eaten of some food types to decrease as the amount available increases, and the relative time and/or effort devoted to obtaining different types is seldom describable by the positive frequency dependence that characterizes many optimally foraging carnivores. Although relatively few food-web models incorporating such functional responses have been studied, those that have suggest that the functional responses may produce "unusual" population dynamics. The dynamics may or may not be atypical of what occurs in nature, but they certainly differ strikingly from those observed in analogous food webs with functional responses appropriate for carnivores. The results provide an additional argument for the need to consider behavioral responses of species when trying to understand community structure and/or dynamics. We are still a long way from knowing how incorporating adaptive behavior would change the conclusions derived from Lotka-Volterra food web models with many species, but preliminary results for very small communities suggest substantial differences in dynamic behavior. Most of the problems addressed by Pimm (1982) and others using Lotka-Volterra type food web models have yet to be addressed using models with adaptive foraging by either herbivores or other species in the food web.

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CHARACTERISTICS OF SPECIES INTERACTIONS OF MACROBENTHOS IN TIDAL FLATS: A SUMMARY WITH A PERSPECTIVE

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INTRODUCTION

For a long time, most patterns of abundance and distribution of invertebrate species in marine soft bottoms have been explained by correlations with physical factors in the environment. Since the 1970s, species interactions have also become recognized as important agents generating patterns. Among various habitats in marine soft bottoms, intertidal flats (both sand flats and mud flats) are systems suitable for investigating species interactions, due to their accessibility and their calmness for maintaining field experimental equipment as compared with exposed sandy beaches.

In this paper, I outline characteristics of the species interactions which organize the benthic communities in temperate-zone tidal flats, and point to several problems in our approaches to these interactions for future research.

The main target organisms here in the size spectrum of tidal-flat benthos are macrofauna, on which studies have been most intensively carried out. Macrofauna are usually defined as those organisms whose adults are retained on a 0.5-mm mesh sieve (Eleftheriou and Holme 1984). Most numerically dominant taxonomic groups of macrofauna are polychaetes, small crustaceans, and mollusks (bivalves and gastropods).

SPECIES INTERACTIONS OF MACROFAUNA

Species interactions of macrofauna prevailing in tidal flats are classified in Table 1. First, the interactions are divided into two categories: I. those between non-carnivorous species (mainly deposit-feeding, suspension-feeding and grazing benthos) and II. the effects of predators on the abundance patterns of prey species. Interspecific interactions in Part I are subdivided into (A) repressive and (B) promotive relationships. Although mutualistic symbiosis (mutualism) and parasitism may be potentially very important interactions in structuring soft-bottom communities, their contributions to the overall dynamics of the benthic communities have received little attention in community-oriented soft-bottom studies; thus, they are not taken up here.

Hereafter, I will give a brief summary of the results of studies for each process of the species interactions listed in Table 1. Most interactions cited in this paper come from those found in tidal flats, but examples from exposed sandy beaches and shallow subtidal soft bottoms are also included. Furthermore, I will point to what I feel to be most serious problems in these studies and give a proposal for better understanding the organization mechanisms of tidal-flat benthic communities.

NICHE DIFFERENTIATION

It may be implicit in most writings on community ecology that most species should interact strongly with only a few other species and mainly those with comparative body sizes (Fenchel 1987, p. 97). Furthermore, it may also be a common belief in the ecological literature that differentiation of niches and/or morphologies through competition in the past should have reduced the intensity of

Table 1. Species interactions in tidal-flat macrobenthos

- I. Between non-carnivorous macrobenthos
 - A. Repressive relationships --- Competition
 - (a) Reduced competition via niche differentiation (? Past competition)
 - (b) Severe competition (Current competition)
 - (1) Inhibition of larval recruitment by adults
 - Direct ingestion or exclusion of larvae
 - Indirect exclusion through changing the sediment properties
 - (2) Competition between adults
 - (2-1) Interference competition
 - Direct exclusion
 - Indirect exclusion through changing the sediment properties
 - (2-2) Exploitation competition for food
 - B. Promotive relationships ---- Commensalism
- II. Influences from predators
 - A. Intermittent predators
 - (1) High-tide carnivores
 - (2) Low-tide carnivores
 - B. Resident predators
 - (1) Epibenthic carnivores
 - (2) Infaunal carnivores

competition and thus brought about coexistence of competitors in the present, although some persons disagree with this view (Connell 1980). For marine soft-sediment benthos, a number of studies have been done in this context, and they often deal with relationships among taxonomically closely related species or those within the same feeding guild; see Branch (1984, pp. 490-508) for examples of such relationships. The partitioned resources involve habitats (horizontal segregation or vertical stratification in the sediment), food resources (particularly for deposit feeders), and time (e.g. breeding seasons), and these partitionings are at times accompanied by character displacement (Fenchel 1975a, b; Fenchel and Kofoed 1976).

However, these niche-differentiation studies are not without problems. The most serious pitfall seems that we are apt to overlook large influences of some species which are operationally removed from the target system for the very simple reason that they are taxonomically remote or belong to different feeding guilds. As shown in the subsequent sections, interphyletic interactions (those between distantly related competitors or those between hosts and commensals) are often prevalent in the benthic communities in tidal flats. Under such large influences, how can we evaluate the significance of resource partitioning between closely related species or between members of a guild to the population dynamics of each species (in particular, for the smaller macrobenthos) and to the organization of the whole benthic community? So far as I know, none of the niche-differentiation studies for tidal-flat macrobenthos have been done bearing this point in mind.

INHIBITION OF LARVAL RECRUITMENT BY ADULTS

Inhibition of larval recruitment by established adults has been considered important in structuring marine soft-bottom communities (Thorson 1966; Woodin 1976). Both laboratory and field manipulative experiments have demonstrated that adults of many macrobenthos, which are non-carnivorous to other adults, can depress recruitment directly by ingesting settling larvae and newly settled juveniles (Highsmith 1982; Tamaki 1985) and indirectly by burying juveniles with sediment displaced by burrowing, feeding, and defecating (Brenchley 1981; Wilson 1981). Ingestion of larvae and juveniles by "non-carnivorous" macrobenthos should make the structure of benthic food webs more complex (Feller et al. 1979). These influential adults may be expected to target or unconsciously involve all larvae and juveniles that they can encounter regardless of the species, including those of their own (Thorson 1966; Woodin 1976). In support of this, several studies have demonstrated that larvae of many species are depressed indiscriminately (Crowe et al. 1987; Hunt et al. 1987), and combined information from various sources on the effects of "villains" on "victims" (Thayer 1983; Woodin 1983) may also support this accidental nature. However, the outcome of the actions of adults varies depending on the functional types (feeding and mobility types, etc.) of the adults and on the size, escaping ability, and susceptibility of the recruits (Woodin 1976, 1983).

Most of the efforts to test the negative influences of established adults on larval recruitment with field enclosures and exclosures could confirm the effects only ambiguously because they do not check, at the same time, the following two other possible causes: the juveniles of a species are absent from an experimental plot because (1) the settling larvae have actively avoided the substrate of this plot due to the lack of attractant cues (Highsmith 1982) or the presence of repellent cues (Woodin 1985), which are associated with the sediment; (2) the larvae have been passively transported to some other places by hydrodynamic forces (i.e. waves, currents, and turbulent flows) (Eckman 1983; Butman 1987). A far more difficult task in the adult-larval interaction studies is to quantitatively evaluate, in the natural conditions, what portion of the population of the planktonic and newly settled larvae is eliminated by established adults and what significance this elimination has for the whole population dynamics of the affected species. The deletion of planktonic larvae in one locality may be replenished from the neighboring localities through the exchange of the waters, but it is also difficult to determine with what certainty this occurs.

INTERFERENCE COMPETITION BETWEEN ADULTS

Recently, studies relating to "interference competition" have remarkably increased in number for soft-sediment benthos. However, as pointed out by Barnes and Hughes (1988, p. 89), many studies only deal with the outcomes of accidental "collisions" resulting from bioturbation (biological disturbance of sediment) caused by the locomotory, feeding, and defecating activities of organisms; identification of the contested resources is often unclear. Interference competition in the strict sense can be seen in several forms of competition for space: (1) In systems composed of taxonomically related, highly mobile crustaceans, inferior competitors are either driven to less preferred habitats (Crocker 1967; Rees 1975; Grant 1981) or experience reductions in survival rates, individual growth rates, and fecundity (Crocker and Hatfield 1980); (2) Several instances have been presented on systems comprised of species with limited mobilities (e.g. bivalves, polychaetes). Intraspecific competition

often causes even spatial patterns in micro-distributions (Holme 1950; Levin 1981). However, caution must be used in explaining the meso-scale distribution patterns; some studies ascribed horizontal segregation of competitors to emigration of adults of inferior species (Levinton 1977; Peterson and Andre 1980), but the more plausible mechanisms may be habitat segregation such as through competition in the past, or through inhibition of larval recruitment by adults, or through spatially different survival rates; (3) Sediment-stabilizing species (e.g. a dense assemblage of tube-building species) and destabilizing species (e.g. a dense assemblage of burrowing species) are sometimes incompatible with each other, and members of each group of species involve a variety of taxa and trophic modes (Woodin and Jackson 1979; Thayer 1983)(but see Sect. 8). The horizontal segregation of these two groups may be brought about through interactions between adults (Brenchley 1982) as well as adult-larval interactions (Brenchley 1981; Wilson 1981).

In demonstrating that adults of species A are absent due to competitive exclusion by species B, we must check possibilities of not only emigration and mortality but also habitat selection and hydrodynamic transportation of species A. Furthermore, competition may result in reductions in individual growth rates and fecundity. No studies have examined all the above demographic population parameters at the same time.

EXPLOITATION COMPETITION FOR FOOD

There are two major feeding modes in marine soft-sediment macrobenthos: deposit-feeding (including grazing of microflora) and suspension-feeding. Many researchers have suggested that natural populations of macrofaunal deposit feeders are food limited. In particular, Levinton (1972) argued that deposit feeders have competed for this limiting resource (bacteria, microalgae, and detrital material) over evolutionary time, resulting in the specialization of feeding niches. Most of the effective demonstrations of the occurrence of current competition for food in deposit feeders are for intraspecific competition (reductions in survival rates, individual growth rates, fecundities, and increase in emigration rates), and the majority of these studies have been done in the laboratory (Tenore and Chesney 1985; Forbes and Lopez 1986; Zajac 1986; Morrissey 1987) with only a few successful experiments carried out in field enclosures (Branch and Branch 1980; Ólafsson 1986; Morrissey 1987). Evidence for current interspecific competition for food is far less (Fenchel and Kofoed 1976; Alongi and Tenore 1985). This scarcity of documented examples of interspecific competition for food may support Levinton's (1972) hypothesis of the trophic specialization between coexisting species. Alternatively, however, most deposit feeders may not actually face shortages of food either owing to its ample supply or owing to the effective regulation of population densities by intraspecific competition, predation (Sect. 9), and/or physical disturbance precluding interspecific competition from taking place.

Levinton (1972) also argued that the supply of phytoplankton, the major food source for benthic suspension feeders, is spatially and temporally variable in terms of quantity and the species present, and that as a consequence, suspension feeders are unlikely to compete for long enough to reach exclusion which can lead to niche specializations. It has been shown that soft-sediment suspension feeders tend to compete for space (Hancock 1973; Peterson and Andre 1980); however, only a few studies showed the operation of intraspecific competition for food (Stiven and Kuenzler

1979; Peterson 1982; Fréchette and Bourget 1985---all for bivalves in the field enclosures), and to my knowledge, no convincing evidence for current interspecific competition for food has appeared on both the micro- and meso-scales except for only a few suggestive results (Peterson and Black 1987).

Thus, it is likely that food limitation is, if anything, more common among deposit feeders than suspension feeders. However, this may simply reflect the difficulty in demonstrating the abundance pattern of foods suspended near the seabed as compared with those deposited in the sediment (cf. Fréchette et al. 1989). Difficulties underlying these exploitation-competition studies -- to identify the food items of each species, to present quantitative data on the extent of depletion of these foods by this species in the natural conditions, and to link this to detrimental influences on other species -- will be hard to overcome.

COMMENSALISM

Although, for a long time, promotive relationships received little attention in community-oriented ecological studies for marine soft bottoms (Dayton and Oliver 1980), the situation has recently been changed. Most of the studies on interspecific promotion deal with commensalism, in particular various effects of the activities of larger macrobenthos on smaller macrobenthos or meiobenthos. Commensalism found so far may be categorized as follows: (1) Body cavities and surfaces, underground burrows, and tubes of large benthos often accommodate uninvited guests within them (e.g. Ricketts et al. (1985) and Nybakken (1988, Ch. 10) for many instances); (2) Large bioturbating infauna irrigate and fertilize the surrounding sediment simultaneously. This alteration of the physico-chemical conditions of the sediment causes attraction of meiobenthos or smaller macrobenthos directly through enlarging underground, habitable oxidized space for them or indirectly through stimulating growth of microorganisms (bacteria, microalgae, ciliates, etc.) which are food of grazing and deposit-feeding benthos (Hylleberg 1975; Reise 1985, Ch. 11; Flint and Kalke 1986); (3) Sediment reworking and tube irrigation by a deposit-feeding polychaete reduces the quantity of particulate organic matter (POM) at the sediment-water interface and increases concentrations of dissolved nutrients in the water column, and these effects cause an increase in the individual growth rate of a smaller filter-feeding bivalve (Weinberg and Whitlatch 1983). The beneficial mechanisms involved may be stimulation of microfloral populations as food for bivalves and preclusion of clogging of the feeding structures of bivalves with POM; (4) Myers (1977) suggests that some burrowing species benefit from decreased compaction and/or cohesion of the sediment which have beforehand been excavated by other burrowing infauna; when they occur in looser sediments, burrowing species should be less subject to epibenthic predators because they quickly hide themselves in the sediment, and hence are able to allocate more energy to life processes other than escape (e.g. growth and reproduction). Such an advantageous behavior of choosing looser sediments is likely to evolve. But only a few examples exist which are suggestive of this behavior (Levinton 1977; Dayton and Oliver 1980, p. 107; Brenchley, 1982; Tamaki 1988); (5) Disturbed patches such as feeding excavations and fecal casts created by large benthos and demersal fish are utilized as suitable microhabitats often with favorable resources (such as detrital food) for smaller benthos (Rhoads and Young 1971; Thistle 1980; VanBlaricom 1982; Tsuchiya et al. 1989; see also a review in Probert 1984); (6) Dense assemblages of protruding tubes of macrobenthos provide suitable microhabitats not only for clinging epibenthos

but also for sediment-dwelling benthos (Mills 1967; Gallagher et al. 1983), probably because tubes increase the topographic complexity of the area and because sediments around tubes can have greater abundances of potential food for macrobenthos (bacteria (Eckman 1985); diatoms (Sanders et al. 1962); meiobenthos (Eckman 1983)). Furthermore, dense tube mats provide stable substrata to function as refuges for smaller macrobenthos against epibenthic predators/disturbers (Mills 1967; Woodin 1981) or wave disturbance (Bailey-Brock 1979).

The connection between commensals and their hosts may be strict in some cases (e.g. (1) above) (obligate commensalism), but in many cases commensals seem to be loosely dependent on the "functions" of the life processes of the hosts (in other words, "types" of microhabitats (or sometimes on larger scales) created by the hosts' bioturbating activities) irrespective of the identity of the host species (facultative commensalism). Colonization by commensals (larvae and/or adults) of these secondary habitats has both active and passive (hydrodynamic accumulation) components, and studies on these processes are now growing. Furthermore, analyses will be needed which pinpoint the life stages that are most important in determining the population growth of commensals and which rank several possible effects of hosts according to their demographic importance. Such an attempt (e.g. Weinberg et al. 1986) has rarely been made.

FUNCTIONAL GROUPS

In the current competitive and commensal relationships among macrobenthic species shown so far (in particular, Sects. 4, 5, and 7), indiscriminate or accidental encounters between species have often been found; in some cases, however, the resultant response types were well predicted in terms of functions of the interacting species (feeding and mobility types, effects of life processes on sediment properties, etc.) irrespective of their taxonomic positions (e.g. Woodin 1976, 1983). But this does not necessarily mean that a group of macrobenthos with a similar function behave as a functional unit. For analysis of the structure of any animal community, it may be fascinating and of great practical value to be able to find infrastructures within it (see Paine 1980). In macrobenthic communities of tidal flats, a burrowing species group (sediment destabilizers) and a tube-building and other sedentary species group (sediment stabilizers), each including a variety of taxa and trophic modes, seem to be incompatible with each other, and to form spatially segregating distinct patches; members of the one group exclude or reduce densities of those of the other group by way of the contrasting effects on sediment characteristics, and within the same group, "help" each other in competition with the opponent group (Woodin and Jackson 1979; Brenchley 1981, 1982; Wilson 1981). But this view, which postulates symmetrical competition and mutualism, is only partially true if at all. As pointed out by Thayer (1983) and Posey (1987), most of the examples which seem to support the above functional-group hypothesis involve asymmetrical interactions in which large or active species exclude smaller forms or exclude organisms that individually have little effect on sediment characteristics. Although a time-delayed reciprocal competition seems potentially possible via adult-larval interactions (e.g. Highsmith 1982; see Sect. 4), few field examples exist where smaller animals, no matter how dense, exclude larger active species (Posey 1987). Also, mutualistic relationships have only been partly demonstrated (e.g. Brenchley 1982). Since the population dynamics of smaller macrobenthos in tidal flats are often organized under the overwhelming hierarchical influences of the larger macrobenthos

either positively (commensalism) or negatively (asymmetrical competition), it may be difficult to detect if any mutualistic beneficial interactions or current reciprocal competitions are occurring among smaller macrobenthos.

Thus, at present, the functional groups as originally suggested may be rather an abstraction; in order to correctly test this hypothesis, it will be necessary to consider at least the following three problems: (1) We should quantitatively measure rates at which each species stabilizes and destabilizes sediments under different regimes of waves and currents (e.g. Jumars and Nowell 1984). But, except for the simplest system in which effects of multiple species on sediments are additive (Peterson 1980), how can we reconstitute a group's total bioturbation rate from each measure?; (2) It must be noted that the component species belonging to one functional group should not only be in "cooperation" with each other against the opponent group but be more or less in competition for limited resources because of the similarity of their niches. These antagonistic interactions will be reflected in benefits and costs, respectively, which may be measured in terms of various demographic population parameters (survival, growth, fecundity, emigration, etc.). Thus, before acknowledging any one set of two opposing functional groups, we must establish a standard with which we can compare these benefits and costs for the component species in each group; (3) These benefits and costs should not be judged only within one locality. For example, inferior competitors in the one functional group may still enjoy benefits by the group's action against the opponent group if they are effectively replenished from the neighboring localities through the exchange of their planktonic larvae. But how can we know these exchange rates?

Despite the limited predictability of the above functional-group hypothesis in the ecological time-scale, competition between sediment destabilizers and stabilizers might have significant evolutionary consequences for the determination of the macrobenthic community structure in soft bottoms. Thayer (1983) summarized the strategies for winning the "war" in sediments as follows: (1) be large; (2) be mobile and/or disturb sediment rapidly; (3) occur in dense populations. Based on this asymmetrical manner of competition, he suggested that biological disturbance of marine sediment has increased over geologic time, especially in causing the reductions of the dominant Paleozoic benthos, the immobile organisms that lived on unconsolidated substrate (bulldozing hypothesis).

INFLUENCES FROM PREDATORS

It is difficult to remove predators from soft-sediment habitats because they are either large and mobile or infaunal and cryptic. Thus, to assess the influences of these predators (both predation and disturbance of sediment) on the structure of macrobenthic communities, enclosure or exclosure cages are usually established in the field. The problems with such caging studies come from the difficulties (1) to separate predator effects from cage artifacts (Virnstein 1978; Dayton and Oliver 1980) and (2) to apply results obtained in a narrow caged area to a far wider natural area without detailed knowledge of the behavior and abundance patterns of predators in time and space. Furthermore, identification of the whole food webs, including consumption of larvae by adults of non-carnivorous macrobenthos (see Sect. 4), is very difficult for soft-bottom communities (see Feller et al. 1979). As a result, only a portion of the predator-prey system can be manipulated.

Predators appearing in tidal flats can be divided into intermittent and resident predators. Intermittent predators include high-tide carnivores (demersal fish and large decapod crustaceans) and low-tide carnivores (birds). Resident predators include epibenthic carnivores (nurslings of demersal fish (e.g. gobiids), shrimp, and crabs, etc.) and infaunal carnivores (turbellarians, nemerteans, polychaetes, gastropods, etc.).

One of the most extensive works to assess the effect of predation in structuring benthic communities in tidal flats has been carried out in the German Wadden Sea (Reise 1985). By means of cages with various mesh sizes installed in several kinds of habitats in the tidal flat, Reise examined the impact of various sizes of epibenthic predators and revealed that (1) intermittent, large predators prey on the older, large-sized individuals, affecting the benthic community only moderately, and that (2) carnivorous nurslings of fish, crabs, hermit crabs, and shrimps, which remain in the tidal flat or migrate back and forth with the tides, indiscriminately consume both meiofauna and juveniles of macrofauna, and hence usually prevent many of macrofaunal species from attaining the carrying capacity of their habitat. However, these effects of predators could be reduced by internal predation within the predators' group, by the presence of refuges (e.g. seagrass) in the sediment surface, and by different physical conditions.

From the above results and a review on the caging experiments to exclude epibenthic predators (Peterson 1979), three tendencies appear general for macrobenthos within cages that exclude predators (Barnes and Hughes 1988, p. 93): (1) an increase in total density; (2) an increase in species richness; (3) no significant tendency toward competitive exclusion by some dominant species. The latter two contrast markedly with results of some predator-exclusion studies conducted in rocky shores (e.g. Paine 1971, 1974), although the data from soft sediments and rocky shores are not really comparable due to the disregard of the smaller benthos in rocky-shore studies. Peterson (1979) suggests a number of explanations for such "anomalies" of soft-sediment macrobenthos: (1) ineffectiveness of both interference competition (the types as seen on rocky shores) and exploitation competition; (2) reduced competition due to vertical habitat partitioning in the sediment; (3) effectiveness of inhibition of larval recruitment by adult macrobenthos to maintain populations at low levels (see Sect. 4), at which adult competition is not likely to be severe. In soft bottoms, however, some top predators may be able to organize the benthic community structure by regulating, for example, the density of large bioturbating infauna (= sediment destabilizers) such as arenicolid polychaetes and thalassinidean decapod shrimps which themselves have large influences on the other macrobenthos (Posey 1986); in such cases, these predators may play a role comparable to a keystone predator (starfish) in rocky shores (cf. Paine 1971, 1974), although large bioturbating infauna are less susceptible to epibenthic predation because of their habitats deep in the sediment. Also, predation within the epibenthic predators' guild can have positive indirect effects on some components of non-carnivorous benthic communities (Kneib 1988).

The roles of infaunal predation in controlling the structure of soft-bottom communities have not been as extensively studied (see Commito and Ambrose 1985). The present interest of the most active researchers seem to detect three-level (epibenthic predators, predatory infauna, other infauna) or more multiple interactions, stressing an indirect positive effect of epibenthic predators on non-carnivorous infauna (Ambrose 1986).

CONCLUSIONS

Among the several categories of species interactions in macrobenthos inhabiting tidal flats (Table 1), inhibition of larval recruitment by adults (Sect. 4), current interference competition between adults (Sect. 5), commensal relationships (Sect. 7), and epibenthic predation of juvenile macrobenthos (Sect. 9) appear to be prevalent, although this may rather reflect the ease with which we can treat and demonstrate the occurrence of these processes as compared with other kinds of interactions. Furthermore, despite the still insufficient data amassed in the benthic studies so far, I predict that the following tendencies will be general concerning these prevailing processes: (1) In predacious aspects of these interactions including consumption of larvae or juveniles by adults of macrobenthos, predators often indiscriminately prey on everything which is small and is present close to the sediment surface; (2) In the other aspects of adult-larval interactions and in interference competition between adults, encounters between species are often accidental; (3) In adult-adult competitions, asymmetrical rather than reciprocal competition is prominent; (4) In commensal relationships, facultative rather than obligate combinations of species are more often found. Based on the results of his extensive work on the benthic community in a tidal flat, Reise (1985) has similarly pointed out the characteristics of the species interactions in macrobenthos, particularly stressing the importance of indiscriminate epibenthic predation in keeping the macrobenthic assemblage below the carrying capacity of its habitat.

If it is true that such loosely connected interactions should prevail over strict or refined relationships between macrobenthic species or between macrobenthos and their predators, several reasons may be proposed for this: (1) Because the environment of tidal flats is variable and marginal, constituting a narrow ecotone between land and sea or between fresh and sea waters, specific interactions between organisms of tidal flats and those either from land or from subtidal seas are unlikely to develop (Reise 1985), and broad-niched species may have been selected (Levinton 1982, p. 388); (2) Tidal flats often occur in an insular pattern interacting with each other through the exchange of planktonic larvae which are unlikely to adapt to local sources of facilitation and mortality (Reise 1985; Underwood and Fairweather 1989). Adaptations of organisms over evolutionary time-scales are more likely to be in response to diffuse, collective processes (Underwood and Fairweather 1989); (3) Tidal flats are geologically young, precluding the development of refined relationships (Reise 1985). To these may be added another reason: in particular, intertidal sandy mud (or muddy sand) flats constitute an ecotone between exposed sandy beaches and protected mud flats, containing species primarily adapted to shifting sedimentary environments and those primarily adapted to very stable substrata. Encounters between these differently adapted organisms will be facultative. In addition, most species primarily adapted to an unstructured and physically controlled habitat of exposed sandy beaches tend to be unspecialized generalists with broad niches (McLachlan 1983). Of course, some of the reasons may be attributable to the characteristics of species interactions which soft-sediment benthic communities in shallow waters in general share.

In contrast to the low connections between species prevalent in tidal flats, outcomes of the interactions between life types or functions of benthic species appear predictable to some extent. In this context, efforts to seek out functional groups (Sect. 8) as an infrastructure of the whole tidal-flat benthic community may not be vain. However, these analyses should not be made in disregard of the

characteristics of the component species. To substantiate analyses of the community organization of macrobenthos based on their functions, at the least it is desirable that changes in the various demographic parameters of each species population caused by the species interactions should be measured in the natural conditions as well as in the laboratory and the field experimental plots. Moreover, using the results of these experiments, simulation studies will be feasible to approximate to the phenomena observed in nature and to rank the importance of the various interactions for the critical life stages in regulating the population dynamics (cf. Weinberg et al. 1986).

I feel that there are three major serious deficiencies in our approaches to the roles of species interactions in shaping the tidal-flat macrobenthic communities. The first problem is in studying various aspects of the interactions separately as if each process proceeds singly; this may miss some more important interactions. The second problem is in synthesizing an image by gathering results obtained in different localities each having different background habitat structures (geomorphological, hydrodynamical, sedimentary, and other physico-chemical conditions, etc.) or obtained at different occasions in a same locality each experiencing different seasonal and episodic events. The third problem comes from our poor knowledge of the ecological links between tidal flats and their adjacent subtidal seas and between neighboring tidal flats; in some cases, the tidal-flat macrobenthic community structure may be determined mainly by the rates and timing of recruitment of macrobenthos from the water column (cf. Underwood and Fairweather 1989) or of the arrival of their predators from land or offshore sea (e.g. Reise 1985, p. 106). In order to overcome these problems, two kinds of approaches will need to be addressed in our empirical research programs: (1) attempts to detect a set of tidal-flat communities with their adjacent subtidal communities which interact via both the exchange of planktonic larvae of macrobenthos and the movement of their predators; (2) studies aiming at elucidating the dynamics of each of these regional communities, taking up as many species interactions as possible.

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Community – Food Web Interactions

By community we mean here a set of species occupying a single trophic level and potentially competing for resources (although often the term is used to refer to all the biota in an ecosystem, and we will make a note of it when the term is used in this way in later discussion). Theoretical community ecologists seldom study communities independently of other aspects of the ecosystem, since abiotic aspects, such as disturbances and nutrients, and biotic aspects, such as predators, are almost crucial in shaping communities. Hence, community ecology by nature has a somewhat wider perspective, as exemplified by the papers at the Seminar dealing with ecological communities.

SOME THEORETICAL APPROACHES TO COMMUNITY ASSEMBLY

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INTRODUCTION

Rather than restrict attention to modelling classical secondary succession per se, I propose to consider the broader question of community assembly and development, for which secondary succession may be but a single important case. This survey, therefore, will concentrate on generic approaches to studying the temporal evolution of communities while omitting the details of classical succession.

As reviewed by Usher in this volume, considerable effort has already been invested in developing predictive models of secondary plant succession (see also Shugart 1984). These range from simple Markovian plant replacement models, suitable for short time predictions (Usher 1979, Horn 1975) to the highly detailed dynamic replacement models designed to simulate long-term histories of vegetation at specific sites (Shugart 1984, Solomon 1986). By contrast, despite having similar roots, the deeper problem of community assembly has not benefitted from such a concentrated or unified modelling effort. Indeed the approaches that exist appear fragmentary, drawn for the most part from several classical topics in population and community ecology. One purpose of this essay will be to begin to survey some of these fragments as they relate to community development in order to suggest the assembly problem as an interesting focus for future research.

I shall organize this review into two parts, statics and dynamics. The section on statics will discuss semi-deductive procedures for extracting process information from static patterns and will include relevant aspects of studies on the topological structure of food webs, the species abundance problem and island biogeography. The section on dynamics will explore a general framework for studying the process of species additions to a system, and will discuss the notion of climax, the invasion problem and the evolution of simple predator-prey systems.

STATICS OF COMMUNITY ASSEMBLY

Each of the approaches below attempts to derive assembly rules from some static aspect of the final structure of an ecological ensemble. These results may be very general or specific depending on the chosen level of analysis: from broad statements such as "gears must mesh according to size", to specific statements such as "part A attaches compatibly to part B in a certain sequence." Although the term "assembly rule" was originally coined in this latter sense, to describe rules for coexistence or exclusion for a specific species assemblage (Diamond 1975), I shall extend its usage here to include fundamental generic constraints on system development.

TOPOLOGY OF NICHE SPACE

This section will discuss a general rule for community assembly deduced as necessary and sufficient from empirical regularities in the topological structure of food webs.

Euler conceived of the generalized graph as a simple way of representing the topological structure of a complex system. A generalized graph consists of a set of vertices, and a set of edges joining vertices. Two useful graphical representations of ecological systems may be constructed from food web data by choosing either the consumers or the resources, as the vertex sets. Here vertices represent subsets of either resources or consumers; pairs of vertices are connected by edges if and only if the subsets that they represent intersect.

If each vertex corresponds to a consumer species, or more precisely, to the subset of resources used by a given consumer species, then we have the consumer overlap graph $G(C)$ (Cohen 1977). On the other hand, if each vertex corresponds to a resource, or to the subset of consumers which use a given resource, then we have the community resource graph $G(R)$ (Sugihara 1983, 1984). The n -pointed "cliques" or fully connected constellations of vertices (resources) in $G(R)$ correspond to n -dimensional trophic niches for consumers. If we inflate $G(R)$ in a higher dimensional space so that each species n -dimensional niche now becomes an n -pointed convex polyhedron or simplex, we can generate the so-called simplicial complex model of the communal niche $K(R)$ (Atkin 1974, Casti 1979, and independently Sugihara 1983). $K(R)$ is similar to $G(R)$ but gives a more robust geometrical portrait of how the n -dimensional species niches are packed together.

As suggested at the outset, the importance of these representations rests in their practical ability when applied to real data to detect deep order in the construction of ecological systems. Such order is revealed in the following temporally robust structural regularities (Sugihara 1984). These patterns were extracted from more than 60 real data sets for natural systems, and place natural systems in an exceedingly narrow subset of mathematical possibilities.

- P1) $G(C)$ can often be collapsed down to a particular 1-dimensional representation known as an interval graph (Cohen 1977).
- P2) $G(C)$ and $G(R)$ have the triangulation or rigid circuit property, i.e., all circuits are effectively paved with triangles (Sugihara 1983).
- P3) $K(R)$ lacks holes. Intuitively, species are packed densely over the space of resources so that $K(R)$ appears as a simple topological solid rather than a multidimensional swiss cheese (Sugihara 1983).

Although the full significance of these patterns has yet to be appreciated, it has been possible to use them to deduce a generic necessary and sufficient rule for sequentially assembling ecological systems. The technical details of this deduction are discussed elsewhere, but the intuitive essence of the rule is that species tend to enter a system (if successful) conservatively, by attaching to single trophic guilds rather than by bridging multiple trophic guilds. That is, insofar as ecological systems develop by the sequential addition of species, their consumer overlap graphs $G(C)$ should tend to grow in a connected tree-like fashion radially, rather than by bridging isolated clusters of species or forming large loops. Ecological assembly, therefore, mirrors the typical case in evolution if convergence is rare, and tends to produce tree-like hierarchically structured systems (Sugihara 1983).

NICHE PARTITIONING THEORY

The tradition of niche partitioning theories, used to explain certain species abundance patterns, is another plausible approach to the assembly problem. The basic idea here is to compare various rules for partitioning the total abundance (biomass or individuals) of an ensemble with the observed pattern of species relative abundance. At the appropriate phenomenological level, it may be reasonable to expect a correspondence between the manner in which abundances are apportioned and underlying system structure. On a more mechanistic level, these different apportionment rules should produce corresponding differences in the distributions for determining the parameters of a dynamic model. Of particular interest here is the presence of ubiquitous empirical regularities in species relative abundances; namely, Preston's canonical lognormal distribution ($\gamma \approx 1$) and the related species-area constant ($z \approx 1/4$). Such robust empirical regularities in static distributions of commonness and rarity could point to the operation of equally general rules of community assembly (Sugihara 1980, however see May 1975, Connor and McCoy 1979, Sugihara 1981).

The three main hypotheses of niche apportionment are Motomura's (1932) geometric series model, MacArthur's (1957) broken stick model, and the niche hierarchy model (Sugihara 1980). In the geometric series or niche preemption model, the community is assembled sequentially by allowing each successive species to preempt a fraction k of the resources left by the previous species. The broken stick model is essentially a null assembly or spontaneous creation hypothesis in that no order or sequence is involved. Rather, abundances are apportioned by simultaneous random subdivisions. Although neither of these apportionment hypotheses produces the observed canonical lognormal distribution, the niche hierarchy model which is intermediate between these two extremes, does produce this distribution and generates the consequent species-area exponent as well. The specific motivation for this model was to duplicate the hierarchical structure seen in a niche overlap dendrogram. Each branch of the dendrogram, therefore, corresponds to a subdivision of abundance, with different subdivisions possibly involving different sets of niche factors. Here communal biomass is sequentially subdivided by randomly choosing (without regard to size) one branch at each step for further subdivision.

Of interest to the previous section is that this simple model for dividing abundances follows consistent from the conservative assembly rule deduced from topology (both contain a suggestive parallel with evolution). A new species does not stem simultaneously (break with) separate branches of an ecological (or evolutionary) tree, but rather arises as a bud from a single branch. That is, new species do not usually enter as a bridge or concatenation of branches. Therefore, it is possible that this rule for sequential breakage of abundances in taxocenes may be an expression of same topologically conservative assembly rule deduced as necessary and sufficient for larger ecosystems.

BIOGEOGRAPHICAL EXPERIMENTAL ASSEMBLY RULES

Darwin established an excellent precedent for using static biogeographical observations to direct thinking about the temporal process of single species evolution. In similar vein, it has been productive to use biogeographical information on the composition of different multispecies assemblages to derive constraints for communities.

Jared Diamond, who originally coined the term "assembly rule" for communities (1975), gathered extensive data on species distributions of birds inhabiting a series of islands in New Guinea. He observed that only certain combinations of species ever occurred together and that others appeared to be forbidden in a statistically significant way (but see Connor and Simberloff's 1979 criticism, and Gilpin and Diamond's 1984 defense). He was thus able to construct, by inference, several partial tables of compatible and forbidden combinations of species to generate a set of empirical exclusion/coexistence rules for birds on these islands. Moreover, he observed that the ability of specific combinations to occur together seemed to depend on the context of the other species in the assemblage. This led Diamond to the following generalizations about community assembly.

- 1) Some stable communities may consist of unstable subcommunities.
- 2) An unstable whole may be produced from stable (subcommunities).
- 3) The invisibility of a subensemble (e.g., guild) may depend on the presence or absence of other species (e.g., from other guilds) in the system.

These properties have a simple dynamic interpretation that will be discussed in section 2.

It is worth mentioning that assembly taken as a compatible parts problem has a long history in experimental and field manipulations (e.g., Dayton 1971, Paine 1966, Davidson 1985). More recently, Philippi et al. (1985) has completed an extensive controlled laboratory study of a 30 species *Drosophila* system designed to produce assembly rules from the combinatorial patterns of coexistence and exclusion (see also Drake 1985). This is the most complete study of its kind that I know of, and verifies many of the phenomena listed above that Diamond inferred circumstantially from biogeographical data.

DYNAMICS OF COMMUNITY ASSEMBLY

This section will explore a heuristic framework for studying the dynamics of community development and will survey some results obtained from simple models of relevance to the assembly problem.

HISTORY INDEPENDENCE AND CLIMAX

The dynamics of community development will depend critically on whether the final composition of the system of interest is or is not dependent on global initial conditions. These global initial conditions describe the inputs in the historical trajectory of the system; i.e., initial population values and the specific timing and order of species introductions.

Let

$$S_p(\bar{t}) = (x_1(t_1), x_2(t_2), \dots, x_p(t_p))$$

be the ordered inoculation vector for the system describing the particular order, the initial population sizes, x_i , and the timing, t_i , of species introductions to the system. Note that if species i and $i+1$ are

added simultaneously, then $t_i = t_{i+1}$. At the other extreme, suppose each i^{th} system generated by the sequential dynamic operator $F(S_i(\cdot))$ has a unique positive global stable equilibrium, $x_i^*(n) > 0$, consisting of some n -sized subset of $\{x_1, \dots, x_i\}$, then we may speak of adding each $i+1$ species sequentially to the positive equilibrium determined by $F(S_i(\cdot))$. Hence, $F(S_i(\cdot))$ may be thought of as sending an initially unordered set of species $\{x_1, \dots, x_p\}$, where initially for each invader $x_i(*) = e$, through a sequence of p equilibria finally to a unique positive globally stable equilibrium consisting of an n species subset of $\{x_1, \dots, x_p\}$. That is,

$$F(S_p(*)) : \{x_1, \dots, x_p\} \rightarrow \bar{x}_p^*(n)$$

where after p steps the dimension of the equilibrium is n , $n \leq p$, $x_i(t) \geq 0$, and \bar{x}_p^* is an e

neighborhood of the p^{th} equilibrium that can be reached in finite time. Furthermore, within each step of $F(S_p(*))$, if a species goes extinct ($x_j = 0$) it remains so for all time unless reintroduced at a later stage in S . Unless otherwise stated, for ease of exposition, we shall only consider the case of p distinct species each appearing only once in S .

In general, and in particular for Volterra systems, for a given unordered set of species $\{x_p, \dots, x_n\}$ and a given F , different $S_p(t)$ may produce different \bar{x}_p^* . This property, as we shall see in section

22, underlies Diamond's assembly rules. If however, $\bar{x}_p^*(n)$ is unique for $\{x_1, \dots, x_p\}$ and F , then it is

independent of $S_p^{\bar{N}}$; i.e., independent of all feasible global initial conditions on the set $\{x_1, \dots, x_p\}$.

In classical secondary succession, if there is a unique climax that can be reached from all feasible starting points, then it must be independent of S . Such a climax system may be modelled, for example, by a Markov process (Horn 1975) since it is history independent. In this case, it is irrelevant to the assembly of the climax whether the initial floristic composition is complete (Egler 1954, Drury and Nisbet 1973) (i.e., $S_p(0); t_i = t_2 = \dots = t_p$) or whether species are added sequentially ($t_1 < t_2 < \dots < t_p$). Such differences may affect the transient dynamics and the sequence of extinctions, but they will not affect the final stationary state \bar{x}^* .

A convenient tool for characterizing the idea of sequence dependence versus independence is a variation of Siljak's (1975) notion of connective stability. An n -species dynamic system is said to be connectively stable if all subsystems generated by the set of all 2^n distinct interconnection matrices is stable. That is, if all possible ways of eliminating specific pairwise interactions among

components is stable. This condition, however, is unrealistically robust and does not address the assembly problem.

A milder and more useful condition may be obtained if we consider, rather, only the subset of interconnection matrices generated by the $n!$ ways of eliminating "whole" species (not just pairwise interactions). A dynamic system is elimination stable if all possible subsets of species are stable.

For example, consider the system:

$$\bar{x}' = \bar{x}f(\bar{x}) \quad (1)$$

and its stability matrix A whose elements

$$a_{ij} = \frac{\partial f(x^*)}{\partial x_j}$$

and where x^* is the independent equilibrium of the n^{th} subset of species. A new stability matrix

BA' is formed by zeroing out corresponding rows and columns defined by the interconnection matrix E , leaving on the n^{th} subset of species. That is, $\{A' = EAE + D\}$ where E and D are diagonal matrices such that the diagonal elements of E and D respectively, are $e_{ii} = 0$ or 1 , and $d_{ii} = 1$ if $e_{ii} \neq 0$ or -1 if $e_{ii} = 0$. Notice that the elements of A will, in general, depend on the new equilibrium defined by E . The system (1) is elimination stable if it is stable for all n .

It is easy to see that if F is a feasibly restricted family of n Volterra equations such that $B = (A + A^T)/2$ is negative definite, and $\bar{x}^*(n)$ is a locally stable positive n -species equilibrium generated by

$$F(S_n(\bar{t})) : \{x_1, \dots, x_n\} \rightarrow \bar{x}^*(n) \quad (2)$$

then the system defined by $\bar{x}^*(n)$ is elimination stable if and only if it is independent of $S_n(\bar{t})$ for a given unordered set of n species $\{x_n, \dots, x_n\}$. That is, because of the global stability of Volterra systems for which B is always negative definite, if one can take them apart in any order, one can reassemble them from the equilibrium components $\{x_1, \dots, x_n\}$ in any order.

In the above system, an n -component climax community is independent of global initial conditions $S_n(\bar{t})$ if and only if it is elimination stable. This ceases to be true, however, with the insertion in S of transient species. If, however,

$$F(S_p(\bar{r})) : \{x_1, \dots, x_n\} \rightarrow \bar{x}_p^*(n),$$

having $p-n$ transient species, is independent of S , then the system defined by $\bar{x}^*(n)$ must be elimination stable. That is, with transient species included in the sequence, elimination stability is a necessary but not sufficient condition for sequence independence. Nonetheless, it should be possible to eliminate the n climax species in any order for $\bar{x}^*(n)$, to generate $n!$ equilibrium sequences $S_n(\cdot)$, $x_i(\cdot) = e$, all leading to $\bar{x}^*(n)$.

HISTORY DEPENDENCE AND ASSEMBLY

Suppose a globally stable n -species equilibrium $\bar{x}^*(n)$ generated by (1) is not elimination stable. That is, there are subsets of $\{x_1, \dots, x_n\}$ for which a stable feasible equilibrium does not exist. This implies that some or possibly all of the ordered additions $S_n(\cdot)$ under F will fail to produce $\bar{x}^*(n)$. Denoting the subset of successful sequences as $\{S'_n(\cdot)\}$, it is clear that the degree to which $\{S'_n(\cdot)\}$ is small compared with $n!$, is the degree to which history dependence or the uniqueness of the assembly sequence is important.

In the sense used by Diamond (1975) and Gilpin and Case (1976), the small size of $\{S'_n(\cdot)\}$ gives definition to their use of the term assembly rule. The extent to which a system or subsystem is not elimination stable, measures the narrowness of possible pathways leading to $\bar{x}^*(n)$. That is, the smaller $\{S'_n(\cdot)\}$, the more precise the assembly rules.

In random simulations of competitive Volterra systems, Gilpin and Case (1976) found that arbitrary removals of single species from stable n -species systems left the remaining $n-1$ species systems stable at a frequency rapidly diminishing as n increased. Therefore, in such randomly generated systems, assembly rules may become more restrictive in the later stages of system development, forming an ever increasing bottleneck. This follows, in part, from the fact that randomly generated dynamic systems are more difficult to stabilize with size (May 1973).

DENSITY MEDIATED FACILITATION AND INVASION RESISTANCE

The results of Gilpin and Case (1976), Pimm and Lawton (1978), May (1973) and Drake (1985), indicate the possibility that a given n -species Volterra system with a stable positive equilibrium sequence of these n stable species $\{x_1, \dots, x_n\}$ will produce $\bar{x}^*(n)$, i.e., $\{FS'_n(\cdot)\} = \Phi$. Rather, as

has been demonstrated in simulation experiments (Drake 1985) it may be possible to achieve $\bar{x}^*(n)$ only by inserting transient species into S^* so that

$$F(S_p(*)) : \{x_1, \dots, x_p\} \rightarrow \bar{x}^*(n) \quad n < p \quad (3)$$

It may be shown that the effect of adding the transient species is to alter the equilibrium densities in the sequential systems in a manner that allows sequential stable coexistence and invasion. This effect may be called density mediated facilitation to distinguish it from physiological facilitation.

It should be noted that even if no equilibrium sequence S_n^* will produce $\bar{x}^*(n)$ there is always some sequence $S_n(\bar{r})$ that will yield $\bar{x}^*(n)$. That is to say that the timing and not just the order of species additions may be important in system assembly.

It is possible that a given finite set of species $\{x_1, \dots, x_n\}$ may contain a subset which is resistant to invasion by all other members of this set. Invasion resistance may be the case in some climax systems and it is easy to construct simple examples using Volterra equations where this is true. Although it is clearly not true in general (e.g., no-transitive species replacement cycles (Buss and Jackson 1979)), simulation studies using Volterra equations have found that long invasion sequences ($p > 1000$) with species drawn redundantly from a fixed randomly generated species pool tend to produce invasion resistant communities (Drake 1985). It should be emphasized, however, that this result clearly depends on having a finite species pool whose interaction parameters do not change. Because one can always "create" a species which can invade any given Volterra system, no natural system will ever be non-invisible in an evolutionary sense.

INVASION SUCCESSION AND EVOLUTION

In the preceding discussion of $F(S^*)$ with $x_i^* = e$ we considered sequential invasions to stable positive equilibria. At each step in $F(S^*)$ an invasion will either fail or it will produce a new equilibrium system possibly not including the invader itself. What are the conditions for successful invasion?

MacArthur and Levins (1967) studied the conditions for the successful invasion of a symmetrical two-species Volterra competition system

$$\dot{x}_i = \frac{r_i x_i (k_i - \sum_j \alpha_{ij} x_j)}{k_i}, \quad (4)$$

where

$$a_{ij} \geq 0; \quad \alpha_{12} = \alpha_{21} = \alpha_R$$

and

$$k_1 = k_2 = k_R$$

for the resident species 1 and 2; and for the invader I

$$\alpha_{1I} = \alpha_{II} = \alpha_{I2} = \alpha_I.$$

They found that the invading species, I , can increase when rare (i.e., invade) when the following inequality is satisfied:

$$k_I > \frac{2\alpha_I k_R}{1 + \alpha_R}. \quad (5)$$

Clearly, the ability to increase when rare is necessary for invasion, and in this particular case, it is also sufficient (condition (5) guarantees a stable 3-species equilibrium). Numerical simulations of generalized Volterra predator-prey systems show that the condition "ability to increase when rare" is sufficient in over 80% of the cases (Post and Pimm 1984). That is, an invader which can initially increase when rare will seldom exit the system without indelibly altering the equilibrium.

It is easy to extend the condition (5) of MacArthur and Levins to the n -species case where competition among the n residents α_R is equal, k_R equal and $\alpha_{iI} = \alpha_{II} = \alpha_I$, $i = (1, \dots, n)$. Condition (5) then becomes

$$k_I > \frac{n\alpha_I k_R}{1 + (n-1)\alpha_R}.$$

If the number of residents, n , is large, we can relax the equality requirement on α_I and α_R and replace them by their expectations $\hat{\alpha}_I$ and $\hat{\alpha}_R$ to obtain

$$1 > \frac{n\hat{\alpha}_I}{1 + (n-1)\hat{\alpha}_R}, \quad (6)$$

where $k_I = k_R$. The term $\hat{\alpha}_I$ in the numerator is the expected competitive effect between the invader and the residents, and the term $\hat{\alpha}_R$ in the denominator is the expected competitive interaction among the residents themselves. This condition shows that it is easier to invade if interactions among residents are stronger (results in smaller resident populations) and/or if the competition between the invader and the residents is weaker. Clearly, as $\hat{\alpha}_I$ decreases, then $\hat{\alpha}_R$ will eventually decrease and invasion will become more and more difficult with time.

Although illustrated in this special case, invasion difficulty in $F(S_n(*))$ as n increases has been observed in a number of computer studies in both linear and Volterra predator-prey systems (Post and Pimm 1983, Drake 1985) and appears to be a robust property.

A criterion similar to (6) for the "ability to increase when rare" has been proposed by Shigesada, Kawasaki, and Teramoto (1984) for Volterra systems with interference competition. Of special significance is their discovery that for special systems like (4) whose interspecific coefficients can be rewritten as $\alpha_{ij} = c_i \beta_j$, where $c_i > 0$ and $\beta_j > 0$ is the coefficient of interspecific interference, the quantity $G_1 = \sum \beta_j x_j^*$ will always increase with each successful invasion. Nakajima further showed

that for equation (4) the quantity $G_2 = \sum K_i x_i^*$ will increase with succession [i.e., $F(S(*))$] if each i^{th} system's stability matrix is symmetric and negative definite. In general, it is possible to show how for a globally stable sequence of equilibria produced by $F(S(*))$ one can measure the development of the system (i.e., shifts in x^*) by a sequence of liapunov functions whose sum is strictly increasing.

A general derivation of the necessary condition for invasion, "ability to increase when rare", may be conveniently obtained from a non-equilibrium neighborhood stability analysis evaluated at the point where the invader population is zero ($x_I(*)=0$) and the resident's populations are at equilibrium $(\bar{x}^*)^N$ (Czapleski 1973, Allen 1976). It can be shown that if the augmented system is unstable at this point, then the invader's population will always increase.

Denoting A_R as the $n \times n$ stability matrix of the resident system Eq. (1) whose elements are $a_{ij} =$

$$x_i^* \left(-\frac{\partial f(x^*)}{\partial x_j} \right),$$

it follows that because $s_I(*)=0$, then $a_{ij} = 0$ for $i (1, \dots, n)$. This simplification allows the determinant of the augmented $(n+1) \times (n+1)$ system having the general form of equation (1) to be expressed conveniently

$$|A_+| = |A_R| |a_U|.$$

Hence, the eigenvalues for the augmented system $\{\lambda_+\}$ are simply the eigenvalues for the original system $\{\lambda_R\}$ plus the new eigenvalue for the invader, $\lambda_I = a_{II}$. Therefore, the condition "ability to increase when rare" is the condition that the invader's eigenvalue at this point have a positive real part, or that

$$a_{II} < 0, \quad (7)$$

which for the general system (1) means that $f_I(\bar{x}) < 0$. Because Volterra systems are a special case of (1), we can use (7) to derive MacArthur and Levin's condition (5) from (4).

Condition (7) has been called the evolution condition because it is required for a newly evolved species to enter the general system (1). A qualitative analysis of this condition for the two species Volterra predator-prey case suggests that such systems tend to evolve toward higher predator/prey biomass ratios (Allen 1975). A more careful analysis (Hirata 1982) confirmed this result by showing how selective drift in parameter values will occur with successive evolutionary replacements of both predator and prey species, moving the system monotonically toward higher predator/prey biomass ratios.

MULTIPLE STABLE STATES AND ORDER THROUGH COLLAPSE

At the other extreme from sequential equilibrium invasions $F(S^*)$, is the idea of building systems from the top down, with the entire n -species pool $\{x_1, \dots, x_n\}$, initially present. As in Egler's (1954) "initial floristic composition hypothesis", assembly here may be thought of as occurring through a process of selective extinctions or dynamic decay. The generated dual under F of the inoculation vector, $S_n(0)$, is the extinction vector, ξ

$$\xi_{n-k}(t) = \{\phi, x_i(t_i), \dots, x_k(t_k)\}, \quad k = [1, 2, \dots, n]$$

which records the order and timing of species departures from the system. If $\xi_{n-k} \neq \phi$, then $F(S_n(0))$

does not lead to a stable positive n -species equilibrium, and we have a sequential collapse of the $n - k$ system, $\bar{x} \neq (n-k)$. What are some properties of $\bar{x} \neq (n-k)$ and ξ ?

Gilpin and Case (1976) used simulations to study the collapse of $F(S_n(0))$ in randomly initialized systems of Volterra competition equations ($S_n(0)$ chosen uniformly from an n -dimensional

simplex). Although they did not study ξ directly, they estimated an empirical rule for the number of distinct $\bar{x}^*(n-k)$ equilibria, so called "multiple stable states", as a function of n . They found that although there are potentially $n!$ combinations of species, the number of observed stable combinations grew much more slowly ($< \exp(0.2(n-1))$). Furthermore, even though the starting conditions were random, certain outcomes were more likely to occur than others.

Both of these results suggest selectiveness in the dynamics of decay, and the possibility, therefore, of a bias toward specific orderings of ξ . It is clear that without singularities, a given system and initialization of these Volterra systems will produce a unique $\bar{x}^*(n-k)$ and ξ .

Section 1.1 listed the triangulation property of niche overlap graphs $G(C)$ as a nonrandom property of natural systems (no $G(C)$ contains minimal circuits of length greater than 3). It is worth noting that the connectance structure of a system of Volterra competition equations may also be described by a consumer overlap graph, $G(C)$. To what extent could the observed triangulation property be selected for in the dynamics of decay?

Numerical simulations of randomly structured (non-triangulated) Volterra competition systems, initialized with all population sizes starting at 1, [$FS(0)$ with $s(0) = (1, 1, 1, \dots, 1)$] show a marked tendency for the collapsed $n-k$ systems to become triangulated (Sugihara 1983). Therefore independent of the topological assembly rule described earlier for the sequential addition of species, it may be possible to obtain topological order from the sequential collapse of randomly structured systems. The basis of this behavior must be due, in part, to the fact that triangulation in $G(C)$ tends to be dynamically stabilizing (Sugihara 1983).

There should be a tendency, therefore, for ξ to contain species involved in non-triangulated (large) circuits.

The triangulation property of real systems, and its relation to stability has a suggestive link with another discovery by Lawlor (1979) and Yodzis (1982) that such natural systems, when modelled by empirically fitted Volterra equations, tend to be more stable (faster return to equilibrium) than equivalent randomly structured (non-triangulated) ones. Here, the triangulation property is seen to be present at all thresholds of interaction strength (Sugihara 1984). This property of real systems, therefore, may be responsible for their high dynamic stability.

SUMMARY

A variety of theoretical approaches for understanding the assembly of ecological systems are surveyed. Among the static approaches, both the topology of real trophic niche spaces and the observed patterns of species abundances suggest a very conservative method for successful species additions to a system. This conservative assembly rule echoes the normal case in evolution in that

it requires that systems grow in a tree-like fashion rather through the concatenation (convergence) of distantly related branches (guilds). On a more tactical level, static biogeographical information on species presence and absence in an area may be used to derive assembly rules as a compatible parts problem. The dynamic basis of compatibility rules is discussed in terms of the concepts of global initial conditions $S(\bar{t})$ sequential dynamics $F(S)$ and elimination stability. This preliminary framework is intended to focus discussion for future mathematical studies of assembly in dynamic systems.

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THE ROLE OF MULTIPLE INVASIONS OF PREDATORS IN ORGANIZING BIOLOGICAL COMMUNITIES

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INTRODUCTION

Much field and laboratory work has suggested that competition and predation have profound effects on shaping community structures. In some communities, a single trophic level in isolation can not sustain many species owing to competition, but the presence of predation from other levels can lead to a community of a higher species richness. For instance, Paine (1966, 1974) showed that removal of the top predator from an intertidal community of marine invertebrates resulted in a decrease in the number of major space-utilizing species. Similar effects have been widely observed in aquatic (Slobodkin 1964; Paine 1966; Dayton 1971; Porter 1972) and terrestrial systems (Darwin 1859; Summerhayes 1941; Connell 1961; Harper 1969). Such a phenomenon is referred to as predator-mediated coexistence. Conversely, it has also been observed that addition of extra predator species can lead to a decrease in the number of constituent species, and we call this situation predator-induced instability (Harper 1969; Paine and Vadas 1969; Hurlbert et al. 1972; Adicott 1974; Janzen 1976; May 1971; Lubchenco 1978).

The Lotka-Volterra models for a 2 prey-1 predator and a 2 prey-2 predator system have been extensively investigated to elucidate mechanisms of predator-mediated coexistence (Cramer and May 1972; Roughgarden and Feldman 1975; Fujii 1977; Caswell 1978; Vance 1978; Teramoto et al. 1979; Freedman and Waltman 1984; Hallam 1986) and predator-induced instability (May 1971, 1973). However, a general analysis of multiple species systems consisting of more than four species has not been fully explored, although there are a great deal of computer simulations based on real communities (Gilpin 1975; DeAngelis 1975; Gilpin and Case 1976; Goh and Jennings 1977; Pimm and Lawton 1977; Yodzis 1978, 1981; Pimm 1984). In multiple species communities, further complicated interactions are expected to occur among prey and predators. Consider a community consisting of multiple competing species. If a predator specializing on one particular prey species invades the community, it may cause a decrease in the density of that species. Subsequently, some of the species not preyed upon may increase their population sizes, being relieved of competition from the prey species. This in turn could lead to a decrease in some other competing species. Furthermore, if more than two predator species feed on competing species, one predator may influence other predators, either detrimentally (indirect competition between predators) or beneficially (indirect

mutualism between predators), through altering the structure of the competition community (Lubchenco 1978; Milton 1947; Dodson 1970; Dungan 1987; Kerfoot 1983; Levine 1976; Vandermeer 1980). Thus the direct and indirect effects of predation and competition may result in various community structures if the number of constituent species is large.

In this article, we focus on a community consisting of multiple interfering competitive prey species, and a number of specialists that consume the prey species. To describe the dynamics of the prey species in isolation, Shigesada et al. (1984) previously presented a simple model using the Lotka-Volterra equation, in which certain restrictions were imposed on the parameters representing interspecific interference competition. They showed that the system in general has multiple stable equilibria and the structure of these equilibria are classified into two types, depending on what characteristic properties the constituent species have in terms of two parameters: the relative strength of intraspecific interference to interspecific interference and the relative intrinsic growth rate (intrinsic growth rate divided by susceptibility to interference from other species). To examine the effect of predation on the structure of this competition community, we assume that a number of predators (specialists) immigrate one after another into the community. If a given invasion is successful, the community will attain a new stable equilibrium state, whose structure is also characterized in terms of the above parameters. By comparing the community structures before and after each invasion, the effects of the invading predator are evaluated. In this analysis we deal with two situations in which the competition community is either closed or open with respect to reimmigration of the species once extinct in the initially isolated competition community. The effect of predation on a closed community is analytically investigated in §3, while an open community needs computer simulations as shown in §4. In both cases, we show under what conditions predator-mediated coexistence or predator-induced instability result and how indirect mutualism or indirect competition arise between predators specializing on different prey species.

STRUCTURES OF COMMUNITIES WITH INTERFERENCE COMPETITION

The competitive community has been extensively studied using a Lotka-Volterra model for N competing species:

$$\frac{dX_i}{dt} = (e_i - \sum_{j=1}^N \mu_{ij} X_j) X_i \quad \text{for } i = 1, 2, \dots, N, \quad (1)$$

where X_i is the population size of species i , e_i is the intrinsic rate of growth and μ_{ij} is the coefficient of competition of the j th species on the i th species.

Here we assume that prey species interact mostly through interference competition. Typical examples of interference competition have been observed in sessile animals and plants that live on rocky shores, and in motile animals that defend territories by aggression or poisoning (Case and Gilpin 1974; Gilpin et al. 1986). To describe interference competition, Shigesada et al. (1984) have previously presented a simple model which adopts the Lotka-Volterra equation. In that model, the competition coefficients μ_{ij} are assumed to be given as a product of two factors as follows:

$$\mu_{ij} = \begin{cases} \sigma_i \alpha_i & (i=j), \\ \sigma_i \beta_j & (i \neq j), \end{cases} \quad (2)$$

where β_i represents the intrinsic interference of the i th species to other species and is termed the *interspecific interference* coefficient. We use α_i to distinguish *intraspecific interference* from interspecific interference, β_i . $\sigma_i (< 1)$ is termed the *susceptibility*, wherein we assume that species i can reduce the effect of interference from other individuals of any species by a factor of σ_i , owing to its defensive ability.

Substituting μ_{ij} defined by (2) for the Lotka-Volterra equation (1) and changing units of variables, we have the following basic equations:

$$\frac{dx_i}{dt} = \sigma_i(e_i - \gamma_i x_i - \sum_{j=1 (j \neq i)}^N x_j)x_i = f_i(x)x_i \quad \text{for } i \in I, \quad (3)$$

where $I = \{1, 2, \dots, N\}$, and

$$x_i = \beta_i X_i, \quad e_i = \epsilon_i / \sigma_i \quad \text{and} \quad \gamma_i = \alpha_i / \beta_i. \quad (4)$$

For the convenience of discussion, we assign subscripts to each species according to rank in decreasing order of $e_i (= \epsilon_i / \sigma_i)$:

$$e_1 > e_2 > \dots > e_N. \quad (5)$$

Thus a species with a higher intrinsic growth rate or a smaller susceptibility occupies a higher rank. Each species is further classified depending on whether its intraspecific interference is larger than its interspecific interference ($\gamma_i = \alpha_i / \beta_i > 1$), or vice versa ($\gamma_i < 1$). Hereafter, we call a species with $\gamma_i > 1$ an *auto-competitor*, and a species with $\gamma_i < 1$ a *hetero-competitor*.

Equations (3) have been extensively analyzed; all the equilibrium states are expressed in explicit forms and their stability properties analytically examined (Shigesada et al. 1984; Kawasaki et al. 1990). Here, we briefly introduce some results of the analysis.

An equilibrium point of (4) is obtained by setting $x_i = 0$ or $f_i(x) = 0$ for all i , and this procedure provides 2^N equilibrium points:

$$x_i^* = (e_i - C(P)) \xi_i \quad \text{for } i \in P, \quad x_i^* = 0 \quad \text{for } i \in I - P, \quad (6)$$

where $I = \{1, 2, \dots, N\}$, P is an arbitrarily chosen subset of I , and

$$\xi_i = \frac{1}{\gamma_i - 1}, \quad C(P) = \sum_{k \in P} e_k \xi_k / (1 + \sum_{k \in P} \xi_k). \quad (7)$$

Among these equilibria, biologically meaningful solutions should be nonnegative (i.e., $x_i^* > 0$ for $i \in P$). Stability properties of these nonnegative equilibrium points can be analyzed by means of the standard linearized method together with a Liapunov function, leading to the following stability criterion:

Stability Criterion Any solution of (3) which starts from an arbitrary positive initial point always approaches an equilibrium state having either of the following structures, I or II:

$$\text{I.} \quad \mathbf{x}^* = (x_1^*, x_2^*, \dots, x_s^*, 0, 0, \dots, 0), \quad (8a)$$

where x_i^* is given by (6) for $P = P_s = \{1, 2, \dots, s\}$, and s ($1 \leq s \leq N$) is an integer for which

$$\xi_i > 0 \quad \text{for } i \in P_s, \quad (8b)$$

$$e_s > C(P_s) > e_{s+1}. \quad (8c)$$

$$\text{II.} \quad \mathbf{x}^* = (x_1^*, x_2^*, \dots, x_t^*, 0, \dots, 0, x_w^*, 0, \dots, 0), \quad (9a)$$

where x_i^* is given by (6) for $P = P_{t,w} = \{1, 2, \dots, t\} + \{w\}$, and t and w ($0 \leq t < w \leq N$) are integers for which

$$\xi_i > 0 \quad \text{for } i \in P_s, \quad \xi_w < 0, \quad (9b)$$

$$e_t > C(P_{t,w}) > e_{t+1}, \quad (9c)$$

$$1 + \sum_{i \in P_{t,w}} \xi_i < 0. \quad (9d)$$

Since species i with $\xi_i > 0$ is an auto-competitor and species i with $\xi_i < 0$ is a hetero-competitor, relations (8b) and (9b) indicate that in case I, all surviving species are auto-competitors, occupying ranks from 1 through s . On the other hand, case II consists of surviving auto-competitors occupying the ranks from 1 through t and one surviving hetero-competitor (species w) whose rank is lower than t . Note that the top rank may be occupied by a hetero-competitor; in such a case none of the auto-competitors can survive (i.e., $w = 1, s = 0$). Figure 1 schematically illustrates the community structures of types I and II.

To summarize the characteristics of stable equilibrium states of interference competition communities: (1) Among all the auto-competitors, survival is hierarchically determined in the rank order of e_i . (2) The number of surviving hetero-competitors is at most one. (3) If a hetero-competitor of rank w can survive, it will exclude all species whose ranks are lower than w .

EFFECTS OF INVASIONS OF PREDATORS ON A CLOSED COMPETITION COMMUNITY

Let us now proceed to analyze the effects of predation on an interference competition community as described in the previous section. Consider an isolated competition community that has already reached a stable equilibrium state having either of the two structures, type I or II as shown in Fig. 1. We then assume that a number of specialist predators immigrate into this competition

I.

| | | | | | | | | | | | | |
|-------|---|---|-----|-----|-----|-------|-----|-------|-----|-------|-----|-----|
| rank: | 1 | 2 | ... | s | ... | w_1 | ... | w_i | ... | w_k | ... | N |
| | ○ | ○ | ○ | ○ | × | × | × | × | × | × | × | × |

II.

| | | | | | | | | | | | | |
|-------|---|---|-----|-----|-----|-------|-----|-------|-----|-------|-----|-----|
| rank: | 1 | 2 | ... | t | ... | w_1 | ... | w_i | ... | w_k | ... | N |
| | ○ | ○ | ○ | ○ | × | × | × | ● | × | × | × | × |

Figure 1. Possible structures of stable communities with interference competition. N species are ranked in decreasing order of e_i/σ_i . These species are further classified into auto-competitors ($\gamma_i = \alpha_i/\beta_i > 1$) and hetero-competitors ($\gamma_i < 1$). The ranks of hetero-competitors are indicated by w_1, w_2, \dots, w_k . I. All the surviving species are auto-competitors which occupy ranks from the top down to s . II. Auto-competitors occupy the ranks from 1 through t and a single heterocompetitor occupies a lower rank. ○, auto-competitor; ●, hetero-competitor; X, extinct species.

community one after another. Suppose that the time intervals between successive immigrations of predators are long enough so that pre-occupant species have already reached a stable equilibrium state before each new predator immigration. We regard a predator as a successful invader if the community colonized by a small propagule of the predator moves into a new stable equilibrium state, in which the predator becomes a constituent member. Once a predator invades successfully, the population sizes of pre-occupant species will change and some may become extinct, thereby altering community structure.

Hereafter, we focus on two situations in which a competition community is either closed or open. We define a competition community as closed if, once competing species in the initially isolated community become locally extinct (species assigned by \times in Fig. 1), they are never allowed to reimmigrate into the community at those times when a new predator invades. On the other hand, the resident species in the initial community (species assigned by ○ in Fig. 1) can reimmigrate, even if they become temporarily extinct upon invasion of predators. We might regard such a closed competition community as a functional group or a guild as termed by Root (1967). We define a competition community as open, if reimmigrations of initially extinct competitors (species assigned by \times in Fig. 1) are also allowed during successive invasions of predators. In this section we treat invasions of predators in a closed competition community. Invasions in an open competition community will be treated in the next section.

Consider a stable equilibrium community, which has been established after successive invasions of the $(n-1)$ th predator. When the n -th predator immigrates to this community, the dynamics of the community are given by the following equations:

$$\begin{aligned}\frac{d}{dt}X_i &= (e_i - \sum_{j \in I} \mu_{ij} X_j) X_i \quad (i \in I-G), \\ \frac{d}{dt}X_i &= (e_i - \sum_{j \in I} \mu_{ij} X_j - \kappa_i Y_i) X_i \quad (i \in G), \\ \frac{d}{dt}Y_i &= (-\eta_i + \kappa'_i X_i) Y_i \quad (i \in G),\end{aligned}\tag{10}$$

where I is the set of species that can stably survive in the closed competition community in isolation: $I=P_s=\{1,2,\dots,s\}$ for case I and $I=P_{t,w}=\{1,2,\dots,t,w\}$ for case II, and G is the set of n predators, each of which specializes on a competitor of rank k_i ($i=1,2,\dots,n$); i.e., $G=\{k_1,k_2,\dots,k_n\}$. X_i ($i \in I$) is the population size of competing species of rank i . Y_i ($i \in G$) is the population size of the predator specializing on competing species of rank i . μ_{ij} and e_i/σ_i (e_i) satisfy (2) and (5), respectively. κ_i is the predation rate of predator i and κ'_i is the product of κ_i and the conversion rate of the prey to the predator. η_i is the death rate of predator i .

Changing units of variables by (4) and

$$y_i = (\kappa_i/\sigma_i) Y_i, \quad d_i = \eta_i \beta / \kappa'_i, \quad K_i = \kappa'_i / \beta_p \tag{11}$$

we express (10) in the form:

$$\begin{aligned}\frac{d}{dt}x_i &= \sigma_i(e_i - \sum_{j \in I} x_j - \gamma_i x_i) x_i \equiv F_i(z) x_i \quad (i \in I-G), \\ \frac{d}{dt}x_i &= \sigma_i(e_i - \sum_{j \in I} x_j - \gamma_i x_i - y_i) x_i \equiv G_i(z) x_i \quad (i \in G), \\ \frac{d}{dt}y_i &= K_i(-d_i + x_i) y_i \equiv H_i(z) y_i \quad (i \in G),\end{aligned}\tag{12}$$

where $z=(x,y)=(x_1,x_2,\dots,x_N,y_{k_1},y_{k_2},\dots,y_{k_n})$. Since we assumed that the preexisting community has attained a stable equilibrium state, \bar{z} , the initial condition of (12) is given by $z(t=0)=\bar{z}+\delta$, where δ is an arbitrarily small vector. If the n -th predator which specializes on a competing species of rank k_n (called predator k_n) can successfully invade the preexistent community \bar{z} , the following should be satisfied:

$$H_{k_n}(\bar{z}) = K_{k_n}(-d_{k_n} + \bar{x}_{k_n}) > 0. \tag{13}$$

We can show that when (13) holds, system (12) always approaches a globally stable equilibrium point, $\hat{z} = (\hat{x}, \hat{y})$, which is given by (Shigesada et al. 1989),

$$\begin{aligned} \hat{x}_i &= \{e_i - C(\hat{S}, \hat{G})\} \xi_i \quad (i \in \hat{S}), & \hat{x}_i &= d_i \quad (i \in \hat{G}), & \hat{x}_i &= 0 \quad (i \in \hat{E}), \\ \hat{y}_i &= e_i - d_i / \xi_i - C(\hat{S}, \hat{G}) \quad (i \in \hat{G}), & \hat{y}_i &= 0 \quad (i \in \hat{E}_p), \end{aligned} \quad (14)$$

where

$$C(\hat{S}, \hat{G}) = (\sum_{i \in \hat{S}} e_i \xi_i + \sum_{i \in \hat{G}} d_i) / (1 + \sum_{i \in \hat{S}} \xi_i). \quad (15)$$

\hat{G} is a set of competing species that serve as prey. Since predator k_n is capable of invading, \hat{G} always contains k_n but not necessarily the preoccupant predators, because the presence of predator k_n may cause extinction of some resident predators. \hat{S} is a set of competing species that survive but are not preyed upon. $\hat{E} (= I - \hat{S} - \hat{G})$ is a set of competing species that go to extinction, and \hat{E}_p is the set of predators that survive in the preexisting community but go to extinction in the resulting community. These sets \hat{S} , \hat{G} , \hat{E} and \hat{E}_p are uniquely determined from the requirements that equilibrium \hat{z} should be nonnegative and locally stable:

$$\hat{x}_i > 0 \quad (i \in \hat{S}), \quad \hat{y}_i > 0 \quad (i \in \hat{G}), \quad F_i(\hat{z}) < 0 \quad (i \in \hat{E}), \quad H_i(\hat{z}) < 0 \quad (i \in \hat{E}_p). \quad (16)$$

If we denote by \bar{z} , \bar{S} , \bar{G} , and \bar{E} the quantities corresponding to the preexisting stable state, \bar{z} is given by (14) in which $\hat{\cdot}$ is substituted for \cdot . Thus the change in the population size of each species after invasion of the n^{th} predator is calculated by subtracting $\bar{z} = \{\bar{x}, \bar{y}\}$ from $\hat{z} = \{\hat{x}, \hat{y}\}$:

$$\begin{aligned} & \left. \begin{aligned} (\hat{x}_i - \bar{x}_i) / \xi_i & \quad (i \in \hat{S} \cap \bar{S}) \\ (\hat{y}_i - \bar{y}_i) & \quad (i \in \hat{G} \cap \bar{G}) \end{aligned} \right\} = C(\hat{S}, \hat{G}) - C(\bar{S}, \bar{G}) \\ & = \left\{ \sum_{i \in \hat{S}} \hat{x}_i + H_{k_n}(\hat{z}) / K_{k_n} - \sum_{i \in \hat{G}} F_i(\hat{z}) \xi_i / \sigma_i - \sum_{i \in \hat{E}_p} H_i(\hat{z}) / K_i \right\} / \left(1 + \sum_{i \in \hat{S}} \xi_i \right). \end{aligned} \quad (17)$$

From (8), (9) and (16),

$$\hat{x}_i > 0 \quad (i \in \hat{S} \cap \bar{E}), \quad F_i(\hat{z}) \xi_i < 0 \quad (i \in \hat{S} \cap \bar{E}), \quad H_{k_n}(\hat{z}) > 0 \quad \text{and} \quad H_i(\hat{z}) < 0 \quad (i \in \hat{E}_p),$$

and hence the numerator in the r.h.s. of (17) is always positive. On the other hand, the denominator becomes negative if the set of surviving competitors that have never been preyed upon (i.e., $\hat{S} - \hat{S} \cap \hat{E}_p$) includes a hetero-competitor, and positive if otherwise. Summarizing the above analyses, we obtain the following (see also Fig. 2):

Remark Consider a closed competition community that has been invaded by a number of specialist predators and has reached a stable equilibrium state. When a new predator (the n^{th} predator) invades this community, the resulting community has the following properties:

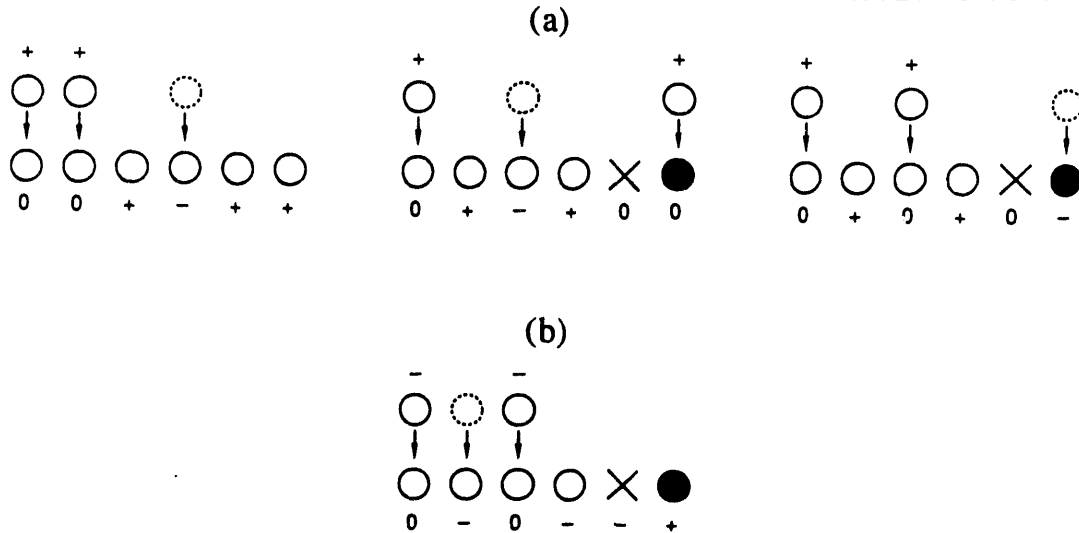


Figure 2. Changes in the community structure by invasion of the n^{th} predator on a closed competition community. In the lower row, the species in a closed competition community are arranged in decreasing order of rank. The surviving species after invasion of the n^{th} predators are indicated by circles (○, auto-competitor; ●, hetero-competitor) and extinct species by cross X. The circle with an arrow in the upper row designates a predator: the dotted version of the circle is a newly invading predator (the n^{th} predator); the solid version is a pre-occupant predator. Signs +, 0 and - indicate an increase, no change and decrease, respectively, in the population sizes compared before and after invasion of the n^{th} predator, all pre-occupant species except the prey species increase their population sizes. Thus predator-mediated-coexistence and indirect mutualism between predators are induced. (b) If there remains a hetero-competitor not preyed upon after invasion of the n^{th} predator, the hetero-competitor increases, while all other pre-occupant species except the prey species decrease their population sizes. Thus predator-induced-instability and indirect competition between predators are induced.

- (a) If there exists no hetero-competitor that is not preyed upon in the resulting community, all the pre-occupant species except prey species increase. Furthermore, some previously extinct species become able to survive in the resulting community. Therefore, predator-mediated coexistence and indirect mutualism between predators are induced (Fig. 2a).
- (b) If there remains a hetero-competitor not preyed upon in the resulting community, the hetero-competitor increases its population size, while all other preoccupant species except prey species decrease. In particular, some preoccupant prey species with lower ranks and their predators may become extinct. Therefore, predator-induced instability and indirect competition between predators are induced (see Fig. 2b).

The above results are explained as follows: because the prey species attacked by the newly invading predator decrease, interference from that prey species will be reduced so that all other species tend to increase (case (a)). However, if there remains a hetero-competitor not predated upon as in case (b), it obtains the greatest advantage from this effect, preferentially increasing its population size. As a result, other species present will be exposed to strong interference from this hetero-competitor, and hence tend to decrease, some occasionally driven to extinction.

INVASIONS OF PREDATORS IN AN OPEN COMPETITION COMMUNITY

In the previous section, we dealt with a closed competition community in which any species initially extinct in the isolated competition community is never allowed to reimmigrate afterward. However, if the community is always exposed to immigration of previously extinct species (an open community), the organization of the community upon each invasion of a predator will take a different course from that of a closed competition community.

To address the above question, we again consider Eq. (10) for $I=\{1,2,\dots,N\}$ and $G=\{k_1,k_2,\dots,k_n\}$. Note that in the present case, I is the set of all the competitors as defined in Sect. 2 ranked from 1 through N in contrast to the case of the closed community in which I is the set of competitors excluding the initially extinct ones.

Let us first consider the case that a single predator, say predator k_1 , invades a competition community, which has already attained a stable equilibrium state having either of the two structures, type I or II, as shown in Fig. 1. The dynamics of such a community is given by (10) for $I=\{1,2,\dots,N\}$, $G=\{k_1\}$, which has been investigated by means of local stability analysis of equilibrium states (Shigesada et al. 1989). The results of the analyses show that the predation effects predicted in the closed communities also appear in the open communities; a predator specializing on a hetero-competitor acts to increase the population sizes of other species, while a predator specializing on an auto-competitor leads to decrease or increase of species richness, depending on whether or not the community contains surviving hetero-competitors not preyed upon. Moreover, some properties specific to the open community are revealed; predation on a hetero-competitor sometimes induces the survival of another hetero-competitor that was previously extinct, and this newly surviving hetero-competitor also acts to change species composition. Therefore, the direction of change of each population size, in this case, is not necessarily fixed as in closed communities.

These properties specific to the open community generally seem to become more prominent with successive invasions of multiple predators. However, if the number of invading predators is greater than two, stability analysis of (10) will no longer be feasible without the help of simulation. Here we carry out a preliminary computer simulation for the special case that $I=G=\{1,2,\dots,N\}$ and parameters are restricted to the following particular values:

The set of prey consists of 10 species ($I=\{1,2,\dots,10\}$) with parameters

$$\begin{aligned} \epsilon_i &= 10 - 0.5 \times (i-1); \quad \alpha_i = \sigma_i = 1 \quad (i \in I), \\ \beta_i &= \begin{cases} 1.42 & \text{for } i \in \{6,7,9\}, \\ 0.6 & \text{for } i \in I - \{6,7,9\}. \end{cases} \end{aligned} \quad (18)$$

Predators have the following parameters:

$$\kappa_i = \kappa'_i = 1; \quad \eta_i = \eta \quad (i=1,2,\dots,10). \quad (19)$$

Among the 10 prey species, species 6, 7 and 9 with $\alpha_i < \beta_i$ are hetero-competitors and other species are auto-competitors. Applying the stability criterion presented in Sect. 2 to the prey community shows that this competition community has the following three locally stable equilibrium states, (a), (b) and (c):

| <i>Equi.</i> | X_1^* | X_2^* | X_3^* | X_4^* | X_5^* | X_6^* | X_7^* | X_8^* | X_9^* | X_{10}^* |
|--------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|------------|
| <i>State</i> | — | — | — | — | — | — | — | — | — | — |
| (a) | 5.15 | 3.90 | 2.65 | 1.40 | 0.15 | 0 | 0 | 0 | 0 | 0 |
| (b) | 0 | 0 | 0 | 0 | 0 | 7.50 | 0 | 0 | 0 | 0 |
| (c) | 0.41 | 0 | 0 | 0 | 0 | 0 | 6.76 | 0 | 0 | 0 |

According to the prior classification scheme, equilibrium state (a) is of type I, and (b) and (c) are of type II (see also Fig. 1).

The 10 predators are assumed to have the identical predation abilities and death rates. Each predator may survive if its food (prey) is abundant enough so that its growth rate exceeds its death rate.

We choose three different initial conditions: The prey species start from the neighborhood of either of the three locally stable states, (a), (b) and (c). For each equilibrium state X^* , we actually set $X(t=0) = X^* + \delta$, where $\delta = (10^{-3}, 10^{-3}, \dots, 10^{-3})$, and the predators initially have the same small size, $Y_i(t=0) = 0.1$ ($i \in I$).

Starting from these initial points, solutions of (10) are numerically calculated for various death rates η . Figure 3 demonstrates an example of numerical data of $z(t)$ for $\eta=2$. The species compositions finally attained after a sufficiently long time are shown in relation to the initial conditions and the death rates η in Fig. 4. When the death rate is large ($\eta > 7.5$), none of the three initial states allow invasion of the predators, because the growth rate of each predator does not exceed its death rate (i.e. $-\eta + X_i^* < 0$ for all i). Let us look at the case of smaller η , for instance, $\eta=6$. When the prey community is at equilibrium (a) in the beginning, no predator can yet invade. On the other hand, if the prey community starts from either (b) or (c), one predator specializing on the hetero-competitor can invade. As a result, some auto-competitors in higher ranks (species 1 and 2 in case (b); species 2 in case (c)) are able to reimmigrate and survive, raising the species richness of the community. These characteristic effects of predation pressures are essentially similar to those exhibited in closed communities as was shown above. When the death rate η becomes still smaller, a new feature emerges. For the case of $\eta=3$, the prey communities starting from either (b) and (c) will approach to the same final state as that from initial state (a), in which the hetero-competitor is excluded, even though it was most abundant initially. This result is explained as follows; among

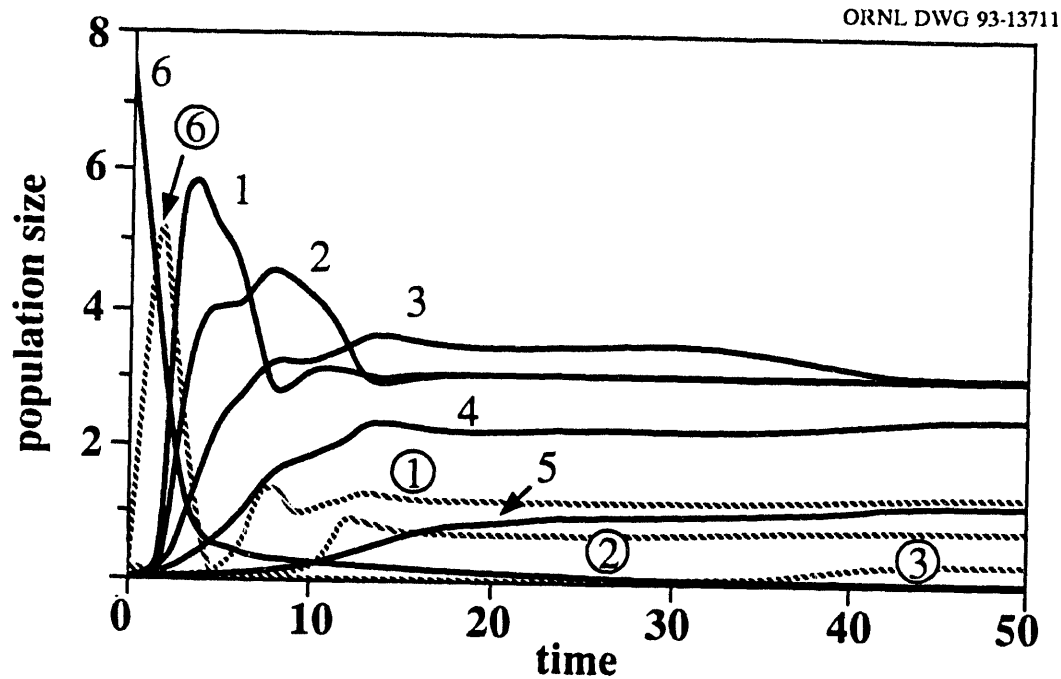


Figure 3. The temporal changes of population sizes of an open community. The solution of (10) with parameters given by (18), (19) and $\eta=3$ with initial condition (b) is presented. Solid curves numbered (1 through 6) represent prey species, and broken curves with circled number (1,2,3 and 6), predators. Predator 6 diminishes its prey (species 6), finally leading to extinction of this prey-predator pair, which in turn stimulates survival of prey and predators of higher ranks.

the invading predators, the one specializing on the most dominant hetero-competitor grows most rapidly at first, and exhausts its prey to a low level. Thus, the interference previously exerted by the prey (the hetero-competitor) will diminish, and auto-competitors in higher ranks will be allowed to grow. As a result, interference from these auto-competitors is intensified so much as to exclude the hetero-competitor along with its predator. When η is further reduced to 1, this tendency is emphasized even more; 7 predators can always invade successfully irrespective of the initial states, and will approach the same equilibrium state in which the 7 prey-predator pairs and a competitor not preyed upon (species of rank 8) can survive. Note that not only auto-competitors but also hetero-competitors which were previously extinct can survive, and that all the prey species retain their sizes at the same level, $X_i^* = \eta$ ($i \in G$). Therefore, the diversity of the community increases in the sense of both species richness and evenness of species abundance. In summary, as the multiplicity of invading predators increases, more competing species are allowed to coexist, leading to higher community diversity.

As demonstrated in the present work, a closed competition community always has a unique stable equilibrium state for a given set of species, so that the dynamical behavior can be completely

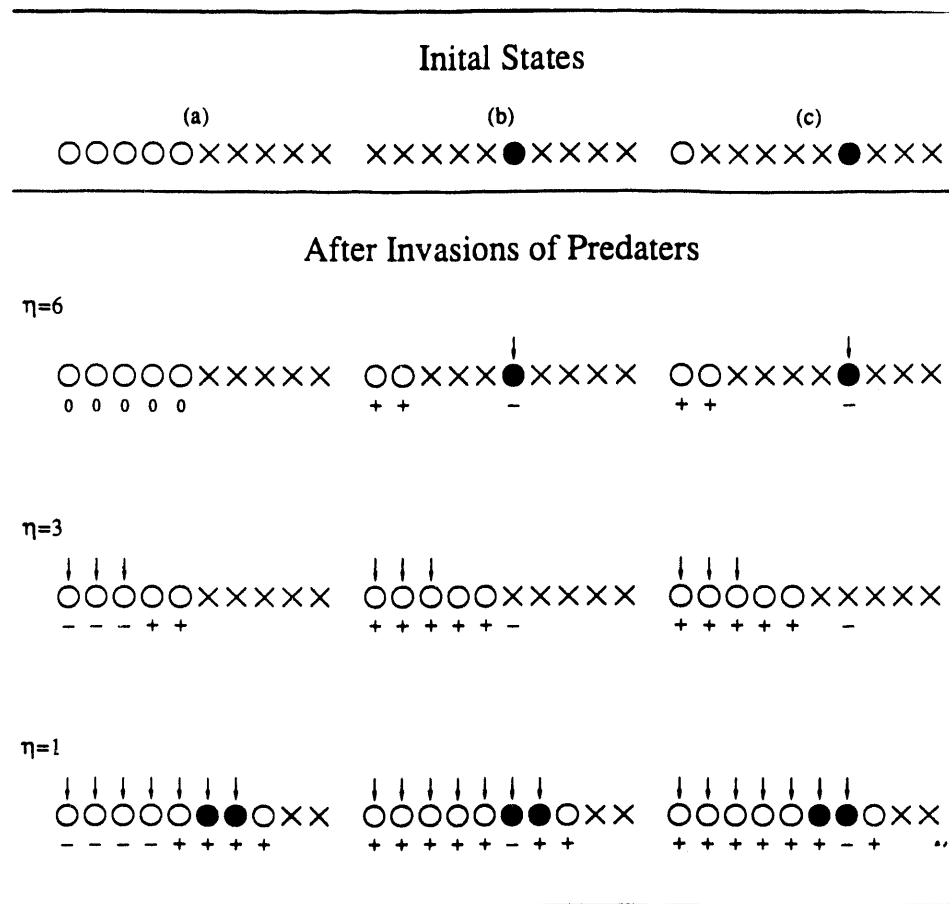


Figure 4. Changes of community structures by invasions of multiple predators into open competition communities. The lower trophic level (consisting of 10 competitors) is initially at either of three stable equilibrium states, (a), (b) or (c). Then small propagules of predators (specialists) and the competitors simultaneously immigrate into this lower trophic community. The dynamical change of the community structure is examined by solving (10) with the aid of a computer. At the ultimate time, each species either persists or goes to extinction; ○, surviving auto-competitor; ●, surviving hetero-competitor; ↓, surviving predator. +, -, and 0 indicate the direction of size change of a competitor compared before and after simultaneous invasions of predators. η denotes the death rate of predators. As η decreases, more predators can successfully invade at the same time. As a result, more competitors which were previously extinct become able to survive, leading to an increase in the species richness of the community.

predicted. In contrast, an open competition community generally possesses multiple stable equilibria; which equilibrium will be actually realized depends on the initial population size of each species. The initial sizes of reimmigrating species play a particularly important role in organizing community structures, because even if they finally become extinct, their temporary invasions may cause the community to shift to another stable state among the multiple equilibrium points. Furthermore, although any solution of (10) for the present case approaches asymptotically a stable equilibrium point, there may exist some unstable equilibria that involve limit cycles or chaos, if the parameter values or initial points are set in different ways. Indirect mutualism or competition between predators will also arise in the open community, although we did not examine it, because we have only dealt with simultaneous invasions of multiple predators (not successive invasions of predators as in the case of the closed community).

Finally, in the present model, we assumed (2) to describe interference competition among prey species. Although this assumption may be too restrictive to represent a real community, it allows us to deduce qualitative features of stability and structures of a competition community. Furthermore, we are only concerned with the case that predators are specialists. The actual community, however, should be more complex, in general including both specialists and generalists. Predation by generalists would operate in a more complex manner compared with that of specialists (May 1973; Vandermeer 1980). Further studies of mixed invasions of specialists and generalists are in progress.

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COMMUNITY STRUCTURE AS A CONSEQUENCE OF COEVOLUTION OF MULTI PREDATOR SPECIES

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SUMMARY

Coevolutionarily stable community (CSC) structures are studied when predators search for several species of prey distributed in a number of patches. A community is called a CSC when no mutant predator with different food preference have a selective advantage over the individuals of the wild type of the same species. We consider not only the equilibrium structure but also the dynamic structure of a CSC, in a food web of two trophic levels. In a CSC, (1) the number of predator species which simultaneously utilize two common patches does not exceed the sum of the numbers of prey species in the two patches. In a simpler model, in which only one species of prey lives in each patch, (2) the number of connections indicating predatory interactions between prey and predator species does not exceed the sum of the numbers of species in the two trophic levels. Especially, when all handling times of predation are sufficiently short, (3) two predator species rarely utilize two common prey species simultaneously. Finally we discuss the relationship between our results based on Darwinian coevolution, Joel Cohen's "non-interval" food webs and George Sugihara's "hole" in the resource graph.

INTRODUCTION

Classical competition theory (MacArthur and Levins 1964, 1967; Levin 1970) predicts that the number of consumer (or predator) species does not exceed the number of resource (or prey) species and that two consumer species cannot be too similar in their resource utilization. These predictions are based on feasible (non-trivial) steady states as a necessary condition for existence.

Whereas a homogeneous resource distribution is assumed in the classical competition theory, Tilman (1982) showed that the number of predator species persisting in a patchy (or heterogeneous) environment may be greater than the number of prey species. Classical theory assumes the system to be at equilibrium, but several authors have developed nonequilibrium theories incorporating nonlinearities in resource utilization (Koch 1974; Levins 1979; Armstrong and McGehee 1980). They pointed out via computer simulations or analytically that two or more species can coexist on one biotic resource.

Classical competition theory is based on the individual selection paradigm. MacArthur and Levins (1967) implicitly considered evolutionary convergence of resource utilization patterns in a niche space. Their idea virtually coincides with the concept of the evolutionarily stable strategy introduced by Maynard Smith and Price (1973; see also Lawlor and Maynard Smith 1978). Matsuda and Namba (1989) considered a community to be coevolutionarily stable. A coevolutionarily stable

community (CSC; termed by Roughgarden 1979, 1983) is a community in which no mutant predator with a different food preference has a selective advantage over individuals of the wild type of the same species. They elucidated an upper limit of the numbers of predator species coexisting in a CSC. Their result shows that the number of predator species which simultaneously utilize two common patches does not exceed the sum of the numbers of prey species in the two patches.

The structure of food webs is an important problem in community ecology. Some authors discuss the relation between ecological stability and the number of species assuming that a food web is randomly connected (May 1972). Gardner and Ashby (1970) used "connectance" (C) as a measure of community complexity. C is defined as the ratio of the actual number of interspecific interactions to all possible combinations of interactions. They and other authors argue that the probability that a steady state is stable decreases as the connectance increases (see Pimm 1982).

However, the connecting pattern of a food web is not random but is directly determined by prey choices of predator species. A predator species may have developed an efficient way to use prey in a patchy environment in the course of Darwinian evolution. Some authors studied the relationship between ecological stability of a prey-predator system and the optimal (or evolutionarily stable) foraging property of one or a few predator species (Comins and Hassell 1979; Matsuda et al. 1986, 1987). In this paper, we examine necessary conditions for a pattern of prey choices and patch uses of some predator species to be coevolutionarily stable. We further discuss the relationship between the CSC structure and Joel Cohen's "non-interval community food webs" or George Sugihara's "hole" of the resource graph.

DOES THE NUMBER OF PREDATOR SPECIES EXCEED THAT OF THE PREY SPECIES?

We assume that many species of prey live in a patchy environment and that predators of some species can move widely and frequently between patches and feed in many patches. We express by I , K and M the numbers of prey species, predator species and patches, respectively. Each prey species lives in some patches. Although an individual predator can search for any prey in any patch, we assume random searching with respect to search for a particular prey in a patch.

We use the following notations:

x_i^μ : the density of the i^{th} prey species in the μ^{th} patch,

$$\mathbf{x}^\mu = (x_1^\mu, x_2^\mu, \dots, x_I^\mu).$$

y_k : the density of the k^{th} predator species, ($\mathbf{y} = (y_1, y_2, \dots, y_K)$).

I^μ : the set of prey species in the μ^{th} patch,

$$I^\mu = \{ i \mid x_i^\mu > 0 \}, \quad (\mu = 1, 2, \dots, M).$$

b_{ik}^μ : the encounter rate of an individual of the k^{th} predator species with individuals of the i^{th} prey species in the

$$\mu^{\text{th}} \text{ patch, } (i=1, 2, \dots, I, k=1, 2, \dots, K).$$

h_{ik} : the handling time of the k^{th} predator species to the i^{th} prey species.

u_{ik} : the net energy gain of the k^{th} predator species when it feeds on an individual of the i^{th} prey species (we assume that h_{ik} and u_{ik} are constants independent of μ).

f_k^μ : the fractional allocation of searching effort (patch use) of the k^{th} predator species to the μ^{th} patch,

$$(0 \leq f_k^\mu \leq 1, \sum_{\mu} f_k^\mu = 1).$$

g_{ik}^μ : the attacking probability (prey choice) when the k^{th} predator species encounters the i^{th} prey species in the

$$\mu^{\text{th}} \text{ patch } (0 \leq g_{ik}^\mu \leq 1).$$

E_k^μ : the per capita prey intake rate of the k^{th} predator species in the μ^{th} patch.

R_k : the per capita total prey intake rate of the k^{th} predator species.

r_i^μ : the growth rate of the i^{th} prey species in the μ^{th} patch.

a_{ij}^μ : the intra- or inter-specific competition coefficient measuring influence of the j^{th} prey species to the i^{th} prey species in the μ^{th} patch.

δ_k : the intrinsic death rate of the k^{th} predator species.

$\Delta_k(y, z)$: the mortality of the k^{th} predator species due to competition between predators and predation by the higher predators.

We assume that R_k is described as the sum of prey intake rates in M patches (E_k^μ) weighted by patch uses (f_k^μ). Namely,

$$R_k = \sum_{\mu=1}^M f_k^\mu E_k^\mu(x^\mu), \quad (1)$$

where

$$E_k^\mu(x^\mu) = \frac{\sum_{i \in I^\mu} g_{ik}^\mu b_{ik}^\mu u_{ik} x_i^\mu}{1 + \sum_{i \in I^\mu} g_{ik}^\mu b_{ik}^\mu h_{ik} x_i^\mu}, \quad (k=1,2,\dots,K, \mu=1,2,\dots,M). \quad (2)$$

Therefore, we can describe the prey-predator system as

$$\begin{aligned} \frac{dx_i^\mu}{dt} &= [r_i^\mu - \sum_{j \in I^\mu} a_{ij}^\mu x_j^\mu - \sum_{k=1}^K f_k^\mu F_{ik}^\mu(x^\mu) y_k] x_i^\mu, \quad (i \in I^\mu, \mu=1,2,\dots,M), \\ \frac{dy_k}{dt} &= [-\delta_k - \Delta_k(y, z) + \sum_{\mu=1}^M f_k^\mu E_k^\mu(x^\mu)] y_k, \quad (k=1,2,\dots,K), \end{aligned} \quad (3)$$

$$F_{ik}^\mu(x^\mu) = \frac{g_{ik}^\mu b_{ik}^\mu u_{ik}}{1 + \sum_{i \in I^\mu} g_{ik}^\mu b_{ik}^\mu h_{ik} x_i^\mu}, \quad (i \in I^\mu, k=1,2,\dots,K, \mu=1,2,\dots,M).$$

To elucidate the coevolutionary change in patch use f_k^μ and prey choice g_{ik}^μ of predators, suppose that a community, in which a wild type predator feeds on prey in a manner specified by coefficients $\{f_k^\mu\}$ and $\{g_{ik}^\mu\}$, is invaded by a sufficiently small number of mutant individuals of the k^{th} predator ($k=1,2,\dots,K$). We assume that the mutant may differ only in patch use f_k^μ and prey choice g_{ik}^μ from the wild type.

For a community described by system (3) to be a coevolutionarily stable community (CSC), it is necessary that any mutant of any species of predator has no larger per capita prey intake rate than the wild type of the same species. Since we have assumed that no loss of searching effort occurs ($\sum_\mu f_k^\mu = 1$), the predator should use only the patch in which the prey intake rate is the highest ($f_k^\nu = 0$ if $E_k^\mu > E_k^\nu$), because if f_k^μ and f_k^ν are positive when $E_k^\mu > E_k^\nu$, a mutant with patch use $(f_k^\mu, f_k^\nu) = (f_k^\mu + f_k^\nu, 0)$ has a selective advantage over the wild type $f_k^\mu E_k^\mu + f_k^\nu E_k^\nu < (f_k^\mu + f_k^\nu) E_k^\mu$. Thus, in a CSC, both f_k^μ and f_k^ν are positive only when $E_k^\mu = E_k^\nu$ (Matsuda and Namba 1989). It would also be related to the "ideal free distribution" of Fretwell and Lucas (1970) in which a population of a predator species distributes among patches so as to keep the instantaneous rates of gain equal at any time for all members of the population (Parker 1984).

Since $\sum_\mu f_k^\mu = 1$ and E_k^μ takes the same value for any patch satisfying $f_k^\mu > 0$,

$$R_k = \sum_\mu f_k^\mu E_k^\mu = E_k^\mu \sum_\mu f_k^\mu = E_k^\mu. \quad (4)$$

Thus, the per capita prey intake rate is the same in any patch so long as the predator uses the patch, and it coincides with the mean per capita prey intake rate of the predator species, R_k .

By the same reasoning as in the optimal diet theory introduced by MacArthur and Pianka (1966), the k^{th} species of predator should ignore the i^{th} species of prey ($g_{ik}^\mu = 0$) if u_{ik}/h_{ik} is smaller than the mean per capita prey intake rate of the k^{th} patch (E_k^μ). Conversely the former should always attack the latter ($g_{ik}^\mu = 1$) if $u_{ik}/h_{ik} > E_k^\mu$.

Joining the result that $E_k^\mu = R_k$ for every k satisfying $f_k^\mu > 0$ with the one that $g_{ik}^\mu = 1$ if and only if $u_{ik}/h_{ik} > E_k^\mu$, Matsuda and Namba (1989) concluded that $g_{ik}^\mu = 1$ if and only if $u_{ik}/h_{ik} > R_k$. Since it is assumed that u_{ik} and h_{ik} are independent of μ , then g_{ik}^μ also becomes independent of μ in a CSC. Namely, if members of a predator species do not attack members of a prey species upon an encounter in a patch, then the predator also ignores the prey in other patches. On the contrary, if a predator species feeds on a prey species in some patch, then the predator should in fact exploit the prey in any patch so long as it contains the prey and is utilized by the predator.

To investigate further properties of patch use and prey choice in a CSC, we assume that a CSC is at steady state. Although system (3) can exhibit a stable limit cycle in which the number of predator species exceeds the number of prey species (Waltman, Hubbell, and Hsu 1980), we may expect that it has a dynamically stable steady state if the handling time and the interspecific competition coefficients are sufficiently small, while the intraspecific competition coefficients are sufficiently large. If we ignore competition between predators and assume absence of higher predators ($\Delta_k = 0$), then $E_k^\mu = \delta_k$ at a steady state in a CSC if $f_k^\mu > 0$.

Since $E_k^\mu = \delta_k$ must be satisfied for every k satisfying $f_k^\mu > 0$, g_{ik}^μ can be uniquely determined;

$$g_{ik}^\mu = 1 \text{ if } u_{ik}/h_{ik} > \delta_k, \quad (5)$$

$$g_{ik}^\mu = 0 \text{ if } u_{ik}/h_{ik} < \delta_k.$$

$E_k^\mu = \delta_k$ is transformed into a system of linear equations with respect to prey densities in the μ^{th} patch x^μ ,

$$\sum b_{ik}^\mu u_{ik} x_i^\mu = \delta_k [1 + \sum b_{ik}^\mu h_{ik} x_i^\mu], \text{ (for all } k \text{ satisfying } f_k^\mu > 0) \quad (6)$$

where the sum is taken for all i satisfying $u_{ik}/h_{ik} > \delta_k$. The number of unknowns x_i^μ is equal to or smaller than the number of prey species in the μ^{th} patch. On the other hand, the number of equations is the number of predator species that utilize the μ^{th} patch. Thus, if these equations are independent, then a necessary condition for existence of positive equilibrium densities ($x_k^\mu > 0$) of prey species to exist is that the number of predators utilizing the μ^{th} patch ($f_k^\mu > 0$) does not exceed the number of prey species in the μ^{th} patch. Thus, as shown in Figure 1, the number of predator species which utilize a particular patch does not exceed the number of prey species in the patch (Matsuda and Namba 1989).

Therefore, the result of classical competition theory (MacArthur and Levins 1964; Levin 1970) holds in every patch, while there remains a possibility that the total number of predator species in the whole system exceeds that of prey species.

ARE THERE "NON-INTERVAL" FOOD WEBS IN A CSC?

In the previous section, we have assumed that $\Delta_k = 0$ and that the system rests at a steady state. If either of these assumptions is relaxed, the above results may require some alterations.

Even if $\Delta_k > 0$ and/or prey densities fluctuate permanently, the following relation must be satisfied in a CSC:

$$g_{ik}^\mu(t) = 1 \text{ if } u_{ik}/h_{ik} > R_k(t) \text{ and } g_{ik}^\mu(t) = 0 \text{ if } u_{ik}/h_{ik} < R_k(t),$$

$$E_k^\mu(t) = R_k(t) \text{ if } f_k^\mu(t) > 0. \quad (7)$$

Thus, g_{ik}^μ is independent of μ in general, while the number of predator species using a particular patch can exceed that of prey in the patch if R_k is not constant. However, if two patches μ and ν are simultaneously utilized by K predator species, then the densities of prey species in the two patches must satisfy K equations, $E_k^\mu = E_k^\nu$. Thus, the number of predator species which simultaneously utilize the two common patches does not exceed the sum of the numbers of prey species which are attacked by at least one predator species among K predator species in the two patches (Matsuda and

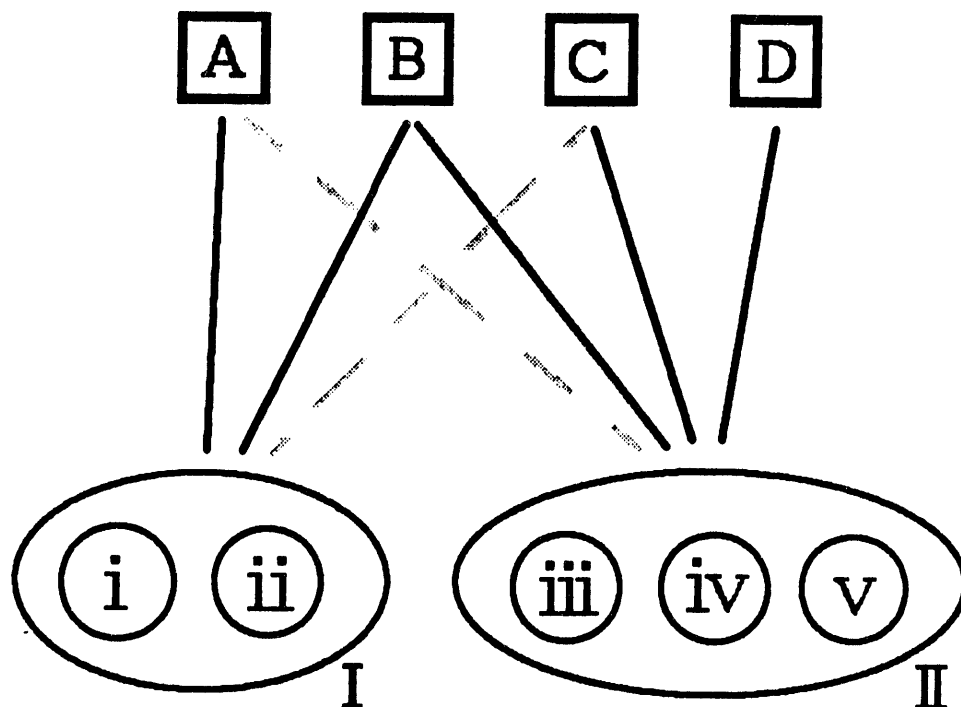


Figure 1. A sketch of CSC structure when $\Delta_k = 0$ and the community is at a steady state. Two and three prey species live in patches I and II, respectively, as well as four predator species. If the patterns of patch use denoted by solid lines are given, then the connection designated by dashed lines are forbidden in a CSC, since the number of predator species utilizing a patch cannot exceed the number of prey species in the patch.

Namba 1989; see Fig. 2 in this paper). Note that if a prey species lives in both patches, the species is doubly counted.

To acquire further information on patch use, we consider a simpler case in which each patch is occupied by only one prey species. We focus on two trophic levels in a food web and concentrate upon K particular predator species and J particular prey species. There may be another predator species which utilizes one of the J prey species, another prey species which is utilized by one of the K predator species, and some other species in the higher or lower trophic levels which interacts with one of the K predator species or one of the J prey species, respectively. If the k^{th} predator species utilizes S_k species of prey ($k=1,2,\dots,K$, $0 \leq S_k \leq J$), then the number of unknowns (x_i) is at most J and the number of equations ($E_k^i = R_k$) is equal to $\sum_k (S_k - 1)$. The total number of connections which indicate actual predatory interactions between predator and prey satisfies

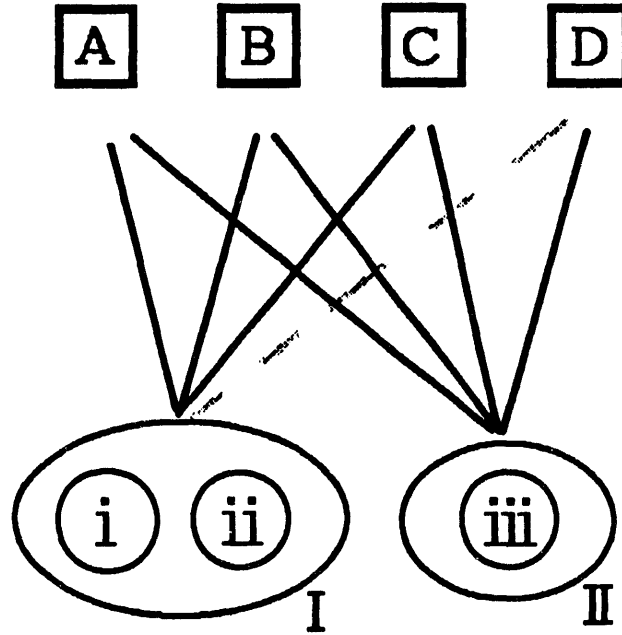


Figure 2. A sketch of CSC structure in the case of $\Delta_k > 0$ and/or in the non-equilibrium case. Two and one prey species live in patches I and II, respectively. If predators A, B, and C utilize both patches, then predator species D cannot use both patches.

$$\sum_{k=1}^K S_k \leq K + J, \quad (8)$$

since $\sum_k (S_k - 1) \leq J$. The maximum number of interactions between the J species of prey and the K species of predator is equal to JK . Thus, the connectance C is not more than $(J+K)/JK$ in a CSC. If the handling times are negligible, then $E_k^i = E_k^j$ becomes a linear equation. There always exists a trivial solution, $x^i(t) = x^j(t) = 0$. For the existence of non-trivial solutions, the CSC condition must be replaced by

$$\sum_{k=1}^K S_k < K + J, \quad (9)$$

(see Fig. 3). This means that the number of connections is smaller than the sum of the numbers of predator species and prey species. Note that the connectance C in a CSC decreases as the numbers of species J and K increase.

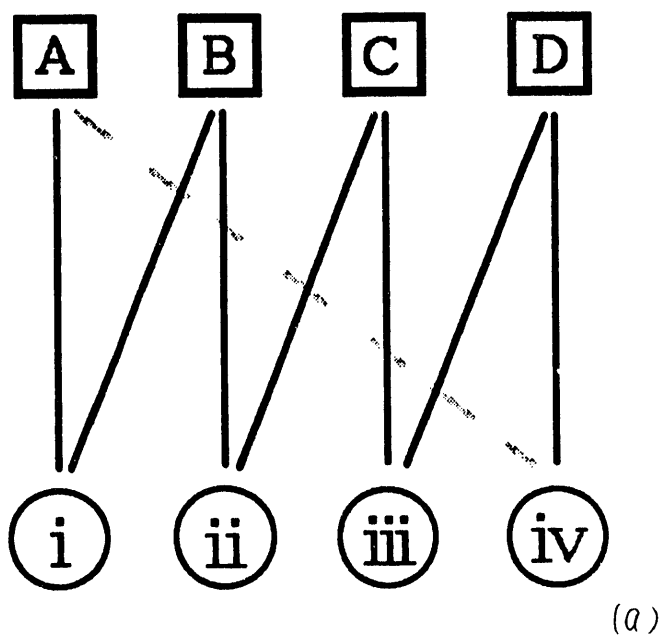
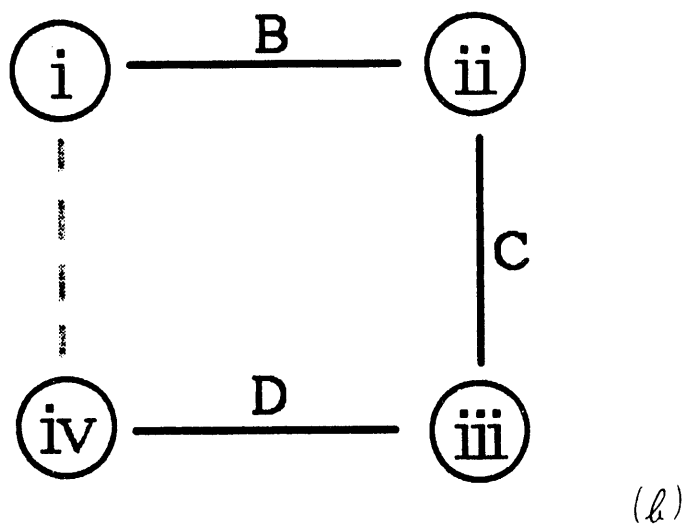


Figure 3. A sketch of part of a CSC and its resource graph, when only one prey species lives in each patch and handling times are negligible. Prey species i and ii are eaten by predator species A, ii and iii are eaten by B, and so on. (a) The number of connections among these eight species is 7. Adding another connection is forbidden in a CSC. (b) The resource graph representing the same structure as (a). A line segment (indicated by B) connecting i and ii means that these prey species are eaten by predator B. In a CSC, any set of segments in a resource graph does not make a "circle".

Cohen (1978) introduced the terms "interval" and "non-interval" (see also Cohen and Palka in press, for some examples of a non-interval graph). Resource utilization of a predator species can be specified by a line segment joining prey species belonging to the predator. For example, if predator *A* and *B* eat prey *i*, *B* and *C* eat *ii*, and *C* and *D* eat *iii*, then four line segments can be arranged along a line (see Fig. 4(a)). Such a food web is called an interval. In addition to these niche overlaps, if both *D* and *A* eat a prey species, *iv*, then this pattern cannot be expressed by segments on a line. However, the pattern can be expressed by overlapping lines in a plane as shown in Fig. 4(b). This is an example of non-interval food webs. Cohen (1978) demonstrated that a fraction of non-interval webs is larger in random webs than in natural webs (see also Cohen and Palka, in press). In a non-interval food web, the number of connections between prey and predators is often (but not always, see Cohen 1978, p. 107, his Fig. 24) greater than or equal to the sum of the numbers of prey and predator species in the web. Thus, we can argue that a non-interval food web is rarely found in a CSC.

Sugihara (1984) used some ideas from graph theory in the study of food web structures. His resource graph, $G(R)$, consists of vertices representing prey species and undirected edges which indicate that the two prey species are eaten by a single predator. In the resource graph, $G(R)$, Sugihara introduced some concepts; a "2-simplex" consisting of three or more vertices is a graph in which all of the prey are utilized by at least one common predator species, and a "one-dimensional hole" is a hollow polygon in which every pair of neighboring prey species (vertices) is utilized by at least one predator, but no predator eat all prey species (see Fig. 5; hereafter we will simply call the 2-simplex and one dimensional hole by "simplex" and "hole", respectively). Sugihara (1984) showed that, of the sixty communities that could possibly have holes, only two in fact did. Thus, he argued that holes are extremely rare in real food webs.

We predict some properties of a CSC in this paper and the previous paper (Matsuda and Namba 1989). Our results are similar (but not exactly the same, as shown by Cohen, personal communication) to Joel Cohen's assertion with respect to non-intervality of the niche overlap graph and also similar to George Sugihara's argument. However, our predictions are derived from coevolutionary stability of a prey-predator system, while the latter two authors based theirs on static analysis of food webs.

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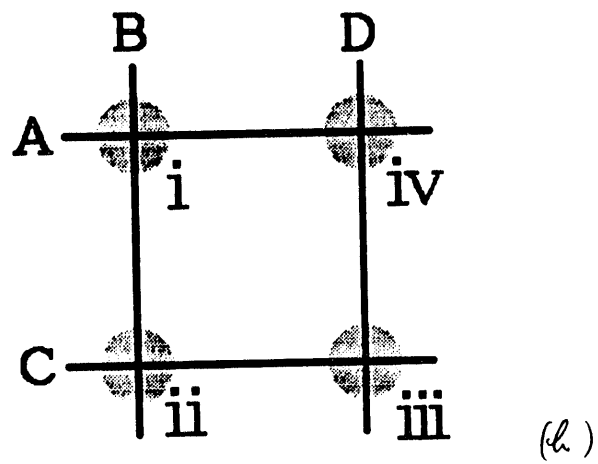
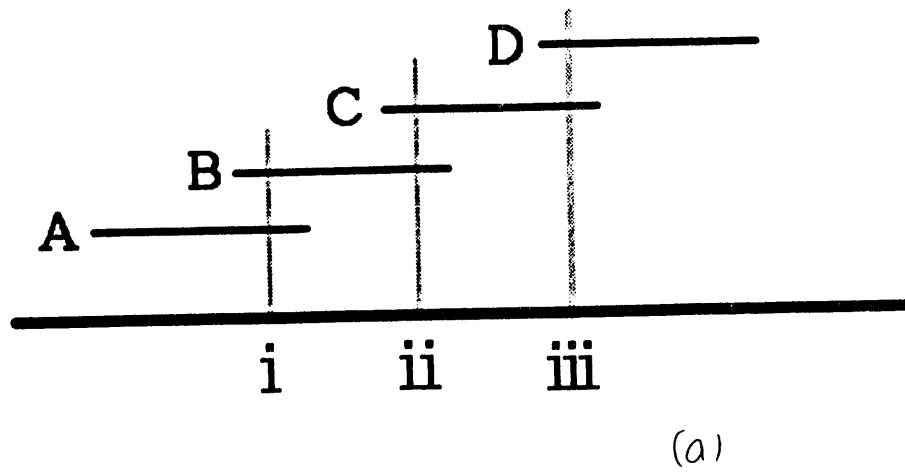


Figure 4. Cohen's (a) interval and (b) non-interval niche overlap graphs. See text.

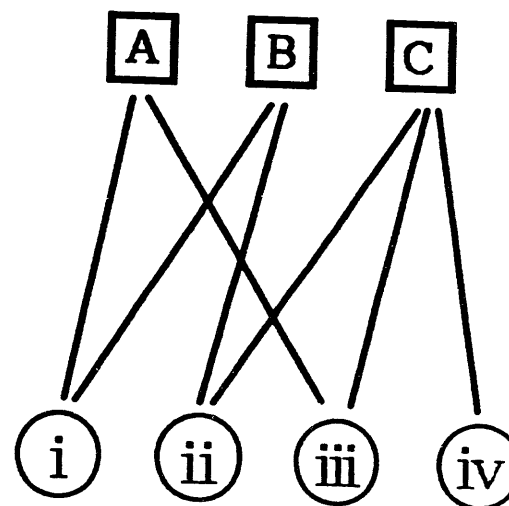
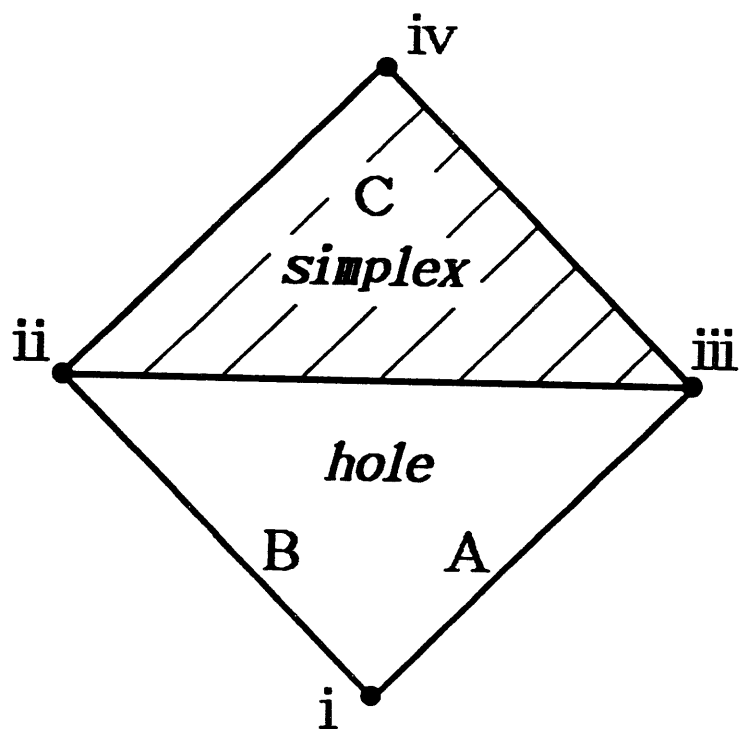


Figure 5. (a) A simplex and one-dimensional hole in a resource graph, and (b) a sketch of a corresponding food web. Predator species *A* eats prey species *i* and *iii*, *B* eats *i* and *ii*, *C* eats *ii*, *iii*, and *iv*, respectively. Since prey *ii*, *iii* and *iv* are eaten by predator *C*, these vertices make a simplex. Prey *i*, *ii* and *iii* make a hole. A community characterized by this graph is not coevolutionarily stable.

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A NOTE ON THE SPECIES ABUNDANCE RELATION: THE GEOMETRIC SERIES DISTRIBUTION

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ABSTRACT

The geometric series distribution has been proposed by several authors as one of the mathematically representative distribution functions of the species abundance relation (May 1975, Pielou 1969). As a supplementary note, we present here several kinds of models of interacting multi-species systems which similarly lead to the geometric series distribution.

INDEPENDENTLY GROWING COLONIES FORMED BY IMMIGRATION

We consider a number of growing colonies on an island which are successively established by a pioneer immigrant from the main land. We assume that the immigration of a new founder occurs in time interval Δt with probability $\lambda \Delta t$ and each colony independently grows with the same Malthusian growth rate e . If the primal colony is established at time $t=0$, the probability that k colonies are found on the island at time t is given by

$$P(k,t) = e^{-\lambda t} (\lambda t)^{k-1} / (k-1)! \quad (1)$$

Then the k^{th} colony which is established in the time interval $(t, t+\Delta t)$ with probability $p(k-1,t) \lambda \Delta t$ has population size $e^{e(T-t)}$ at time T ($>t$), while the size of the primal colony is $n_1 = e^{eT}$. Therefore the expected relative value of population size of the k^{th} colony at time T can be calculated as

$$\begin{aligned} \langle n_k / n_1 \rangle &= \int_0^T e^{-e t} p(k-1,t) \lambda dt \\ &= \lambda^{k-1} / (k-2)! \int_0^T e^{-(e+\lambda)t} t^{k-2} dt = \{\lambda / (e+\lambda)\}^{k-1}, \end{aligned} \quad (2)$$

where a sufficiently long time T is assumed.

Thus, in this case, it has been shown that the population sizes of colonies are given by a geometric series distribution. On the other hand, if the colonies are formed by the pioneers from members of preexisting colonies on the island, the population sizes are given by a hypergeometric series distribution, as already shown by Yule (1924) in his discussion on the speciation process in general.

THE LOGISTIC GROWTH OF COLONIES

Here, in the same model, let us consider the case that the growth rate of colonies diminishes as the total population on the island increases. The equations of the population growth of colonies are given by

$$dn_k/dt = (e - \nu \sum_{j=1}^i n_j) n_k = (1 - N/K) n_k, \quad k=1,2,\dots,i, \quad (3)$$

where i and N_i are the number of established colonies and the total population on the island at time t , respectively. $K = e/\nu$ is the carrying capacity for the total population. Summing Eqs. (3) gives

$$dN/dt = (1 - N/K) N_i \quad (4)$$

and the solution

$$N_i(t) = KN_i(t_0)[N_i(t_0) + \{K - N_i(t_0)\}e^{-e(t-t_0)}]^{-1}. \quad (5)$$

Notice that this solution can be used until an additional new colony is formed. Comparing (3) and (4), we have the relation

$$\ln\{n_k(t)/n_k(t_0)\} = \ln\{N_i(t)/N_i(t_0)\}. \quad (6)$$

Thus the solution of Eq. (3) can be obtained as

$$\begin{aligned} n_k(t) &= \{n_i(t)/N_i(t_0)\} n_k(t_0) \\ &= Kn_k(t_0)[N_i(t_0) + \{K - N_i(t_0)\}e^{-e(t-t_0)}]^{-1}. \end{aligned} \quad (7)$$

Now, we shall consider again the formation of colonies at times $t_0 = 0, t_1, t_2, \dots, t_i, \dots$ successively. If the i^{th} colony is formed at time t_{i-1} , then clearly there exist i colonies in the time interval $t_{i-1} \leq t < t_i$. By Eq. (7), the population size of the k^{th} colony $n_k(t_i)$ for $k=1,2,\dots,i$ at time t_i is given by

$$n_k(t_i) = Kn_k(t_{i-1})[N_i(t_{i-1}) + \{K - N_i(t_{i-1})\}e^{-e(t_i-t_{i-1})}]^{-1}, \quad (8)$$

and the total population of i colonies $N_i(t_i)$ at time t_i is

$$N_i(t_i) = KN_i(t_{i-1})[N_i(t_{i-1}) + \{K - N_i(t_{i-1})\}e^{-e(t_i-t_{i-1})}]^{-1}. \quad (9)$$

In the next time interval (t_i, t_{i+1}) , we must take into account the supposition that the $(i+1)^{\text{th}}$ colony with population size $n_{i+1}(t_i) = 1$ is newly added at the instant t_i , so that the initial value of the total population in this time interval is

$$N_{i+1}(t_i) = N_i(t_i) + 1. \quad (10)$$

Thus, using the following notations

$$N_i(t_{i-1}) = N_i^*, \quad \beta_i = e^{-a(t_i - t_{i-1})}$$

we can obtain the coupled recurrence formulae

$$N_i^* = 1 + KN_{i-1}^*[N_{i-1}^* + (K - N_{i-1}^*)\beta_{i-1}]^{-1}, \quad i=1,2,\dots \quad (11)$$

$$n_k(t_i) = Kn_k(t_{i-1})[N_i^* + (K - N_i^*)\beta_i]^{-1}, \quad k=1,2,\dots,i, \quad (12)$$

where $N_0^* = 0$ and $n_k(t_{k-1}) = 1$.

The formation of new colonies can successively occur until the total population reaches the carrying capacity K . Therefore, the upper limit of the possible number of colonies $i_{\max} = S$ is decided by the condition $N_S^* < K < N_{S+1}^*$ and the last colony is formed at time t_{S-1} . Then, using the recurrence formulae (11), (12) and (7) with $t_0 = t_{S-1}$, we can obtain the population sizes of colonies at time $t > t_{S-1}$ as

$$n_k(t) = K[N_S^* + (K - N_S^*)\beta]^{-1} \prod_{j=k}^{S-1} K[N_j^* + (K - N_j^*)\beta_j]^{-1},$$

$$k = 1, 2, \dots, S, \quad (13)$$

where $\beta = e^{-a(t - t_{S-1})}$. Thus, taking the limit $t \rightarrow \infty$, we finally obtain

$$n_k(\infty) = (K/N_S^*) \prod_{j=k}^{S-1} K[N_j^* + (K - N_j^*)\beta_j]^{-1}, \quad k=1,2,\dots,S \quad (14)$$

where N_j^* can be evaluated by the recurrence formula (11).

Now, as we assumed previously, if the colonies are formed by a Poisson process, the average time t_j of the formation of the $(j+1)^{\text{th}}$ colony becomes $t_j = j/\lambda$ and, using these average values we have $\beta_j = e^{-a/\lambda}$. Figure 1 shows the growth of the total population calculated by Eqs. (11), where the parameter values are $e^a = 1.2$ and $1/\lambda = 5$. In this case there are 19 colonies ($S = 19$) at the final stage. In Fig. 2, the logarithm of population sizes $n_k(\infty)$ is plotted as a function of rank k (rank size relation), which shows a linear relation that is a geometric series distribution in the wide range of k values, excepting cases in which population sizes are small.

A STRONG COMPETITION MODEL

In 1932, Motomura showed that the data of population sizes of bottom fauna obtained by Miyadi (1931) can be fairly represented by a geometric series distribution, and a possible explanation was given by Uchida (1943) and Motomura (1947), using a simple competition model.

They considered that each of S species (1,2,...,S) ranked in descending order of competitive dominance has n individuals and these nS individuals are randomly distributed over the area A . It is assumed that each individual occupies its own habitat area $a < A$, but in each of these habitats only one individual of the most dominant species can survive.

The probability that this unit habitat area contains no individual of species 1 is

$$(1 - a/A)^n = r^n, \quad (15)$$

where $r = 1 - a/A$ and the probability that at least one individual of species 1 occupies this area is $1 - r^n$. On the other hand, the number of available habitat areas is A/a ; therefore, the average number of survivors of species 1 is given by

$$\begin{aligned} \langle n_1 \rangle &= (1 - r^n) A/a = (1 - r^n)/(1 - r) \\ &= 1 + r + r^2 + \dots + r^{n-1} < n. \end{aligned} \quad (16)$$

The probability that no individual of species 1 but at least one individual of species 2 is found in this area is $r^n(1 - r^n)$; thus, the average number of survivors of species 2 is given by

$$\langle n_2 \rangle = r^n(1 - r^n) A/a = r^n(1 - r^n)/(1 - r). \quad (17)$$

Similarly, the probability that no individual of species 1,2,..., $k-1$ but at least one individual of species k is found in this area is $r^{(k-1)n}(1 - r^n)$, and the average number of survivors of species k is given by

$$\langle n_k \rangle = r^{(k-1)n}(1 - r^n)/(1 - r). \quad (18)$$

This Motomura-Uchida model may be the simplest intuitive model which exhibits the geometric series distribution.

Now we show a stochastic version of the above model. Let us again consider a unit habitat area which can be occupied by only one individual. From the species pool consisting of S species, an individual invades this area with probability $\lambda \Delta t$ in the time interval Δt and the success of invasion occurs only when the former habitant is one of the lower-ranked species.

The probability that this area is occupied by an individual of species k at time t , $P_k(t)$, satisfies the equation

$$dP_k(t)/dt = \lambda \{1 - \sum_{j=1}^k P_j(t)\} - \lambda(k-1)P_k(t), \quad k=1,2,\dots,S, \quad (19)$$

where the first term represents the probability that the former inhabitant of lower rank is replaced by the invasion of an individual of species k , and the second term is the probability that the individual of species k which already occupied this habitat is replaced by an invader of higher rank.

If we introduce the generating function

$$F(z, \tau) = \sum_{k=1}^S P_k(\tau) z^k, \quad (20)$$

where $\tau = \lambda t$, we have

$$\frac{\partial F}{\partial \tau} + z \frac{\partial F}{\partial z} = \frac{z}{1-z} (1-F). \quad (21)$$

The solution with initial condition $P_i(0) = \delta_{i,i_0}$, $F(z,0) = z^{i_0}$ can be obtained as

$$\begin{aligned} F(z, \tau) &= 1 - (1-z)(1-z^{i_0}e^{-i_0\tau})/(1-ze^{-\tau}) \\ &= 1 - (1-z)[1+ze^{-\tau}+z^2e^{-2\tau}+\dots+z^{i_0-1}e^{-(i_0-1)\tau}]. \end{aligned} \quad (22)$$

The probability $P_k(t)$ is given by the coefficient of z^k , and we have

$$\begin{aligned} P_k(t) &= (1-e^{-\lambda t})e^{-\lambda(k-1)t}, \quad k = 1, 2, \dots, i_0-1, \\ &= e^{-\lambda(i_0-1)t}, \quad k = i_0, \\ &= 0, \quad k > i_0. \end{aligned} \quad (23)$$

Therefore, if there are M available unit habitat areas, the expected population size of species k at time t , $\langle n_k(t) \rangle = M P_k(t)$ is given by a geometric series distribution, though due to the assumptions all habitats are occupied by the most dominant species 1 at the final stage.

A LOTKA-VOLTERRA MODEL OF ONE-SIDED COMPETITION

In this section, in order to re-examine the above competition model from the standpoint of population dynamics, we shall consider a Lotka-Volterra competition model of S species ranked again in descending order of competitive dominance. Here we assume that each species suffers competitive interference only from species of higher rank. Then the dynamical change of a population of the k^{th} species is given by

$$dn_k/dt = (r_k - \sum_{j=1}^k a_{kj} n_j) n_k, \quad k = 1, 2, \dots, S. \quad (24)$$

Here, for mathematical simplicity, we assume that the coefficients a_{kj} can be written as

$$\begin{aligned} a_{kj} &= \sigma_k \alpha_k \quad \text{for } j = k, \\ &= \sigma_k \beta_k \quad \text{for } j \neq k, \end{aligned} \quad (25)$$

where α_j and β_j are intrinsic factors of intra- and interspecific interference respectively, and these effects on the k^{th} species are reduced by a factor σ_k (< 1) owing to the defensive ability of the k^{th} species. Then Eq. (24) can be rewritten as

$$dx_k/dt = \sigma_k (e_k - x_k - \sum_{j=1}^{k-1} v_k x_j) x_k, \quad k = 1, 2, \dots, S, \quad (26)$$

where $x_k = \alpha_k n_k$, $e_k = r_k / \sigma_k$ and $v_k = \beta_k / \alpha_k$.

Here let us consider the positive stationary state which can be obtained as a solution (x_k 's > 0) of the equations

$$e_k - x_k^* - \sum_{j=1}^{k-1} v_k x_j^* = 0, \quad k = 1, 2, \dots, S, \quad (27)$$

from which we can readily have the relation

$$x_k^* = (e_k - e_{k-1}) + (1 - v_{k-1}) x_{k-1}^*, \quad k = 1, 2, \dots, S, \quad (28)$$

where $e_0 = 0$. Thus we can obtain the solution of Eqs. (27) in a form

$$x_k^* = (e_k - e_{k-1}) + \sum_{j=1}^{k-1} \Lambda_{kj} (e_j - e_{j-1}), \quad k = 1, 2, \dots, S, \quad (29)$$

where

$$\Lambda_{kj} = \prod_{i=j}^{k-1} (1 - v_i). \quad (30)$$

Therefore, if we consider a special case such that

$$v_i = \beta_i / \alpha_i < 1 \quad \text{and} \quad e_i \geq e_{i-1} \quad \text{for all } i,$$

the Eqs. (29) give a positive stationary solution and its global stability can also be shown; the Lyapunov function is given by

$$H(x_1, x_2, \dots, x_S) = \sum_{k=1}^S (v_k/\epsilon_k) [x_k - x_k^* - x_k^* \log(x_k/x_k^*)].$$

Furthermore, if $\epsilon_i = \epsilon$ for all i , we have

$$x_1 = \epsilon \quad \text{and} \quad x_k = \prod_{j=1}^{k-1} (1-v_j) \quad k = 1, 2, \dots, S. \quad (31)$$

Hence, the population size distribution is given by a geometric series distribution, where $\alpha_i = \alpha$ and $v_i = v$ for all i :

$$n_k = (\epsilon/\alpha)(1-v)^{k-1}. \quad (32)$$

SUMMARY

As a supplementary discussion on the species abundance relation, we present several kinds of models which similarly lead to the geometric series distribution. It has been shown that, in the case of size distribution of growing colonies, the geometric series distribution is derived from a compound process of the Poisson process of immigration of new pioneers, and the Malthusian growth of established colonies. It is also shown that a similar rank-size relation can be obtained even when taking into account logistic growth of the total population.

On the other hand, populations of a multi-species system with a strictly ordered rank of competitive dominance seem to show the characteristic pattern of the geometric series distribution, as shown by the original model given by Motomura and Uchida, and by its stochastic version given in Sect. 3. This supposition has also been supported by considering the solution of Lotka-Volterra's equation of a one-sided competition model.

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Food Web Theory

At the level of the food web a broad array of research directions exists. In recent years, the ecological theory of food webs has to some extent broken away from the classical equilibrium theory approach and is more oriented towards studying the dynamical implications of detailed mechanisms at lower levels (e.g., interactions between populations or subpopulations) without making prior assumptions about stability at the system level. This is reflected in the emphasis on spatial scale, temporal variability and disturbances in some of the talks. The search for general unifying principles is still a driving force behind much of the work in food web theory, however.

THE TEMPORAL VARIABILITY OF SPECIES DENSITIES

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INTRODUCTION

Ecologists use the term 'stability' to mean a number of different things (Pimm 1984a). One use is to equate stability with low variability in population density over time (henceforth, temporal variability). Temporal variability varies greatly from species to species, so what affects it? There are at least three sets of factors: the variability of extrinsic abiotic factors, food web structure, and the intrinsic features of the species themselves.

We can measure temporal variability using at least three statistics: the coefficient of variation of density (CV); the standard deviation of the logarithms of density (SDL); and the variance in the differences between logarithms of density for pairs of consecutive years (called annual variability, hence AV, by Wolda 1978). There are advantages and disadvantages to each measure (Williamson 1984), though in our experience, the measures are strongly correlated across sets of taxonomically related species. The increasing availability of long-term data sets allows one to calculate these statistics for many species and so to begin to understand the various causes of species differences in temporal variability.

THE VARIABILITY OF THE ENVIRONMENT

Temporal variability will depend on the variability of the abiotic factors that directly determine a species' survivorship and reproduction. We might expect a population's temporal variability to be higher where key abiotic variables are themselves more variable. British bird populations, for example, have densities determined, in part, by the severity of cold winters (Pimm 1984b). So we might expect communities experiencing more variable abiotic conditions to have species whose densities are similarly more variable. Malicky (1976), for example, found that the numbers of emerging caddisflies were more variable from year to year in a stream that varied in temperature from 0 to 19°C, than in a nearby similar one that varied from only 6.0 to 6.3°C. Similarly, McGowan and Walker (1985) noted the high similarity of species composition of plankton samples taken years apart from the Central Pacific Gyre. The Gyre is a gently-circulating, well-mixed body of water. These high similarities contrast with the low similarity of plankton samples taken only hours apart from turbulent areas in the California current. Salinities were much more variable in the Current than in the Gyre.

Not all such comparisons succeed. Wolda (1983) tested Elton's (1958) assertion that tropical species have populations that fluctuate less (are "more stable") than those of temperate species. Using

data on a variety of insect taxa, Wolda concluded that "tropical insects are about as stable, ...as temperate insects, even insects from a relatively undisturbed tropical forest".

Pimm (1984b) suspected that resident species of British birds, which experience occasional hard winters, should be more variable than migrant species. For whatever reasons, migrant species are marginally more variable than resident species.

FOOD WEB EFFECTS

While changes in physical variables may affect a species' density directly, they must also affect density indirectly by changing the density of the species' food supply, competitors, predators and parasites, and mutualists. We should expect the patterns of interactions within a community, i.e. the food web, to affect population variability. Comparisons have involved different systems of putatively different food web complexities: tropical systems versus simple temperate systems and natural systems versus simple agricultural systems. These systems differ in ways other than just complexity, however, and so differences in population variability may be due to other causes. As already noted, there do not appear to be obvious differences in variability between tropical and temperate populations. Insect species in agricultural systems, however, do appear to be more variable than those in forest communities (Wolda 1983, Rejmanek and Spitzer 1982).

An alternative way to explore the role of food web structure on temporal variability is to consider the arguments that relate temporal variability to the diet breadth of a species. MacArthur (1955) argued that species exploiting many food species should be less temporally variable than more specialized species. If one food species failed, then a polyphagous species could switch to alternative supplies, while a more specialized species could not. In fact, host switching is not necessary for this argument. Some polyphagous insect species may be composed of separate sub-populations that each specialize on different local hosts (Fox and Morrow 1981). The failure of one of these hosts may severely affect the sub-population, but the total population may be little affected.

Interestingly, Watt (1964) suggested a diametrically opposite affect to MacArthur's. Consider species that are usually rare -- held there by inclement conditions or effective predators. During rare favorable conditions, polyphagous species have the potential to exploit a larger proportion of the environment and to spend less time searching for suitable resources than specialized species. Thus, polyphagous species may increase more rapidly, attain higher densities, and so be more temporally variable. Specialized species living in monocultures of their prey will also be able to increase quickly and be highly variable. (Perhaps this explains why insect herbivores in agricultural communities are so variable.)

These two opposing arguments are summarized in Fig. 1. MacArthur's idea relates to the effects of deviations below the norm (crashes), while Watt's idea relates to deviations above it (outbreaks). There may be data to support both MacArthur's and Watt's arguments. For aphids and moths in Britain, we (Redfearn and Pimm 1988) have found either no correlation or negative correlations between temporal variability and the degree of polyphagy (Fig. 2a). Rejmanek and Spitzer (1982) found a positive correlation between temporal variability and the degree of polyphagy in Noctuid moths in South Bohemia (Fig. 2b).

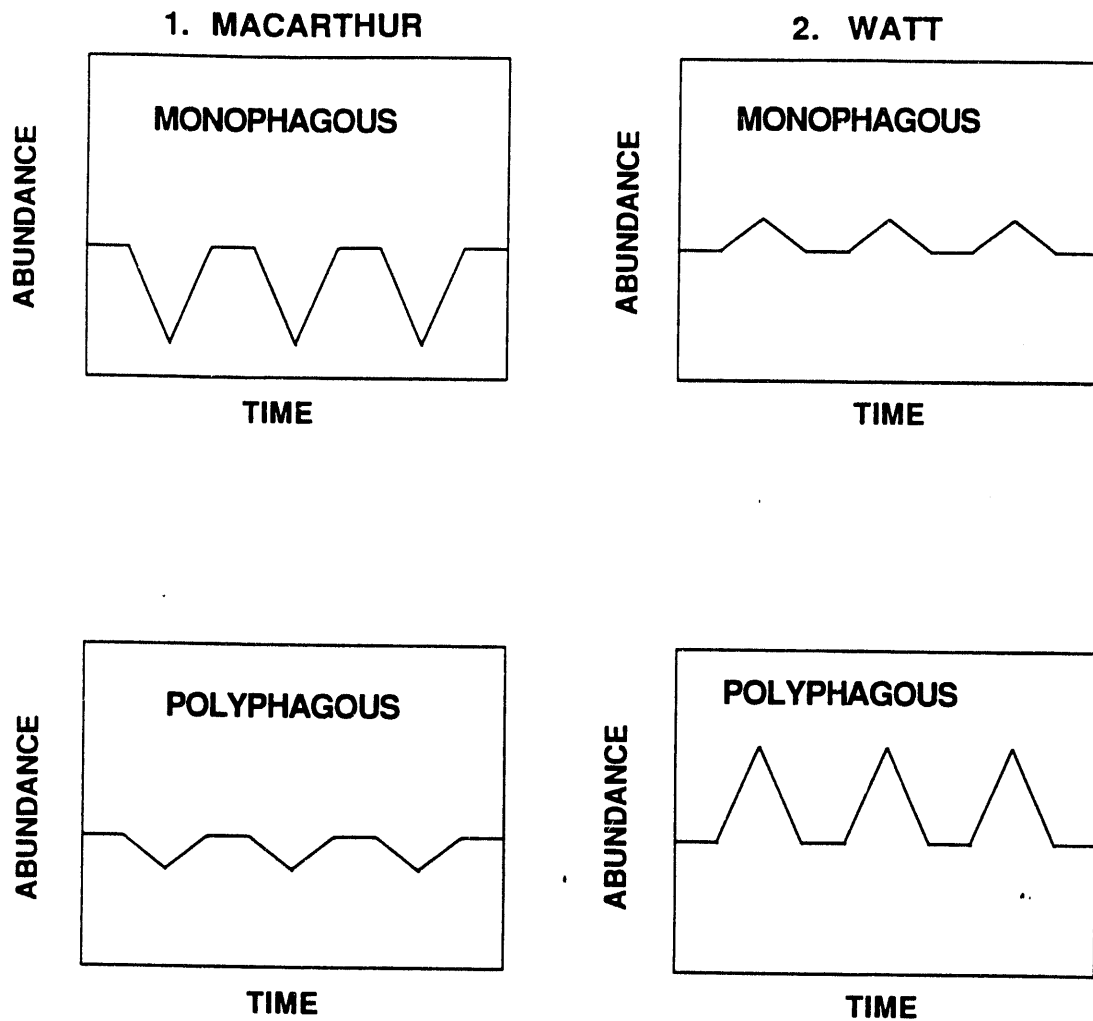


Figure 1. Caricature of the two opposing arguments of MacArthur (1955) and Watt (1964). MacArthur suggested that specialist species may be more variable because they are likely to be more susceptible to population crashes. Watt said that polyphagous species may be more variable because they may be able to attain higher numbers during favorable periods. (After Redfearn and Pimm 1988.)

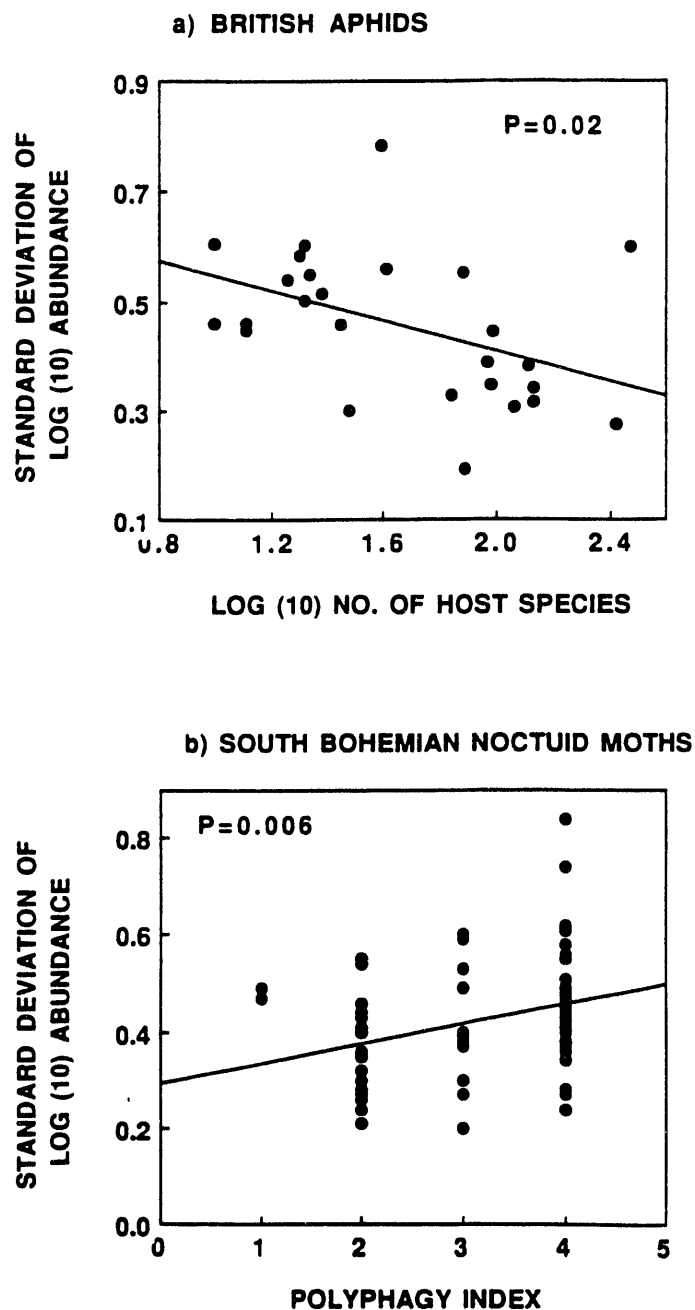


Figure 2. Variability versus polyphagy for (a) 26 species of British aphids analyzed by Redfearn and Pimm (1988) and collected by the Rothamsted Insect Survey at Silwood Park, England (see Redfearn and Pimm, 1988 for references to the raw data) and (b) 72 species of South Bohemian Noctuid moths analyzed and collected by Rejmanek and Spitzer (1982). Variability is measured as the standard deviation of the $\log_{10}(N_t)$, where N_t is the annual density in year t , calculated over (a) 13 to 16 years and (b) 12 years. Polyphagy is estimated a) by the logarithm of the number of recorded host plants and (b) as the following categories: 1-on one plant genus, 2-on one family, 3-on two to three families, and 4-on more than three families of plants (Rejmanek and Spitzer 1982).

Parallel arguments may be applied to the diversity of predators a species suffers: more diverse communities might be predicted to provide more reliable control of a set of prey species, which would then have less variable densities. Hansson and his colleagues (Hansson 1987, (and see review in Hanski 1987) have shown that voles (*Clithrionomys* and *Microtus* species) are more variable in the north of Scandinavia than in the south. High variability is associated with multi-annual cycles, which, moreover, are synchronous across species, including insectivorous shrews and birds. These latitudinal differences, Hansson argues, stem from there being only one important (and specialized) vole predator in the north (the least weasel, *Mustela nivalis*). In the south, there are a variety of generalized predators (e.g. the fox, *Vulpes vulpes*). These predators, though important to the voles gain most of their food from other herbivores (e.g. rabbits, *Oryctolagus cuniculus*). Thus, it is the greater diversity of predators in the south that ultimately result in the voles being less variable there.

INTRINSIC SPECIES DIFFERENCES

Species differ in many ways that could affect the responses of their densities to abiotic variables and the densities of the species with which they interact. One approach to investigating these species differences is to examine the relationship between body size and temporal variability. We have assembled 202 previously published population studies of terrestrial animals that were conducted at least annually and for at least 15 years. The data comprise 116 bird studies, 43 mammal studies, and 43 insect studies. The majority of the bird data were collected by the British Trust for Ornithology's (B.T.O) Common Bird Census and are published annually in Bird Study. The data were supplied to us by the Trust's director, R. J. O'Connor. Many of the insects are British moths and aphids collected by the Rothamsted Insect Survey. References to the annual reports presenting these data are given in Redfearn and Pimm (1988). Most of the remaining studies were used or referred to by two other comparative studies of population dynamics (Tanner 1966, Peterson et al. 1984). Finally, 19 miscellaneous studies were assembled by Stuart L. Pimm's graduate ecology class of 1986. Both references and data for all but the B.T.O. studies are available on request on IBM-compatible 5.25" discs.

We have calculated three indices of variability (CV, SDL, AV) for each population over just 15 years. Temporal variability increases continuously as more years of data are included in the estimate of temporal variability. Whatever the measure of temporal variability, small-bodied species were significantly more variable than large-bodied species ($P < 0.0001$, in all cases; Fig. 3). This correlation was probably anticipated by most of our readers, but it is not inevitable, nor is its explanation obvious. The correlation may be due to body size directly or through correlations of body size with reproductive rate, longevity, or other factors.

BODY SIZE

Small-bodied species may be more vulnerable to inclement weather and so be more temporally variable than large-bodied species (Lindstedt and Boyce 1985). Data on the percentage decline of British bird species, of various body sizes, during hard winters support this idea (Cawthorne and Marchant 1980).

RATE OF POPULATION INCREASE

The rate of population increase, r , has a strong correlation with body size (Southwood 1981): large-bodied species have low rates of increase. Rate of increase may affect temporal variability in diametrically opposite ways (Pimm 1984b).

(i) Populations with high r will recover from population crashes more rapidly than those with low r . Thus, following the same initial decline, high r populations will spend less time at low densities and may, therefore, be less variable than low r species. This relationship holds for British bird populations (Pimm 1984b), in which temporal variability depends on the decrease in abundance following hard winters and the rate at which normal abundances are recovered.

(ii) Populations with high r may be more temporally variable than those with low r , for one of two reasons. (1) If there are time delays in mortality and natality, populations with sufficiently high r may first overshoot, then undershoot equilibrium, leading perhaps to simple two-point cycles, or to much more complicated dynamics as r increases (May et al. 1978). In our collection of population studies, obviously cycling species were not always small-bodied (hence high r). But, cycling species tended to be more temporally variable than non-cycling species of the same body size (Fig. 3). This suggests that if high r causes cycling and this contributes to high temporal variability, the effects are independent of, and additional to, the main effect of body size in determining temporal variability. Small-bodied species are highly variable even when no cycles are apparent. We have an important caveat: many of the populations may show simple cycles, but these may not be apparent in only 15 years of data. (Many of the species for which we did detect simple cycles were counted for much longer than 15 years.) Nor can we exclude the possibility that populations show complex, yet deterministic changes of density; the analyses of Schaffer and Kot (1986) show that such populations may be much more common than once thought. (2) The second reason for a positive correlation between reproductive rate and temporal variability, involves our supposing that the equilibrium density of a population is itself variable. Species with high r will track this variable equilibrium, while populations with low r will respond more slowly, and not tend to track the equilibrium. This possibility may hold for Noctuid moths, in which high r species are the more variable (Spitzer et al. 1984). (This is the opposite result from that which we have discussed for British birds.)

Whether one finds a positive or a negative correlation between r and temporal variability may reflect the time-interval between counts and the time over which the population is counted relative to the life-span of the organism, as much as species-to-species differences. Thus, we would expect all populations to track very long-term environmental changes, and to have corresponding changes in density. Over short periods, high r populations may track better than low r populations, and so low r populations will vary less. And over intervals dominated by rare, but severe population crashes, high r species will vary less.

LONGEVITY

Large-bodied species also tend to be long-lived (Bonner 1965), so large-bodied species might be expected to vary less in density, because, in the extreme, it may be the same individuals that are counted in each of the years of the study. In contrast, small-bodied species may have gone through

several generations in each of the years. A hypothetical population of adult redwood trees might show no density variation at all over, say, 15 years!

In order to evaluate this effect, we would need to calculate temporal variability from generation to generation rather than from year to year. There is a simpler alternative though. Animals that weigh less than 0.1kg (small birds, small mammals, and insects) are likely to complete their lives within a year, or to have generation times on the order of a year (Bonner 1965). The negative relationship between temporal variability and body size not only holds for this subset of the data (Fig. 3), but the associated regressions have even more negative slopes than for the combined data. For this subset, the different years of data must generally involve different individuals, and so large-bodied species averaging out fluctuations cannot be the reason for why there is a negative correlation.

OTHER FACTORS

Small-bodied species may be more variable because they are more specialized than large-bodied species. This seems the least likely explanation for the overall negative correlation. First, as we have already mentioned, polyphagy does not necessarily decrease variability, and when it does, the correlation is rarely a strong one. Second, although within taxa, large-bodied species tend to be more polyphagous (Wasserman and Mitter 1978), it seems unreasonable to suggest that mammals are less variable than insects because they are sufficiently more polyphagous than insects.

There must be many other correlates of body size that also affect temporal variability. However, the species that contribute to the relationship in Fig. 3 are diverse both trophically and taxonomically. The very smallest species (aphids) are herbivorous as are the very largest species (mammals). So the negative relationship is not due to trophic differences.

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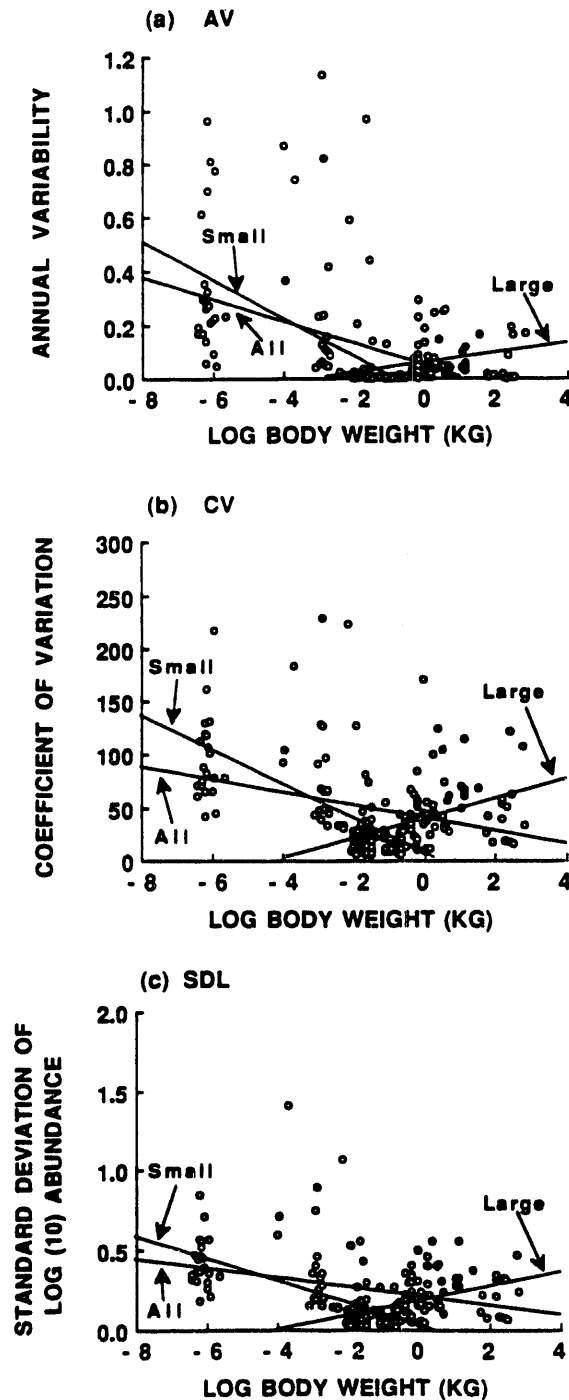


Figure 3. Three measures of population variability versus body weight. All estimates are calculated for 15 years of estimates of annual density, N_t . AV is the variance of $(\log_{10}(N_t) - \log_{10}(N_{t+1}))$, CV is the coefficient of variation of the N_t , and SDL is the standard deviation of the $\log_{10}(N_t)$. Solid circles are species that show pronounced cycles of abundance. For each measure of variability, separate regression lines are given for small species (weighing less than 0.1 kg), and all species combined. Small species might be expected to have life spans of about a year or less.

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PERFECT AND APPROXIMATE AGGREGATIONS IN MODEL ECOSYSTEMS

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SUMMARY

Simple ecosystem models sometimes work much better than complex and realistic ones both in understanding and in predicting an ecosystem's behavior. Here I report a recent advancement in the theoretical study of simplification of models by the aggregation of variables. First, the necessary and sufficient condition for perfect aggregation of nonlinear dynamics is presented and applied to several examples of ecological models, including the growth of a cohort, an exploiter and its resource, a population with spatial structure, a stage-structured population, and a multi-species system. The perfect aggregation condition can be extended to stochastic dynamic models. These support the aggregation of similar or substitutable variables. Next, the best approximate aggregation of dynamical systems is studied, which minimizes a certain criterion of inconsistency between aggregated and original systems. Aggregation giving the least square deviation of a vector field is obtained for any nonlinear dynamical system. Best aggregations of linear systems around the equilibrium is then examined by using various criteria to minimize, such as (1) difference in vector field, (2) difference in variables at a certain point in time, (3) difference in temporally averaged variables, and (4) the temporal average of the square difference in variables. In short, the best aggregated dynamics greatly depend on the choice of criterion, in particular the selection of the time horizon and of the weighting according to the initial state.

INTRODUCTION

The reduction of dimensionality of models by aggregating variables is a fundamental aspect of ecological modelling. Every ecological description includes some degree of aggregation, because any model, no matter how large and detailed it is, is made possible by neglecting further details within each component.

A realistic model includes all the processes that potentially affect the system we study, in order to explain and predict as many aspects of the system's behavior as possible. As the model becomes more complex, the parameter estimate from available data becomes increasingly difficult and unreliable.

Even when computation capacity allows us to deal with a large and realistic model, an aggregated or otherwise simplified model may work better than a corresponding complex one. For example, Ludwig and Walters (1985, and also Ludwig 1983) constructed optimal fishing policies using different mathematical models whose parameters were calculated from simulated data. They demonstrated that a small and highly aggregated model may be much better in estimating the true optimal fishing policy than a large model, even for data generated using the latter model. In addition, smaller models are easier to comprehend, and thereby give better intuition about the systems they describe. Small models also have an obvious economic advantage.

The study of general properties of model aggregation is therefore an important issue in theoretical systems ecology, and has been studied for conservative flow systems (O'Neill and Rust

1979; Gardner et al. 1982; Cale et al. 1983), and also in more general systems (Luckyanov et al. 1983; Luckyanov 1984; see Sugihara et al. 1984 for a general discussion).

In this paper I summarize recent theoretical studies of the aggregation of dynamics in ecological modelling (Iwasa et al. 1987, 1989; Gard 1988). If a detailed model as a system of (nonlinear) differential equations and the manner of combining the variables into a smaller number of macrovariables are given, the perfect aggregation condition tells us whether there exists a simplified dynamical system for the macrovariables which is consistent with the original system (Iwasa et al. 1987). The perfect aggregation condition can be extended to stochastic dynamic models (Gard 1988). When the perfect aggregation is not possible, the best approximate aggregated dynamics may be searched, which minimizes a given measure of the inconsistency (Iwasa et al. 1989).

PERFECT AGGREGATION

PERFECT AGGREGATION THEOREM

The general framework of the aggregation problem for dynamical systems is as follows (Fig. 1). There exist microdynamics which describe the full behavior of the system:

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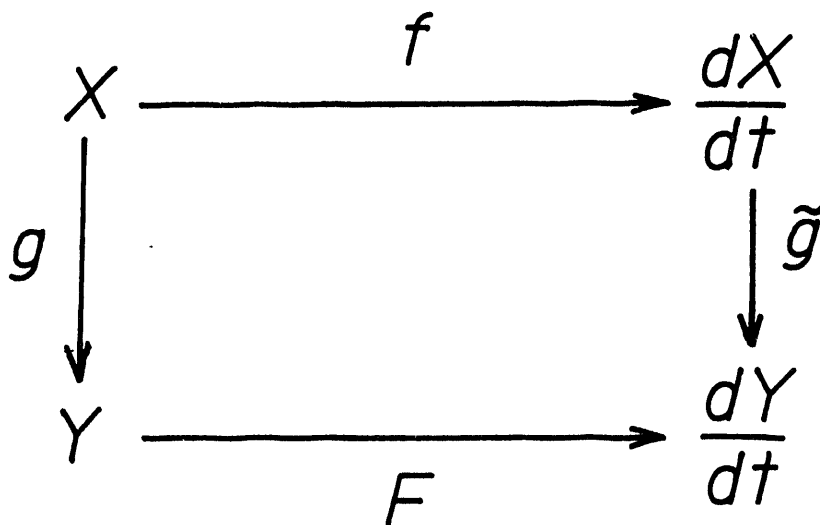


Figure 1. Scheme for aggregation of nonlinear dynamics. Here microdynamics f , (active) aggregation function g , and aggregated dynamics F are all regarded as mapping. Together with passive aggregation function (\tilde{g}), which is naturally induced by g , the consistency of these four mappings is equivalent to the perfect aggregation condition.

$$dX_i/dt = f_i(X_1, \dots, X_n), \quad (1)$$

where $i = 1, \dots, n$. There are m *macrovariables* calculated from the microvariables using the *aggregation function* $g_j(X_1, \dots, X_n)$.

$$Y_j = g_j(X_1, \dots, X_n), \quad (2)$$

where $j = 1, \dots, m$, with $m < n$. One then wonders whether there are *aggregated dynamics* for these macrovariables, such that

$$dY_j/dt = F_j(Y_1, \dots, Y_m), \quad (3)$$

where $j = 1, \dots, m$, and these could be consistent with the microdynamics (1). If so, we say that perfect aggregation is realized in the scheme of microdynamics (1) and aggregation function (2).

The study of when exact aggregation is possible gives a general idea of what the systems are which allow us to aggregate without large mistakes in macrovariables. The aggregated dynamics give the rate of change in macrovariable Y_j ($j = 1, \dots, m$) as

$$(dY_j/dt)_{\text{aggregated}} = F_j(g_1(X), \dots, g_m(X)), \quad (4)$$

where $X = (X_1, \dots, X_n)$, while the microdynamics combined with the aggregation function (2) yield

$$(dY_j/dt)_{\text{micro}} = \sum_{i=1}^n (\partial g_j / \partial X_i) f_i(X). \quad (5)$$

Two dynamics are perfectly consistent if (4) and (5) are the same for all X (Luckyanov et al. 1983; Iwasa et al. 1987).

Theorem 1 (Perfect Aggregation Theorem) Suppose the functions f_j and g_j are continuously differentiable on an open set D . Assume for each Y , the set $g^{-1}(Y) = \{X \in D: g(X) = Y\}$ is connected. Define the $m \times n$ matrix-valued functions $B = \{B_{ji}\}$ and $A = \{A_{ji}\}$ on D by

$$B_{ji} = \partial g_j / \partial x_i \quad \text{and} \quad A_{ji} = \partial \left(\sum_{k=1}^m B_{jk} f_k \right) / \partial x_i. \quad (6)$$

Then perfect aggregation of (1) is implemented by (2) if and only if

$$AB^+B = A \text{ on } D, \quad (7)$$

where B^+ is the generalized inverse of the matrix B .

See Iwasa et al. (1987) for proof. The generalized inverse B^+ of an $m \times n$ matrix B is an $n \times m$ matrix defined by the symmetry of both B^+B and BB^+ and by the equation

$$(BB^+ - I)B = 0 = B^+(BB^+ - I), \quad (8)$$

where I is the $m \times m$ identity matrix (Penrose 1955). When the matrix B has full row rank, $B^+ = B^T(BB^T)^{-1}$ (superscript T denoting transpose).

ECOLOGICAL EXAMPLES OF PERFECT AGGREGATION

To illustrate how to apply the perfect aggregation theorem, I now examine several examples from ecological modelling.

(1) *A community of competitors*

The most familiar model for interacting species is the Lotka-Volterra system. For three competitors, the dynamics may be written:

$$dX_i/dt = r_i X_i (1 - \sum_{j=1}^3 a_{ij} X_j / K_i), \quad (9)$$

where $i = 1, 2, 3$, and X_i indicates the abundance of species i . Assume $a_{ii} = 1$, for each i . Suppose we are interested only in the abundance of one of the species, say X_3 , and ask whether we can aggregate the abundance of the other two into a single variable. Namely, we are asking about the possibility of perfect aggregation with the aggregation function:

$$Y_1 = X_1 + X_2, \quad Y_2 = X_3. \quad (10)$$

In examining this system we are led to set

$$B = \begin{pmatrix} 1 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \quad \text{and therefore } B^+ = \begin{pmatrix} 1/2 & 0 \\ 1/2 & 0 \\ 0 & 1 \end{pmatrix}.$$

The condition Eq. (7) becomes:

$$r_1 = r_2, \quad K_1 = K_2, \quad a_{31} = a_{32}, \quad a_{13} = a_{23}, \quad \text{and } (a_{12} + a_{21})/2 = 1. \quad (11)$$

The first four equalities indicate that the two species to be lumped must be functionally similar, for no error to result. However, the last equality in (11) implies that there may be asymmetry in inter-

specific competition between the two species if their average effect is the same as for intra-specific competition.

(2) *A size structured population*

The second example is the dynamics of a stage structured population. Individuals are classified into several life history stages or size classes, N_1, N_2, \dots, N_n , which follow the dynamics:

$$\begin{aligned} dN_1/dt &= \sum_{i=2}^n m_i N_i - (u_1 + vN_1)N_1 - g_1 N_1, \\ dN_i/dt &= g_{i-1} N_{i-1} - u_i N_i - g_i N_i, \quad (i=2,3,\dots,n-1), \\ dN_n/dt &= g_{n-1} N_{n-1} - u_n N_n, \end{aligned} \quad (12)$$

where m_i and g_i are the fertility and growth rate, respectively, of an individual of stage i . Only the youngest stage is assumed to receive density dependent mortality $(u_1 + vN_1)$.

Let us consider separating the juveniles into their own class but lump all the older stages into a single group:

$$\begin{aligned} Y_1 &= b_1 N_1, \\ Y_2 &= b_2 N_2 + \dots + b_n N_n. \end{aligned} \quad (13)$$

Here we have weighted each class by its biomass b_i so that Y_1 and Y_2 represent the total biomasses of juveniles and adults.

Theorem 1 tells us that the aggregation (13) can be perfect if and only if

$$m_2/b_2 = m_3/b_3 = \dots = m_n/b_n, \quad (14a)$$

and

$$\begin{aligned} (b_2/b_2 - 1)g_2 - u_2 &= (b_3/b_3 - 1)g_3 - u_3 = \dots \\ &= (b_n/b_{n-1} - 1)g_{n-1} - u_{n-1} = -u_n. \end{aligned} \quad (14b)$$

Equation (14a) indicates that the fertility of an adult at various stages must be proportional to the weight, and (14b) says that relative growth rate minus mortality loss is common to all the adult stages. The aggregated dynamics are:

$$\begin{aligned} dY_1/dt &= (b_1 m_n/b_n) Y_2 - (u_1 + (v/b_1) Y_1) Y_1 - g_1 Y_1, \\ dY_2/dt &= (b_2 g_1/b_1) Y_1 - u_n Y_2 \end{aligned} \quad (15)$$

(3) *Cohort dynamics*

Both examples above are linear aggregation. The theorem can apply to nonlinear aggregation too. Consider the following dynamics of the number of individuals X_1 of a cohort and the average individual weight X_2 :

$$\begin{aligned} dX_1/dt &= -(u + v(X_2)X_1)X_1, \\ dX_2/dt &= rX_2(1 - X_2/K(X_1)). \end{aligned} \quad (16)$$

Now we examine the possibility of aggregating into 1-dimensional dynamics with the total biomass $Y = X_1 + X_2$. The necessary and sufficient condition for perfect aggregation is

$$v(X_2) = v_0 X_2 \text{ and } K(X_1) = K_0/X_1. \quad (17)$$

The aggregated dynamics are then:

$$dY/dt = Y((r - u) - (r + v_0 K_0)Y/K_0). \quad (18)$$

(4) *Exploiter and resource*

Another example of nonlinear aggregation is a population of size X_1 and its resource species X_2 :

$$\begin{aligned} dX_1/dt &= rX_1(1 - X_1/K(X_2)), \\ dX_2/dt &= mX_2 - X_1 a(X_2). \end{aligned} \quad (19)$$

X_1 grows logistically, with a carrying capacity $K(X_2)$ that depends on the abundance of the resource. The resource X_2 multiplies with Malthusian parameter m , but is consumed by the species X_1 , whose per capita rate of resource consumption is $a(X_2)$. Calculations show that the ratio $Y = X_1/X_2$ lead to perfect aggregation if and only if

$$K(X_2) = rX_2/(a(X_2) + c), \quad (20)$$

where c is an arbitrary constant. The aggregated dynamics are:

$$dY/dt = ((r - m) - cY)Y. \quad (21)$$

(5) *A spatially structured population*

One of the most common applications of variable aggregation is neglect of spatial heterogeneity in population dynamics. As the simplest example, consider a species living in two subhabitats (indicated by $i=1,2$). Suppose that the organisms interact within each subhabitat and migrate randomly between them. The population sizes of organisms in two subhabitats, u_1 and u_2 , follow:

$$\begin{aligned} du_1/dt &= f_1(u_1) + D(u_2 - u_1), \\ du_2/dt &= f_2(u_2) + D(u_1 - u_2), \end{aligned} \quad (22)$$

where $f_i(u_i)$ is the rate of population growth in the i -th subhabitat, and D is the migration rate.

Under what conditions can we neglect spatial structure without incurring error? We usually assume that, if the migration rate between habitats is sufficiently large, the size of the whole

population can be treated as a single variable instead of following the population size within each subhabitat. Perfect aggregation, however, is not possible in the realistic situation. Consider the aggregation into the total population size $U = u_1 + u_2$. Theorem 1 tells us that perfect aggregation is possible only when both $f_1(u)$ and $f_2(u)$ are linear with the same coefficient for the first-order term, which is severely restrictive.

From these studies, we conclude that similar or substitutable variables may be aggregated without causing a large error, and that perfect aggregation condition is sometimes too stringent to hold widely.

A STOCHASTIC DYNAMICS AGGREGATION MODEL

Recently Gard (1988) extended the above perfect aggregation theorem for deterministic models to models expressed as stochastic differential equations. For example, cohort dynamics (16) become

$$dX_1/dt = -(u + v(X_2)X_1)X_1 + X_1 dB_1/dt, \quad (23a)$$

$$dX_2/dt = rX_2(1 - X_2/K(X_1)) + X_2 dB_2/dt, \quad (23b)$$

where dB_i/dt is the white noise indicating purely random stochastic fluctuation without autocorrelation. Consider the aggregation into a 1-dimensional model with the total biomass $Y = X_1 + X_2$. Following the chain rule of stochastic differential equation (Ito integral), we can derive the set of stochastic differential equations for the macrovariable Y , and the perfect aggregation holds if the latter can be written using macrovariable(s) only.

Perfect aggregation now requires conditions for stochastic terms in addition to those for deterministic terms. Gard (1988) shows that the perfect aggregation of stochastic model (23) is not more restrictive than that for the deterministic model (16), because the conditions for stochastic terms are automatically satisfied. In general, however, the perfect aggregation of stochastic dynamics is more restrictive than that of a corresponding deterministic model.

APPROXIMATE AGGREGATION

AGGREGATION OF MINIMUM DIFFERENCE IN A VECTOR FIELD

The study of perfect aggregation made it clear that the perfect consistency requirement is unpractically restrictive. In the following, we study the *best approximate aggregation* of dynamical systems which attain the minimum inconsistency between aggregated and original systems.

The perfect aggregation condition is derived from the consistency of the vector field. As a measure of the inconsistency between two dynamical systems, we might use the difference in vector field:

$$\Phi = \int \|dY/dt(X)_{\text{aggregated}} - dY/dt(X)_{\text{micro}}\|^2 w(X) dX, \quad (24)$$

where $\|\cdot\|$ indicates the Euclidean vector norm, and $w(X)$ is a positive function ($w(X) > 0$) indicating a weighting with respect to variables $X = (X_1, \dots, X_n)$, and is normalized as $\int w(X) dX = 1$. The measure (24) is zero when perfect aggregation is realized.

The optimally aggregated dynamics (or the *best aggregated dynamics*) corresponds to the choice of functions $F_j(Y_1, \dots, Y_m)$ which minimize (24) for given microdynamics, $f_i(X_1, \dots, X_n)$, and given aggregation functions, $g_i(X_1, \dots, X_n)$. When perfect aggregation is impossible, the dynamics which give the best fit in one part of the state space may not give a good fit in other regions; then weighting factor $w(X)$ is necessary to specify the desired compromise.

Let $h(X)$ be an m -dimensional vector whose j th element is the right hand side of Eq. (5), the rate of change in Y_j by microdynamics. From (4) and (5), we can rewrite (24) as

$$\Phi = \int \|F(g(X)) - h(X)\|^2 w(X) dX. \quad (25)$$

Then we have the following:

Theorem 2 Let $F(Y)$ be the best aggregated dynamics, i.e. those that minimize F as given by (25). At every point Y at which $F(Y)$ is continuous,

$$F(Y) = \lim_{\delta \rightarrow 0} \int_{U_\delta} h(X) w(X) dx / \int_{U_\delta} w(X) dX \quad (26)$$

holds, where U_δ is the set of X for which $g(X)$ is in δ -neighborhood of Y , $U_\delta = \{X \mid \|g(X) - Y\| < \delta\}$.

This theorem says that the best aggregation, if no constraint is placed on the choice, can be calculated as the appropriately weighted average value of $h(X)$.

A more convenient expression is obtained if we regard the weighting function $w(X)$ as the probability distribution of a random variable X , although there is no element of stochasticity in the original formulation. Then Eq. (26) can be expressed in terms of the conditional expectation of $h(X)$:

$$F(Y) = E[h(X) \mid g(X) = Y]. \quad (27)$$

The measure of deviation F for the best aggregated dynamics (27) can be interpreted as the variance of microdynamics $h(X)$ remaining after that explained by the value of macrovariables $g(X)$.

For a given point in time t , the difference between aggregated dynamics and microdynamics for general nonlinear dynamical systems can be made small if the difference in the two vector fields is sufficiently small. The minimum difference in the rate of change in variables implies the best fitting of macrovariables on a short time scale. However, the difference in macrovariables produced by a

small difference in vector fields grows exponentially with time t , indicating that the aggregation is accurate only for the finite time horizon.

Good fitting in vector fields does not in general preserve important features of the dynamical systems after aggregation of variables. In Iwasa et al. (1989) this is illustrated by two examples: In the first example, the best vector field fitting around the origin causes the shift of the equilibrium. In the second example, the best vector field aggregation keeps the location of the equilibrium consistent with the original dynamics but its stability is now changed. Both the location of equilibria and their stability are related to the system's behavior in the far future, and may not be guaranteed by the best vector field fitting.

AGGREGATION CRITERIA WITH DIFFERENT TIME SCALES

Sometimes, prediction of models in the far future, for example, may be more important than those in the near future, when we discuss the long term consequences of continued application of stress. In other circumstances, it may be the short term which is of interest. In this section, we investigate systems aggregated according to several criteria which emphasize different time scales.

Unlike vector field fitting (Theorem 2), mathematics here requires the explicit solution of the dynamics, and therefore we restrict our attention to linear dynamical systems with a steady state at the origin:

$$dX/dt = \sum_{k=1}^n M_{ik} X_k; \quad (28)$$

such a system could arise from linearization around a singular point in a nonlinear system, with X representing deviations from that point. We assume that the matrix M is stable, i.e., all the eigenvalues have a negative real part. We further assume that the aggregated dynamics are also linear:

$$dY/dt = \sum_{k=1}^m C_{jk} Y_k. \quad (29)$$

If the main objective is to predict the state of the system at some future time t , then we require that $Y(t)$, as produced by the aggregated dynamics, be close to the vector predicted by the microdynamics. We may regard a dynamical system as a mapping from an initial state $X(0)$ to a future state $X(t)$ at time t with matrix $\exp(Mt)$, and the aggregated dynamics with matrix $\exp(Ct)$. In the aggregation scheme illustrated in Fig. 2, the same linear aggregation, with matrix B , is used for mapping from $X(0)$ to $Y(0)$ and that from $X(t)$ to $Y(t)$. At time t , the aggregated dynamics give:

$$Y_{\text{aggregated}}(t) = \exp(Ct) B X(0), \quad (30a)$$

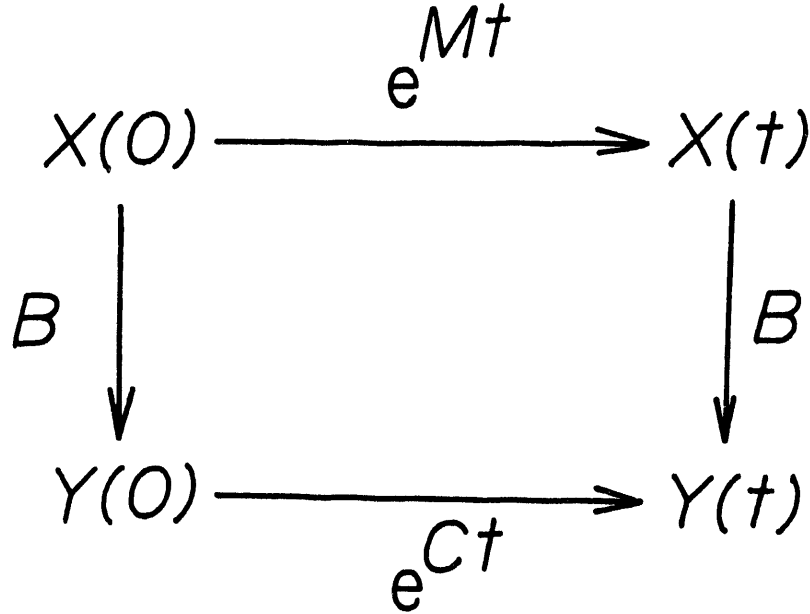


Figure 2. Scheme of the aggregation of a linear dynamical system. The microdynamics translate the initial state $X(0)$ to the state $X(t)$ by multiplication by the matrix $\exp(Mt)$, whereas the aggregated dynamics replace M by C . Perfect aggregation requires that Be^{Mt} equal $e^{Ct}B$; the best approximate aggregation minimizes a weighted difference between these when perfect aggregation is impossible.

and $Y(t)$ calculated from the microdynamics is:

$$Y_{\text{micro}}(t) = B \exp(Mt) X(0). \quad (30b)$$

If these two are the same for all initial states $X(0)$ for all t , the aggregated dynamics provide a perfect surrogate according to the given criterion.

(1) *Minimum difference in vector field*

First, we apply the vector field approximation developed in the last section. If the weighting $w(X)$ is a spherically symmetric normal distribution centered at the origin, the best aggregated dynamics which minimizes (24) are with matrix

$$C = B M B^*. \quad (31)$$

This is the case in which the consistency of aggregation in the immediate future is of large importance.

(2) *Minimum difference in variables at a particular time*

A candidate for the measure of inconsistency between two dynamics is the difference in the variables calculated by the two dynamics at a particular point in time t :

$$\Phi = \int \|Y_{\text{aggregated}}(t) - Y_{\text{micro}}(t)\|^2 w(X_0) dX_0, \quad (32)$$

where $w(X_0)$ is a normal distribution spherically symmetric about the origin. A particular aggregated dynamical system which is very good if the original system starts from one choice of initial conditions, may be quite poor along another trajectory. The weighting $w(X_0)$ in (32) defined a compromise which gives acceptable consistency for various initial conditions.

The dynamics C which achieve the minimum of (32) are:

$$C = \log(B \exp(Mt) B^+)/t, \quad (33)$$

which depend on the specified point in time t .

(3) *Minimum difference in the temporal average of variables*

We may be interested in predicting variables suitably averaged over time rather than those at a single time point. For example, the average value of variables $X(t)$ weighted according to a negative exponential distribution:

$$\langle X \rangle_\tau = \int_0^\infty X(t) \exp(-t/\tau) dt / \tau, \quad (34)$$

will emphasize the behavior of the system on a time scale of order t . Then, the optimal aggregation which minimizes the difference

$$\Phi = \int \| \langle Y_{\text{aggregated}} \rangle_\tau - \langle Y_{\text{micro}} \rangle_\tau \|^2 w(X_0) dX_0$$

is:

$$C = (I - [B(I - M\tau)^{-1}B^*]^{-1})/\tau. \quad (35)$$

If we let $\tau \rightarrow 0$, we obtain

$$\lim_{\tau \rightarrow 0} C = B M B^*, \quad (36)$$

which is the same as (31), the best dynamics when the short time scale is emphasized. In contrast, for a very large t , the optimal C in (35) tends to the limit

$$\lim_{\tau \rightarrow \infty} C = (B M^{-1} B^*)^{-1}. \quad (37)$$

(4) *Minimum temporal average of difference in variables*

We may use, as a measure, the time average of squared distance in macrovariables:

$$\Phi = \int_0^{\infty} \int \|Y_{\text{aggregated}}(t) - Y_{\text{micro}}(t)\|^2 p(t) dt w(X_0) dX_0, \quad (38)$$

where $p(t)$ is a weighting factor over time,

$$p(t) > 0, \text{ and } \int_0^{\infty} p(t) dt = 1.$$

Equation (38) is zero if and only if the aggregation is perfect. A set of conditions determining the best aggregated dynamics can be derived (Iwasa et al. 1989), but unfortunately they are too complicated to be practical.

To illustrate the difference between the best aggregated dynamics corresponding to the various criteria above, we consider the special case in which M is real and diagonal, and the aggregation matrix B is of size $1 \times n$:

$$M = \begin{pmatrix} \lambda_1 & & 0 \\ & \lambda_2 & \\ 0 & & \ddots \\ & & & \lambda_n \end{pmatrix}, B = (b_1, \dots, b_n). \quad (39)$$

We assume $0 > \lambda_1 > \dots > \lambda_n$. The aggregation is the lumping of the n variables into a weighted sum; hence C is a scalar (1×1 matrix). The problem is to approximate a summation of n exponential functions with different exponents by a single exponential function, provided that the initial condition is consistent.

The results are summarized in Table 1. The best coefficient depends on the criterion to minimize: (1) The vector field fitting gives the arithmetic mean of eigenvalues as the optimal aggregation. The same result is obtained for other criteria if weighting over time emphasizes the short

term (either $t \rightarrow 0$ or $\tau \rightarrow 0$). (2) In contrast, if the long term horizon is of concern, the result depends on the particular choice of criteria. The optimal coefficient may be the dominant eigenvalue, the harmonic mean of eigenvalues, or something else. (3) The result for minimizing the average of the difference in macrovariables is too difficult in computation to be practical.

CHOICE OF AGGREGATION FROM A RESTRICTED CLASS

For the best aggregation in Theorem 2, we assumed that the aggregated dynamical system can be freely chosen, provided only that it is autonomous. However, often one must restrict the choice. For example, when the best linearly aggregated system is sought for a given linear dynamical system, usually the aggregated dynamics are also assumed to be linear. Similarly, the search for aggregation in the Lotka-Volterra system is often restricted to models of the same Lotka-Volterra form, with a smaller number of components. In these cases, Theorem 1 may not be useful except when the best aggregated dynamics happen to be in the restricted class of systems.

One approach for finding the optimally aggregated dynamics from a restricted set is to search for the best (set of) parameters. The general theorem for this procedure is given in Iwasa et al. (1989), which is too complicated to be useful.

A more practical way to find a reasonably good aggregated system is to determine free parameters by using either the consistency of the location of equilibria or of the linearized dynamics at several different points sequentially, in a suitable order according to the importance of characteristics of the model. For example, the location of a particular equilibrium may be regarded as the most important characteristic of the given model; after satisfying this, one can add other criteria to guarantee consistency of the second steady state, or of the linearization about the first, etc.

DISCUSSION

In the present paper, I reviewed recent theoretical studies of the perfect aggregation and the best approximate aggregation of dynamical systems used in ecological modelling. By regarding a system of differential equations as mapping from space variables to their rate of changes, we can extend the aggregation theory of *linear functions* developed in economics and statistics (Theil 1954, 1957, 1959; Ijiri 1968, 1971; Chipman 1976) to that of *nonlinear dynamical systems*.

The condition for perfect aggregation is here presented in a form comparable to the one for linear dynamics in automatic control theory (Aoki 1968, 1978) and that for linear functions in economics (Ijiri 1968, 1971; Chipman 1976). The theory for aggregation in ecological systems now fits well to the framework of general aggregation problems.

Analysis of examples for linear aggregation seems to support the idea that lumping of variables which are functionally similar or substitutable produces good aggregation (e.g. Vemuri 1978), which in turn may justify "natural" ways to aggregate variables, based on concepts such as the guild, trophic level, block, and clique.

In practice, however, it is rare for a given nonlinear system to satisfy the condition for perfect aggregation, although it may be approximately so. The perfect aggregation condition is often too stringent to deal with all the practically important applications of variable aggregation, as demonstrated in particular by the aggregation of the spatially structured population.

Table 1

(1) Vector Field Approximation

$$C = \sum_i b_i^2 \lambda_i / \sum_i b_i^2, \quad [\text{the arithmetic mean of } \lambda_i]$$

(2) Approximation at a Time Point

$$C = (1/t) \log[\sum_i b_i^2 \exp(\lambda_i t) / \sum_i b_i^2].$$

$$\text{When } t \rightarrow 0, \quad C = \sum_i b_i^2 \lambda_i / \sum_i b_i^2, \quad [\text{the arithmetic mean of } \lambda_i]$$

$$\text{When } t \rightarrow \infty, \quad C = \lambda_1, \quad [\text{the dominant eigenvalue}]$$

(3) Approximation of Temporal Average

$$\text{When } \tau \rightarrow 0, \quad C = \sum_i b_i^2 \lambda_i / \sum_i b_i^2, \quad [\text{the arithmetic mean of } \lambda_i]$$

$$\text{When } \tau \rightarrow \infty, \quad C = \sum_i b_i^2 / \sum_i b_i^2 (1/\lambda_i), \quad [\text{the harmonic mean}]$$

(4) Minimum Temporal Average of Difference in Variables

Let the weighting with respect to time be
 $p(t) = \exp(-t/\tau)/\tau, \quad (\text{for } t > 0).$

C is a positive solution of a polynomial

$$0 = \sum_k b_k^2 \{1/(1/\tau - 2c)^2 - 1/(1/\tau - c - \lambda_k)^2\}.$$

$$\text{When } \tau \rightarrow 0, \quad C = \sum_i b_i^2 \lambda_i / \sum_i b_i^2, \quad [\text{the arithmetic mean of } \lambda_i]$$

When $\tau \rightarrow \infty$, C is the solution of

$$|2c|^2 = \sum_k b_k^2 / \sum_k b_k^2 (1/(|\lambda_k| + |c|))$$

A more practical problem is to find the approximate aggregated dynamics which minimize some measure of inconsistency between the aggregated and the true dynamics. The approximate function problems in economics (Ijiri 1971; Chipman 1976) are extended to the best aggregation with the least square deviation in a vector field in nonlinear dynamics (Theorem 2).

In spite of the generality of Theorem 2, however, the shortcoming of the vector-field fitting is evident. The location of equilibria and their stability may be changed as the result of best aggregation of vector-field fitting, in spite of the fact that these are often considered to be the most important feature of dynamical systems (e.g. Zeigler 1976; O'Neill and Rust 1979; Cale and Odell 1979; 1980).

We therefore studied other criteria for inconsistency. Our study shows that, when perfect aggregation is impossible, the best aggregated dynamical system depends on (1) the time scale and (2) the region in which high accuracy of approximation is required.

Procedures used in previous studies on aggregation in ecological modelling can be examined from the general theoretical framework of aggregation developed here. The nature and magnitude of inconsistency produced by aggregation of variables in model ecosystems have been examined extensively either in linear systems (O'Neill and Rust 1979; Cale and Odell 1979, 1980), or in conservative flow systems (Gardner et al. 1982; Cale et al. 1983). In population genetics, Cohen (1985) considered the aggregation of "fitness in each environment" rules giving rank among genotypes. Hirata and Ulanowicz (1985) developed aggregation of a system of steady flows between compartments by evaluating the performance of aggregation using an index based on information theory.

Another technique to simplify model ecosystems is to separate fast and slow dynamics, in which variables changing much faster than the ones concerned are regarded as being at the quasi-equilibrium, while variables changing very slowly are treated as constants. This method is widely used in ecology (e.g. MacArthur 1972; Schaffer 1981; Ludwig et al. 1978; Mangel 1982). Such time scale differences often accompany hierarchical structure of interaction (Simon and Ando 1961), and graph theoretical techniques are sometimes useful in finding suitable way of aggregation and decomposition of models. Simplification using time scale difference is also related to aggregation (see Iwasa et al. 1989).

In the present paper, we searched for the aggregated dynamics assuming the set of macrovariables given. In some cases, however, the number and identity of macrovariables may also be left at the modeler's discretion. In that case, a much larger dimensionality is often needed, than the number of variables to predict by the model. In automatic control literature, aggregation of linear dynamical systems is discussed when the aggregated system is used to predict the "output" (Aoki 1968, 1978; Hickin and Sinha 1975a, b; Sinha and Kuszta 1983). We can examine the question of model dimensionality in the context of ecological modelling if the model is used to predict a given set of aspects from a given set of data (Iwasa and Levin manuscript).

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The Ecosystem and Macroscopic Concepts

The ecosystem level unites the biotic components of populations, communities, and food webs with the abiotic components of energy flux, nutrient flux and other physical factors related to these flows (e.g., temperature, weather events) into a total system perspective. Few of the papers classed as dealing with the ecosystem level actually deal with all of these things simultaneously. They do, nevertheless, shift the emphasis away from the purely biological phenomena to the concomitant flows of matter and energy. They also attempt to understand total system behavior through analogies from information, cybernetic, or thermodynamic theory through macroscopic indices borrowed from these fields. Hence, theoreticians approaching ecological systems from this viewpoint attempt a unified perspective by integrating ecology into the physical sciences (whereas theoreticians beginning from individual adaptations attempt a unified perspective oriented around the concept of natural selection at the individual level).

**PRODUCER-DECOMPOSER MATCHING IN A SIMPLE MODEL ECOSYSTEM:
A Network Coevolutionary Approach to Ecosystem Organization**

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ABSTRACT

The present note is concerned with how the ecosystem maintains its energy and matter processes, and how those processes change throughout ecological and geological time, or how the constituent biota of an ecosystem maintain their life, and how ecological (species) succession and biological evolution proceed within an ecosystem. To advance further Tansky's (1976) approach to ecosystem organization, which investigated the characteristic properties of the developmental process of a model ecosystem, by applying Margalef's (1968) maximum maturity principle to derive its long term change, we seek a course for deriving the macroscopic trends along the organization process of an ecosystem as a consequence of the interactions among its biotic components and their modification of ecological traits. Using a simple ecosystem model consisting of four aggregated components ("compartments") connected by nutrient flows, we investigate how a change in the value of a parameter alters the network pattern of flows and stocks, even causing a change in the value of another parameter, which in turn brings about further change in the network pattern and values of some (possible original) parameters. The continuation of this chain reaction involving feedbacks constitutes a possible mechanism for the "coevolution" or "matching" among flows, stocks, and parameters.

ECOSYSTEM ORGANIZATION AND CONSTITUENT BIOTA COEVOLUTION

A general question of concern is: What are the characteristic properties of ecosystem organization, and how does the ecosystem work? More specifically, how does the ecosystem maintain its energy and matter processes, and how do those processes change throughout ecological and geological time? Or, from a different point of view, how do the constituent biota of an ecosystem maintain their life, and how does the ecological (species) succession and biological evolution proceed within an ecosystem? As for trends in the developmental process of ecosystems, several alternative hypotheses have been proposed in terms of various optimality principles, such as maximum energy flux (Lotka 1922a,b), power (Odum 1971), maturity (Margalef 1968), and ascendancy (Ulanowicz 1986). Tansky (1976) investigated the characteristic properties of the developmental process of a model ecosystem, applying Margalef's maximum maturity principle to derive its long-term change. To

advance further Tansky's approach to ecosystem organization, we now seek a course for deriving the macroscopic trends along the organization process of an ecosystem as a consequence of the interactions among its biotic components and their modification of ecological traits.

To make a first step in this direction, we will consider a simple ecosystem model consisting of four aggregated components, referred to as the ecosystem "compartments", connected by flows of nutrients to each other. Using this simple system, we will illustrate a new general idea for investigating how a change in the value of a parameter alters the network pattern of flows and stocks, even causing a change in the value of another parameter, which in turn brings about further change in the network pattern and values of some (possible original) parameters; the continuation of this chain reaction involving feedbacks constitutes a possible mechanism for the "coevolution" or "matching" among flows, stocks and parameters.

A SIMPLE ECOSYSTEM MODEL WITH A PRODUCER-DECOMPOSER CYCLE

Consider a simple ecosystem model depicted in Fig. 1, which consists of four compartments,

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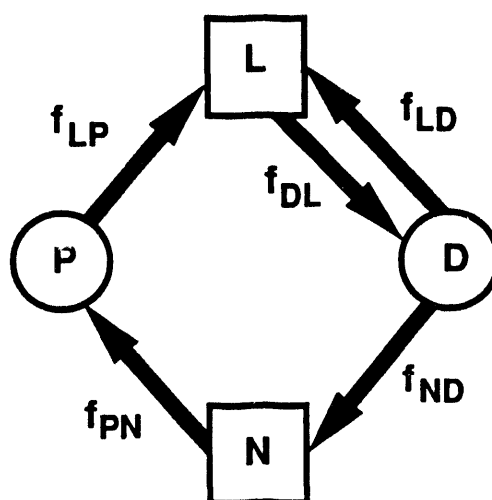


Figure 1. A model ecosystem consisting of four compartments which are connected to each other by flows of nutrient transfer.

primary producer (compartment P), litter and detritus (compartment L), decomposer (compartment D), and nutrient pool (compartment N), connected by flows of nutrient transfer. Let P , L , D , and N also be used to denote standing stocks of nutrients in the corresponding compartments, and f_{XY} denote the flow to compartment X from compartment Y . Then, the dynamics of this model system are given by the following set of differential equations:

$$\frac{dP}{dt} = f_{PN} - f_{LP} \quad (1a)$$

$$\frac{dL}{dt} = f_{LP} + f_{LD} - f_{DL} \quad (1b)$$

$$\frac{dD}{dt} = f_{DL} - f_{LD} - f_{ND} \quad (1c)$$

$$\frac{dN}{dt} = f_{ND} - f_{PN} \quad (1d)$$

We assume that the flows are determined by (are functions of) the standing stocks in several compartments and some parameters that characterize local (compartment level) processes such as the nutrient uptake rate of the primary producer. Specifically, we will assume that the flows have the following functional dependencies:

$$\begin{aligned} f_{PN} &= f_{PN}(P, N; a), & f_{LP} &= f_{LP}(P; a), & f_{DL} &= f_{DL}(D, L; b), \\ f_{LD} &= f_{LD}(D; b), & f_{ND} &= f_{ND}(D), \end{aligned} \quad (2)$$

where a and b are parameters that represent the coefficients of some local processes and satisfy the conditions that

$$\begin{aligned} \partial f_{PN} / \partial a &\geq 0, & \partial f_{LP} / \partial a &\geq 0, \\ \partial f_{DL} / \partial b &\geq 0, & \partial f_{LD} / \partial b &\geq 0. \end{aligned} \quad (3)$$

For example, parameters a and b may be considered to represent the nutrient uptake rate of the primary producer (P) and the decomposition rate for the decomposer (D), respectively. Furthermore, we assume that

$$\partial f_{XY} / \partial Y > 0 \quad (4)$$

for all flows, i.e., any flow increases as its donor increases in stock.

STABILITY AND SENSITIVITY ANALYSES OF THE MODEL SYSTEM

Equations (1), representing a closed system, imply $\frac{dP}{dt} + \frac{dL}{dt} + \frac{dD}{dt} + \frac{dN}{dt} = 0$, from which we have $P+L+D+N = c$ (constant). Thus, for instance, substituting $c - (P + D + N)$ for L in $f_{DL}(D, L; b)$, we have a closed form for the dynamics of three variables P, D, N :

$$\frac{dP}{dt} = f_{PN}(P,N;a) - f_{LP}(P;a) = f_P(P,N;a) \quad (5a)$$

$$\frac{dD}{dt} = f_{DL}(D, c-(P+D+N);b) - f_{LD}(D;b) - f_{ND}(D) = f_D(P,D,N;b) \quad (5b)$$

$$\frac{dN}{dt} = f_{ND}(D) - f_{PN}(P,N;a) = f_N(P,D,N;a) \quad (5c)$$

The dynamics of L is determined from the other variables' dynamics through the equation $L = c - (P + D + N)$.

Given values of parameters a and b , let $P_1(a,b)$, $D_1(a,b)$ and $N_1(a,b)$, respectively, be values for variables P , D , and N at a steady state of the dynamical system defined by Eqs. (5); then $(P_1(a,b), D_1(a,b), N_1(a,b))$ is a solution for a set of algebraic equations:

$$f_P(P,N;a) = 0, f_{PN}(P,N;a) = 0 \quad (6a)$$

$$f_D(P,D,N;b) = 0 \quad (6b)$$

$$f_N(P,D,N;a) = 0 \quad (6c)$$

The local stability condition for this steady state can be readily derived by linearizing the system (5) around the steady state; a simple form of sufficient condition for stability is that

$$\partial f_P / \partial P < 0, \quad \partial f_D / \partial D < 0, \quad (7)$$

i.e., the biotic compartments P and D are both self-regulatory. In the following we assume that the model system under consideration satisfies this stability condition for steady states, and further that the changes in values of the parameters are slow relative to those of the variables so that the system traces its trajectory on a "slow" manifold consisting of points that "map" different values of the parameters into the corresponding stable steady states.

The sensitivities of the steady state $(P_1(a,b), D_1(a,b), N_1(a,b))$ with respect to changes in the values of parameters a and b can be evaluated in terms of the sets of partial derivatives $(\partial P_1 / \partial a, \partial D_1 / \partial a, \partial N_1 / \partial a)$ and $(\partial P_1 / \partial b, \partial D_1 / \partial b, \partial N_1 / \partial b)$, respectively. Taking the partial derivatives with respect to a of the functions $P_1(a,b)$, $D_1(a,b)$ and $N_1(a,b)$ of a and b which are implicitly defined by Eqs. (6), we have

$$R \begin{bmatrix} \partial P' / \partial a \\ \partial D' / \partial a \\ \partial N' / \partial a \end{bmatrix} = - \begin{bmatrix} \partial f_P / \partial a \\ \partial f_D / \partial a \\ \partial f_N / \partial a \end{bmatrix} \quad (8)$$

where R is the linearization (community matrix) of the system (5) around the steady state $(P_1(a,b), D_1(a,b), N_1(a,b))$:

$$R = \begin{bmatrix} \partial f_P / \partial P & \partial f_P / \partial D & \partial f_P / \partial N \\ \partial f_D / \partial P & \partial f_D / \partial D & \partial f_D / \partial N \\ \partial f_N / \partial P & \partial f_N / \partial D & \partial f_N / \partial N \end{bmatrix} \quad (9)$$

Thus we have

$$\begin{bmatrix} \partial P' / \partial a \\ \partial D' / \partial a \\ \partial N' / \partial a \end{bmatrix} = S \begin{bmatrix} \partial f_P / \partial a \\ \partial f_D / \partial a \\ \partial f_N / \partial a \end{bmatrix} \quad (10)$$

where $S = -R^{-1}$. This result may be interpreted as follows [for a full development of this point, see article by Nakajima in this volume]: change in parameter a may directly cause a change in the net inflow (growth) for each of compartments P and N , which may in turn bring about changes in the value of $P'(a,b)$ directly and indirectly through a causal chain; these chained influences together constitute the change in the value of $P_1(a,b)$ due to a change in parameter a . Likewise, we have for parameter b

$$\begin{bmatrix} \partial P' / \partial b \\ \partial D' / \partial b \\ \partial N' / \partial b \end{bmatrix} = S \begin{bmatrix} \partial f_P / \partial b \\ \partial f_D / \partial b \\ \partial f_N / \partial b \end{bmatrix} \quad (11)$$

THE BASIC IDEA

ESS-LIKE VALUES OF PARAMETER A GIVEN PARAMETER B

Given a specific value for parameter b , let $a^*(b)$ denote an ESS-like value for parameter a [ESS stands for evolutionary stable strategy (Maynard Smith and Price 1973)], i.e., a value of a such that once the primary producer with $a^*(b)$ prevails, a primary producer with any value for parameter a other than $a^*(b)$ can not invade; then $a^*(b)$ must satisfy the following conditions:

$$\frac{\partial f_P}{\partial a} = \frac{\partial(f_{PN} - f_{LP})}{\partial a} = 0 \quad (12)$$

$$\frac{\partial^2 f_P}{\partial a^2} = \frac{\partial^2(f_{PN} - f_{LP})}{\partial a^2} < 0 \quad (13)$$

for $a = a^*(b)$, $P = P_1(a^*(b), b)$, $D = D_1(a^*(b), b)$, $N = N_1(a^*(b), b)$. Therefore, $a^*(b)$ is given as the fourth component of the solution $(P^*(b), D^*(b), N^*(b), a^*(b))$ of the set of Eqs. (6) and (12) for a given value of parameter b . These four equations, each defining a surface, together determine a curve as the intersection of the surfaces they define in the five-dimensional Euclidian space of (P, D, N, a, b) . $(P^*(b), D^*(b), N^*(b), a^*(b))$ constitutes a one-parameter expression of the curve with b the parameter, and function $a = a^*(b)$ represents the projection of this curve onto the (a, b) -plane (Fig. 2).

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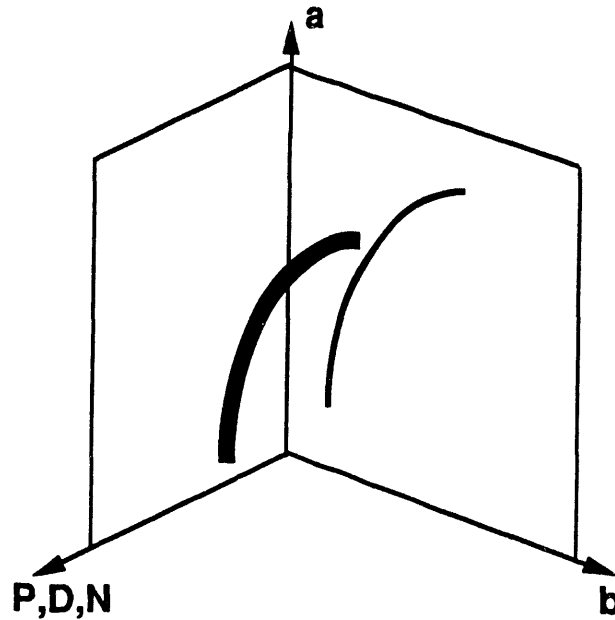


Figure 2. The curve determined as the intersection of the surfaces each of which is defined by one of four equations (6) and (12) in the five-dimensional Euclidian space of (P, D, N, a, b) , and the projection of this curve onto the (a, b) -plane, which is represented by the function $a = a^*(b)$.

To investigate the dependency of the ESS-like value of a on the value of b , we consider the derivative da^*/db . By taking derivatives of the functions $P^*(b)$, $D^*(b)$, $N^*(b)$, $a^*(b)$ of b defined implicitly by equations (6) and (12), we have

$$R' \begin{bmatrix} dP^*/db \\ dD^*/db \\ dN^*/db \\ da^*/db \end{bmatrix} = - \begin{bmatrix} \partial f_P / \partial b \\ \partial f_D / \partial b \\ \partial f_N / \partial b \\ \partial(\partial f_P / \partial a) / \partial b \end{bmatrix} \quad (14)$$

where R' is the linearization of Eqs. (6) and (12) around the solution $(P^*(b), D^*(b), N^*(b), a^*(b))$, thus

$$R' = \begin{bmatrix} \partial f_P / \partial P & \partial f_P / \partial D & \partial f_P / \partial N & \partial f_P / \partial a \\ \partial f_D / \partial P & \partial f_D / \partial D & \partial f_D / \partial N & \partial f_D / \partial a \\ \partial f_N / \partial P & \partial f_N / \partial D & \partial f_N / \partial N & \partial f_N / \partial a \\ \partial^2 f_P / \partial a \partial P & \partial^2 f_P / \partial a \partial D & \partial^2 f_P / \partial a \partial N & \partial^2 f_P / \partial a \partial a^2 \end{bmatrix}$$

$$= \begin{bmatrix} & & 0 \\ & 400R & 0 \\ & & \partial f_N / \partial a \\ \partial^2 f_P / \partial a \partial P & 0 & \partial^2 f_P / \partial a \partial N & \partial^2 f_P / \partial a^2 \end{bmatrix} \quad (15)$$

By multiplying R'^{-1} from the left to both sides of this equation, we get

$$\begin{bmatrix} dP^*/db \\ dD^*/db \\ dN^*/db \\ da^*/db \end{bmatrix} = S' \begin{bmatrix} \partial f_P / \partial b \\ \partial f_D / \partial b \\ \partial f_N / \partial b \\ \partial^2 f_P / \partial a \partial b \end{bmatrix} = S' \begin{bmatrix} 0 \\ \partial f_D / \partial b \\ 0 \\ 0 \end{bmatrix} \quad (16)$$

where $S' = -R'^{-1}$. Thus, derivative da^*/db can be expressed as follows:

$$\frac{da^*}{db} = -\frac{1}{|R'|} \frac{\partial f_N}{\partial D} \left(\frac{\partial f_P}{\partial P} \frac{\partial^2 f_P}{\partial a \partial N} - \frac{\partial f_P}{\partial N} \frac{\partial^2 f_P}{\partial a \partial P} \right) \frac{\partial f_D}{\partial b} \quad (17)$$

where $|R'|$ denotes the determinant of matrix R' .

Note in (17) that da^*/db equals zero when $\partial f_D / \partial b$ is zero. Further, using this formula (17) the following can be proved. Assume that $|R_1| [(\partial f_P / \partial P)(\partial^2 f_P / \partial a \partial N) - (\partial f_P / \partial N)(\partial^2 f_P / \partial a \partial P)] < 0$. Then, because $\partial f_N / \partial D > 0$, the sign of the derivative da^*/db coincides with that of $\partial f_D / \partial b$; thus, as far as

a larger decomposition coefficient b is favored for the decomposer (D), the ESS-like value $a^*(b)$ for the producer's parameter a increases with b . Within the value range of b where da^*/db is positive, a lower level of b would induce a lower level for a^* , while a higher level of b would select a matched higher level of a^* ; that is, the ESS-like value of the producer's parameter a matches the decomposer's parameter b (Fig. 3).

ESS-LIKE VALUES OF PARAMETER B GIVEN PARAMETER A

We can make a similar analysis for a dual case in which, given a specific value for a , we consider the ESS-like value $b^*(a)$ for parameter b . First, consider the following set of equations:

$$g_D(D,L;b) \equiv f_{DL}(D,L;b) - f_{LD}(D;b) - f_{ND}(D) = 0 \quad (18a)$$

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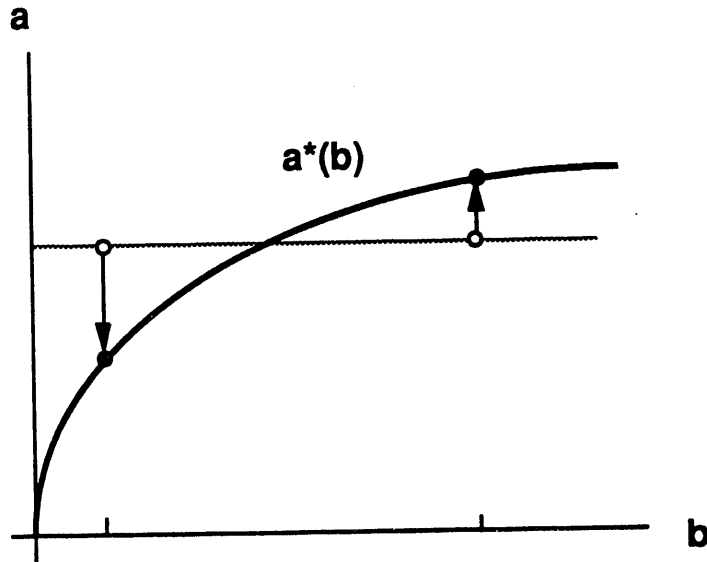


Figure 3. An illustration of the ESS-like value a^* of parameter a matching to the level of parameter b within the value range of b where da^*/db is positive; that is, a lower level of b would induce a lower level for a^* , while a higher level of b would select a matched higher level of a^* .

$$g_P(D,P,L;a) \equiv f_{PN}(P,c-(P+L+D);a) - f_{LP}(P;a) = 0 \quad (18b)$$

$$g_L(D,P,L;a,b) \equiv f_{LP}(P;a) + f_{LD}(D;b) - f_{DL}(D,L;b) = 0 \quad (18c)$$

$$\frac{\partial g_D}{\partial b} = \frac{\partial(f_{DL} - f_{LD})}{\partial b} = 0 \quad (18d)$$

Let $(D_2(a,b), P_2(a,b), L_2(a,b))$ be a solution of the set of equations (18a), (18b) and (18c), representing a steady state of the dynamical system (1) for a given pair of values of parameters a and b . The ESS-like value $b^*(a)$ for a specific value of a is given as the b -component of the solution $(D^*(a), P^*(a), L^*(a), b^*(a))$ of the set of four Eqs. (18).

Using the same method used in the case for $a^*(b)$, we have the following formula for the derivative db^*/da :

$$\frac{db^*}{da} = -\frac{1}{|T'|} \left(\frac{\partial g_D}{\partial D} \frac{\partial^2 g_D}{\partial b \partial L} - \frac{\partial g_D}{\partial L} \frac{\partial^2 g_D}{\partial b \partial D} \right) \left(\frac{\partial g_L}{\partial P} \frac{\partial g_P}{\partial a} - \frac{\partial g_P}{\partial P} \frac{\partial g_L}{\partial a} \right) \quad (19)$$

where $|T'|$ is the determinant of the matrix that represents the linearization of equations (18) around the solution $(P^*(a), L^*(a), D^*(a), b^*(a))$.

PRODUCER-DECOMPOSER MATCHING: COEVOLUTIONARY PROCESS OF THE A AND B VALUES

An intersection of two curves $a = a^*(b)$ and $b = b^*(a)$ of the ESS-like values for parameter a and b , respectively, represents a pair of CSS-like values (a_0, b_0) for parameters a and b [CSS stands for coevolutionary stable state (Roughgarden 1983 Matsuda and Namba 1989)], i.e., a pair of values (a_0, b_0) for a and b such that once the parameters a and b attain those values, a primary producer with any a value other than a_0 or a decomposer with any b value other than b_0 may not invade, and thus the parameters a and b remain at those values.

Depending on the shape of, and the relationship between, two curves $a = a^*(b)$ and $b = b^*(a)$ of the ESS-like values, there may be alternative patterns, and two cases of particular interest here are a stable or unstable CSS-like state (a_*, b_*) such as that illustrated in Fig. 4. In the case of a stable CSS-like state (Fig. 4a), an initial state (a_0, b_0) on the curve $a = a^*(b)$ is stable (ESS-like situation) with respect to parameter a of the producer, but it is not stable with respect to parameter b of the decomposer, which, with the stable parameter a unchanged, would seek a new value $b_1 = b^*(a_0)$, the ESS-like value of b given $a = a_0$. This new state (a_0, b_1) , however, is no longer stable with respect to parameter a , thus it is now the producer's turn to seek a change in the value of parameter a to $a_1 = a^*(b_1)$, while the stabilized parameter b remains unchanged. Repeating the same process again and again will finally lead to a CSS-like state (a_*, b_*) , as illustrated in figure 4a.

THE ROLE OF INDIRECT EFFECTS IN THE COEVOLUTIONARY PROCESS

PROPAGATION OF EFFECTS FROM B TO A^*

Given a value of N , the solution sets of Eqs. (6) and (12) provide an alternative one-parameter expression with N the parameter for the five-dimensional curve discussed above (Fig. 2); combining the two alternative one-parameter expressions allows us to derive the following relationship:

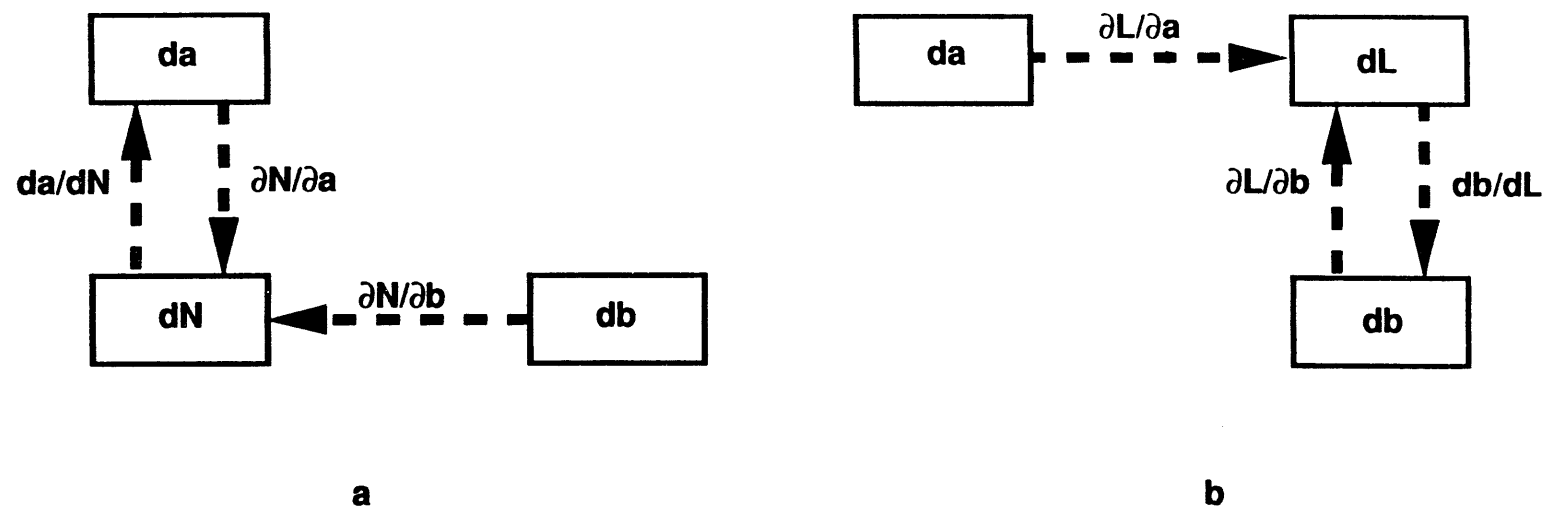


Figure 4. Illustration of (a) stable and (b) unstable CSS-like state (a_0, b_0) .

$$\frac{da}{db} = \frac{\frac{da}{dN}}{\frac{db}{dN}} = \frac{da}{dN} \frac{dN}{db}, \quad (20)$$

where each derivative is the derivative of a function that represents a projection of the curve in terms of either of these two one-parameter expressions. Further, from the relationship $N^*(b) = N_1(a^*(b), b)$, we have

$$\frac{dN^*}{db} = \frac{\partial N_1}{\partial a} \frac{da^*(b)}{db} + \frac{\partial N_1}{\partial b}. \quad (21)$$

Eqs. (20) and (21) yield the following relationship:

$$\begin{aligned} \frac{da^*(b)}{db} &= \frac{\partial N_1}{\partial b} \frac{da}{dN} \frac{1}{1 - \frac{\partial N_1}{\partial a} \frac{da}{dN}} \\ &= \frac{\partial N_1}{\partial b} \frac{da}{dN} \left[1 + \left\{ \frac{\partial N_1}{\partial a} \frac{da}{dN} \right\} + \left\{ \frac{\partial N_1}{\partial a} \frac{da}{dN} \right\}^2 + \dots \right]. \end{aligned} \quad (22)$$

Figure 5a illustrates an interpretation of this relationship from the viewpoint of direct and indirect influence propagation. Note that given N , the ESS-like value a^* for parameter a (a trait of the primary producer) is determined completely from two equations:

$$f_p = 0 \quad \text{and} \quad \left(\frac{\partial f_p}{\partial a} \right) = 0. \quad (23)$$

The derivative da/dN represents the direct influence of a change in available nutrient level N upon the ESS-like value a^* for parameter a . $\partial N_1/\partial b$ and $\partial N_1/\partial a$, as already mentioned, represent the total (direct plus indirect) influence of a change in the b and a values, respectively, propagated upon the available nutrient level N^* through all available paths in the functional network. Therefore, Eq. (22) indicates the following: A change in the parameter b value will cause some change in nutrient

PROPAGATION OF EFFECTS FROM A TO ESS B

In a similar way as we derived Eq. (22), for the dual case we have the following:

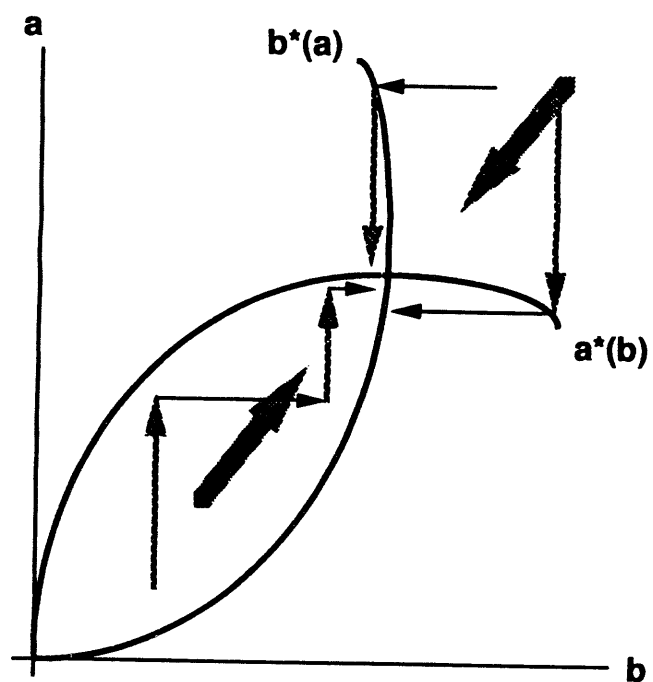
$$\begin{aligned}
\frac{db^*(a)}{da} &= \frac{\partial L_2}{\partial a} \frac{db}{dL} \frac{1}{1 - \frac{\partial L_2}{\partial b} \frac{db}{dL}} \\
&= \frac{\partial L_2}{\partial a} \frac{db}{dL} \left[1 + \left\{ \frac{\partial L_2}{\partial b} \frac{db}{dL} \right\} + \left\{ \frac{\partial L_2}{\partial b} \frac{db}{dL} \right\}^2 + \dots \right] \quad (24)
\end{aligned}$$

Figure 5b explicitly indicates the causal chains (or paths) connecting a cause (a change in the parameter a value) to its effects on the ESS-like value b^* . level N , which will in turn directly cause a change in the ESS-like value a^* . But this change may cause a further change in the N value, which will again change the a^* value. This process will repeat again and again until the influence dissipates completely. The effect da^*/db caused by a unit change in parameter b upon the ESS-like value a^* is thus the sum of these indirect influences propagated through all available paths.

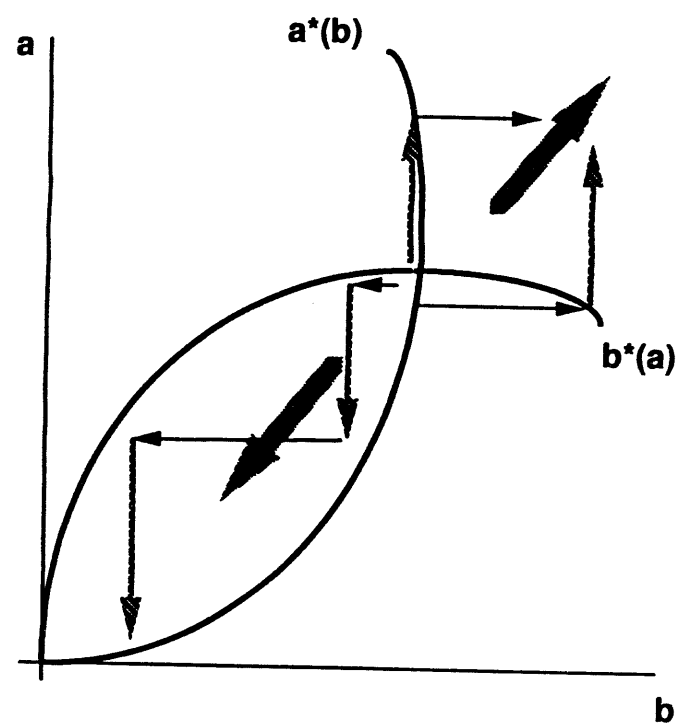
NETWORK COEVOLUTION AS A MECHANISM FOR SELF-ORGANIZATION OF THE ECOSYSTEM

If we look at the producer-decomposer matching represented as a matching race between the two parameters a and b , in the scope of the whole ecosystem it may appear as the ecosystem organizing itself.

As the two parameters evolve in such an interactive fashion so that one parameter's change triggers the other's and this interaction repeats with alternate directions, the biomasses of the producer and decomposer may both grow up under certain conditions, but because of indirect effects that a change in parameter a (or b) causes upon the value of $P_1((a,b))$ (or $D_1(a,b)$), an increase in the value of the parameter does not imply an unconditional increase in biomass of the producer P (or decomposer D). Also, the stocks of the non-living compartments as well as all the flows in the ecosystem would change accordingly, constituting a "network coevolution" of the whole ecosystem. If we imagine an ecosystem that starts with a very low level of biomasses and parameter values of biota, this network coevolutionary process would appear as a process of building up the system toward a biologically richer regime. Since the process does not require any external force to cause changes, but instead is proceeded through an internal mechanism built in the system in terms of its biotic components' evolution of interaction, it may be viewed as a self-organizational process. To generalize, therefore, a coevolutionary process at the system components' level, exemplified here by the network coevolution of a simple ecosystem model, may provide a mechanism for the self-organization of a system.



a



b

Figure 5. Diagram to illustrate an interpretation of (a) relationship (22) and (b) relationship (24) from the viewpoint of direct and indirect influence propagation.

APPLICATIONS OF THE IDEA TO SPECIFIC THEORETICAL PROBLEMS ON ECOSYSTEMS

The approach based on the notion of network coevolution as described above is in principle applicable to a general class of ecological networks that are defined in terms of a set of differential equations of n variables with m parameters, though involving a larger number of variables and parameters elevates the difficulty in carrying out the analysis. It may therefore provide a unified framework for dealing with the following theoretical issues in ecosystems study:

(1) The issue of tropical versus temperate ecosystems in terms of their characteristic structure. The case in which the producer-decomposer matching takes place to grow the biota of the system, thus reducing the level of the nutrient pool, may correspond to the well known fact that the tropical rainforest is, while rich in standing stock of its biota, very poor in soil nutrients. Further, high productivity of the tropical forest may not be solely the product of the rich physical conditions such as high solar input and temperature, but may be achieved in part as the result of coevolution with the decomposer. For, should the decomposer not be able to change its parameter b in response to an increase in value of the producer's parameter a , the producer would not be able to further increase its parameter a . By the same token, the decomposer is expected to have a higher decomposition rate or a decomposing system with a higher decomposition rate tends to be favored than the level estimated solely from a curve that represents the physiological response to primary physical condition factors such as temperature.

(2) The issue of food web structure, in particular grazing versus detrital food chains, regarding their relative state of growth (in terms of their length, richness in biomass, species diversity, and so on) in aquatic versus terrestrial ecosystems.

(3) Among terrestrial systems, the issue of forest versus grassland ecosystems, in particular the cause for their bifurcation, i.e., what makes a forest a forest and not a grassland, and vice versa. The case with an unstable CSS may serve as a model for explaining this bifurcation such that a system should either lead to a forest or a grassland depending on its initial condition (a_0, b_0) ; with values too low for a_0, b_0 the system should be reduced to a grassland, while with large enough values for a_0, b_0 it should build up a forest.

The exploration of each of these issues requires further elaboration and extension of the simple model and its analysis than we have presented.

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CELLULOSE DYNAMICS AND TERMITE ECOLOGY AS KEY FACTORS TO STRUCTURING TERRESTRIAL COMMUNITIES

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INTRODUCTION

How can the earth, which teems with plant-eating animals ranging in size from aphids to elephants, be so green? Plant-eating animals kill more plants than drought or logging does, yet they do not wipe out all the plants (Howe and Westley 1988). Why is it so? Approximately half of the ca. 800,000 species of insects are phytophagous, and they account for one-quarter of all living species excluding algae and microorganisms (Strong et al. 1984). As for the evolution of plants in relation to phytophagous animals, especially insects, much attention has been paid to the chemical defenses that plants exert by use of their secondary compounds (Ehrlich and Raven 1964; Whittaker and Feeny 1971; Feeny 1975; Rosenthal and Janzen 1979; Strong et al. 1984; Howe and Westley 1988). In contrast, very little attention has been paid to another important aspect of plant-animal interactions that is no less relevant to the green coverage of the earth; most animals lack the ability to produce the enzymes necessary for decomposing cellulose, the primary cell-wall component of higher plants and the most abundant organic compound on earth, whereas various kinds of microorganisms are able to produce these enzymes (Nielsen 1962; Janzen 1981; Begon et al. 1986). For the earth to be so green, it is "ideal" that a plant should not be consumed by heterotrophs when it is alive, but that it should be consumed promptly when it is dead, to return nutrients back to the living portion of plants. Thus, the spatial distribution pattern of the organisms that can digest cellulose plays a crucial role here; in terrestrial communities, microorganisms, which can produce cellulase, the cellulose-decomposing enzymes, are to large extent confined in the soil, to decompose the cellulose not in living plants but in fallen dead plants.

Cellulose, long viewed as the master construction material of plants, was probably evolutionarily selected for the same reason that we choose concrete to construct houses in areas of high termite activity (Janzen 1985). The distribution of cellulose is directly related to the morphology of plants, thus that of forests and grasslands. But, cellulose is also a major energy resource, potentially available and explicitly so when this hard substance encounters cellulose-digesting organisms such as microorganisms in the soil. In view of its super-abundance and dominance in quantity, its physical robustness and the restricted distribution of its consumers despite its potential as an energy resource, cellulose may be a "key substance" for understanding community structure. Furthermore, differences in the distribution pattern of cellulose and its digesting organisms may explain differences in community structure between forests and grasslands, such as those in the relative significance of grazing and detritus chains (Odum 1953; Begon et al. 1986).

One of the primary consumers of cellulose and the most abundant animals in tropical terrestrial communities, termites are conspicuous in that they can produce cellulase partly by

themselves (Yokoe 1964; Mishra 1980; O'Brien and Slaytor 1982) and have a symbiotic association with the other organisms that produce enzymes to decompose cellulose and sometimes lignin, an even harder substance (Grasse and Noirot 1959), and they may play a significant role, especially in tropical regions a deterministic role, in structuring the community in which they reside.

In the present essay, we examine the relationship of cellulose to animals, especially insects, to provide a new perspective for understanding terrestrial communities based on cellulose dynamics, and highlight for tropical ecosystems the role that termites play in determining community structure.

CELLULOSE AND COMMUNITY STRUCTURE

TWO TYPES OF FOOD: CELL WALL AND CYTOPLASM

One of the most significant differences between plant and animal cells is the presence of a cell wall. Although the cell wall and cytoplasm of plant cells are both potential food sources for heterotrophs (consumers), they are quite different in their chemical compositions.

The cell wall of higher plants, containing little protein and lipid, consists mainly of cellulose, hemicellulose (complex polysaccharides) and lignin (complex phenolic polymer), which are inversely located almost exclusively in the cell wall. These three cell-wall substances in weight compose about 47%, 22% and 22%, respectively, of deciduous wood, 16%, 13% and 21% of deciduous leaf, and 30%-33%, 18%-24% and 11%-14% of grass (Swift et al. 1979). Therefore, cell wall is the primary component of trees (ca. 90%) and grasses (60%-70%) in biomass. Because most plant material (98%) on earth is terrestrial, and 75%-90% of it is located in forests (Whittaker 1975), cell-wall components, especially cellulose, are the most abundant organic matter on earth. Further, noting that cellulose is degraded into glucose, we may state that cell wall provides the most abundant food resource, if only potentially, on this planet. Except for some types of molluscs, silverfish and a few earthworms, animals cannot directly utilize this abundant food resource, because they cannot produce a complete set of cellulases (Nielsen 1962; Begon et al. 1986; Martin 1987). Therefore, animals must have direct or indirect associations with microorganisms to make it available.

On the other hand, cytoplasm, which is abundant in pollens, seeds and new leaves, is rich in proteins, lipids and starches, thus potential high quality food for animals. Higher plants produce, however, various kinds of toxic secondary substances such as alkaloids, terpenoids and hydrogen cyanides, and keep them in cytoplasm (Howe and Westley 1988). Therefore, animals that feed on plant cytoplasm must solve the problem of the chemical defences plants devise using these secondary compounds.

CELL-WALL CONSUMERS AND CYTOPLASM CONSUMERS

On the basis of the foregoing observations, we propose a new categorization for the heterotrophs or consumers of plants: cell-wall consumers and cytoplasm consumers. The former category of consumers, having acquired a means to manage the hard construction materials of cell wall, utilize a food of low quality but of high quantity, whereas the latter, having acquired a means to manage toxic secondary substances in the cytoplasm of plant cells, utilize a food of low quantity but of high quality.

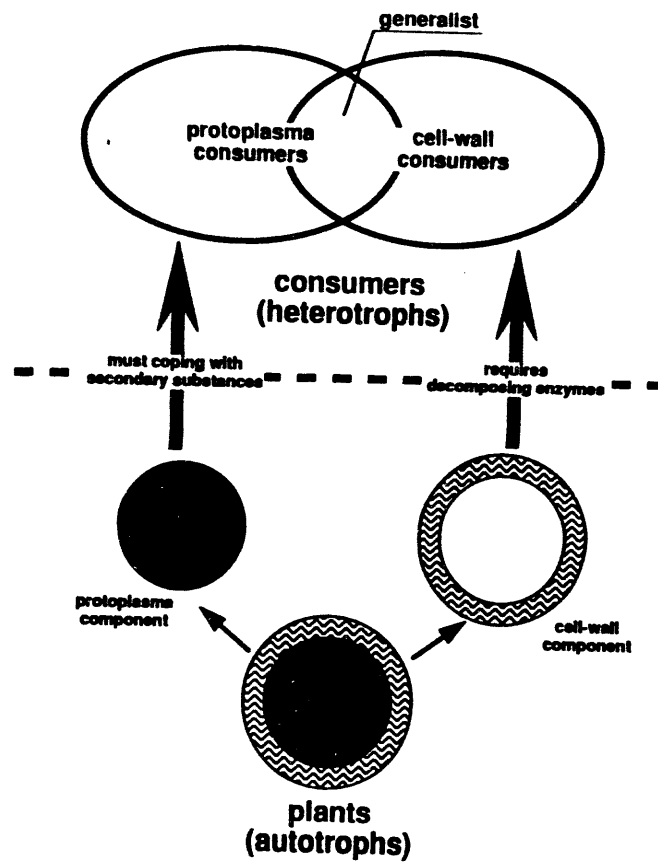
How effective is this categorization of heterotrophs when applied to insects? As stated above, phytophagous insects make up approximately half of all insect species, including nine of 29 orders: Coleoptera (Scarabaeidae, Languridae, Coccinellidae, Tenebrionidae, Mordellidae, Chrysomelidae, Cerambycidae, Curculionidae and Apionidae), Collembola, Diptera (Cecidomyiidae, Dolichopodidae, Drosophilidae, Ephydriidae, Anthomyiidae, Agromysidae, Chloropidae and Tephritidae), Hemiptera, Hymenoptera (Xyelidae, Cephidae, Blasticotomidae, Diprionidae, Tenthredinidae), Lepidoptera, Orthoptera (Tettigoniidae, Acrididae and Eumastacidae), Phasmida and Thysanoptera. Hemiptera, Lepidoptera, Orthoptera and Phasmida are almost entirely phytophagous, but only about one-third of Coleoptera and one-tenth of Hymenoptera feed on the living tissues of higher plants (Strong et al. 1984).

On the other hand, as Martin (1987) reviewed, cellulose-digesting insects have associations with microorganisms to obtain acquired enzymes: Thysanura, Isoptera, Plecoptera, Trichoptera, Blattaria, Orthoptera (Gryllidae: *Acheta domesticus*), Diptera (Tipulidae: *Tipula abdominalis*), Hymenoptera (Siricidae: *Sirex* spp.), Coleoptera (many species of Buprestidae, Coccinellidae, Anobiidae, Scarabaeidae, Cerambycidae and Curculionidae). Although there is insufficient information on cellulose-digesting insects, the comparison of phytophagous and cellulose-digesting insects at the family level shows that no cellulose-digesting insects are phytophagous except for some Coleopterans and probably Orthopterans. Therefore, we may summarize that most insects that consume plant materials have succeeded in solving either but not both of two problems: (i) the detoxification of secondary substances in cytoplasm, and (ii) the degradation of cell-wall components with the aid of microorganisms.

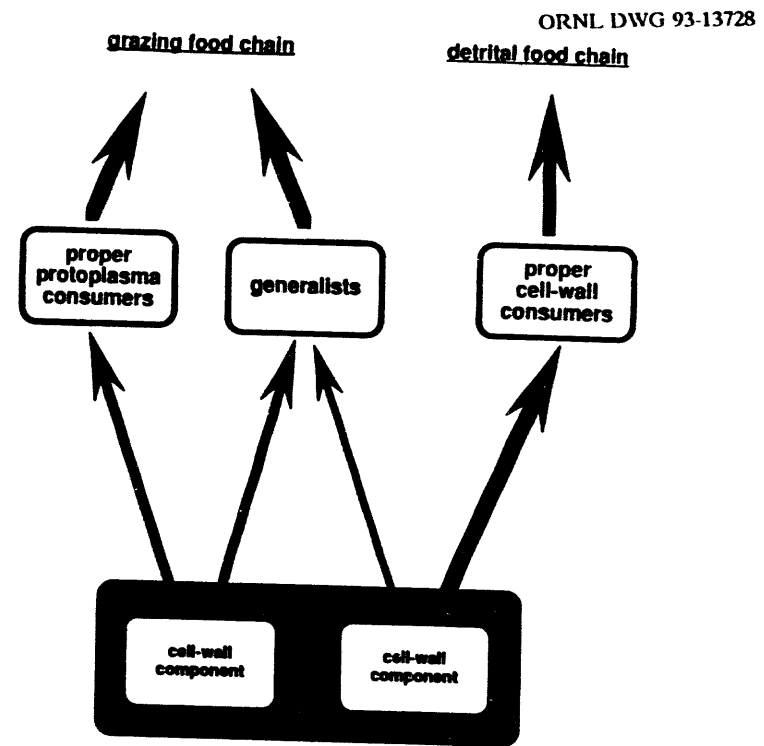
From the point of view based on this fundamental classification of heterotrophs into cell-wall consumers and cytoplasm consumers, an insect that utilizes the seeds of two plant species is more specialized than an insect that feeds on stem and seed of a single species of plant. This idea can be extended to all animals. Cell-wall consumers include dead plant feeders of great variety besides termites (LaFage and Nutting 1978), while cytoplasm consumers include most animals feeding on plants, especially human beings, ants, and bees. Herbivorous ruminant mammals, which can utilize both cell wall and cytoplasm (Dobson and Dobson 1988), are called "generalists". It is notable that eusociality has evolved in both classes of consumers; termites have developed their eusociality based on quite different food resources from those for ants, bees, and wasps.

A NEW PERSPECTIVE ON COMMUNITY STRUCTURE AND EUCARYOTES MACROEVOLUTION

The new categorization of heterotrophs leads to an alternative view of community structure. A division of a plant cell, representing the primary producer space (or the resource space), into cell wall and cytoplasm, is projected into the classification of consumers into two corresponding categories, cell-wall consumers and cytoplasm consumers (Fig. 1a). The overlap of cell-wall consumers and cytoplasm consumers corresponds to generalist consumers such as herbivorous mammals with rumens, which transmit into grazing food chains some portion of cell-wall components. The rest of the cell-wall components flow into detrital food chains, because it is consumed as dead organic materials by proper cell-wall consumers which are not cytoplasm consumers, such as bacteria in the soil, fungi, and



a



b

Figure 1a. An alternative view of the community structure that is derived from a new categorization of (primary) heterotrophs that classifies them into cell-wall consumers and cytoplasm consumers.

Figure 1b. Flows from the cell-wall and cytoplasm components of plants into grazing and detrital food chains.

insects with symbiotic microorganisms. Most of the consumed cytoplasm flows into grazing food chains through cytoplasm consumers (Fig. 1b).

This new view on community structure suggests the following clear-cut perspective on the macroevolution of eucaryotes. After the emergence of eucaryotic life, three kingdoms of plants, animals and fungi evolved from protists, the most primitive form of eucaryotes supposed to have evolved through intracellular symbiosis of prokaryotes (Margulis 1970). The emergence of animals, super-active and effective consumers, might have selected plants, the emerging eucaryotic autotrophs, to devise a harder structure of cell wall, by using not only cellulose but also other hard substances combined with it to produce a harder new material. The enzymes for decomposing the hard cell-wall substances including lignin are mainly produced by fungi. Therefore, it may be said that plants have evolved as the producer of two distinct types of food resources, cell wall and cytoplasm, and that animals have evolved as cytoplasm consumers, while fungi evolved as cell-wall consumers (Fig. 2a). The macroevolution of eucaryotes is thus a process of specialization or "speciation" into three directions based on the trophic interactions among the three groups of organisms, each of which has come to occupy a unique trophic niche (Fig. 2b).

VARIATIONS IN COMMUNITY STRUCTURE

The community structure of forests and grasslands are different in the relative significance of detrital and grazing chains. The quantitative significance of detrital chains relative to grazing chains is greater in forests than in grasslands (Odum 1953; Begon et al. 1986).

Comparing grass and trees, the major plant components of grasslands and forests, respectively, the former contains more cell-wall components and less nitrogen contents than the latter (Swift et al. 1979; Martin and Martin 1978). Nitrogen contents of grasses and wood (in parenthesis, tree and shrub foliage) are 1.2%-4.5% and 0.04%-0.3% (0.6%-6.6%), respectively. Thus, in the context of the basic structure that Fig. 1b depicts, the relative availability of cell-wall components is higher in forests than in grasslands. In terrestrial ecosystems, microorganisms, the major cellulose decomposers, are located on the ground surface and in the soil, thus cell-wall components are mainly decomposed after they are dead and have fallen down on the ground, to flow into detrital food chains (Fig. 1b). These two facts alone would suggest that the quantitative significance of detrital food chains relative to grazing food chains is greater in forests than in grasslands.

This basic scheme can, however, be modified by the animals, in particular various kinds of insects and mammals, that depend on plants. In forests, the insects which can decompose cellulose with the aid of microorganisms usually do not attack living plant tissues, while most phytophagous insects, having no association with microorganisms for cellulase, are restricted to consume only nutritious portions of plants such as fruits, seeds, pollens and young leaves, and do not destroy major parts of trees, such as old leaves, branches and stems. Herbivorous mammals, which harbor microorganisms in their guts and decompose cell-wall substances, and other generalist consumers (Fig. 1b) are scarce in forests (Fittkau and Klinge 1973). On the contrary, in grasslands herbivorous mammals represented by ungulates are abundant, and sometimes consume much of living grasses, to increase the flow into grazing chains. But, herbivorous mammals with rumens can not digest cellulose completely but only in the range of 43%-73%, mainly due to the presence of lignin and silica, and

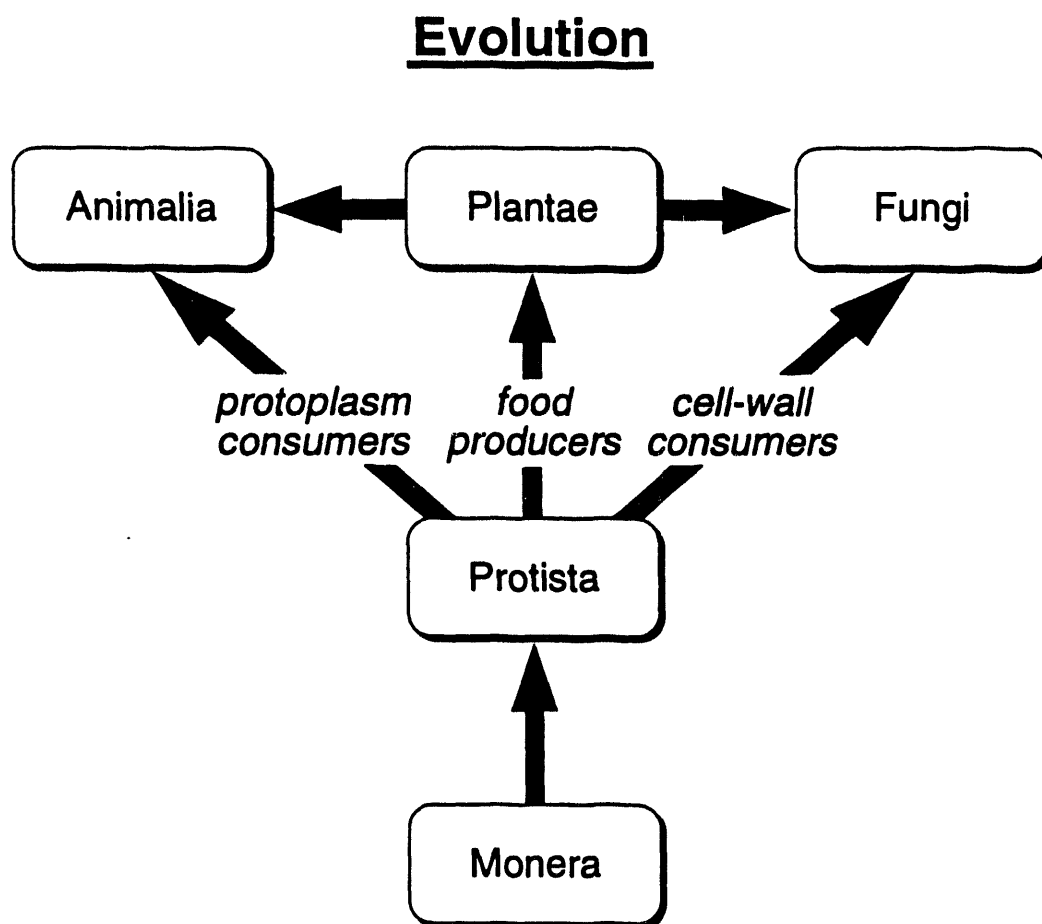


Figure 2a. Evolutionary structures of five kingdoms: Monera, Protista, Plantae, Fungi, Animalia. The macroevolution of eucaryotes as the process of specialization into three categories of life.

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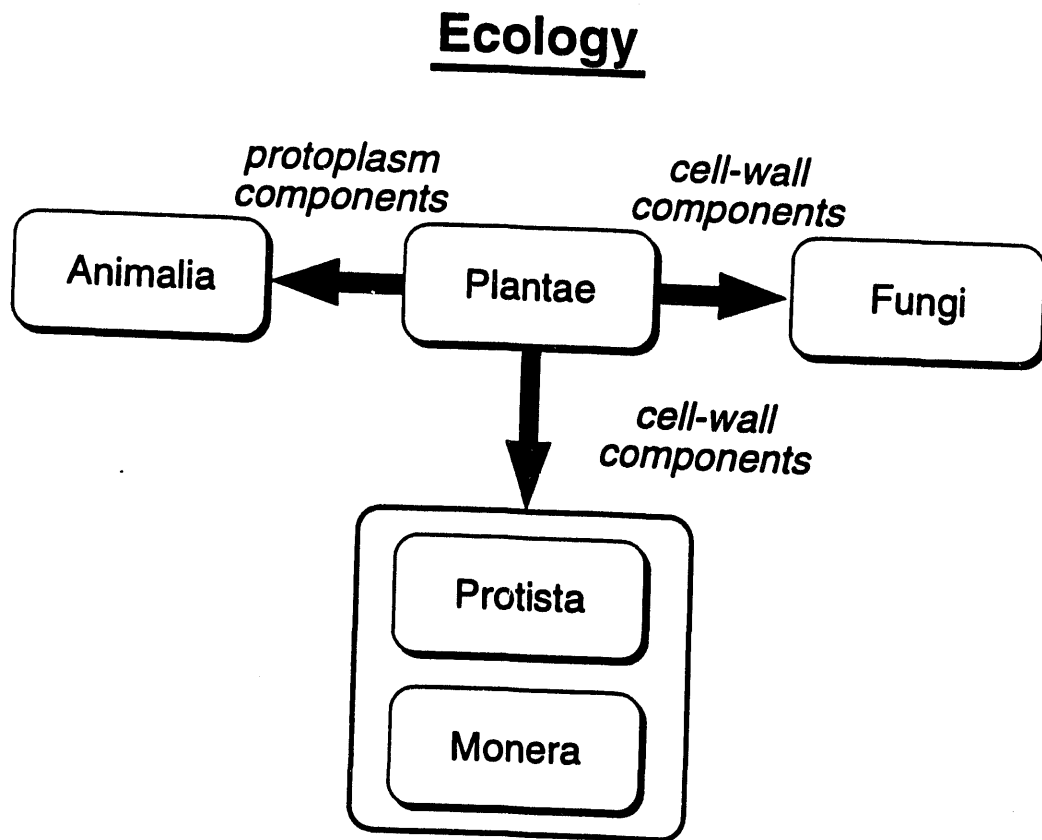


Figure 2b. The trophic interactions among the five kingdoms of organisms, each of which occupies a unique trophic role niche.

further the inclusion of cellulose, lignin and silica in grass places a utilization limit on herbivores below the availability level of this potential food, because their feeding ecology can be explained to large extent by the behavioral adaptation to maximize protein consumption and minimize consumption of tough lignified or silicated fiber (Howe and Westley 1988). The scarcity of generalist consumers in forests and the contrasting abundance in grassland only increases the difference between forests and grasslands in the relative significance of detrital and grazing food chains, because generalists redirect some portion of cell-wall components flow toward grazing food chain (Fig. 1b).

Another structural comparison can be made between communities in tropical regions and those in temperate regions. A key for this comparison lies in the interaction of cell-wall substances with the termite, one of the most abundant animals with the greatest consumption of plant products in tropical terrestrial communities. Therefore, we will start with a summary of termite ecology focusing on the role of termites in the community in which they reside.

TERMITES AND COMMUNITY STRUCTURE

ABUNDANCE OF TERMITES AND THEIR LITTER CONSUMPTION

Termites (Isoptera containing 2200 living species) are widely distributed in tropical and subtropical regions, and their number of species and biomass are especially large in the tropical zone, where they play a major role in the decomposition of dead plant materials rich in cellulose, hemicellulose and lignin (Lee and Wood 1971; Wood and Sands 1978; Josens 1985; Wood and Johnson 1986). Termites are largely classified into two groups: lower termites (Families Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae and Rhinotermitidae) and higher termites (Termitidae). Major differences between the two groups are in the symbiotic organisms they are associated with; the former's symbionts are protozoa, and the latter's are bacteria.

The maximum density and biomass of termites are roughly the same in the tropical rain forest and wet savanna: 4,000 to 5,000/m² and ca. 10 g.w.w./m² (Table 1). The relative abundance of humus feeders increases with an increase in precipitation, whereas that of fungus growing termites (in Africa and Asia) is higher in savannas and dry forests.

Termites are predominant among all animals in the tropical terrestrial ecosystems. In a Brazilian rain forest, about 80% of total biomass of animals (21 g.w.w./m²) was due to soil invertebrates, 30% of which were termites (Fittkau and Klinge 1973). In a Malaysian forest, the density and biomass of all soil macrofauna and termites (in parentheses) are as follows: 5387/m² (3485/m²) and 12.5 g.w.w./m² (9.4 g.w.w./m²), respectively (Abe 1979;). In East Africa savannas, the biomass of termites roughly equals that of wild ungulates.

If we take 10 g.w.w./m² as a criterion for an abundant animal, only four groups pass this criterion: herbivorous mammals in African savanna, termites in tropical regions, human beings (250/km² and 40 kg/person) and earthworms in the temperate regions (Edwards and Lofty 1972). Ants seem everywhere abundant, yet rarely exceed this criterion.

Some attempts have been made to measure the role of termites in energy flow and material cycling in tropical forests (Matsumoto and Abe 1979; Abe 1980, 1982; Collins 1983, and savannas

Table 1. Density (number/ m^2) and biomass (g wet weight/ m^2), indicated in parentheses, of termites in tropical ecosystems.

| ecosystems | Tropical rain forests | | Savannas | | |
|----------------|-----------------------|------------|-------------|-------------|-----------|
| Locality | Mulu | Pasoh | Lamto | Mokwa | Fete-Ole |
| Country | Malaysia | Malaysia | Ivory Coast | Nigeria | Senegal |
| Rainfall (mm) | 5107 | 2000 | 1290 | 1175 | 375 |
| Latitude | 4N | 3N | 6N | 9N | 16N |
| Authors* | (1) | (2) | (3) | (4) | (5) |
| Humus feeder | 621(1.02) | 1505(2.52) | 100(0.16) | 163(0.66) | 0 |
| Fungus growers | 5(0.03) | 960(6.12) | 554(0.64) | 2193(6.39) | 93(0.72) |
| Others | 909(1.35) | 1020(0.78) | 213(0.93) | 1652(3.54) | 138(0.24) |
| Total | 1526(2.4) | 3485(9.41) | 867(1.75) | 4001(10.59) | 231(0.96) |

*(1) Collins (1983), (2) Abe (1979), (3) Josens (1972), (4) Wood and Sands (1978), (5) Lepage (1974).

(Josens 1972; Lepage 1974; Ohiagu 1979; Ohiagu and Wood 1979; Collins 1981, 1983; Buxton 1981; Gentry and Whitford 1982), as reviewed by Wood and Sands (1978) and Josens (1985). Estimates of litter consumption by termite populations are shown in Table 2. Ecological impacts of termites in savannas seem to be greater than those in tropical forests. In Southern Guinea Savanna of Nigeria, termites consume 63% of annual grass litter supply, consuming 36% of all litter supply.

INTERACTION OF TERMITES WITH OTHER ORGANISMS

In the lower termites, cellulose is digested by enzymes secreted by termites themselves and their gut protozoa, while in the higher termites (about 75% of all species), cellulose digestion is mediated by cellulase secreted by termites, their gut bacteria and the fungi in their nests (Grasse and Noirot 1959). The fungus growing termites among the higher termites (Macrotermitinae), which are dominant in tropical Asia and Africa, cultivate fungi of *Termitomyces* placing their faeces on fungus gardens in their nests, and obtain cellulase mainly from the fungi (Abo-Khatwa 1978; Martin and Martin 1978). Furthermore, the fungi of *Termitomyces* also produce lignin-degrading enzymes (Rohrman and Rossman 1980), and the repetition of the cyclic process formed by the cultivation of fungi by faeces and the reingestion of old portions of fungus gardens, which contain plant materials partially degraded by fungi, results in a complete decomposition of plant litter.

In the tropical forests, termites consume mainly dead plant materials such as fallen trunks, branches, leaves and humus, and they rarely attack living parts of trees (Abe 1979). The process of wood decomposition by termite activity is an interesting one. Termites transfer into wood a lot of soil that contains microorganisms with cellulases and probably lignin-decomposing enzyme. The part of

Table 2. Estimates of consumption by termite populations derived by combining field measurements and calculation from mean weight-specific rate of consumption, based on Josens (1972), Lepage (1974), Wood and Sands (1978), Wood and Sands (1978), Matsumoto and Abe (1978) and Collins (1981, 1983).

| Locality (Subregion) <i>Sources of litter</i> | Annual rain fall (mm) | Total litter (g/m ²) | <u>Litter consumed by termites</u> | | | |
|---|-----------------------------|--|------------------------------------|------------------------|---------------------|------------------------|
| | | | <u>Field measurements</u> | | <u>Calculated</u> | |
| | | | (g/m ²) | (% of total litter) | (g/m ²) | (% of total litter) |
| Sahel savanna, Senegal | 375 | 125 | 12.5 | 10.0 | 18.4 | 14.7 |
| S. Guinea savanna, Nigeria | 1115 | 533 | 189 | 35.3 | 179 | 33.5 |
| <i>Wood</i> | | 139 | 84 | 60.1 | | |
| <i>Leaves</i> | | 239 | 6.8 | 2.8 | | |
| <i>Grass</i> | | 155 | 98 | 63.2 | | |
| Derived savanna, Ivory Coast | 1290 | 480 | 135 | 28.1 | 24.2 | 5.0 |
| Rain forest, West Malaysia | 2000 | 1276 | | | 155-173 | 12.2-13.6 |
| <i>Leaves</i> | | 703 | 150-200 | 24-32 | | |
| <i>Wood</i> | | 573 | | | | |
| Rain forest East Malaysia | | | | | | |
| (Kerangas) | 5698 | 1050 | | | 35 | 3.4 |
| (Alluvial) | 5087 | 1280 | | | 11 | 0.9 |
| (Dipterocarp) | 5107 | 960 | | | 20 | 2.1 |

wood in contact with the soil becomes soft enough to be easily removed by termites. Most of fallen trunks and branches seem to be decomposed rapidly by a termite-microorganism complex (Abe 1980).

In temperate forests and grasslands, plant litter is decomposed in several stages (Burges 1967; Dickinson and Pugh 1974; Collins 1981). After development of phylloplane microflora, the litter is colonized by saprophytic microorganisms and the degradation of plant polysaccharides by them is essential for soil invertebrates to begin to feed. The litter is then comminuted and ingested by soil invertebrates, and litter fragments and invertebrate faeces are incorporated into the soil, where further microbial actions result in the formation of humus. In other words, the litter decompositions by microorganisms and soil animals proceed "sequentially" in temperate regions. In contrast, the ability of many termites to feed on fresh litter opens up a completely new pathway in the tropical decomposition process (Wood 1976; Collins 1981). Litter decomposition by microorganisms and soil animals proceeds "concurrently" in the tropical regions where fresh litter feeding termites are abundant and this may enhance the rate of litter decomposition, although the accelerating effect of

high temperature on microorganisms' activity in these regions must also be taken into account (Anderson and Swift 1983).

In spite of their ability to consume cell-wall components, few termites attack living trees in the forest, although in the savanna, a significant proportion of termites consume living grasses (Lee and Wood 1971; Abe 1979;). In this context, it is noteworthy that some species of termites are serious pests of agricultural plants (Harris 1961). For example, in Malaysia termites are pests of rubber trees and tea bushes (Dhanarajan 1969; Tho 1974), and in Zambia they are pests of Eucalyptus trees (Nkunika 1980). Interestingly, those agricultural plants attacked by termites are all introduced species. Although little is known about whether the same plant species are attacked by termites in their native habitats, an observation by the first author of this essay suggests that Eucalyptus trees in Australia, their native lands, are not attacked so severely as in Africa and India. Abe and Watanabe (1983) showed that two species of termites which consume only dead wood and/or fallen leaves in a subtropical rain forest began to attack cassava (an introduced plant) in cultivated areas adjacent to the forest. Although chemical information is lacking, one possible explanation to this phenomenon is that a native tree species which coexists with a species of termites has developed a chemical defence against that species of termites.

NESTED SYMBIOSIS: THE ROLE OF THE TERMITE IN COMMUNITY STRUCTURING

The trophic interactions (i.e., interactions of nurturing) surrounding termites, as have been discussed, constitute two cycles of different scales: the larger one is the nutrient (mineral) cycling of the entire ecosystem scale formed by the primary producer (autotrophs, plants), the litter, the decomposer, including termites, and nutrient pool, whereas the smaller one is the cycle formed by the termite and its symbionts (protozoa or bacteria and fungi) in their exchange of cell-wall materials gradually decomposed in the transfer (Fig. 3). The larger cycle might be developed, to increase flows and build up the standing stocks of its living components, the primary producer and decomposer, through the coadaptation or coevolutionary process between these two components (for more details on this point, see Higashi et al. in this report). The smaller cycle may be also developed through an analogous process of coevolution between the termite (host) and its symbionts (guest), to enhance their symbiotic (mutualistic) interaction. Then, the termite would play the conjunctive point through which the development of these two cycles are interrelated.

As an example of this linked development of the two cycles, we might consider the following situation: An increase of the symbiotic reward from the termite's guest (symbiont) to the host (termite) induces (or evolutionarily favors or selects) an increase of the litter processing effort by the termite, which in turn enhances the primary producer's production effort (or evolutionarily selects a producer with a higher production rate). This would further enhance the decomposer (termite)'s litter processing effort, which would in turn induce an increase of the symbiotic reward from the termite's guest to the host termite. In this example, tracing the temporal development along an evolutionary causal chain, we find ourselves in the smaller cycle at first, then switch into the larger cycle, and later comes back to the smaller cycle again. It illustrates a typical manner in which the coevolutionary development of the two cycles are interconnected.

Noting the scale and magnitude of the impact that the termite has in terrestrial communities, particularly in tropical regions, these two interconnected cycles, "nested symbiosis", appear to constitute the infrastructure on which an entire terrestrial community is built up in the tropics. A central feature of the infrastructure of a community is represented by the larger cycle formed by the primary producer, the litter, the decomposer, and nutrient pool. In comparison between temperate and tropical regions, we have pointed out that the internal structure of the decomposer subsystem in this cycle serves for a clear distinction; it has a "sequential" structure in decomposition of dead plant materials by microorganisms and soil animals in the former, whereas a "concurrent" structure in the latter, due to the smaller cycle of decomposition made by the soil animals, mainly termites, associated with symbiotic microorganisms, beside other decomposers, resulting in higher total decomposing efficiency of the decomposer subsystem, which might in turn lead, through the coevolutionary mechanism between the primary producer and the decomposer, to a greater primary production than would be expected solely from physiological response of the plant to a higher temperature and solar radiation.

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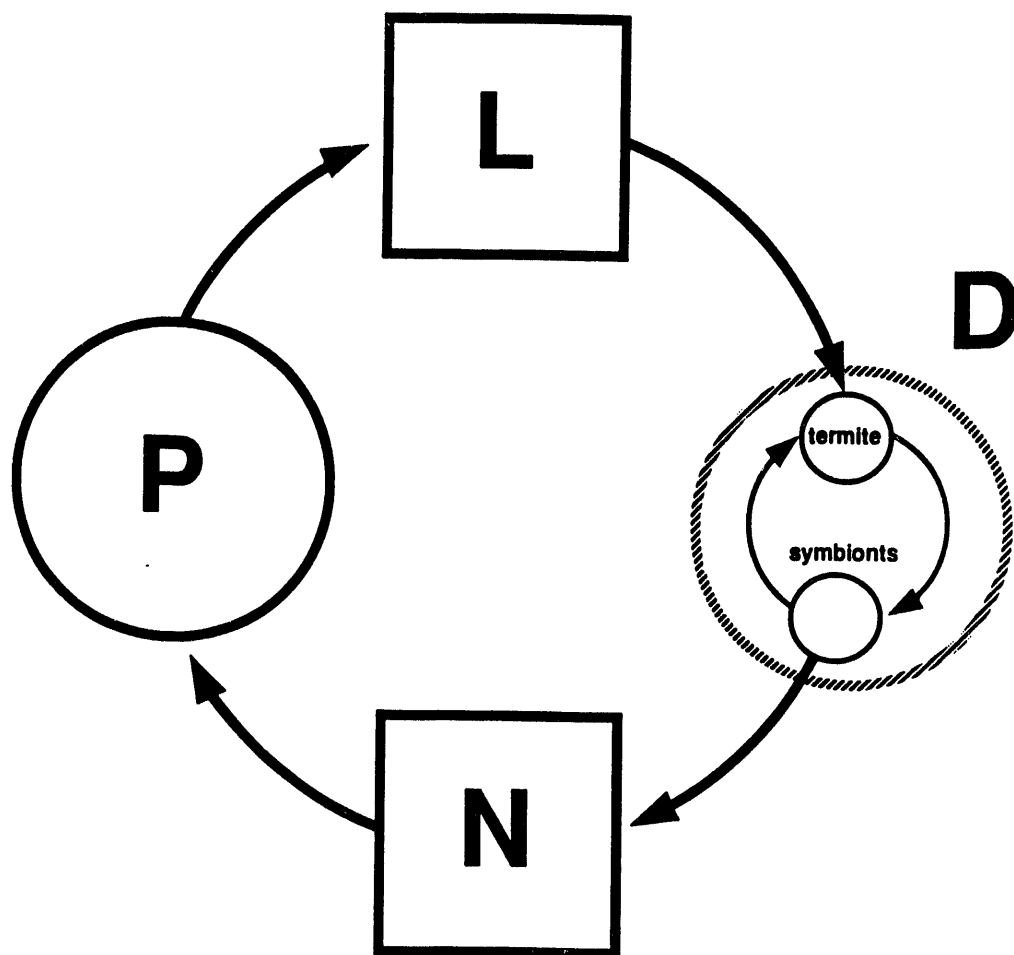


Figure 3. The two cycles of trophic interactions involving termites. The larger cycle represents the nutrient cycling of the entire ecosystem scale formed by the primary producer, the litter, the decomposer, including termites, and nutrient pool, whereas the smaller one is the cycle formed by the termite and its symbionts in their exchange of cell-wall materials gradually decomposed in the transfer.

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NON-NEWTONIAN CAUSALITIES IN ECOSYSTEM DEVELOPMENT

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Ecodynamics differ from the more familiar Newtonian dynamics in that they result in part from causes that are not wholly mechanical or material in nature.

In the aftermath of Newton there followed a concerted effort by natural philosophers to limit consideration of the causes of phenomena to only mechanical (efficient) and material agents. The neo-Darwinian view of evolution and development remains within these Newtonian confines, but only at the expense of assuming that the developing system is cybernetically decoupled from its environment. As ecology is concerned specifically with the interaction between the biological system and its environment, one might ask whether causes of ecological events are strictly newtonian in nature and, if not, whether one can describe ecodynamics in a rational and quantitative fashion?

Prior to Newton one of the most influential Western thinkers to write about causality was Aristotle, who suggested that causes in nature are usually not simple. A single event may have several simultaneous causes, and Aristotle taught that any cause could be assigned to one of four categories: (1) material, (2) efficient, (3) formal, and (4) final. For example, in building a house the material cause resides in the bricks, lumber and other tangible elements that go into its structure. The efficient cause is provided by the laborers who actually assemble these materials. The design or blueprints are usually taken as the formal cause, and the need for shelter on the part of those who contracted for the construction is considered to be the final agent.

Autocatalytic feedback is an example of formal cause at work in living systems. By autocatalysis is meant a cyclical configuration of two or more processes or entities wherein the activity of each member positively catalyzes the activity of the next element in one direction around the loop. At first glance it might appear that autocatalysis can be readily decomposed into its material and efficient components, but further reflection reveals otherwise. Autocatalysis (AC) possesses at least six properties that reveal its stature as a formal agency. (1) As the prefix "auto" suggests, AC is to at least some degree autonomous of its composite parts. Whenever the network of causal influences can be mapped, it becomes feasible to identify and enumerate all the circular causal routes. Furthermore, if the individual links can be somehow quantified, it is then possible to separate abstractly the autocatalytic nexus from the supporting tree of causal events upon which it remains contingent (Ulanowicz 1983). (2) If one observes only a subset of the elements in an autocatalytic cycle, these components form a distinctly nonautonomous chain. However, if one increases the scale of observation to include all the members of the cycle, AC is seen to emerge as a phenomenon. (3) By its very nature AC serves to accelerate the activities of its constituents, i.e., it is growth-enhancing. (4) Chance perturbations in any element of a loop that enhance AC are themselves enhanced, and vice-versa. That is, AC exerts selection pressure upon deviations in the loop to foster only those characteristics which contribute to the ensemble behavior. It is a short step from selection for character traits to selection among possible replacement components. Once one recognizes that the ensemble exerts selection upon its replacement parts, it becomes clear that the characteristic lifetime

of the configuration exceeds that of any of its parts, and selection becomes a key element of the autonomy mentioned in (1) above. In particular, changes in any element that result in its drawing increased resources into the loop will be rewarded, giving rise to a central tendency, or, as Denbigh put it, a form of "chemical imperialism". (5) Both selection and central tendency result inevitably in competition for resources among multiple AC loops. The result is an ever-more streamlined, or articulated topology of interactions. (6) Finally, AC is manifestly the result of a dynamical structure, thereby making it formal in nature. The six properties of AC constitute a strong case that it be considered a formal agent. In the absence of major, destructive perturbation AC serves to increase the level of activity of the system (an extensive effect), while at the same time it prunes the less effective causal pathways from the network (an intensive result). It remains to quantify the dual effects of this unitary agency. Towards this end it is useful henceforth to confine discussion to networks of material or energy transfers as they occur in ecological communities or in other systems of interest. Thus, the activity level of the system becomes synonymous with the magnitude of the aggregate transfers occurring in the network. This latter sum is known in economic theory as the total system throughput (TST), a term which has carried over into ecology (Hannon 1973).

Quantifying the tendency towards an ever more articulated network topology is a slightly more difficult proposition. Suffice it here to note that in more articulated, or highly defined networks there is less uncertainty as to which medium at any given mode will flow next. Less uncertainty implies more information, and Rutledge et al. (1976) show how the average mutual information (AMI), as estimated from the relative magnitudes of the flows, captures the degree of articulation inherent in the flow topology.

However, the AMI, being an intensive attribute, lacks physical dimensions. It is, nonetheless, multiplied by a scalar constant which can be used to give dimensions to the measure (Tribus and McIrvine 1971). Thus, scaling the AMI by the total system throughput gives rise to a quantity known as the network "ascendency"--a surrogate for the "efficiency" with which the system processes the medium in question. Because any increase in the level of activity can be characterized as growth (e.g., the increase in the gross national product of a country's economy), and because the augmented definition of its topology may be termed development, an increase in the product of the TST by the AMI (the ascendency) serves to measure the unitary process of growth and development (Ulanowicz 1986).

Of course, growth and development can never continue unabated, and the limits to a system's rise in ascendency can be quantified using similar quantities from information theory. The AMI, for example, is bounded from above by the Shannon-Wiener index of uncertainty. Scaling this latter measure by the TST yields a quantity called the development capacity--a measure of the size and complexity of the network. The limits to rising development capacity (and also to ascendency) are recognizable from the mathematical form of the development capacity. One constraint is the finitude of external sources available to the system. A second limitation exists on the number of compartments. Disaggregation cannot continue beyond a point where the finite resources become spread over too large a number of categories. Otherwise, some compartments would come to possess so little resources that they would be highly vulnerable to chance extinction by the inevitable perturbations to which any real system is always subjected.

Even if the development capacity has leveled off, the ascendancy may continue to increase by diminishing the amount by which it falls short of the capacity, a difference called the "overhead". The overhead in turn can be traced to four sources: (1) the multiplicity of external inputs, (2) the exports of usable medium from the system, (3) the dissipations inherent in the activities at each node and (4) the redundancy among various pathways joining any two arbitrary compartments. Rather than being an unmitigated encumbrance upon the system's performance, the overhead is seen at times to be essential for system persistence. That is, diminishing any term in the overhead beyond some unspecified point will eventually place the given system at risk. For example, relying completely upon a single external source of medium makes the system highly vulnerable to chance disruptions in that source. Similarly, it would be counterproductive to cut back on exports which might be coupled autocatalytically to the system's inputs at the next higher hierarchical level. Furthermore, the resources that are dissipated at each node often underwrite structural maintenance at a lower level of the hierarchy. It would be detrimental to decrease such support to very low levels, even if such arbitrary cutbacks were thermodynamically feasible (which they are not). Finally, a channel of flow between two nodes or species having no redundant backup is susceptible to disruption by perturbation in the same way as discussed above for the external sources.

The quantitative description of growth and development is far from complete, and there are numerous opportunities for US-Japanese collaboration in extending the theory. For example, the AMI is estimated using only direct interactions, and investigators such as Patten argue that indirect influences are cardinal to any description of ecodynamics. To incorporate indirect influences into the ascendancy measure Magahiko Higaski (personal communication) has suggested using information theory as applied to fuzzy sets. Other expansions upon the ascendancy narrative include how to define the measure for a system in which more than one medium is circulating (as is inevitably the case), or how best to implement the principle of increasing ascendancy as a problem in operations research (Cheung 1985).

Finally, it should be acknowledged that ascendancy theory stands upon a very sparse inventory of data. A comparative study of selected Japanese and American ecosystems would be a very desirable objective for a cooperative research program and should further test the suitability of this still unconventional way to describe living phenomena.

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SENSITIVITY AND STABILITY OF FLOW NETWORKS

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ABSTRACT

The input sensitivity is defined by the ratio of the steady state change to the amount of an extra input added to the system. This sensitivity gives us information relating to dynamical properties about steady states, because the input sensitivity matrix has a simple relation with the coefficient matrix obtained by linearization of the dynamical system. The interactive structures of the system are reflected in the input sensitivity of steady state introduced here, thus the analysis of this sensitivity offers a key to understanding other sensitivities; for example, parameter sensitivity, inter-flow sensitivity, etc. Indirect effects among elements can also be estimated in the context of input sensitivity as the accumulation of effects along all possible paths of interactive links from one compartment to another. The relationship between two concepts of stability, resilience and resistance, is discussed in terms of input sensitivity. For donor-dependent systems, it is found that these stability properties are closely related to each other.

INTRODUCTION

Dynamical system approaches have attained great success in the analysis of systems consisting of small numbers of elements. For example, the population dynamics approaches have had fruitful results (e.g., on periodic phenomena, catastrophic change, and stability of steady state) for simple ecological systems (e.g. May (1973)). However, dynamical system approaches are not the most suitable for complex systems, because we cannot get enough information about interactions among elements of a system to describe its precise dynamical behavior.

Cohen (1978, 1989) discussed the structure of food webs in terms of feeding relations without requiring knowledge of flow amounts from prey to predators. He used a topological rule in the structure of prey-predator relations and derived from a simple model scale invariant laws which many food webs satisfy. His work gives us an idea about underlying laws relating to predator-prey connections in food webs. On the other hand, flow analysis of ecological systems was developed by Patten et al. (1976) and Finn (1976) to estimate how elements of the system control each other through flows. An extension of the analysis given by Patten and Higashi (1984) and Higashi (1986a) took into account storage as well as flow to get information on the interaction between storage and flow. Results associated with residence time (Higashi 1986b) and degree of cycling (Finn 1976, Patten and Higashi 1984) were obtained from these analyses, though the analyses were concerned only with steady states. However, these analyses contain no information about dynamic aspects such as dynamic control and dynamic stability.

Knowledge of dynamical properties of a system is useful for understanding the interactive structure of the system, beyond that gained through the study of steady states. Element controls and stability are important characteristics of an ecological system in steady state, since these factors affect the formation of interactive structure in the succession or evolutionary process of the system

(Nakajima 1985). Puccia and Levins (1985) developed loop analysis which provides the bridge between networks and their representations as dynamical systems.

As an extension of their work, we here introduce the input sensitivity analysis of steady states, which measures the change of a steady state due to an extra input added to one element of the system.

From this sensitivity, knowledge can be obtained on dynamical properties about the steady state of the system. This analysis may give us insight into dynamical properties for complex systems.

INPUT SENSITIVITY ANALYSIS

We consider a flow network consisting of n compartments, and the interflows, inputs, and outputs associated with each of them. Let x_i denote storage of compartment i . We denote interflow from compartment i to j by f_{ji} . It is assumed that each flow f_{ji} depends on storage x_1, \dots, x_n and parameters p_1, \dots, p_m . We have the following dynamical equation for each storage,

$$\frac{dx_i}{dt} = \sum_{j=0}^n f_{ij} - \sum_{j=0}^n f_{ji}, \quad (i=1, \dots, n), \quad (1)$$

where f_{i0} and f_{0i} are input and output of the i^{th} compartment, respectively (i.e. compartment 0 represents the environment of the system). At a steady state, total inflow equals total outflow for each compartment; that is,

$$\sum_{j=0}^n f_{ij} = \sum_{j=0}^n f_{ji}, \quad (i=1, \dots, n). \quad (2)$$

Now, we add a small amount of input Δz_j to compartment j . When this extra input is added to the system, the steady state storage for each compartment changes to $x_i + \Delta x_i$ ($i=1, \dots, n$), according to the following steady state condition,

$$\sum_{j=0}^n f_{ij}(x_1 + \Delta x_1, \dots, x_n + \Delta x_n) + \Delta z_i = \sum_{j=0}^n f_{ji}(x_1 + \Delta x_1, \dots, x_n + \Delta x_n), \quad (3)$$

$$\sum_{j=0}^n f_{kj}(x_1 + \Delta x_1, \dots, x_n + \Delta x_n) + \Delta z_i = \sum_{j=0}^n f_{jk}(x_1 + \Delta x_1, \dots, x_n + \Delta x_n), \quad (k \neq i).$$

We call the ratio $\Delta x_i / \Delta z_j$ the sensitivity of x_i with respect to the change of input z_j . Let s_{ij} denote this sensitivity; that is,

$$s_{ij} = \lim_{\Delta z_j \rightarrow 0} \frac{\Delta x_i}{\Delta z_j}, \quad (i, j = 1, \dots, n), \quad (4)$$

and let S be the matrix whose (i, j) element is s_{ij} ; i.e., $S = (s_{ij})$. We can also add an extra output to the system, which is treated simply as a negative extra input; i.e., $\Delta z_j < 0$. We assume here the following continuity of $\Delta x_i / \Delta z_j$:

$$\lim_{\Delta z_j \rightarrow +0} \frac{\Delta x_i}{\Delta z_j} = \lim_{\Delta z_j \rightarrow -0} \frac{\Delta x_i}{\Delta z_j} \left(= \lim_{\Delta z_j \rightarrow 0} \frac{\Delta x_i}{\Delta z_j} \right), \quad (i, j = 1, \dots, n). \quad (5)$$

Let matrix A be the coefficient matrix deduced from the linearization of dynamical system (1) about the steady state; i.e., elements of this matrix, a_{ij} , satisfy the following equation:

$$a_{ij} = \frac{\partial}{\partial x_j} \left(\sum_{k=0}^n f_{ik} - \sum_{k=0}^n f_{ki} \right), \quad (i, j = 1, \dots, n), \quad (6)$$

where partial derivatives are evaluated at the steady state. This matrix A is usually called the community matrix in community ecology. When an extra input is added, steady state conditions (3) are satisfied, thus we have

$$d \left(\sum_{k=0}^n f_{ik} - \sum_{k=0}^n f_{ki} \right) = -\partial_{ij} dz_j, \quad (i = 1, \dots, n). \quad (7)$$

From the Taylor expansion of the left-hand side of Eq. (7), we get

$$\sum_{k=1}^n a_{ik} dx_k = -\partial_{ij} dz_j, \quad (i = 1, \dots, n). \quad (8)$$

Thus, we have the following simple relationship between the input sensitivity matrix S and the community matrix A :

$$S = -A^{-1}. \quad (9)$$

The influence of an extra input spreads throughout the whole system until the system reaches a new steady state. Thus, sensitivity is the accumulation of influences made by the extra input at every

moment on each compartment. Therefore, Eq. (9) can be interpreted in the following way: If an extra input Δz_j is added during the small time interval Δt , its influence on storage x_i is equal to

$$(e^{At})_{ij} \Delta z_j \Delta t \quad (10)$$

after time interval t . The change of storage x_i due to an extra input Δz_j can be expressed as the integral of Eq. (10) from the infinite past to the present, thus we have

$$\Delta x_i = \int_{-\infty}^0 (e^{-At})_{ij} \Delta z_j dt = (-A^{-1})_{ij} \Delta z_j. \quad (11)$$

This relationship means that sensitivity equals the total effect of an extra input added to the system throughout the infinite time interval. From Eq. (11), Eq. (9) follows.

According to Eq. (9), the community matrix can be obtained from the sensitivity matrix. The sensitivity s_{ij} can be obtained from the measurement of change in storage x_i , when a constant input to compartment j is introduced for a long period compared to relaxation time. The change in x_i is measured after the influence of this injection spreads over the system. These measurements are easier than the measurements of the elements of community matrix, because in the latter case, measurements should be made before the influence of injection spreads to other compartments of the system; i.e., before compartments other than i get no influence from compartment j .

When a system has more than one extra input, we have

$$dx = S dz, \quad (12)$$

where

$$dx = \begin{pmatrix} dx_1 \\ \vdots \\ dx_n \end{pmatrix}, \quad dz = \begin{pmatrix} dz_1 \\ \vdots \\ dz_n \end{pmatrix}. \quad (13)$$

When one of the system parameters is changed by a small amount, the steady state is also altered. We get the following relationship between the change of parameter p_i and the steady state change,

$$dx = S df, \quad (14)$$

where

$$d f = \begin{pmatrix} \frac{\partial}{\partial p_l} \left(\sum_{k=0}^n f_{1k} - \sum_{k=0}^n f_{k1} \right) \\ \frac{\partial}{\partial p_l} \left(\sum_{k=0}^n f_{2k} - \sum_{k=0}^n f_{k2} \right) \\ \vdots \\ \frac{\partial}{\partial p_l} \left(\sum_{k=0}^n f_{nk} - \sum_{k=0}^n f_{kn} \right) \end{pmatrix} dp_l, \quad (15)$$

This equation means that the storage changes due to a parameter change are expressed by the products of the sensitivities of storage with respect to the extra input and the flow changes due to the parameter change. The sensitivity matrix S reflects the structure of connections among elements, and has nothing to do with the sensitivities of flows with respect to parameters. Flow changes $d_i f$ are caused by parameter change dp_l , and have no influence from any storage changes. Equation (15) implies that effects of the flow changes due to parameter change dp_l spread into the system, and that this propagation is described by the sensitivity matrix S , so that the storage changes are equal to the product of S and $d_i f$.

When a parameter p_l has an influence on only interflow f_{ij} , we obtain the sensitivity with respect to interflow from Eq. (15):

$$dx_k = (s_{ki} - s_{kj}) \frac{\partial f_{ij}}{\partial p_l}, \quad (k = 1, \dots, n). \quad (16)$$

Interflow f_{ij} has direction from j to i , thus compartment i has a positive effect from this interflow and compartment j has a negative one.

DIRECT AND INDIRECT EFFECTS

Input sensitivity gives us a better understanding of mutual effects among elements, especially in systems which have cycles of effects, because this sensitivity consists of total effects among compartments including direct and indirect effects. Here, we define the direct effects in the sense of steady state,

$$d_{ij} = \left(\frac{\partial x_i}{\partial x_j} \right)_{x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_{j-1}, x_{j+1}, \dots, x_n}, \quad (i, j = 1, \dots, n; i \neq j). \quad (17)$$

When an extra input is added to compartment j , storage of this compartment changes, and other compartments receive the effects of this storage change. The suitable extra inputs (positive or negative) are added to compartments other than i and j , to keep storage levels of those compartments constant. These extra inputs absorb the effects of compartment j on compartments other than i and j , thus compartment i has no effect from other compartments except j . If no extra input is added to compartment i , then compartment i has the effect only from compartment j . We consider Eq. (17) as the direct effect from j to i , in the sense of the steady state.

We say that

$$d_{ii} = 0, \quad (i = 1, \dots, n). \quad (18)$$

Every compartment has the temporal direct effect on itself, which corresponds to the diagonal elements of the community matrix, a_{ii} . However, every compartment has no direct effect on itself in the steady state, because storage of a compartment does not change without the effect of an extra input to this compartment and the effects of all other compartments. From Eqs. (7) and (18) for compartment i with conditions $dx_k=0$ ($k \neq i, j$), we have

$$d_{ij} = -\frac{a_{ij}}{a_{ii}} + \partial_{ij}, \quad (i, j = 1, \dots, n). \quad (19)$$

If every compartment has self regulation, that is, $a_{ii} < 0$ for all i , then each steady state direct effect has the same sign as the corresponding temporal direct effect. In this case, the structure of the steady state direct effects preserves the sign relationship of interactions in general dynamical systems. Direct effect matrix D consists of elements d_{ij} .

The direct effects from the environment of a system can be estimated in the same way as direct effects among compartments. We define d_{j0} as

$$d_{j0} = \left(\frac{\partial x_j}{\partial z_j} \right)_{x_1, \dots, x_{j-1}, x_{j+1}, \dots, x_n}, \quad (j = 1, \dots, n). \quad (20)$$

From Eq. (7) for compartment j with conditions $dx_k=0$ ($k \neq j$), we have

$$d_{j0} = -\frac{1}{a_{jj}}, \quad (j = 1, \dots, n). \quad (21)$$

The matrix of environmental direct effects \tilde{D} is a diagonal matrix whose elements are d_{j0} . We have a relationship among community matrix A , direct effect matrix D , and the environmental direct effect matrix \tilde{D} ,

$$D = \tilde{D}^{-1}A + I. \quad (22)$$

Matrix \tilde{D} represents the direct effects of extra inputs added to the system on the compartments having the extra input. Matrix product $D\tilde{D}$ represents the effects of extra inputs on each compartment through a link from the compartment having an extra input to the compartment under consideration. Matrix $D^2\tilde{D}$ represents the sum of the effects from an extra input along all paths having two links, say $j \rightarrow k \rightarrow i$, where compartment j has an extra input, i is the compartment under consideration, and compartment k has a link from j and a link to i . Thus, the total effects of the extra input is the sum of the power series,

$$\tilde{D} + D\tilde{D} + D^2\tilde{D} + D^3\tilde{D} + \dots = (I - D)^{-1}\tilde{D}. \quad (23)$$

From Eqs. (22) and (23), we get

$$\tilde{D} + D\tilde{D} + D^2\tilde{D} + D^3\tilde{D} + \dots = -A^{-1} = S. \quad (24)$$

In the previous section, the input sensitivities are interpreted as total effects with respect to time [cf. Eq. (11)]. Another interpretation of the input sensitivities can be given here; namely, the total effects along all possible paths from one compartment to another.

We have direct effects from extra input itself and from other compartments due to extra inputs, as follows

$$\tilde{D} + D\tilde{D}. \quad (25)$$

From Eqs. (24) and (25), we get indirect effects due to extra inputs

$$D^2\tilde{D} + D^3\tilde{D} + \dots = S - (I + D)\tilde{D}. \quad (26)$$

Applying the operator \tilde{D}^{-1} to the right-hand side of Eq. (26) from the right, we have indirect effects

$$S\tilde{D}^{-1} - I - D. \quad (27)$$

Equation (27) can be also interpreted as the indirect effects between one compartment and another, which can easily be compared with direct effects defined by Eq. (17).

INPUT SENSITIVITY OF DONOR-DEPENDENT SYSTEMS

In donor-dependent systems, all flows depend only on the storage of donors; that is,

$$f_{ij} = f_{ij}(x_j), \quad (i = 0, 1, \dots, n; j = 1, \dots, n). \quad (28)$$

Inputs depend on the state of environment, but this state is assumed constant so that all inputs are assumed constant. We also assume that the amount of each flow increases when storage of the donor increases; i.e. the flows $f_{ij}(x_j)$ are increasing functions of x_j . Therefore, we have

$$b_{ij} = \frac{df_{ij}}{dx_j} \geq 0, \quad (i = 0, 1, \dots, n; j = 1, \dots, n), \quad (29)$$

where equalities hold when the flows are identically equal to zero. From Eqs. (6) and (29), we obtain the community matrix, as follows:

$$A = \begin{pmatrix} -\sum_{k=0}^n b_{k1} & b_{12} & \dots & b_{1n} \\ b_{21} & -\sum_{k=0}^n b_{k2} & \dots & b_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ b_{n1} & b_{n2} & \dots & -\sum_{k=0}^n b_{kn} \end{pmatrix}. \quad (30)$$

Diagonal elements of this community matrix are negative, and its off diagonal elements are nonnegative. This community matrix is diagonal dominant, because the sum of all elements in each column is negative. Thus, $-A$ is the so called M -matrix (cf. Chapters 6 and 9 of Berman and Plemmons (1979)). According to a theorem on M -matrices, matrix $S = -A^{-1}$ is nonnegative and the following relations hold:

$$s_{jj} \geq s_{ij} \quad (i, j = 1, \dots, n). \quad (31)$$

From the above nonnegativity of sensitivity matrices and Eq. (31), we have the following results: "There is no negative sensitivity in donor-dependent systems"; "The compartment having an extra input receives the greatest influence of this extra input among all compartments in the system, so that influences decrease along the paths of interaction links".

Now, we analyze the effects of interflow changes on each storage. Let p_{ij} be the parameter in a function of interflow from j to i , namely f_{ij} . From Eq. (16), we have

$$dx_k = (s_{ki} - s_{kj}) \frac{\partial f_{ij}}{\partial p_{ij}} dp_{ij} \quad (k = 1, \dots, n). \quad (32)$$

The storage change of compartment i has the same sign as the interflow change $(\partial f_{ij} / \partial p_{ij}) dp_{ij}$, because $s_{ii} - s_{ij}$ is positive according to inequality (31). On the other hand, the storage change of compartment j has the opposite sign to the interflow change, because $s_{ij} - s_{jj}$ is negative according to

inequality (31). When the interflow is increased by the parameter change, the direct effect of this interflow change on compartment j decreases the storage of compartment j , since compartment j is a donor of this interflow, and the outflow of compartment j increases. The compartment j has indirect effects through other compartments. However, the total effects on j decrease storage of compartment j , even if indirect effects on compartment j increase storage of compartment j . The storage change of other compartments depends on the difference of the sensitivity from i and j to each compartment under consideration.

In donor-dependent systems, the input sensitivity matrix agrees with matrix $-(A'')^{-1}$ in the environ analysis proposed by Matis and Patten (1981). The storage of every compartment is divided by the portion originally coming from each input, in the following way:

$$x = -(A'')^{-1}z, \text{ where } x = (x_1, \dots, x_n)^t, z = (f_{10}, \dots, f_{n0})^t. \quad (33)$$

RESILIENCE AND RESISTANCE

There has been much discussion on the relationship between the complexity and stability of ecosystems, since MacArthur (1955) and Elton (1958) and especially May (1973) came to a conclusion conflicting with earlier studies. However, confusion arose through use of the same word in different senses. Pimm (1984) listed several concepts on stability and complexity to clear away this confusion. Here, we focus on two stability concepts, resilience, and resistance.

The resilience of a system refers to how fast the system returns to an original steady state following a perturbation. This stability concept is a characteristic of the system, and can be defined as the reciprocal of the time taken for the system to damp the deviation from the steady state by $1/e$. Resistance is defined as the degree to which a state variable is changed following a perturbation. This stability is concerned with each state variable in the system and not with the whole system. It also depends on what parameter or component of the system is perturbed. We now derive mathematical expressions for these stability concepts. Let λ_m be the eigenvalue having the maximum real part in all eigenvalues of community matrix A . Let the left and right eigenvectors of λ_m be denoted by u' and v , respectively. These eigenvectors satisfy the following equations:

$$u'A = \lambda_m u', \quad Av = \lambda_m v. \quad (34)$$

Let T_m denote return time of the system. We have the following relationship between λ_m and T_m ,

$$T_m = -\frac{1}{\text{Re}\lambda_m}. \quad (35)$$

Equation (35) represents resilience, since resilience can be estimated by the return time, T_m , of the system. Another type of stability, resistance, can be interpreted as the reciprocal of the input sensitivity; i.e., $1/s_{ij}$ represents the resistance of compartment i to the input change of compartment j . From Eqs. (14) and (15), the resistance of compartment i to the change of parameter p_i can be defined as

$$\frac{1}{\sum_{j=1}^n s_{ij} \frac{\partial}{\partial p_i} \left(\sum_{k=1}^n f_{jk} - \sum_{k=1}^n f_{kj} \right)} \quad (36)$$

Resilience and resistance express the degree of stability, and the changes of these degrees of stability are calculated from the above results. Taking the derivative of the first equation of Eq. (34) and multiplying vector v to both sides of the equation from the right, we have

$$(du^t)Av + u^t(dA)v = (d\lambda_m)u^t v + \lambda_m(du^t)v. \quad (37)$$

From the second equation of Eq. (34) and simple algebra, we get

$$d\lambda_m = \frac{u^t dA v}{u^t v}. \quad (38)$$

From Eq. (9), it is clear that if λ , u^t , and v are an eigenvalue of the community matrix, and left and right eigenvectors of this eigenvalue, respectively, then $-1/\lambda$ is an eigenvalue of the corresponding sensitivity matrix, and u^t and v are also left and right eigenvectors, respectively, of the sensitivity matrix for eigenvalue $-1/\lambda$. In donor-dependent systems, $-A$ is the M -matrix. From Kellogg's (1972) theorem, λ_m is real, and $T_m (= -1/\lambda_m)$ is the maximal eigenvalue of sensitivity matrix S . We have the following equation, corresponding to Eq. (38),

$$dT_m = \frac{u^t dS v}{u^t v}. \quad (39)$$

From the Perron-Frobenius theorem of nonnegative matrices (see e.g. chapter 2 of Berman and Plemmons (1979)), all elements of eigenvectors u^t and v are positive. Therefore, in donor-dependent systems, if one or more elements of the sensitivity matrix decrease, then the return time of the system also decreases. This means that a more resistant system is more resilient, in donor dependent systems.

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THERMODYNAMICAL ENTROPY IN ECOLOGICAL SYSTEMS

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ABSTRACT

The thermodynamical entropy concept is applied to ecological systems.

(1) Although entropy content of living systems has not been measured so far, entropy flow and entropy production - process variables - can be estimated from corresponding energetic data by use of some physical methods. Examples of entropy flow and entropy production in nature (white-tailed deer, plant leaf, lake, and the earth) are presented.

(2) Ecological systems can be considered to be composed of a number of compartments; flows among compartments constitute networks. The entropy concept is applied to the input-output flow analysis of ecological networks at steady state, and entropy laws in ecological systems are presented; these laws are stated in terms of network theory, that is, throughflow, total system throughflow, path length, and cycling index.

(3) The study of large and complex systems, such as lakes, may be approached in two different ways: holological (holos = whole) and merological (meros = part). As a holological study of lakes, monthly entropy productions of Lake Mendota (eutrophic) and the northern basin of Lake Biwa (oligo-mesotrophic) are investigated, and holological and entropic indices which characterize the lakes are determined. A comparative study of the two lakes suggests that processes of eutrophication or succession of lakes are accompanied by an increase in magnitude of these entropic indices. A hypothesis for the whole span of ecological succession is proposed.

INTRODUCTION

The energy concept, originated in physics, has been intensively employed in natural (and even social) science. In biological sciences, we can speak of bioenergetics, ecological energetics, or more specifically energy-flow analysis in ecosystems, as examples of the use of the energy concept. However, little has been known about implications of entropy in nature, although entropy is as important as energy from a thermodynamical viewpoint: the First Law of Thermodynamics is concerned with the concept of energy and the Second Law with entropy. Hence, the importance of the study from an entropy viewpoint should be emphasized.

The Second Law of Thermodynamics is the law of the entropy concept. It states for an isolated system that the change of entropy content of the system in irreversible processes (ΔS (irrev)) is always larger than that in reversible processes (ΔS (rev)), and the latter is zero:

$$\Delta S \text{ (irrev)} > \Delta S \text{ (rev)} = 0. \quad (1)$$

Since biological objects are not isolated systems, Eq. (1) can not be applied to biology. Biological systems are open systems which exchange energy and matter with their surroundings. For open systems, the change of entropy content of a system (ΔS) is the sum of two terms: entropy flow ($\Delta_e S$)

and entropy production (ΔS). The entropy flow is the entropy that is brought into or out of the system associated with flows of energy and matter, and the entropy production is the entropy that is produced by irreversible processes occurring within the system. The Second Law for open systems asserts that the entropy production in irreversible processes (ΔS (irrev)) is always larger than that in reversible processes (ΔS (rev)), and the latter is zero:

$$\Delta S \text{ (irrev)} > \Delta S \text{ (rev)} = 0. \quad (2)$$

Thus, the Second Law for open systems is formulated in terms of entropy production.

Entropy is produced anywhere at any time when processes are irreversible. The higher the irreversibility of a process, the more entropy produced. Hence, entropy production is a measure of the extent of irreversibility of processes. Since all motions and reactions actually occurring in nature are irreversible, entropy production is also a measure of the extent of activity of natural processes, which consists of physical activity (the strength of processes of heat flow and transportation of matter), chemical activity (the strength of chemical reaction) and biological activity (the strength of biological interaction).

Thermodynamical variables are divided into two classes: state variables and process variables. With regard to the entropy concept, the state variable is entropy content and the process variables are entropy flow and entropy production. As for the state variable, entropy content, it should be noted that no one has yet been able to measure it in living systems. It is questionable whether or not it will be measured in the near future. Hence, at present it is impossible to develop thermodynamical discussions based on measured entropy content of biological systems. However, entropy flow and entropy production - process variables - can be quantitatively estimated by use of some physical methods from observed energetic data of biological objects. Thus, we can develop entropy considerations based on values of entropy flow and entropy production obtained by calculations. Some examples of entropy flow and entropy production in nature are given in the next section.

EXAMPLES OF ENTROPY FLOW AND ENTROPY PRODUCTION

Figure 1 shows the entropy flows and the entropy production for a 50 [kg] white-tailed deer on a maintenance diet during a winter night (Aoki 1987a). The values are in units of [$J s^{-1} K^{-1}$]. The infrared radiation from the sky and from the ground is incident upon and absorbed by a white-tailed deer. The entropy inflow into the deer due to this infrared radiation is 1.66 units. The entropy of 0.46 units is produced by irreversible processes within the body of the white-tailed deer. The entropy outflow from the deer is 2.12 units, which consists of 1.82 units by emission of infrared radiation from the deer, 0.21 units by convection to the surrounding air, 0.07 units by evaporation of water from the skin and the lungs of the deer, and 0.02 units by heat conduction to ingested food.

The entropy flows and entropy production for a deciduous plant leaf under sunlight (the energy flux of solar radiation is $1.20 [cal cm^{-2} min^{-1}]$) are shown in Fig. 2 (Aoki 1987b). Units are $10^{-4} [J cm^{-2} s^{-1} K^{-1}]$. The entropy inflows into a leaf due to absorption of solar radiation and absorption of infrared radiation are 0.30 units and 2.87 units, respectively. The entropy production in a leaf is 1.79 units. The entropy outflow from a leaf is 4.96 units, which consists of 3.88 units by

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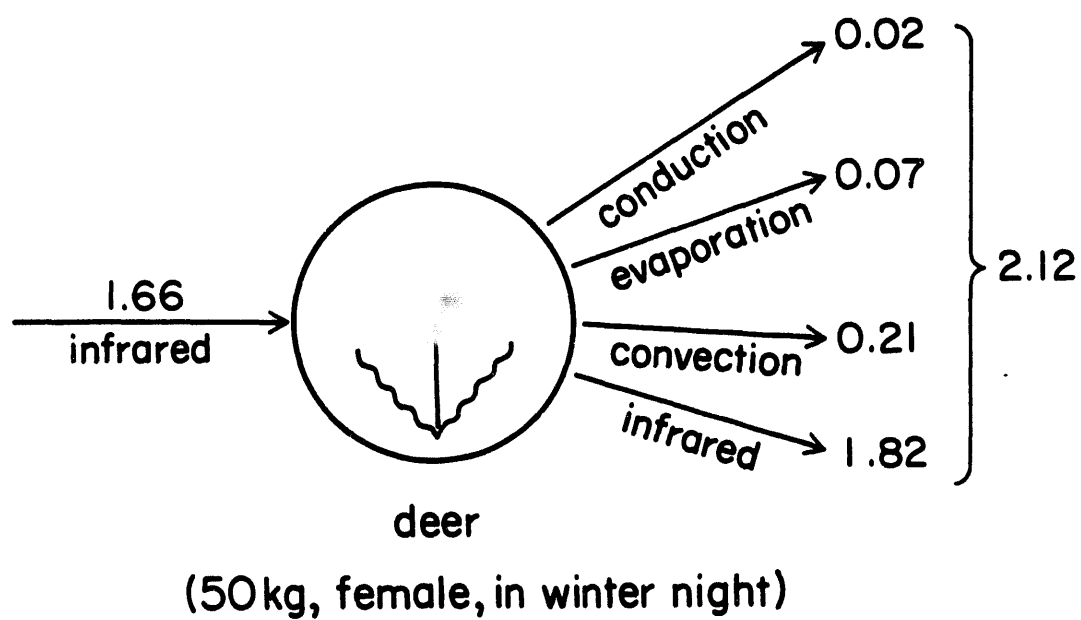
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Figure 1. Entropy flow and entropy production for a white-tailed deer during a winter night.

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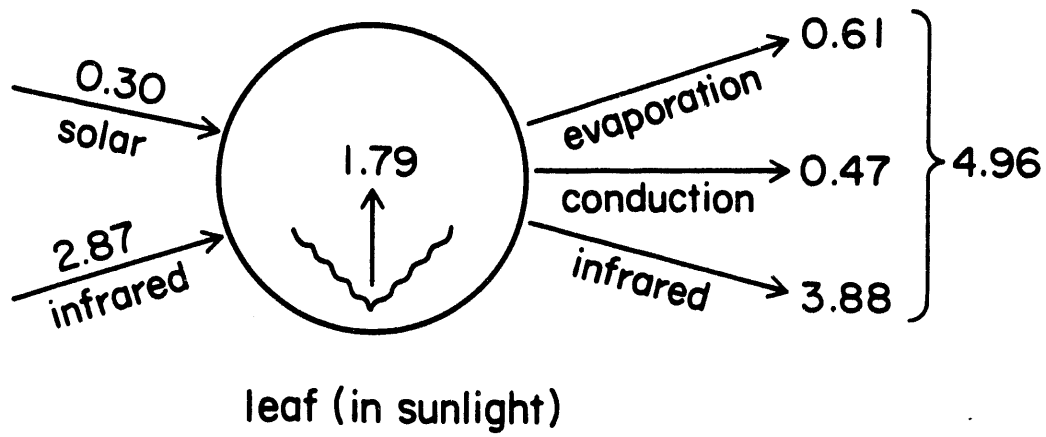
units : $10^{-4} [\text{Jcm}^{-2} \text{s}^{-1} \text{K}^{-1}]$ 

Figure 2. Entropy flow and entropy production for a deciduous plant leaf under sunlight.

emission of infrared radiation, 0.47 units by heat conduction and 0.61 units by evaporation of water. On the other hand, the entropy production in a leaf is nearly zero at night (Aoki 1987b, 1987c). It is shown that the entropy production in leaves is proportional to the solar radiation energy absorbed by leaves, which oscillates with a period of one day. Hence, the entropy production in leaves also oscillates, keeping pace with solar radiation. Since entropy production is a measure of activity as stated in the introduction, the activity of leaves is high during the day and almost zero at night. That is, a large portion of the activity in plant leaves is "on" during the day and "off" at night (except perhaps for CAM plants). Most of the activity in leaves may be triggered by solar radiation.

The annual values of entropy flow and entropy production per unit surface area of Lake Biwa (Japan), as an example of an ecosystem, are shown in Fig. 3 (Aoki 1987d). Units are [$MJ\ m^{-2}\ year^{-1}\ K^{-1}$]. This work is intended to treat a lake-ecosystem as a whole (holistic approach) from an entropy viewpoint. More detailed entropic studies of lakes are given in a later section. Figure 4 shows results of the entropy study of the whole earth (Aoki 1988a). Units are [$J\ cm^{-2}\ year^{-1}\ K^{-1}$]. The earth is considered here to consist of two compartments: the atmosphere and the earth's surface. The entropy inflow to each compartment is due to incident solar radiation, and the entropy outflow from each compartment is due to reflected solar radiation and infrared radiation emitted by each compartment. There is an extensive circulation of entropy between the two compartments. The ratio of the incoming entropy into the earth to the outgoing entropy from the earth is 1:18; the earth amplifies incoming entropy by 18 times.

In the above four cases, the net entropy flows into a white-tailed deer, a plant leaf, the lake, the atmosphere, and the earth's surface are all negative. That is, they absorb "negative entropy" (Schrödinger 1944) from the surroundings. This fact is the physical basis for organized structures and functions of organisms, ecosystems, or the earth to be maintained, as Schrödinger (1944) asserted.

Also, the entropy productions in the above cases are all positive. This shows that the Second Law of Thermodynamics holds in the above four cases, as is evident from Eq. (2). This is contrary to the erroneous arguments made earlier that the Second Law can not be applied to living systems.

ENTROPY LAWS IN ECOLOGICAL NETWORKS AT STEADY STATE

In considering a large and complex system like an ecosystem, the system-theoretical approach has been frequently adopted as a useful tool for investigating such a system. The system-theoretical approach treats a large and complex system as being composed of numbers of subsystems or compartments; each compartment is dealt with as a whole and details of structures and processes within compartments are not scrutinized, that is, each compartment is regarded as a black-box. The main concern in this approach is patterns of networks of flows into and out of each compartment. Thus far, only flows of conservative quantities, energy and matter, have been considered. However, the non-conservative quantity, entropy, also flows in networks associated with flows of energy and matter, and is produced within each compartment of a system.

In this section, the thermodynamical entropy concept is applied to the input-output flow analysis of ecological networks at steady state, and entropy laws in ecological systems are presented (Aoki 1988b).

units: $[\text{MJm}^{-2}\text{yr}^{-1}\text{K}^{-1}]$

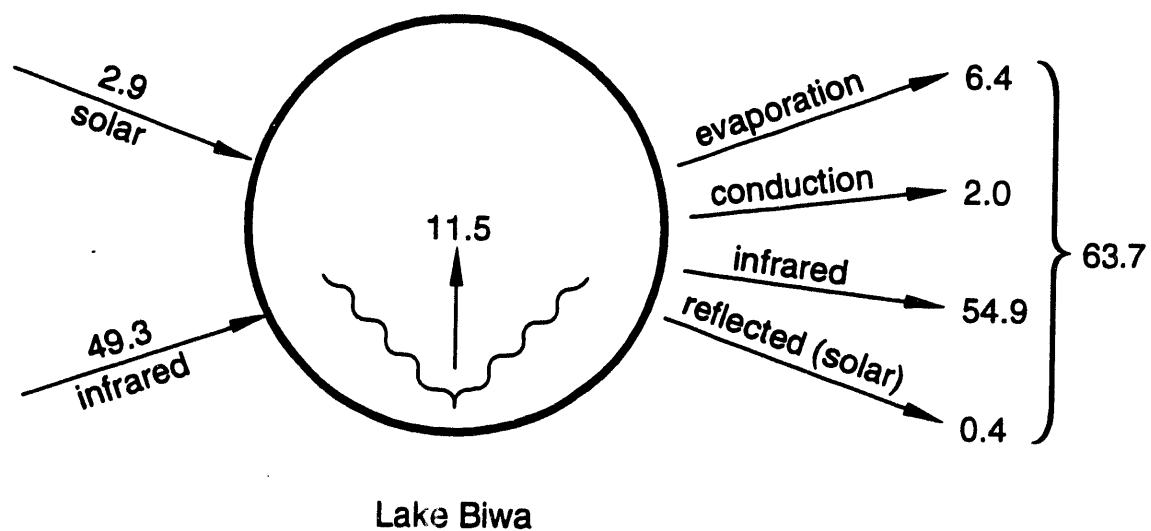


Figure 3. Entropy flow and entropy production for the northern basin of Lake Biwa.

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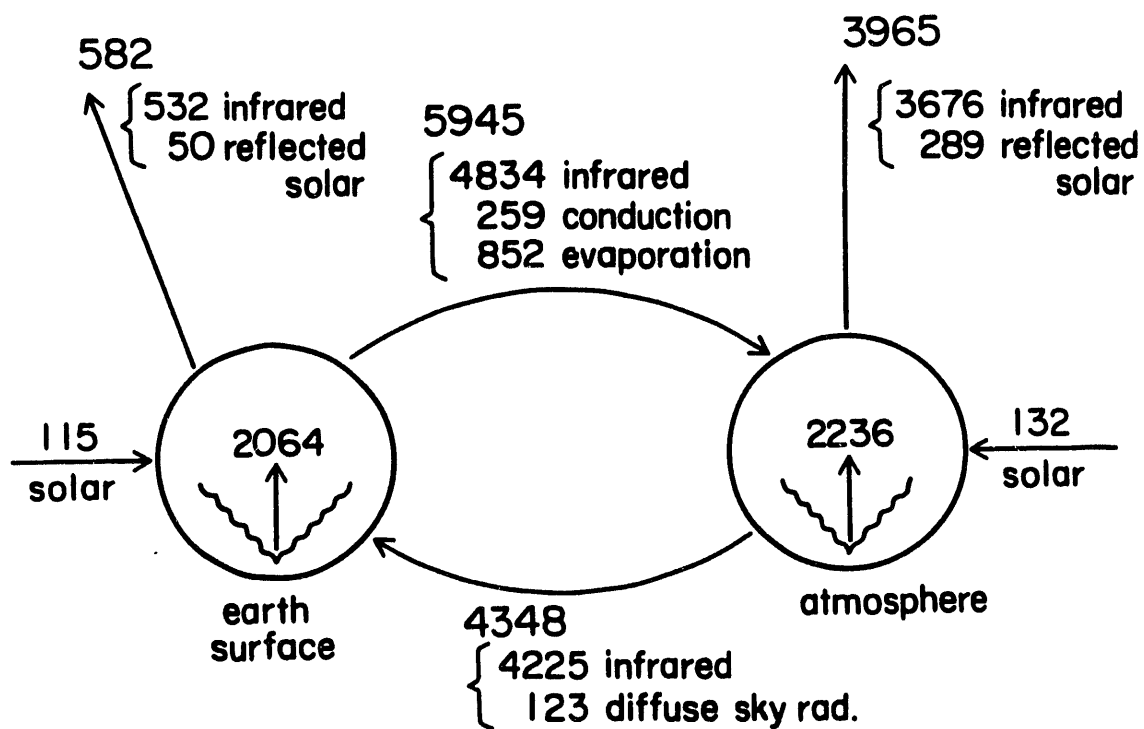
units : $[\text{J cm}^{-2} \text{yr}^{-1} \text{K}^{-1}]$ 

Figure 4. Entropy flow and entropy production for the earth's surface and the atmosphere.

DEFINITION OF TERMS (FIG. 5)

Let a system H be composed of n compartments H_k , $k=1,2,\dots,n$. The compartment H_k has a state variable x_k associated with it, which is in the present case the entropy content of the compartment H_k . The compartment H_k may receive entropy inflow z_k from the environment (the outside of the system H), and donate entropy outflow y_k to the environment. Within the system H , entropy flows f_{ij} pass from H_j to H_i . Entropy is produced within H_k ; the entropy production s_k (notation is different from Eq. 2) is non-negative according to the Second Law of Thermodynamics for open systems (Eq. 2). (It is assumed that entropy is kept constant in flowing between compartments; if entropy is increased at some place between compartments, that place should be included as part of the compartment.)

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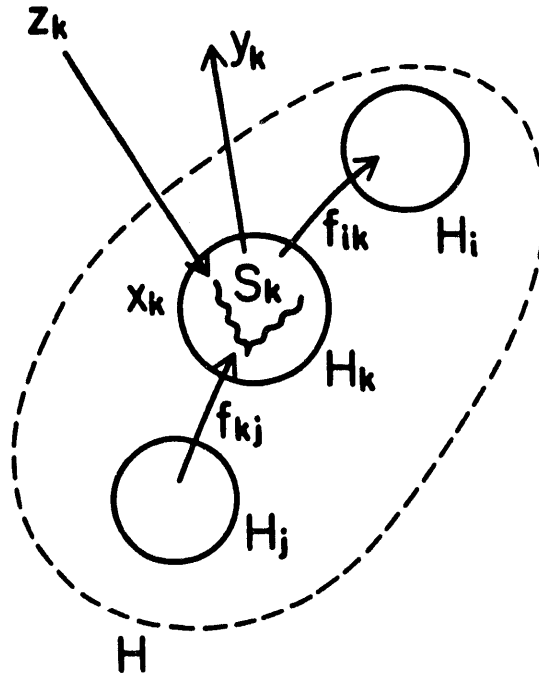


Figure 5. Illustration of definition of terms in the input-output flow analysis from an entropy viewpoint.

The derivative of x_k with respect to time is equal to the incoming entropy into H_k plus the entropy production within H_k minus the outgoing entropy from H_k :

$$\dot{x}_k = \sum_{j=1}^n f_{kj} + z_k + s_k - \sum_{i=1}^n f_{ik} - y_k. \quad (3)$$

Now we only consider entropy under steady state conditions, in which x_k is kept constant with time: $x_k = 0$, hence

$$\sum_{j=1}^n f_{kj} + z_k + s_k = \sum_{i=1}^n f_{ik} + y_k ,$$

from Eq. (3). Each side of the above equation defines entropy throughflow (T_k) at the compartment H_k :

$$T_k = \sum_{j=1}^n f_{kj} + z_k + s_k = \sum_{i=1}^n f_{ik} + y_k . \quad (4)$$

The first equation of Eq. (4) is the sum of all entropy inflows into H_k plus the entropy production within H_k . The second equation of Eq. (4) is the sum of all entropy outflows from H_k . Either expression of entropy throughflow T_k represents the rate at which entropy is moving through H_k . Total system throughflow in the entropy version (TST) is defined as

$$TST = \sum_{k=1}^n T_k . \quad (5)$$

Entropy structure matrix

Starting from Eq. (4) and following the ordinary procedures in the input-output flow analysis (e.g., Hannon 1973; Finn 1976; Patten et al. 1976), we obtain the following expressions for T_k :

$$T_k = \sum_{j=1}^n y_j n_{jk}^* = \sum_{j=1}^n n_{kj}^{**} (z_j + s_j) = T_k^{(Z)} + T_k^{(S)} , \quad (6)$$

where n_{jk}^* is an element of the matrix

$$N^{**} = [I - Q^*]^{-1} = [n_{jk}^*], \quad Q^* = [q_{ik}^*], \quad q_{ik}^* = f_{ik}/T_i;$$

n_{kj}^{**} is an element of the matrix

$$N^{**} = [I - Q^{**}]^{-1} = [n_{kj}^{**}], \quad Q^{**} = [q_{kj}^{**}], \quad q_{kj}^{**} = f_{kj}/T_j;$$

$$T_k^{(Z)} = \sum_j n_{kj}^{**} z_j, \quad T_k^{(S)} = \sum_j n_{kj}^{**} s_j$$

All n_{jk}^* and n_{kj}^{**} are non-negative.

Also, TST is expressed as

$$TST = TST^{(Z)} + TST^{(S)}, \quad (7)$$

where

$$TST^{(Z)} = \sum_k T_k^{(Z)} = \sum_k \sum_j n_{kj}^{**} z_j$$

$$TST^{(S)} = \sum_k T_k^{(S)} = \sum_k \sum_j n_{kj}^{**} s_j$$

The matrix $N^* = [n_{jk}^*]$ or $N^{**} = [n_{kj}^{**}]$ is the entropy version of the structure matrix (Hannon 1973), or the fundamental matrix (Kemeny and Snell 1976), or the transitive closure matrix (Patten et al. 1976).

ENTROPY THROUGHFLOW

As already shown, the Second Law of Thermodynamics claims that entropy production is non-negative; it is positive when processes are irreversible and is zero when processes are reversible (Eq. 2). If processes occurring in all the compartments are reversible, then $s_j = 0$ for all j and T_k

becomes $T_k(\text{rev}) = \sum_j n_{kj}^{**} z_j$ which is smaller than T_k when processes are irreversible ($s_j \neq 0$):

$$T_k(\text{irrev}) = \sum_j n_{kj}^{**} (z_j + s_j).$$

That is,

$$T_k(\text{irrev}) > T_k(\text{rev}). \quad (8)$$

Thus, when processes occurring in compartments are irreversible, the entropy throughflow is always larger than if all the compartments are in reversible processes.

Also for TST , we obtain

$$TST(\text{irrev}) > TST(\text{rev}), \quad (9)$$

where

$$TST(\text{irrev}) = \sum_k T_k(\text{irrev}) = TST^{(Z)} + TST^{(S)},$$

$$TST(\text{rev}) = \sum_k T_k(\text{rev}) = TST^{(Z)}.$$

ENTROPY PATH LENGTH

Entropy path length (PL) is defined as the average number of compartments through which will pass an average entropy outflow to the environment, or the average number of compartments through which will pass an average entropy inflow from the environment plus an average entropy production within the system. It is shown similarly to the case of energy and matter (Patten et al. 1976) that

$$PL = \frac{TST}{Y} = \frac{TST}{Z + S} = \frac{TST^{(Z)} + TST^{(S)}}{Z + S}, \quad (10)$$

where $Y = \sum_k y_k$ is the total entropy outflow from the system H ; $Z = \sum_k z_k$ is the total entropy

inflow into H ; $S = \sum_k s_k$ is the total entropy production in H ; and $Y = Z + S$ at steady state as

is easily shown. When processes in all the compartments are reversible, $S = 0$ and $TST^{(S)} = 0$ and the entropy path length becomes $PL(\text{rev}) = TST^{(Z)}/Z$. On the other hand, when processes are irreversible, the entropy path length $PL(\text{irrev})$ is expressed by Eq. (10).

Let us introduce two more path lengths: those due to entropy production within the system and those due to entropy inflow from the environment. Path length due to entropy production in the system is defined as

$$PL^{(S)} = \sum_k (s_k / \sum_i s_i) \sum_j n_{jk}^{**} = \frac{TST^{(S)}}{S}, \quad (11)$$

which represents the average number of compartments through which will pass an average entropy production in the system. Path length due to entropy inflow from the environment is defined as

$$PL^{(Z)} = \sum_k (z_k / \sum_i z_i) \sum_j n_{jk}^{**} = \frac{TST^{(Z)}}{Z}, \quad (12)$$

which represents the average number of compartments through which will pass an average entropy inflow from the environment.

It is shown that relations

$$PL(\text{irrev}) \begin{matrix} > \\ < \end{matrix} PL(\text{rev}) \quad (13a)$$

hold paralleling relations

$$PL^{(S)} \begin{matrix} > \\ < \end{matrix} PL^{(Z)}. \quad (13b)$$

That is, $PL(\text{irrev})$ is equal to (or larger or smaller than) $PL(\text{rev})$ when $PL^{(S)}$ is equal to (or larger or smaller than) $PL^{(Z)}$.

ENTROPY CYCLING INDEX

Entropy cycling efficiency at the compartment H_k is defined as the fraction of entropy throughflow T_k that returns to H_k and given by (as the case of energy and matter; Finn 1978)

$$RE_k = 1 - \frac{1}{n_{kk}}. \quad (14)$$

The cycled portion of TST is expressed as

$$TST_C = \sum_k RE_k \cdot T_k = TST_C^{(Z)} + TST_C^{(S)}, \quad (15)$$

where $TST_C^{(Z)} = \sum_k RE_k \cdot T_k^{(Z)}$ and $TST_C^{(S)} = \sum_k RE_k \cdot T_k^{(S)}$. The entropy cycling index (CI) is the fraction of TST that is cycled and given by (Finn 1978)

$$CI = \frac{TST_C}{TST} = \frac{TST_C^{(Z)} + TST_C^{(S)}}{TST^{(Z)} + TST^{(S)}}. \quad (16)$$

When processes in all the compartments are reversible, $TST_C^{(S)} = 0$, $TST^{(S)} = 0$ and the entropy cycling index becomes $CI(\text{rev}) = TST_C^{(Z)} / TST^{(Z)}$. On the other hand, when processes are irreversible, the entropy cycling index $CI(\text{irrev})$ is expressed by Eq. (16).

Let us introduce two more cycling indices: those due to entropy production within the system and those due to entropy inflow from the environment. The cycling index due to entropy production within the system is defined as

$$CI^{(S)} = \frac{TST_C^{(S)}}{TST^{(S)}}, \quad (17)$$

which represents the entropy cycling index if there is no entropy inflow from the environment. The cycling index due to entropy inflow from the environment is defined as

$$CI^{(Z)} = \frac{TST_C^{(Z)}}{TST^{(Z)}}, \quad (18)$$

which represents the entropy cycling index if there is no entropy production within the system.

It can be shown that relations

$$CI(\text{irrev}) \begin{matrix} > \\ < \end{matrix} CI(\text{rev}) \quad (19a)$$

hold paralleling relations

$$CI^{(S)} \begin{matrix} > \\ = \\ < \end{matrix} CI^{(Z)}. \quad (19b)$$

That is, $CI(\text{irrev})$ is equal to (or larger or smaller than) $CI(\text{rev})$ when $CI^{(S)}$ is equal to (or larger or smaller than) $CI^{(Z)}$.

SUMMARY AND REMARKS

Up until now only two entropy laws were known, Eq. (1), for an isolated system:

$$\Delta S (\text{irrev}) > \Delta S (\text{rev}) = 0,$$

and Eq. (2) for an open system:

$$\Delta_p S (\text{irrev}) > \Delta_p S (\text{rev}) = 0.$$

I have presented here four more entropy laws applied to networks at steady state, that is, Eq. (8) :

$$T_k (\text{irrev}) > T_k (\text{rev}),$$

Eq. (9) :

$$TST(\text{irrev}) > TST(\text{rev}),$$

Eq. (13) :

$$PL(\text{irrev}) \begin{matrix} > \\ = \\ < \end{matrix} PL(\text{rev}) \sim PL^{(S)} \begin{matrix} > \\ = \\ < \end{matrix} PL^{(Z)},$$

Eq. (19) :

$$CI(\text{irrev}) \begin{matrix} > \\ = \\ < \end{matrix} CI(\text{rev}) \sim CI^{(S)} \begin{matrix} > \\ = \\ < \end{matrix} CI^{(Z)}.$$

These four entropy laws are expressed in the terms of network theory: throughflow, total system throughflow, path length, and the cycling index. They are derived from Eq. (2) by use of the procedures in the input-output flow analysis of ecological networks at steady state. They are exact laws without any approximation. They can be applied to any networks (not only ecological) at steady state, if entropy flow and entropy production can be estimated.

ENTROPY PRINCIPLE FOR ECOLOGICAL SUCCESSION

As pointed out by Hutchinson (1964), the study of large and complex ecosystems, such as lakes, consists of two different approaches: holological (holos = whole) and merological (meros = part). In the holological approach, an ecosystem is treated as a black-box without scrutinizing internal

structures and processes of a system, and the attention is focussed on input and output to and from an ecosystem. On the other hand, in the merological approach, components or parts of a system are studied in detail.

Let us focus our attention on holological approaches to lakes. Holological studies of lakes were first made by Birge (1915) and later by Hutchinson (1957) and many others from an energy viewpoint. Jørgensen and Mejer (1979, 1981) applied the thermodynamical energy concept to the analysis of lake ecosystems; the energy is a measure of the distance of a system from thermodynamic equilibrium and is closely related to the entropy concept. Aoki (1987d) estimated annual values of entropy flow and entropy production in Lake Biwa and thus characterized it from holological and entropic standpoints.

In the present section, monthly values of entropy flow and entropy production in Lake Mendota (eutrophic) and in Lake Biwa (oligo-mesotrophic) are investigated, and a comparison is made between the two lakes. Then, an entropy principle for ecological succession is presented (Aoki 1989).

LAKE MENDOTA

Lake Mendota in Wisconsin is the most thoroughly studied lake in the world (Brock 1985). Dutton and Bryson (1962) estimated monthly variation of each term of the heat balance equation for Lake Mendota. Terms in the heat balance equation consist of: energy flows due to direct, diffuse and reflected solar radiation; energy flows due to infrared radiation incident upon the lake, and due to infrared radiation emitted by the lake; energy flows due to evaporation, and due to sensible heat; and changes of heat storage in the lake. They are expressed per unit area of the lake surface. From monthly values of the terms of energy flow, we can calculate corresponding entropy fluxes into and out of the lake using some physical methods described in Aoki (1987d, 1989). Then, the net entropy flow into the lake ($\Delta_e S$) can be estimated. The change of entropy content of the lake (ΔS) is computed from the change of heat storage in the lake and from the mean temperature of the lake water (Stewart 1973). Thus, the entropy production ($\Delta_p S$) per unit area of the lake surface is obtained as $\Delta_p S = \Delta S - \Delta_e S$. Dividing by the mean depth of the lake, we obtain the entropy production (S_{prod}) per unit volume of lake water.

The net entropy flows into the lake ($\Delta_e S$) become negative in all months. That is, the lake absorbs "negative entropy" (Schrödinger 1944) from its surroundings. Schrödinger (1944) asserted that biological organisms absorb "negative entropy" from their surroundings and that this is the physical basis for ordered structures and functions of organisms to be maintained. Thus, in this respect (absorption of "negative entropy"), the lake as a whole can be regarded as something like a "superorganism" (Clements and Shelford 1939) which has ordered structures and functions in it similar to a biological organism.

The entropy production in each month is shown in Fig. 6. It is larger in summer and smaller in winter. The monthly entropy production in the lake (S_{prod}) becomes a linear function of the monthly solar radiation energy absorbed by the lake (E_{solar}); that is, $S_{prod} = a + bE_{solar}$, $a = 0.006$ [$\text{MJ m}^{-3} \text{ month}^{-1} \text{ K}^{-1}$] and $b = 2.29 \cdot 10^{-4}$ [$\text{m}^{-1} \text{ K}^{-1}$]. The values (a, b) are holological indices which

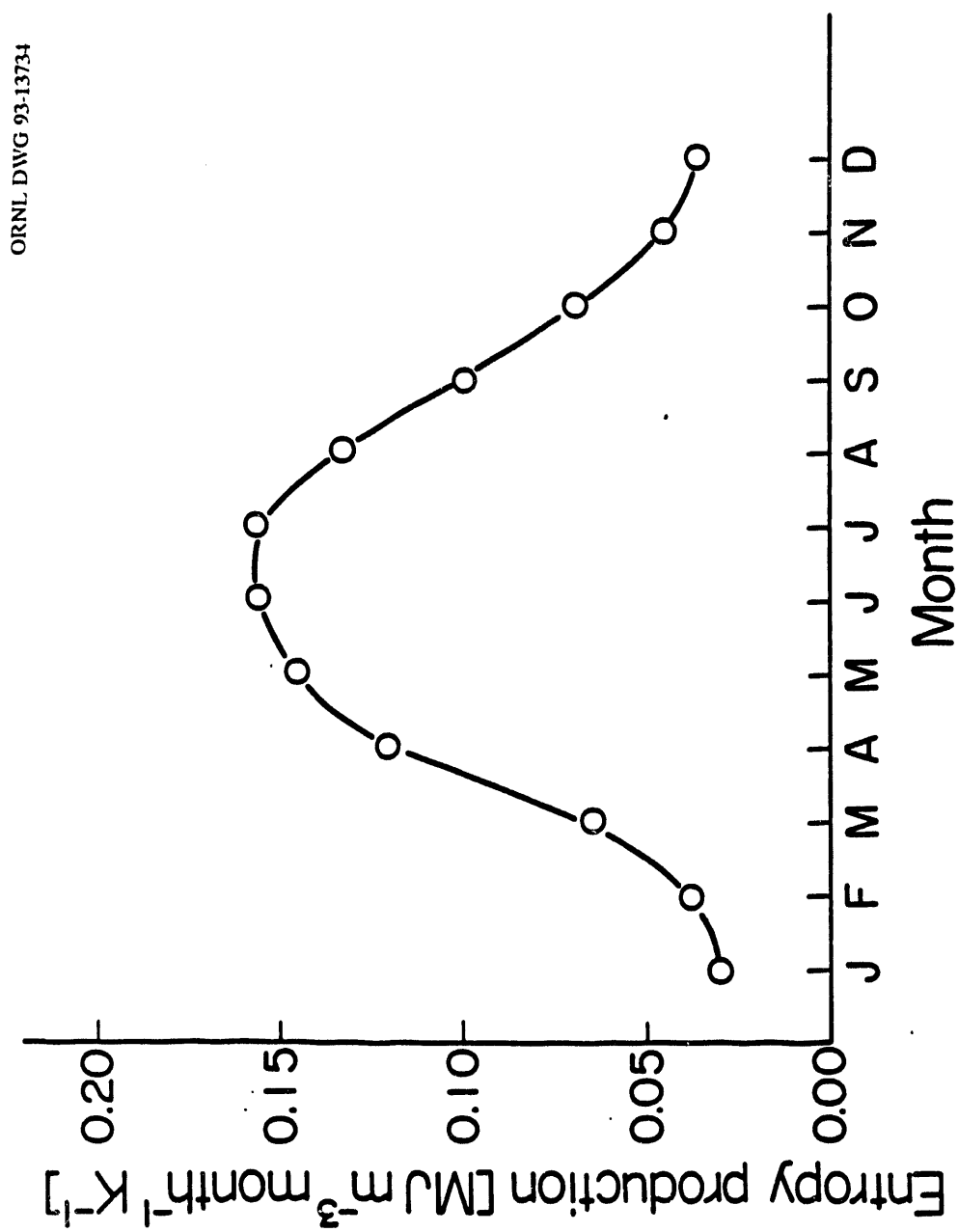


Figure 6. Annual march of entropy production in Lake Mendota.

characterize the lake from an entropy viewpoint: a is the entropy production independent of absorbed solar radiation, and b is a sensitivity of entropy production to absorbed solar radiation energy. Or as another index similar to b , we may introduce the entropy production per unit volume of lake water per year divided by the absorbed solar radiation energy per unit area of lake surface per year. This quantity (say, b') may be called "normalized entropy production" in the sense that it represents entropy production divided (normalized) by an environmental factor of the lake: the solar radiation. The value b' for Lake Mendota is $2.44 \times 10^{-4} [m^{-1} K^{-1}]$.

LAKE BIWA AND A COMPARATIVE STUDY

Similar calculations are carried out for the northern basin of Lake Biwa, the most studied lake in Japan, and the corresponding values of holological indices (a, b, b') are obtained (Aoki, in preparation). Comparison of these indices in Lake Mendota and in Lake Biwa is made and shown in Table 1. As shown, these values (a, b, b') in Lake Mendota (eutrophic) are larger than those in the northern basin of Lake Biwa (oligo-mesotrophic). Thus, the eutrophication process is accompanied by an increase in magnitude of these entropy production indices. This is a trend in processes of eutrophication in lakes specified from an entropy point of view. Ecological succession in lakes proceeds from oligotrophic to eutrophic. Hence, the increase of entropy production will be an entropy principle of ecological succession in lakes, and also in other ecological systems.

TABLE 1

Comparison of indices a, b, b' in Lake Mendota and the northern basin of Lake Biwa. a is in units of $[MJ m^{-3} month^{-1} K^{-1}]$ and b, b' in units of $10^{-4} [m^{-1} K^{-1}]$. Total-P in units of $[mg l^{-1}]$.

| Lake | Total-P | Type | a | b | b' |
|-----------------|-------------|-------------------|-------|-----|------|
| Biwa (northern) | ~ 0.01 | oligo-mesotrophic | 0.002 | 0.6 | 0.6 |
| Mendota | ~ 0.14 | eutrophic | 0.006 | 2.3 | 2.4 |

The above statement, which may be called "the increasing entropy production principle" can be compared with Lotka and Odum's maximum power principle (Odum 1971), which asserts that power (= flow \times force) is maximized in processes of succession. Entropy production is also expressed as flow \times force (the same expression as power), although definitions of force are of course different between power and entropy production. Thus, since power and entropy production are expressed in similar forms, "the increasing entropy production principle" can be considered to be similar to Lotka and Odum's maximum power principle. However, "the increasing entropy production principle" is opposite to Prigogine's minimum entropy production principle (Nicolis and Prigogine 1977), which states that entropy production decreases with time and reaches a minimum. Prigogine's principle holds only near the thermal equilibrium; on the other hand, ecosystems will be far from equilibrium. Hence, it is not surprising nor strange that Prigogine's principle does not hold in ecological systems.

THE OVERALL TREND IN ECOLOGICAL SUCCESSION

In the above, we proposed that entropy production increases with time in some stage of succession. Does this trend continue over the whole period of ecological succession? The description of how living systems develop with time is one of the most important problems in biological sciences. In this connection, I present here one probable hypothesis: entropy production increases with time in a developmental stage (early stage) of succession, and is kept constant in a stationary stage (intermediate stage) and decreases with time in a senescent stage (later stage) of succession, as shown in Fig. 7. Thus, processes of succession will not be uni-directional, but consist of three different phases (increasing, constant, and decreasing). I think that this trend will be applied to the time-course of Lotka and Odum's power, and also Hirata and Ulanowicz's ascendancy that is an information theoretical index describing growth and development of organisms and ecosystems (Hirata and Ulanowicz 1984; Ulanowicz 1986). This trend will be of universal nature in biological or ecological processes which have two opposing phases: growth and senescence.

The non-unidirectionality of processes discussed above means that maximum-minimum principles, which assert that actual processes in nature proceed so as to maximize or minimize some fundamental quantities, do not necessarily hold in some aspects of biological and environmental sciences. Maximum-minimum principles may be used in a restricted period of time (e.g., only in a developmental stage), but they can not be used for the whole span of processes. The origins of maximum-minimum principles are in physics; hence the above discussions present the case in which physical principles can not necessarily be applied to biological and ecological objects.

Discussion

Hirata and Ulanowicz (1986) made the following comment on ecological succession: "Even though ecological succession is clearly in the domain of non-equilibrium thermodynamics, there is still no consensus on a formal method for treating these phenomena." The present section has presented one methodology to treat ecological succession from a thermodynamical, or more specifically, from an entropic point of view. Also, we have proposed an entropy principle for ecological succession. Of course, in order to get a solid conclusion on succession from an entropy standpoint, it is necessary to obtain more data on entropy production in many ecological systems at different stages.

The methods for calculating entropy production in lakes described in Aoki (1987d, 1989) can be applied to any ecosystems if their energy budgets are completely known. Ulanowicz and Hannon (1987) proposed a hypothesis that living systems create more entropy than their non-living complements and suggested that one compare entropy productions in forests with those in deserts in order to substantiate this hypothesis. Computation of entropy production in forests will be made soon by use of the methods described in Aoki (1987d, 1989). Thus, this line of research on entropy production in ecosystems will make it possible to answer quantitatively the key question posed by Ulanowicz and Hannon (1987): "Do living systems serve to increase the entropy production rate over what it would be in the absence of life?"

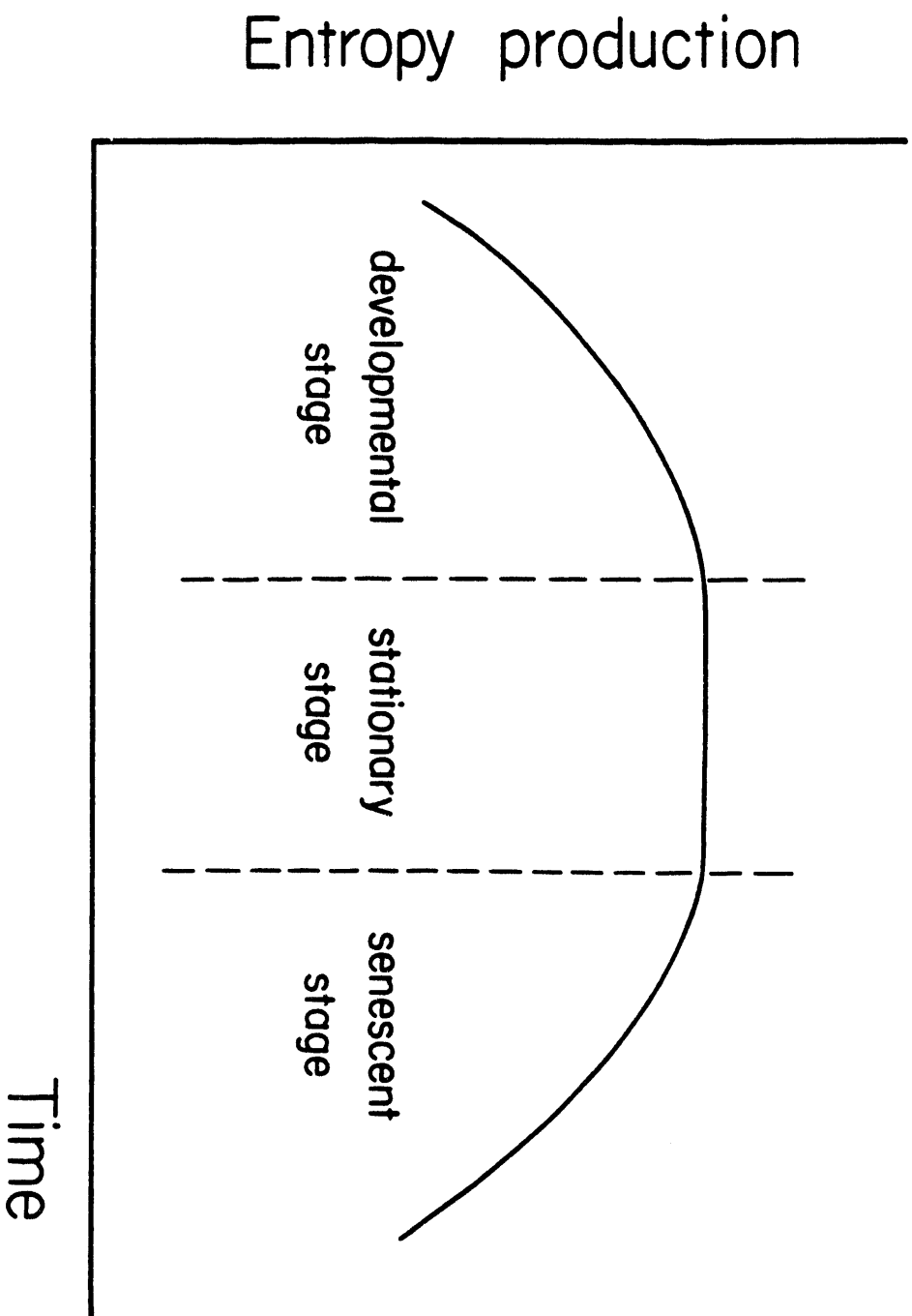


Figure 7. Proposed trend for the time-course of entropy production.

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INFORMATION IN ECOLOGICAL COMMUNITIES

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ABSTRACT

Here we define a new index of information contained in the structure of ecological communities. We call it the " H^2 -information index." Using H^2 -information, we lend theoretical support to several ecological insights, especially those concerned with stability; e.g., those concerned with the relation between the structure of a foodweb and its environment, or the relation between stability and average turnover rate. We also show on the basis of H^2 -information that mineral systems are generally more highly organized than carbon and energy systems.

INTRODUCTION

An ecological community may be defined as an information based system which has the ability to store the information necessary for its own persistence or adaptation to the environment through succession (or evolution).

An ecological community may be regarded as a system transmitting various media such as energy, carbon, or nitrogen from input to output. Each medium has its inherent routes between the entrance and exit. The structure of the ecological community may be characterized by coding the routes using sequences of the names of elements.

Gatlin (1972) discussed the genetic code using information theory. Although the actual meanings of information indices for the genetic code and those for the ecological community are not completely congruent, we use the same symbols as Gatlin used, so that researchers who are familiar with his work will understand it easily.

From the view point of information theory, we newly define the H^2 -information index R of the ecological community, which is a measure of how much the entropy has been lowered from its maximum value and also a measure of all the ordering, constraints, rules, etc., that have been imposed upon the ecological system. R is a direct measure of the structure of the ecological community; i.e., the size of the elements and the direct or indirect relations among elements, such as predation, competition, or symbiosis.

The H^2 -information index R consists of two parts, $RD1$ and $RD2$. $RD1$ represents the divergence from equiprobability with respect to the distribution of elements; i.e., in some sense the distribution of storage. $RD2$ represents the divergence from independence with respect to the relation between elements; i.e., the distribution of flows. $RD1$ depends on the distribution of storage (or the population). Thus if we use a species as an element of the system, $RD1$ relates to species diversity. On the other hand, $RD2$ depends on the distribution of both storage and flow; i.e., community structure. If the system is at steady state, $RD2$ relates to mutual information of network structure which we have already defined (Hirata and Ulanowicz 1984, 1985; Hirata 1990). Therefore, the H^2 -information index represents the information contained in both the entity (or storage) distribution and the flow structure.

In Sect. 2, we explain how we can represent the structure of ecological communities as a coding problem.

In Sect. 3, we develop theoretical definitions of the divergence from equiprobability and the divergence from independence. Finally we define H^2 -information of ecological communities. We also define several related indices.

In Sect. 4, we try to find the role of H^2 -information for stability. We find out the relation between H^2 -information and the stability of ecological communities using Shannon's second theorem (e.g., Shannon and Weaver 1949): ecological communities should keep H^2 -information high in order to adapt to severe environments; i.e., to be stable. This coincides with Johnson's statement (1989) that in harsh environments increased redundancy is necessary for a species to withstand the greater natural fluctuation and the greater prevailing variability, and Ulanowicz's (1980) statement that perturbations probably act to increase the amount of redundancy. This result also gives theoretical support to the following two experimental results.

1. The structure of a foodweb under fluctuation is simpler than it would otherwise be under a constant environment (Briand 1983).
2. Arctic aquatic ecosystems are relatively simple in their structure (Johnson 1989).

These results coincide with Briand (1983)'s insight that environmental constraints will impose a far greater rigidity of web shapes and a much smaller choice of trophic patterns than previously assumed. The proposed information index has some relation to May's stability condition (1972). We also study the relation between average turnover rate and stability through information theoretical discussion: ecological communities should keep average turnover rate small in order to adapt to severe environments; i.e., to be stable. This result lends theoretical support to the following insights.

1. The Production/Biomass ratio in lakes tends to decrease with increasing latitude (Mann and Brylinsky 1975).
2. Tropical forest systems have a much more rapid turnover rate than temperate forest systems (Whittaker 1966; Golly 1972; Burger 1981).
3. Arctic lakes support a high biomass relative to the very low primary productivity (Johnson 1989).

It also coincides with Leigh's theoretical result (1968) on Volterra's equations: the higher the turnover rate, the less stable the community.

In Sect. 5, we discuss some properties of H^2 -information. Eutrophic versus oligotrophic conditions are discussed using H^2 -information. By computationally comparing H^2 -information of a eutrophic ecological community with that of an oligotrophic one, we get the result that H^2 -information of the oligotrophic lake is larger than that of the eutrophic lake. We use data from four lakes (Richey et al. 1978). Marion Lake (British Columbia), Findlay Lake (New Hampshire) and Mirror lake (New Hampshire) are oligotrophic, and Lake Wingra (Wisconsin) is eutrophic. These

lakes are similar in size, climate, and altitude, except Findlay Lake, which is at a higher elevation. If we suppose that ecological systems succeed in reaching a more stable state, this result coincides with the following insights since larger H^2 -information means higher stability.

1. Oligotrophy should succeed eutrophy, not precede it. A decisive experiment to test this would be to reduce the input of nutrients to a eutrophic lake and follow its evolution. We are positive it would change in the direction of oligotrophy (Margalef 1968).
2. Eutrophication of a lake results when nutrients are imported to the lake from the outside. This is equivalent to adding nutrients to a laboratory microecosystem or fertilizing a field: the system is pushed back, in successional terms, to a younger state (Odum 1971).
3. Lakes can and do progress to a more oligotrophic condition when the nutrient input from the watershed slows or ceases (Mackereth 1965; Cowgill and Hutchinson 1964; Harrison 1962).

Furthermore, we show that each kind of medium (carbon, energy, nitrogen, etc.) has its special characteristic relation between $RD1$ and $RD2$.

CODING OF ECOLOGICAL PATHS

As in Fig. 1, an ecological community may be regarded as a system transmitting various media such as energy, carbon, or nitrogen, from input to output. Each medium has its inherent routes between the entrance and exit. The structure of ecological communities may be defined by coding the routes using sequences of the symbolic names of elements.

Let us define the sample description space X_1 , which is referred to below as the community alphabet, of the random phenomenon of choosing an element along a route:

$$X_1 = \{x_i\}_{i=1, \dots, n, n+1} \quad (1)$$

where x_i , which is referred to below as a community letter, gives the symbolic name of the i^{th} element ($i = 1, \dots, n$) and x_{n+1} implies the outside of the community. $P(x_i)$ is defined as the probability of x_i 's occurrence.

Let us define the space of doublets of community letters, X_2 , which is necessary for discussing a sequence of community letters:

$$X_2 = \{x_i x_j\}_{i, j=1, \dots, n+1}, x_i \in X_1 \quad (2)$$

Here the conditional probability $P(x_j | x_i)$ is defined.

Let us define the set of paths, PATH, from input to output:

$$PATH = \{l_k\}_{k=1, \dots, q} \quad (3)$$

where

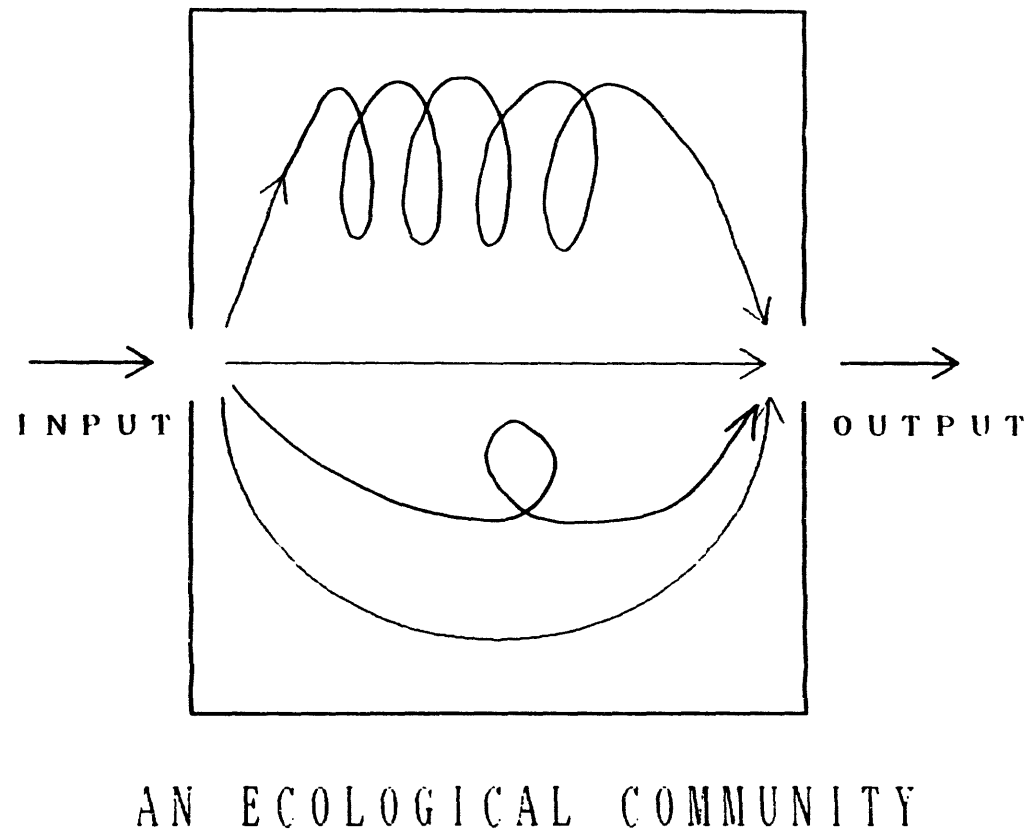


Figure 1. Paths of media in an ecological community.

$$l_k = y_1^k y_2^k \dots y_{m_k}^k \quad (4)$$

$$y_j^k \in X_j, m_k = |l_k| \text{ (the length of } l_k\text{)}. \quad (5)$$

Here $y_{m_k}^k$ is x_{n+1} , which works as the stopping code. Although q may be theoretically infinite if there exists a cycling loop, $P(l_k)$ of such a long sequence tends to zero. This sequence of symbols is ordered along a set of constraints which constitutes an ecological community.

H^2 -INFORMATION

Let us discuss the properties of a set of paths, PATH, which represents characteristics of an ecological community. We can define information of the set PATH to evaluate two kinds of entropy with different meanings. Evaluating the entropy of X_1 gives the divergence from equiprobability and that of X_2 yields the divergence from independence. Let P_i be $P(x_i)$ and P_{ij} be $P(x_j | x_i)$ below.

THE DIVERGENCE FROM EQUIPROBABILITY: D_1

The entropy of X_1 is

$$H_1 = - \sum_{i=1}^{n+1} P_i \log P_i. \quad (6)$$

H_1 has the maximum value

$$H_1^{\max} = \log(n+1) = \pi(n) \quad (7)$$

when P_i has a uniform distribution; i.e.,

$$P_i = 1/(n+1) \quad (i = 1, \dots, n+1) \quad (8)$$

which is the equiprobable state. We will substitute $\pi(n)$ for $H_1^{\max} = \log(n+1)$ below.

The divergence from the equiprobable state is the difference between the entropy of the equiprobable state, H_1^{\max} , and that of the actual state, H_1 :

$$D_1 = H_1^{\max} - H_1 \quad (9)$$

$$= \log(n+1) - H_1 = \pi(n) - H_1. \quad (10)$$

D_1 can be defined on the storage (or population) distribution. If we use species as elements, H_1 means species diversity in some sense. Thus, D_1 is the difference between the capacity of an ecological system and its diversity.

THE DIVERGENCE FROM INDEPENDENCE: D_2

The entropy of X_2 is

$$H_2^d = - \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} P(x_i, x_j) \log P(x_i, x_j) \quad (11)$$

$$= - \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} P(x_j | x_i) P(x_i) \log P(x_j | x_i) P(x_i) \quad (12)$$

$$= - \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} P_i P_{ij} \log P_i P_{ij} \quad (13)$$

H_2 has the maximum value

$$H_2^{ind} = - \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} P_i P_j \log P_i P_j \quad (14)$$

when x_i and x_j are independent.

The divergence from the independent state is the difference between the entropy of the independent state, H_2^{ind} , and that of the dependent state, H_2^d :

$$D_2 = H_2^{ind} - H_2^d. \quad (15)$$

D_2 is defined on the distribution of flow and storage, and is especially based on flow structure.

We can easily show the following relations.

$$H_2^{ind} = 2H_1 \quad (16)$$

$$H_2^d = H_1 + H_M \quad (17)$$

where

$$H_M = - \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} P_i P_{ij} \log P_{ij} \quad (18)$$

From (15)-(17), D_2 is finally expressed as

$$D_2 = H_1 - H_M \quad (19)$$

The sum of D_1 and D_2 measures exactly how much the entropy has been lowered from the maximum entropy state. Since the maximum entropy state means the random state (or unorganized state), the sum of D_1 and D_2 evaluates to what degree the ecological community is self-organized by storing information. Let us define stored information as follows.

H^2 -Stored Information: I_s

Let us define H^2 -stored information as the sum of the total divergence from the maximum entropy state:

$$I_s = D_1 + D_2. \quad (20)$$

The reason why we call it the H^2 -information index is because two meanings of entropy are evaluated in this index.

Substitution of (10) and (19) into (20) yields:

$$I_s = \log(n+1) - H_M = \pi(n) - H_M \quad (21)$$

H^2 -Information: R

Normalization of I_s by the maximum value $\pi(n)$ can define normalized stored information, which is simply referred to below as H^2 -information.

Let us define H^2 -information, R :

$$R = \frac{I_s}{\pi(n)} = \frac{D_1 + D_2}{\log(n+1)}. \quad (22)$$

Here,

$$0 \leq R \leq 1 \quad (23)$$

and R is dimensionless because it is a fraction. H^2 -information is the same quantity as Shannon's redundancy in information theory.

H^2 -information, R , measures how much the entropy has been lowered from its maximum value and is a measure of all the ordering, constraints, and rules that have been imposed upon the system. R is a direct measure of the structure of an ecological community; i.e., the size of the elements and the direct or indirect relations among elements, such as predation, competition, or symbiosis.

STRUCTURE INDICES OF H^2 -INFORMATION: $RD1$ AND $RD2$

Separation of R into two parts is useful in studying the structure of H^2 -information, R .

$$R = R_1 + R_2 \quad (24)$$

where

$$R_i = D_i/\pi(n). \quad (i = 1,2) \quad (25)$$

Let us define an index to characterize two parts:

$$RD1 = \frac{R_1}{R} = \frac{D_1}{D_1+D_2} \quad (26)$$

$$RD2 = \frac{R_2}{R} = \frac{D_2}{D_1+D_2}. \quad (27)$$

Here,

$$RD1 + RD2 = 1 \quad (28)$$

and

$$0 \leq RD_i \leq 1. \quad (i = 1,2) \quad (29)$$

$RD1$ and $RD2$ are dimensionless because they are fractions. $RD1$ is the contribution of D_1 to R ; i.e., it shows the effect of storage distribution. $RD2$ is the contribution of D_2 to R ; i.e., it is the effect of structure. These indices are referred to below as structure indices of H^2 -information. If we are given two identical values of H^2 -information R , each with significantly different structure indices $RD1$ and $RD2$, we would have an ecological community with the same amount of H^2 -information but of different kinds. The H^2 -stored information I_s or the H^2 -information R tells us how much divergence there has been from the maximum entropy state. And the structure indices $RD1$ and $RD2$ tell us what kind of divergence it is; i.e., whether it is composed mostly of D_1 or D_2 .

The three fundamental quantities which one calculates are H_1 , H_M and $\pi(n)$. From these one can calculate all the useful values like D_1 , D_2 , I_s or R , $RD1$ and $RD2$. H_1 can be defined only on the distribution of storage in some sense; i.e., it depends on the individuals of the ecological system, and it shows the population (storage) diversity (variety). On the other hand, H_M is defined mainly on the transition rate corresponding to the distribution of flows; i.e., it depends on the structure of the ecological community, and it shows flow diversity.

Whenever we calculate the entropy of a sequence of symbols, it represents the capacity to transmit. When we evaluate the entropy of a divergence from the maximum value, $\pi(n)$, this is a measure of the capacity to store information. Stored information is also a capacity to combat error (or to adapt to the environment). It is possible for the entropy to be so high that transmission error makes communication impossible. Reducing the entropy to the point where the stored information becomes maximal, we can make transmission highly reliable (or stable as concerns ecological communities); but the message variety is so low that we cannot hold successful variety in the message (or the ecological community).

Generally we need an optimum blend of variety and stored information for successful or meaningful communication (or successful succession of ecological communities).

The capacity to combat error (or the capacity to adapt to the environment) depends not on an entropy maximum or minimum but rather on a delicate optimization of the two opposing elements of variety and reliability. In an ecological community a delicate optimization of two opposing factors, variety and stability, is necessary to adapt to the environment.

STABILITY OF ECOLOGICAL COMMUNITIES

FUNDAMENTAL CONDITION OF STABILITY

Let us discuss stability against perturbation of ecological communities.

When a sequence of community symbols is ordered according to a set of constraints which constitutes an ecological community, the sequence of community symbols shows a route for moving media. It may be called the ecological message. We may regard an ecological community as an information source. The encoding of the ecological message occurs at the source. A channel is simply any medium over which the message is transmitted. In the discussion of ecological communities, a time tunnel with environmental perturbation such as climate change may be regarded as a channel. That is, there exists noise, which interferes with the transmission in the channel. Environmental perturbation like climate change may be regarded as noise for ecological communities.

Let us describe Shannon's second theorem.

Shannon's Second Theorem: If

$$U < C \quad (30)$$

where U is the rate of emission from the information source and C is channel capacity, there is a code such that transmission over the channel is possible with an arbitrarily small number of errors.

The channel has a certain capacity; i.e., an upper limit to the rate at which it can transmit a sequence of symbols without incurring gross error due to overloading the channel. The essential concept of Shannon's second theorem is this: we cannot eliminate noise in the channel, but we can under certain conditions ($U < C$) transmit a message without error in spite of this noise if the message has been properly encoded at the source. The code is the crux of the matter. The more efficient the code becomes, the closer it approaches this error-free limit. A fundamental condition under which Shannon's theorem is valid is that $U < C$; i.e., the rate of emission from the source, which is measured by the source entropy, must not exceed the channel capacity.

In studying ecological communities, U may be expressed as

$$U = kH_M \quad (31)$$

where k is the average turnover rate in all transitions between elements. Therefore, an interpretation of Shannon's second theorem for ecological communities is represented as follows.

Proposition 1: Ecological communities can be stable against perturbation under the condition

$$kH_M < C; \quad (32)$$

i.e., ecological communities can be stable with respect to disturbance of the environment, if it has been properly organized or structured. Here, C is a decreasing function of the strength of the perturbation and

$$C = \pi(n) \quad (\text{no perturbation}) \quad (33-a)$$

$$C < \pi(n). \quad (\text{perturbation}) \quad (33-b)$$

Proposition 1 shows that ecological communities should keep U , or H_M and k , small in order to adapt to severe perturbation; i.e., to keep itself stable.

THE RELATION BETWEEN STABILITY AND H^2 -INFORMATION

Because there is a relation between H_M and H^2 -information R as

$$H_M = \pi(n) \quad (1-R) \quad (34)$$

we can rephrase Proposition 1 as follows:

Proposition 2: Ecological communities should keep H^2 -information R large in order to adapt to severe environments; i.e., to be stable.

It may be said that H^2 -information R of ecological communities in cold and severe regions should be larger to defend against perturbation than the R of those in warm and mild regions. Proposition 2 also means that smaller H^2 -information is enough for tropical ecological communities but not for arctic communities. H^2 -information, R , is a measure of all the constraints on an ecological community which make the ecological community stable. Proposition 2 coincides with Johnson's statement (1989) that in harsh environments increased redundancy is necessary for a species to withstand the greater natural fluctuations and the greater prevailing variability and Ulanowicz's statement (1980) that perturbations probably act to increase the amount of redundancy.

Because larger R 's generally mean relatively simple structures of food webs, Proposition 2 gives theoretical support to the following two experimental results.

1. The structure of foodwebs undergoing fluctuation is simpler than those under constant environments (Briand 1983).
2. Arctic aquatic ecosystems are relatively simple in their structure (Johnson 1989).

Proposition 2 or the results derived from it coincide with Briand's (1983) insight that environmental constraints will impose a far greater rigidity of web shapes and a much smaller choice of trophic patterns than previously assumed.

Proposition 2 also lends some support to the results of the relation between the complexity and stability of ecological communities (May 1972; Pimm 1982, 1984 and 1987; and others). Actually, although the details have been omitted in this paper due to space limitation, we see both theoretically

and experimentally that H_M has a strong correlation with May's stability index $(n\sigma)^{1/2}$ (n is the number of species, and σ is connectance).

THE RELATION BETWEEN STABILITY AND AVERAGE TURNOVER RATE

As a relation between stability and the average turnover rate over all transitions, k , the following proposition can be derived from Proposition 1.

Proposition 3: Ecological communities should keep average turnover rate k small in order to adapt to severe environments; i.e., to be stable.

It may be said that the average turnover rate k of ecological communities in cold and severe regions should be smaller than the k of those in warm and mild regions in order to defend against severe environments. Proposition 3 also means that tropical ecological communities can support larger turnover rates than arctic ecological communities.

When we can assume that the average turnover rate is approximated by the Production/Biomass ratio, Proposition 3 gives some theoretical support to the following insights.

1. The Production/Biomass ratio in lakes tends to decrease with increasing latitude (Mann and Brylinsky 1975).
2. Tropical forest systems have a much more rapid turnover rate than temperate forests (Whittaker 1966, and Golly 1972).
3. Arctic lakes support a high biomass relative to the very low primary productivity (Johnson 1989).

Proposition 3 also coincides with Leigh's (1968) theoretical result on Volterra's equations: the higher the turnover rate, the less stable the community.

SOME PROPERTIES OF H^2 -INFORMATION

EUTROPHIC VERSUS OLIGOTROPHIC

Let us compare H^2 -information R 's between eutrophic and oligotrophic ecological communities. We use data from four lakes (Richey et al. 1978). Marion Lake (British Columbia), Findlay Lake (New Hampshire) and Mirror Lake (New Hampshire) are oligotrophic, and Lake Wingra (Wisconsin) is eutrophic. These lakes are similar in size, climate, and altitude, except Findlay Lake, which is at a higher elevation. Because the data include only flow values, we calculated H^2 -information using the approximation of probabilities $\{P(x_i)\}$ shown by flows (e.g., Hirata 1990).

The results are:

| <u>Lake</u> | <u>R</u> |
|-------------|----------|
| Marion | 0.943 |
| Findley | 0.776 |
| Mirror | 0.560 |
| Wingra | 0.521 |

H^2 -information R of oligotrophic lakes is larger than that of the eutrophic lake. If we suppose that ecological systems succeed in reaching a more stable state, this result coincides with the following insights since larger H^2 -information means higher stability.

1. Oligotrophy should succeed eutrophy, not precede it. A decisive experiment to test this would be to reduce the input of nutrients to a eutrophic lake and follow its evolution. We are positive it would change in the direction of oligotrophy (Margalef 1968).
2. Eutrophication of a lake results when nutrients are imported to the lake from the outside. This is equivalent to adding nutrients to a laboratory microecosystem or fertilizing a field: the system is pushed back, in successional terms, to a younger state (Odum 1971).
3. Lakes can and do progress to a more oligotrophic condition when the nutrient input from the watershed slows or ceases (Mackereth 1965; Cowgill and Hutchinson 1964; Harrison 1962).

RD1 VERSUS RD2

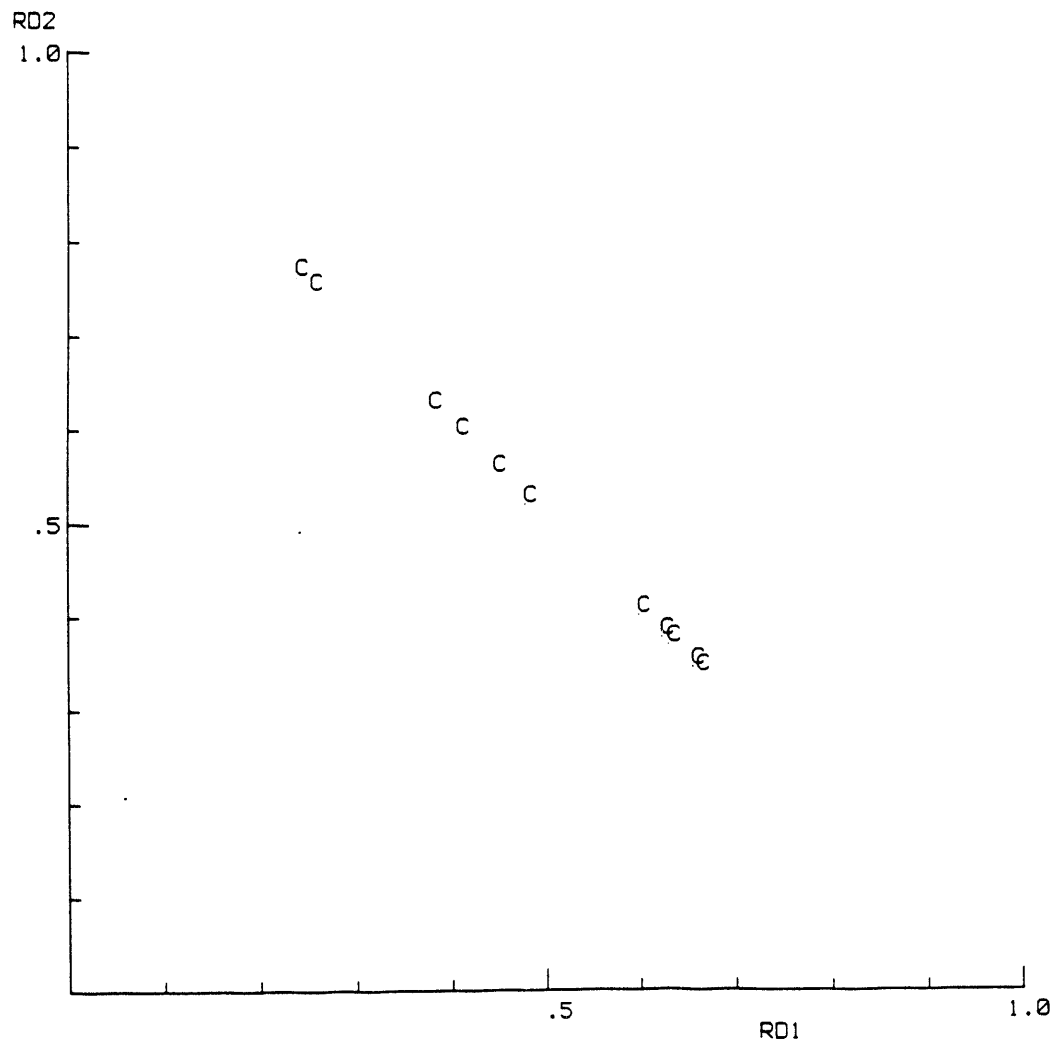
H^2 -information, R , is a measure of all the constraints on an ecological community which make the ecological community stable, or persistent.

In terms of entropy, the highly organized system does not necessarily have the lowest values of H_M , but rather the lowest values of H_M relative to H_i ; i.e., it has the highest values of D_2 . The larger $RD2$ becomes, the more highly organized the structure.

Figure 2 shows there are some differences among media in the distribution of the ratio between $RD1$ and $RD2$. Carbon (C) distributes in the whole part on the line; Energy (E), more in the upper part than in the middle; Minerals (Potassium (K) and Nitrogen (N)), in the upper quarter part on the line; with Nitrogen (N) in the part near the axis. Energy is an exception in the figure. Perhaps this is because its data is not real but estimated. Fig. 2 characterizes mineral systems (similar to the Nitrogen system) as more highly organized than energy and Carbon systems on the basis of an information theoretic measure.

CONCLUSION

We defined a new index of the information contained in the structure of ecological communities, namely H^2 -information. We discussed several properties of the stability of ecological communities from the viewpoint of information. The proposed H^2 -information index will come to play an important role in discussions of ecological succession.



(1) Carbon (C)

Figure 2a. RD1 versus RD2: Carbon (C).

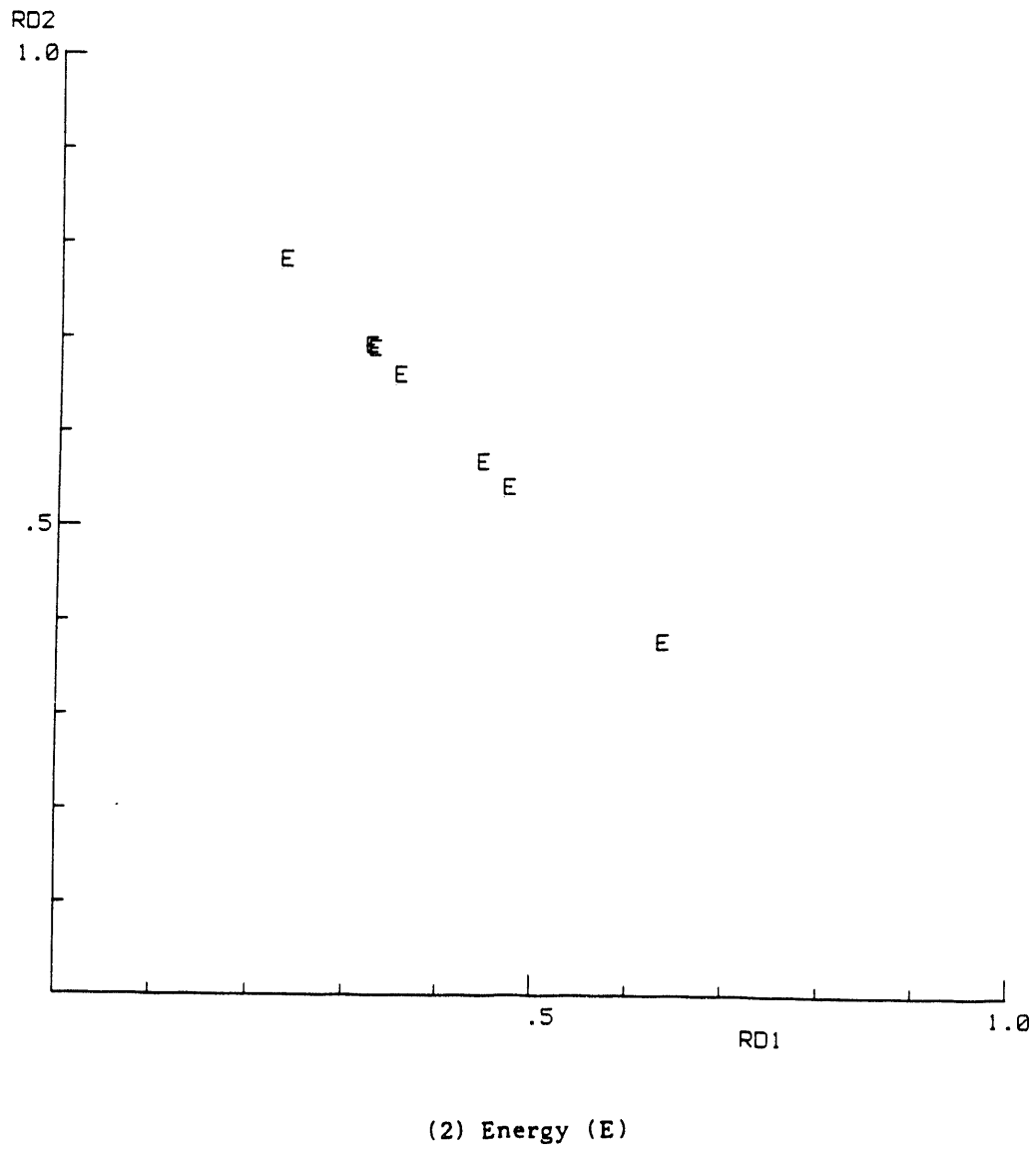
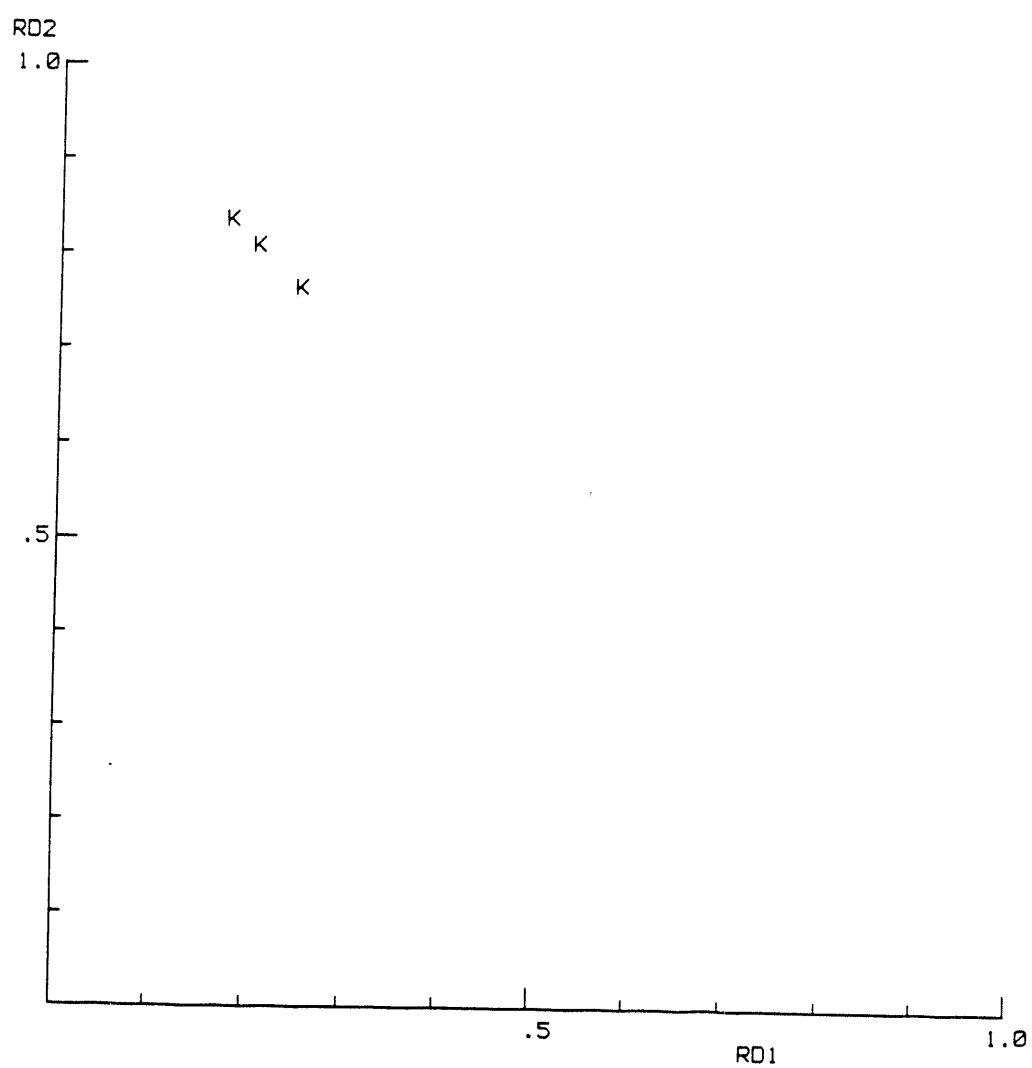


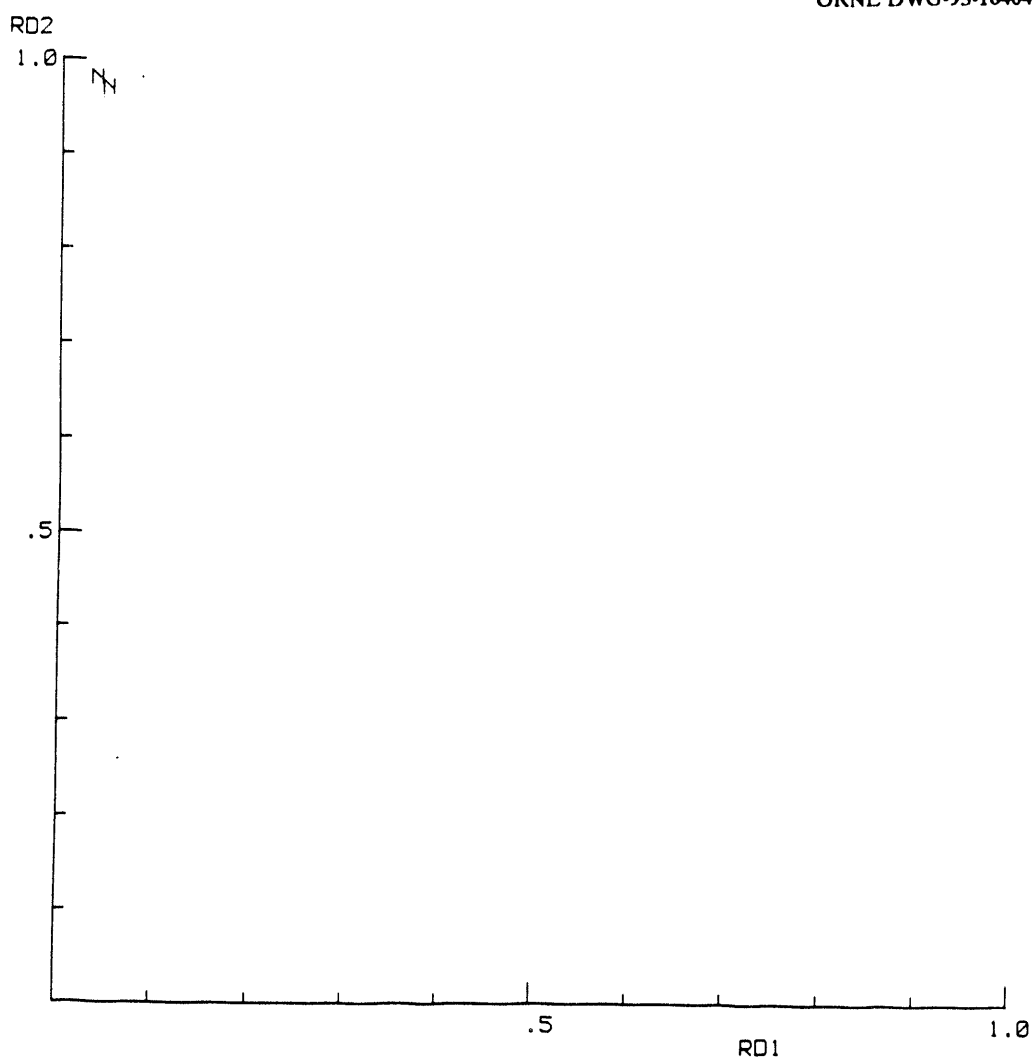
Figure 2b. RD1 versus RD2: Energy (E).



(3) Potassium (K)

Figure 2c. RD1 versus RD2: Potassium (K).

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(4) Nitrogen (N)

Figure 2d. RD1 versus RD2: Nitrogen (N).

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Other Papers

The paper by GILPIN ("Community Collapse: Perspectives on Prediction") expanded to communities in the broad sense, comprising all of the species in a given place. Gilpin pointed to the four evils that will increasingly impact ecological systems: habitat loss, pollution, introduction of alien species, and the secondary effects of the first three. The first three of these may directly cause the extinction of species. The fourth, secondary effects, produces additional extinctions that will occur before the system reaches its final steady state.

Gilpin inquired into the degree to which community ecologists will be able to predict the extinctions produced by these disturbances. Scientists in other fields are often able to predict the consequences of disturbances, shocks, and perturbations to their systems. In fact, this ability is often the strength of their science.

The first problem faced by community ecologists is to identify what they intend by a "community" and to come up with a language by which scientific discourse is possible. It must nonetheless be understood that community ecologists do speak different languages, that these languages resolve different parts of the system, and that the character of the predictions made will be a function of the language spoken.

At levels below and above the "community," the abstractions "population" and "ecosystem," while entailing problems of their own, have been easier to utilize in scientific discourse. The population is the fundamental unit of evolution, while the ecosystem is governed by physical constraints. These connections can allow the use of terminology from other disciplines, for example, population genetics and thermodynamics.

Gilpin acknowledged that there is probably no such thing as the "real community;" at least it is nothing humans can know. By this term is meant the least abstracted, most exhaustively detailed description of the system that we can obtain. Such a description would include detail on single individuals and their inner workings. Clearly, this is not an appropriate level at which to do community theory.

The three levels of state identification listed above represent successively greater degrees of abstraction. Closest to "reality" is the species interaction model, in which all kinds of species interactions, including interference and mutualism, are incorporated. The resource competition model ignores species interactions other than direct consumption, while the feeding web model only considers the presence or absence of a consumption link between two species.

The simplification from the first two levels of abstraction to the third is, from a practical standpoint, quite large. There are no instances where long-term data exist giving the densities of, and interaction strengths between, any set of species. Yet there are many complete descriptions of feeding webs. This means that, at the level of food webs, one has the possibility of empirical patterns that are beyond dispute. For the two higher levels, however, different community ecologists have generalized from the systems with which they are familiar, producing alternative "theories," actually hypotheses, concerning the nature of species interactions: which interactions exist, how strong they are, whether they are constant or vary with time, whether they have coevolved, and so forth. Thus,

at levels 1 and 2 there are competing alternative theories. It is possible that ecosystem and community construction and collapse may help to select the most realistic of these theories.

HASTINGS ("Stability of Food Webs") questioned the basic usefulness of the concept of stability as applied to natural systems. Stability has been extremely difficult to define for such cases. Local stability, or the tendency for a system to return towards a well-defined equilibrium point, seems particularly unsuitable for most real ecological systems. There are many examples of coexisting species in which population numbers do not settle down to stable levels. The less restrictive concept of persistence seems more appropriate in such cases.

One important problem with respect to defining stability is the question of scale. What level of spatial scale does one mean? Systems may be unstable at the level of a patch but can be somewhat stabilized via dispersal that couples together many patches over large spatial areas.

Many models used to describe such food web characteristics as stability do not take into account factors such as age and spatial structure, which can often be crucial. Hastings argued that the important common features of food webs (features that can be usefully compared) may not be the general descriptors such as stability, but instead the lower level mechanisms (interactions between subpopulations on small patches, age-, or size-specific behavior, etc.). The search for sets of commonalities at their lower levels and their incorporation into models is an important goal of theoretical ecologists.

Food web assembly is another key topic in food web theory and **YODZIS** ("The Interface Among Dynamics, Energy, and Assembly") presented a unified perspective that encompassed the rival ideas that (1) either energy constraints or (2) dynamic stability considerations govern structure or that (3) structure is generally "loose" and not strongly controlled by any factor. Yodzis noted that the build-up of communities through a process of assembly by a more or less random sequence of colonizing species has been studied from several viewpoints; energetic constraints (Yodzis 1981, 1984), mild specialists (Sugihara 1982, 1984), and dynamics (Post and Pimm 1983, Drake 1983). His talk explicated the relationship between the energetic and dynamic viewpoints, and proposed, very tentatively, a unified perspective on the structuring of assembled communities.

The dynamic assembly models are based on Lotka-Volterra dynamics for a community of *s* species. In order for a potential invading species to succeed in joining such a community, three criteria must be met (if we assume only equilibrium dynamics): (1) the invader must be capable of increase when rare, (2) the new community must have a feasible equilibrium, and (3) this equilibrium must be stable. As communities are built up in this way, one finds that two things happen (Post and Pimm 1983, Drake 1983): the return time of the system equilibrium decreases, and it becomes more difficult to fulfill the "increase when rare" criterion. Eventually, the assembly process terminates with all further attempted invasions failing already at step 1: "invasion resistant" endstates are reached, with no potential invaders able to increase when rare.

Yodzis showed that the condition (2) for increase when rare is an energetic consideration: it expresses that the invading species must have a positive population energy balance when rare in

order to invade. The invasion resistant endstates of the dynamic assembly process are constrained by energy flow.

This view of the assembly process suggests that communities might fall into at least three different classes:

- (1) If the assembly process terminates, structure will be energetically constrained. This might be the case in relatively undisturbed habitats.
- (2) If small-scale disturbances are sufficient to destabilize the equilibrium before the energetically constrained endstate can be attained, structure will be constrained by dynamical stability (Pimm 1982).
- (3) If assembly is disrupted by larger-scale disturbances, we will get something else - perhaps the "loosely structured" communities discussed in this symposium by Prof. Kawanabe.

The search for universal principles was exemplified by COHEN's study, based on phenomenological rules of predator-prey allometry in food chains. He used an observed allometric relation between the weight of terrestrial vertebrate predators and the weight of their prey to predict an upper limit to the weight of a terrestrial vertebrate predator that is very close to the observed largest weight.

If W_{pred} denotes the weight (in kg) of a terrestrial vertebrate predator and W_{prey} the weight (in kg) of its prey, then the two weights are related approximately by a power function

$$W_{pred} = A W_{prey}^B = f(W_{prey}) . \quad (1)$$

where $B = 0.58$ and $A = 8.6$ approximately. According to (1), a terrestrial vertebrate predator that takes prey weighing 1 kg is predicted to weigh approximately 8.6 kg. A terrestrial vertebrate predator of prey weighing 1 mg is predicted to weigh approximately 3 g.

Applying (1) to a food chain, Cohen determined that for sufficiently long food chains (i.e., the number of links approaches infinity), the weight of a terrestrial vertebrate top predator is predicted to be independent of both the number n of links up to that predator and of the weight W_{prey} of the basal prey in the food chain.

For example, the heaviest terrestrial vertebrate predator considered is the East African lion (*Panthera leo*) at 160 kg. With $A = 8.6$ and $B = 0.58$, (1) predicts a maximum predator weight of 168 kg. However, the number of trophic links in real food chains is not infinite. In 113 community food webs (Cohen et al. 1986), the longest reported chain (from a tropical Pacific plankton community) has 10 links. Using $n = 10$ gives a predicted top predator weight of 155 kg for basal prey weight of 1 g. For chains of length 10, the predicted weight of the top terrestrial vertebrate predator increases by less than 3 percent when the weight of the basal prey increases by a factor of 1000.

That predator-prey allometry can be used to predict approximately the absolute individual size of the largest predator (at least among contemporary terrestrial vertebrate predators) appears not to have been noticed previously. This finding leaves open the problem of explaining the origin of predator-prey allometry.

DeAngelis ("Some Stability Relations in Nutrient-Limited Systems") explored some relationships between system resilience and nutrient availability (through nutrient input and recycling) in nutrient-limited ecological food chains. The results point to the existence of a broad generalization on the level of the total system, but also to great complexities when the internal structure of the food chain has to be taken into account.

At the level of the whole system, when nutrient input is limiting in the system, the ratio of the steady state flux of nutrient to standing stock of nutrient in the system appears to be an accurate measure of resilience, as had been previously noted in computer simulations by Jordan et al. (1972), Dudzik et al. (1975), DeAngelis (1980), and Harwell et al. (1981). The present work adds analytic corroboration to this generalization.

The relationships involving resilience of the system become more complex and interesting when perturbations act on only part of the system and/or the post-perturbation behavior of only part of the system is of interest. Several examples involving perturbations to either the autotroph alone or to the whole system were considered. It was shown that it made a great deal of difference to resilience whether, in steady state, the autotroph exerted control over the level of available nutrient in the system or whether the autotroph was itself controlled by the herbivore trophic level. In the latter case, the ratio of nutrient flux through the ecosystem to its standing stock of nutrients was generally higher, so that resilience was greater than in the former case. Since the autotroph is generally controlled from above when the number of trophic levels above it is odd, autotroph-herbivore and autotroph-herbivore-carnivore-supercarnivore food chains are likely to be more resilient than are autotroph and autotroph-herbivore-carnivore chains.

It was shown that the relative sizes of components of the ecological system also make a difference to resilience when only part of the system is perturbed. A detritus compartment, for example, can act as a buffer to perturbations affecting other parts of the system, if the detritus compartment is large in comparison. The large standing stock of nutrients in the detritus is ready to go back into the pool of available nutrients faster than this pool can be filled by external inputs of nutrient.

The study by DeAngelis was meant only to suggest the variety of behaviors that can occur in nutrient-limited food chains with nutrient cycling. The models examined special functional forms and special sets of parameters. A more thorough study would doubtless reveal more complex patterns of behavior that were beyond the scope of the present work.

CONCLUSIONS: IS THERE A UNIFIED APPROACH IN THEORETICAL ECOLOGY?

Rather than attempting to synthesize all ideas into one summary, it may be better to present verbatim the thoughts of a few different participants, and then make some concluding remarks.

Thomas Burns:

"Unified perspective" clearly means "one view," but this immediately raises the questions "What is being viewed?" and "At what scale or resolution is it being viewed?". At a gross scale or low resolution, the majority of participants at the US-Japan Seminar in the Environmental Sciences shared an underlying interest in ecological theory as it pertains to ecosystems and how they are organized. So from this level a unified perspective has already been achieved. This does not deny that there are ecologists who are primarily concerned with the dynamics of populations, even if they recognize that the "environment" or ecosystem partially determines those dynamics. At a finer scale or resolution, at the level of particular approaches to the problem of how ecosystems are organized, there is no single view. Some are concerned with whether a single population will go to extinction or not under a perturbation to ecosystem organization, some with the "horizontal" organization of guilds, some with the "vertical" organization of feeding webs, and others with the interactive (causal) structure and phenomenology of ecosystems. This diversity is entirely acceptable, perhaps desirable, especially if the different "schools" recognize the existence and validity of alternatives.

At least three pairs of alternative approaches to the problem of ecosystem organization were manifested at the meetings: Applied vs. Basic, Empirical vs. Theoretical, and Population Dynamical (Food Web) vs. Ecosystem Phenomenological (Energy-flow Network). Gilpin, in the morning session of Day 1, made an almost impassioned plea for applied ecological theory, especially towards the protection of species from extinction. Tamaki, in the morning of Day 1, and Kawano and Hara, in the afternoon, were the first of several Japanese researchers to present their empirical field studies. Although not explicitly addressing the problem of ecosystem organization, they demonstrated the need for ecosystem theory to help focus and interpret empirical studies of populations and guilds, and they reminded the theoreticians that it is real ecosystems we are attempting to understand. These presentations also strongly suggested that non-reductionistic approaches were necessary to understand real systems. Ecology cannot be reduced to physiology and demography, because interactions of all types are significant. The first two pairs of alternatives will not be discussed further because it is evident to most ecologists that both are necessary for science to progress.

More than any other, the "unified perspective" sought was that between "food web" and "ecosystem" approaches to ecological theory. While these two will and probably should continue as distinct approaches to distinct problems, common ground was uncovered: a concern with whole ecosystems and not merely the local relationships between populations or guilds, a focus on trophic interactions, and an awareness that their indirect effects influence ecosystem organization, including the species-abundance relations within guilds. This was exemplified by Shigesada et al.'s paper, on the morning of Day 1, where they considered the effect of a predator on a set of competing species and by the work on food web assembly presented on Day 2, as well as the "ecosystem" papers on Days

3 and 5. Teramoto's presentation on the first afternoon also tied in nicely with this theme. He discussed how, from its very beginning with Motomura in 1932, ecology's concern with empirically observed species-abundance relations has been modeled by assuming interspecific competition within guilds. However, he then presented work of Nakajima demonstrating that the geometric series distribution can be generated by null models (with respect to competitive interactions); i.e., a probabilistic invasion process. Assuming that the world is not truly random, these results suggest that the usual level of explanation (interspecific competition within guilds) is perhaps inappropriate or insufficient for understanding (modeling) what determines species-abundance relations. Many at the meeting would agree that trophic interactions at least must be included in such models.

Whereas explicitly considering how both predators and resources determine the dynamics of populations may be a "revolutionary" advance for ecological theory (Fretwell 1987), approaches that account for energy and nutrient flows from all resources to all consumers, no matter how small the direct interactions, are equally important to understanding the trophic structure and hence the organization of ecosystems. The trophic structure of ecosystems cannot be reduced, however, to a simple chain of feeding interactions (e.g., Lindeman 1942) without significant loss of information (Burns ms.). It is hubris to make claims that any approach is more important or "central" to ecological theory, and doing so only further divides ecology. A unified perspective may simply be an open-minded recognition that many approaches are needed to understand organisms and their environments; that is, ecosystems.

Peter Abrams:

There are probably few areas of science today that are more lacking in a unified perspective than ecology. Scientists who call themselves ecologists may read totally nonoverlapping subsets of the scientific literature, use totally different approaches, and fervently believe that many of the other approaches are not only less productive areas of inquiry, but do not even qualify as science. Given this state of affairs, the title of the Joint U.S.-Japan Seminar was perhaps overly optimistic. Nevertheless, the fact that most of the participants were theorists, and the fact that they represented a selected subset of theorists, might have been expected to produce a more unified view than exists for the field as a whole. To determine whether this expectation was met, one must first address the problem of how to define a "unified perspective," and related issues.

By definition, if an area of science is active, there will be differences of opinion on some significant problems, and the perspectives of different workers will not be identical. Thus, if a truly unified perspective existed in ecology, it would imply that we should seek employment in other fields. The question is really whether the field has a sufficiently narrow range of perspectives with gaps that are sufficiently few and narrow, that problem solving is not inhibited by differences in approaches. The papers and discussions at the U.S.-Japan Seminar suggested both that existing differences may have inhibited problem solving, but also that such differences need not do so. The major dichotomy in approaches among the U.S. participants was that between the population/community ecologists and the ecosystem ecologists. O'Neill et al. (1986) have recently discussed the dichotomy in a book on hierarchy theory, and I can add little to that discussion here. The major difference between these two factions is the set of variables that each group usually examines. Ecosystem ecologists typically follow

a variety of aggregated variables such as carbon flow or biomass per trophic level, and population/community ecologists focus on the population densities of species. Many ecologists (especially ecosystem ecologists in the United States) have, I think, wrongly equated this with the distinction between holism and reductionism. There has been considerable antagonism between the two camps as a result. There is an equally large difference between the variables of interest to population geneticists/evolutionary ecologists and population ecologists, but there has never been the illusion of a holist/reductionist dichotomy. Because of this lack of philosophical baggage, the differences have been seen as an intellectual gap to be bridged rather than as a barrier separating more and less worthy approaches. Several of the papers presented by the Japanese participants and that of DeAngelis were attempts to span the gap between population and ecosystem approaches. These provide some rays of hope for filling in holes that exist in ecology's theoretical framework, which I see as the closest we can come to a unified perspective on theoretical approaches to ecology.

Filling the holes in "theory space" has the potential benefit that patterns observed in one set of variables can be related to mechanisms operating on another set of variables, with a resultant increase both in explanatory and predictive power. As Michael Gilpin pointed out, an increase in predictive power is necessary if ecological theory is to make significant contributions to solving ecological problems. The major gaps that I see in present ecological theory are (i) the lack of attempts to provide population dynamical mechanisms to explain phenomena observed in the aggregated variables typically monitored in ecosystem studies, and (ii) the lack of behavioral mechanisms in models of interactions within and between populations. The fact that there were several papers presented that addressed each of these areas suggests that the lacunae are being eliminated. The work of DeAngelis and Sugihara seems to be related to the first gap, and that of Matsuda, Yamamura and colleagues, as well as my own is related to the second. Needless to say, it would not be desirable for all ecologists to have the filling of these gaps as their first priority. If this were to happen, the resultant decline in diversity would more than offset any advantage in connectedness. The diversity of views presented at the meeting suggests that we do not have to worry about this yet.

Michael Gilpin:

A variety of views at population, community, and ecosystem levels have been expressed in this joint meeting with Japanese and United States ecological scientists. A "unified approach" is sought. As a paradigm of unification, DeAngelis offered the great thermodynamic reduction. What was that? Two sciences working at very different levels of resolution - 10 raised to the 23rd power apart - speaking very different languages. One language spoke of temperature and heat capacity. The second spoke of kinetic energy and statistical distributions. The problem was really one of aggregation. The likes of Gibbs, Maxwell, and Helmholtz produced a $g()$ function that mapped variables at the lower level and totally explained all the experimental phenomena at the higher level with molecular processes at the lower level. Molar thermodynamics was reduced (yet it continues to be used!).

Is the situation we face as grim in its separation or as potentially promising with the prospect of reduction? One encouraging sign is that we basically speak the same language. The basic problem is with aggregation. The population dynamicist lumps all species beyond those he wants to study into

the environment. The community ecologist keeps 3 to 30 species as his state variables. The ecosystem person works with about the same range of variables, but many of these variables are aggregations of species.

Are we trying to reduce ecosystems and community ecology to population dynamics? Yes and no. I have, for example, explained the molar properties of island biogeography with statistical distributions of species extinction and colonization rates -- successfully, I believe. The food web people have done a number of similar things.

But this seems to strike terror into holists. Yet I think we have seen, and quite profitably so, that there is not this great chasm between the holists and reductionists. All ecologists are holists. And it is exactly this that draws us from mathematics, physics, and other basic sciences. Patten believes that I have extracted my *Drosophila* system away from reality, from context, from, I think he would say, the Aristotelian purposes of the ecosystem.

It seemed that so-called indirect effects were one expression of this. Whole ecosystems had them; abstractions did not. Yet this quickly proved to be false. Contrary to Patten, people at the meeting had demonstrated the consequences of indirect effects in many ways. And everyone seemed to agree, at least for certain phenomena, that they were of predominate importance. Indeed, indirect effects are found at all levels of population biology. Even in population genetics they are seen in epistasis, and in correlated responses. So, perhaps this is a red herring. What then is the axis over which we need to establish a unification.

Information is one such axis. Population genetics is awash and floundering in too much information. Population dynamics has almost enough, though it is not as long-term as one would like. Community ecology has very little beyond two and three species interactions (e.g., agriculture, pest control). With ecosystems the situation is even worse, for there are almost no long term studies, and questions of aggregation boundaries are still vexing problems. I feel that a unification can only occur when the availability of system information is more uniform.

There is another problem that is probably producing just as much discord. We rarely make clear what it is that we expect from our modeling exercises. Let me consider three works:

1. Shigesada, Kawasaki, and Teramoto on theory;
2. Gilpin's *Drosophila* work on laboratory species assembly;
3. Food web links and dynamic stability by DeAngelis, Yodzis, Pimm, Cohen, and others in the real world.

We shall consider them with regard to the role of interference competition.

Shigesada assumed interference competition and proved theorems about it; except for my own laboratory *Drosophila* model these theories have no connection to reality. I worked with a possible world, as Haldane put it -- not the real world. The purpose of my experiments was to find alternative domains of attraction, as Case and I have predicted in 1974 and which were the basis for Diamond's assembly rules. The generalized interference we found was not expected and was somewhat discouraging for our goal of alternative domains. Yet the domains existed for other reasons.

The food web people start solidly in reality. They work with data from real systems. Their goal is one of reduction. They want to explain a pattern they see based on a process they believe they understand - the persistence of systems based on resilience as indexed by eigenvalues. They fail altogether to recognize or to mention interference. Yet, given their goal, this might be justifiable - for generalized interference is neither universal nor dominating, and it is not obvious that it biases their results. Nonetheless, they have not fully justified this.

What we need to do to integrate our ecological science more fully is to focus on mechanisms and to explicitly consider them as they run the gamut of aggregation. Interference is a place to start.

George Sugihara:

I agree with the comments made earlier by several participants (in order: N. Shigesada, P. Abrams, Y. Iwasa, and J. Cohen) that a diversity of approaches is healthy. I also agree with the somewhat paradoxical view that effort toward some kind of unification is also healthy.

From a naive system dynamical point of view, maintaining diversity in a system appears opposite to forces tending towards unification. Indeed, the positive effect of a meeting such as this one, whose purpose is to find bridges or conduits for interactions among a diverse community of interests, is precisely to generate instability within the community. The dynamical analogy may not be entirely facetious. Such instability is caused by stronger interaction among players (unification). It may represent progress even though the outcome may involve the loss or absorption of one set of interests by another. This is a desirable dynamic as long as new ideas are continuously created, so that the process will not run out of steam. That is, the striving toward unification (especially cross checking for consistency) combined with the steady creation of new viewpoints seems to be a very desirable condition for progress. Therefore, insofar as this complexity-stability metaphor seems reasonable, progress viewed in terms of the dynamism of the field can best be fostered by encouraging efforts toward unification and encouraging the generation of new ideas.

Mathematics can be described as the axiomatic study of objects and relations. Science, on the other hand, is at best only semi-axiomatic. The art in science comes in choosing these objects and relations in meaningful and insightful ways so that nature becomes more comprehensible (i.e., so that we can create order out of complexity).

This difficult question of the art in science is, I believe, a fundamental one that deserves more prominence in our thinking. In this regard, one of the dangers that we as theorists have to avoid is illustrated by the story of the man in a lighted room who is looking for something he knows was lost in the darkened room next door. When asked why he is not looking next door he replies, "the light is better here." There is a temptation in ecology to restrict our search to lighted rooms, using models, formalisms, and techniques that are familiar and tractable rather than necessarily informative about nature.

Ecological systems are complex; consequently it may be difficult to succeed solely with a classical bottom-up approach involving theoretical investigations that begin with assumed microscale mechanisms and are extrapolated to predict large-scale behavior and patterns. It is possible that more rapid progress would be made if the flow of information from theory to field test were reversed. That is, it may be useful, at least as a complementary strategy, for the flow of information to proceed from

nature to theory. The idea is to exploit existing data and measurements to find large-scale or whole-system regularities (symmetries and invariances) that can be used to characterize real ecosystems. Modern physics has developed largely through the systematic use of such symmetry principles. This idea of creating a more empirically informed community-ecosystem theory based on the phenomenology of actual data has been made by May, Ulanowicz, Pimm, and Cohen, among others.

Within the context of this meeting, and to complete this thought with an example, I was particularly intrigued by Hirata's empirical result that when an estuarine system is viewed in terms of nitrogen and phosphorus cycling, it appears to be more well-organized than when the classical quantities, energy or carbon, are used. This is interesting because it demonstrates how data for a real system can potentially inform us as to how to construct ecosystem flow models. In terms of Hirata's mutual information criterion, characterizing systems by their nitrogen or phosphorus cycles may yield a more coherent picture (i.e., a system having greater predictability, and implicitly giving rise to a more successful model) than when the classical quantities carbon or energy are used.

Joel Cohen:

A concrete opportunity to unify different areas of ecological theory arose at the meeting. For example, Ulanowicz spoke at length about the increase in his measure of ascendancy over time, without giving any empirical or theoretical foundation for his claim. Ascendancy is a product of two factors, one a measure of system size, the other an entropy-like measure of system complexity. During the meeting, Iwasa distributed a paper that demonstrates that entropy increases in time under the operation of a variety of linear systems, such as discrete-time or continuous-time Markov chains on discrete or continuous state species. Iwasa's paper provides a theoretical justification for a temporal increase in the entropy factor of Ulanowicz's ascendancy, provided one accepts a linear approximation to the dynamics of a system. As another example, the models of Aoki on entropy flow in ecological systems are closely related, it seems, to those of Patten. My image of a unified perspective in ecological theory is captured by the biological term "anastomosis." The way to encourage this anastomosis is by bringing together people with different perspectives at precisely the sorts of meetings as the present one.

GENERAL CONCLUSIONS:

It is reasonable to conclude that most participants felt that a "unified perspective" is still somewhat ambitious for theoretical ecology. Major differences in approach still divide some aspects of theory - particularly theory at the ecosystem level versus that at other levels. To attempt to get beyond the enormous complexity of ecosystems, theorists working at this level are looking for holistic concepts from thermodynamics and information theory. Still, the community/food web theorists, while often working in a reductionist manner, are also oriented towards a holistic perspective. Thus, while the gap between the ecosystem level and other levels seems wide and a diversity of approaches appears to be inevitable and probably desirable for some time, connections between the two views are being made.

At the lower levels -- food webs, communities, populations, and individual adaptations -- a unified perspective may be emerging, as the scientific programs in each of these areas seem to be converging rapidly.

APPENDIX A

**Participants of the U. S.- Japan Seminar in the
Environmental Sciences**

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|---------------------|---|
| Takuya Abe | Associate Professor, Department of Zoology, Kyoto University, Sakyo-ku, Kyoto 606, Japan |
| Peter A. Abrams | Associate Professor, Department of Ecology, University of Minnesota, 318 Church Street, Minneapolis, Minnesota 55455 USA |
| Ichiro Aoki | Associate Professor, Department of Physics, Osaka Medical School, 2-41 Sawaragi-cho, Takatsuki 569, Japan |
| Thomas P. Burns | Institute of Ecology, The University of Georgia, Athens, Georgia 30602 USA |
| Joel E. Cohen | Professor, The Rockefeller University, 1230 York Avenue, New York, New York 10021 USA |
| Donald L. DeAngelis | Senior Scientist, Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, Tennessee 37831 USA |
| James A. Drake | Assistant Professor, Department of Zoology, The University of Tennessee, Knoxville, Tennessee 37996 USA (absent due to illness) |
| Michael E. Gilpin | Professor, Department of Biology, University of California at San Diego, La Jolla, California 92093 USA |
| Toshohiko Hara | JSPS Fellow, Institute of Plant Ecology, Kyoto University, Sakyo-ku, Kyoto 606, Japan |
| Alan M. Hastings | Professor, Department of Mathematics, University of California at Davis, Davis, California 95616 USA |
| Masahiko Higashi | JSPS Fellow, Department of Biophysics, Kyoto University, Kyoto University, Kyoto 606, Japan |
| Hironori Hirata | Associate Professor, Department of Electronics, Chiba University, 1-33 Yagi-cho, Chiba 260, Japan |
| Yoh Iwasa | Instructor, Department of Biology, Kyushu University, Higashi-ku, Fukuoka 812, Japan |
| Hiroya Kawanabe | Professor, Department of Zoology, Kyoto University, Sakyo-ku, Kyoto 606, Japan |
| Shoichi Kawano | Professor, Department of Botany, Kyoto University, Sakyo-ku, Kyoto 606, Japan |

- Kohkichi Kawasaki Associate Professor, Science and Engineering Research Institute, Dohshisha University, Kamigyo-ku, Kyoto 606, Japan
- Hiroyuki Matsudo Information Processing Center of Medical Sciences, Nippon Medical School, Sendagi 1-1-5, Bunkyo-ku, Tokyo 113, Japan
- Hisao Nakajima Associate Professor, Department of Mathematics and Physics, Ritsumeikan University, Kita-ku, Kyoto 603, Japan
- Bernard C. Patten Professor, Institute of Ecology, The University of Georgia, Athens, Georgia 30602 USA
- Stuart L. Pimm Associate Professor, Department of Zoology, The University of Tennessee, Knoxville, Tennessee 37996 USA
- Nanako Shigesada Instructor, Department of Biophysics, Kyoto University, Kyoto University, Kyoto 606, Japan
- George Sugihara Assistant Professor, Scripps Institution of Oceanography, La Jolla, California 92037 USA
- Akio Tamaki Instructor, Department of Fishery, Nagasaki University, 1-14 Bunkyo-cho, Nagasaki 852, Japan
- Ei Teramoto Professor, Department of Biophysics, Kyoto University, Sakyo-ku, Kyoto 606, Japan
- Robert E. Ulanowicz Professor, The University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland 20688 USA
- Norio Yamamura Associate Professor, Department of Natural Sciences, Saga Medical School, Nabeshima-cho, Saga 840-01, Japan
- Peter A. Yodzis Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

APPENDIX B

**Topics of Participants of U.S.-Japan Seminar
in the Environmental Sciences**

Abe, Takuya - "Ecology of Termites: Do Mutualistic Relationships Decide the Community Structure?"

Abrams, Peter A. - "Representing Biological Communities Containing Optimally Foraging Herbivores: Implications of Adaptive Behavior for Community Structure"

Aoki, Ichiro - "Entropy Laws in Ecological Networks at Steady State"

Cohen, Joel E. - "Why the Lion is not Larger: Predator-Prey Allometry and Food Chains"

DeAngelis, Donald L. - "Some Stability Relations in Nutrient-Limited Systems"

Drake, James A. - "Towards a General Theory of Community Organization Using Assembly Rules" (presented by Pimm)

Gilpin, Michael E. - "Community Collapse: Perspectives on Prediction"

Hastings, Alan M. - "Stability of Food Webs"

Hirata, Hironori - "Information in Ecological Communities"

Iwasa, Yoh, and Simon A. Levin - "Perfect and Approximate Aggregation in Model Ecosystems"

Kawanabe, Hiroya - "Facultative Mutualism in Fish Communities"

Kawano, Shoichi, and Toshihiko Hara - "Spatio-Temporal Changes in Growth, Structure, and Fecundity of a Plant Population over the Environmental Gradients"

Matsudo, Hiroyuki - "Coevolutionary Stable Community Structures in a Patchy Environment"

Nakajima, Hisao - "Sensitivity and Stability of Flow Networks"

Patten, Bernard C., Masahiko Higashi, and Thomas P. Burns - "Trophic Dynamics in Ecosystem Networks: Significance of Cycles and Storage (Network Theory)"

Pimm, Stuart L. - "Food Web Structure and Temporal Variation"

Shigesada, Nanako, Kohkichi Kawasaki, and Ei Teramoto - "Effects of Invasions in a Patchy Environment"

Sugihara, George - "Some Theoretical Approaches to Community Assembly"

Tamaki, Akio - "Characteristics of Species Interactions Organizing the Benthic Community on an Intertidal Flat"

Teramoto, Ei - "A Note on the Population Size Distributions of Competing Species"

Ulanowicz, Robert E. - "Further Research to Quantify the Effects of Non-Newtonian Causalities in Ecosystem Development"

Yamamu , Norio, Hisao Nakajima, and Masahiko Higashi - "Flow-Matching and Flow Compensation in Simple Model Ecosystems: A Network Coevolutionary Approach to Ecosystem Organization"

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