

**IDEA**

**Increasing resource specialization among competitors shifts control of diversity from local to spatial processes**

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**Abstract**

We argue that an increase in the number of specialized consumers can shift the control of ecological dynamics from local to spatial processes. When there are only a few specialized types, local dynamics maintains most types within each patch. As the number of types increases, the probability of local extinction rises. Subsequent colonizations perturb local dynamics, setting off another round of extinctions and the potential for later recolonization. Global processes of colonization and extinction reduce local diversity and increase differentiation among patches. We draw an analogy between the specificity of host-parasite genetics and the specificity of consumer–resource pairs.

**Keywords**

Colonization, competition, dispersal, extinction, host-parasite, metapopulation.

Suppose that several species compete for a limited resource. The competitive vigor of each species depends on the abundance of a distinct resource on which that species is uniquely specialized. Define the dimensionality of the system as the number of different resources available for specialization. We argue that changes in dimensionality cause qualitatively different ecological dynamics and patterns of diversity.

Low-dimensional systems maintain most of the few possible species in each local patch, with dynamics controlled by local processes of competition. As the number of species rises, the average abundance per species declines (Tilman & Pacala 1993). Lower average abundance increases the probability that one or more species become extinct locally by deterministic nonequilibrium fluctuations and by demographic stochasticity (May 1974).

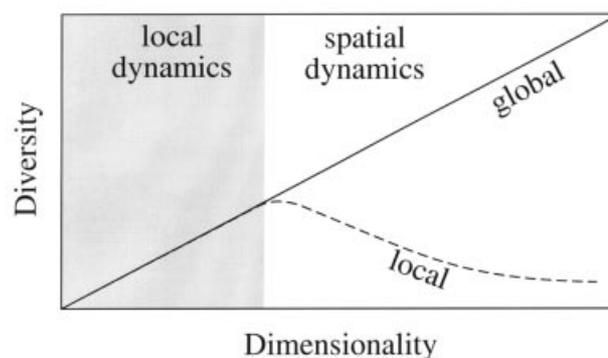
Local extinctions make individual patches prone to rapid growth of colonists. Suppose a particular species has recently become extinct in a particular patch. The unique resource consumed by that species will increase. Then a colonist of that species can invade and increase rapidly because its competitive ability will be boosted by an

abundant supply of its special resource. The rapid increase of the colonist will drive down the abundance of competitors, making them prone to local extinction. Any extinctions will be followed by an increased supply of the matching resources. Another round of colonization, competition, and extinction is inevitable. Cycles of local colonizations and extinctions continue, each bout coupled with a turnover in local diversity.

Figure 1 summarizes the comparative predictions about dynamics and diversity. The dynamics of low-dimensional systems are governed by local processes of competition. Each additional specialist that can be stably maintained locally increases both local and global diversity. As dimensionality rises, the risk of local extinctions increases. At some point, spatial processes of colonization and extinction dominate and periodic, extreme competition from colonists drives down local diversity. Thus a rise in the number of specialist types decreases average local diversity but increases the diversity maintained in the metapopulation.

Frank (1989, 1993, 1997) developed a similar argument for host-parasite genetics. The host-parasite models can be considered part of a wider class of genetic models of specific recognition. In those models, the consumer genotype must avoid specific recognition and defence by the resource genotype. Successful attack leads to a benefit to the consumer at a cost to the resource. Empirical studies of plant-pathogen genetics, cytoplasmic male sterility, and other genetic systems of recognition and antagonism often reveal high dimensionality of specificity and a strong influence of colonization-extinction dynamics (Gouyon & Couvet 1985; Thompson & Burdon 1992; Frank 1997). But there is not enough comparative evidence to analyse the main prediction – that a shift in dynamics and diversity occurs as systems change from low to high dimension.

We suggest that the logic connecting dimensionality to dynamics applies both to host-parasite genetics and to a broad class of consumer–resource models of competition.



**Figure 1** Increasing dimensionality causes a shift in the control of dynamics from local to spatial processes.

Frank (1993, 1997) illustrated host-parasite dynamics with a simple model. Here we introduce a similar model to illustrate consumer–resource dynamics.

Each of  $m$  consumer species, with abundance  $N_i$ , is specialized on a resource with abundance  $R_i$ . The dynamics are given by

$$\Delta N_i / \Delta t = cbN_i(R_i - \sum R_k N_k / K)$$

$$\Delta R_j / \Delta t = a(S - R_j) - bR_j N_j,$$

where each individual of species  $i$  consumes  $bR_i N_i$  units of resource per time period and converts those resources into reproduction at a rate  $c$ . The supply of resource  $i$  increases at a rate  $a(S - R_i)$ , where  $S$  is a carrying capacity for resource abundance and  $a$  is a rate constant (Tilman 1982). Competition among consumers for another, limited resource sets the carrying capacity of all consumers at  $K$ .

The dynamical system is easier to analyse when written in nondimensional form (Segel 1972; Murray 1989) by using the following substitutions:

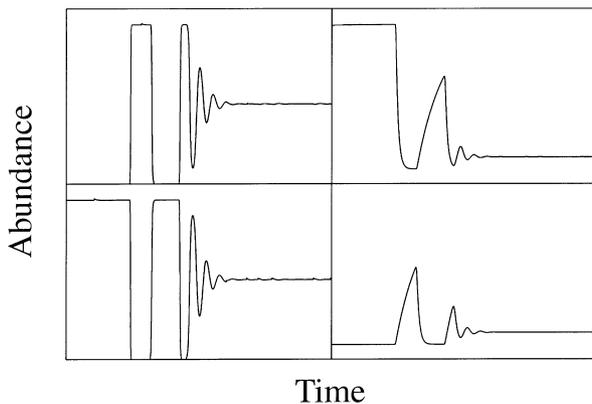
$$n_i = N_i / K, r_i = R_i / S, \alpha = a / bcS, \beta = K / cS, \Delta\tau = bcS\Delta t,$$

yielding

$$\Delta n_i / \Delta\tau = n_i(r_i - \sum r_k n_k)$$

$$\Delta r_j / \Delta\tau = \alpha(1 - r_j) - \beta r_j n_j$$

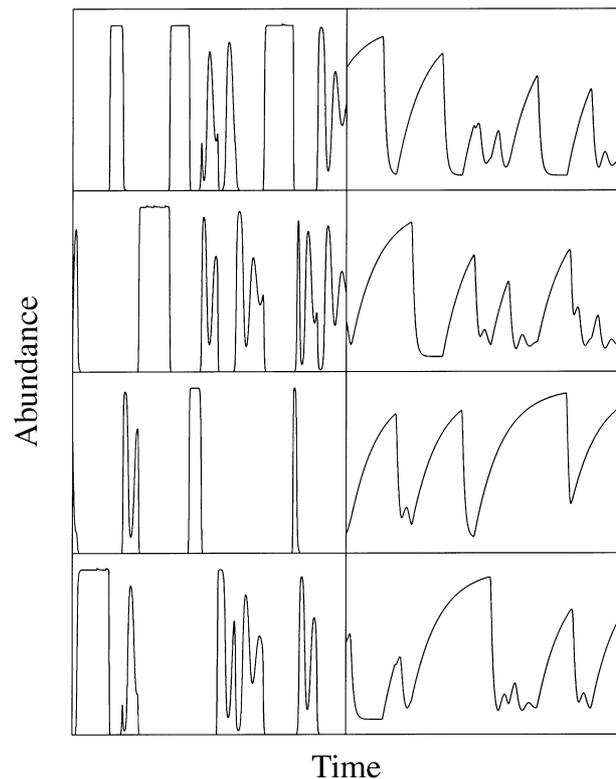
for  $i, j, k = 1, \dots, m$ . The system is controlled by the four parameters  $\alpha$ ,  $\beta$ ,  $m$ , and  $\Delta\tau$ . These difference equations become continuous (differential) as  $\Delta\tau \rightarrow 0$ .



**Figure 2** Time series of the dynamical system described in the text. The parameters are  $\alpha = 0.005$ ,  $\beta = 0.05$ ,  $\Delta\tau = 0.1$ , and  $m = 2$ . The system was run for an initial 15,000 iterations (not shown); the following 20,000 iterations are plotted. Each iteration is a nondimensional time step of length  $\Delta\tau$ . Extinction is simulated by setting to zero any abundance less than 0.01. Colonization is simulated by adding 0.01 to the abundance of each consumer in each iteration if a random number between 0 and 1 is less than  $5 \times 10^{-4}$ . Thus the average number of iterations between each colonization event is 2000.

Figures 2 and 3 illustrate the change in dynamics as the dimensionality,  $m$ , increases. In Fig. 2, the two consumers ( $m = 2$ ) specialize on two different resources. The temporal dynamics for consumers are shown in the left column of panels. In each row, the right panel shows the matching dynamics of the resource on which the consumer specializes. After initial transients of local extinctions and recolonizations, the system in Fig. 2 settles to an equilibrium with both consumers maintained locally.

Figure 3 has identical parameters except that there are four consumer–resource pairs. This system could, in theory, settle to an equilibrium with all types equally abundant. But the transient dynamics caused by repeated extinctions and stochastic colonizations tend to keep the system fluctuating away from the basin of attraction to the equilibrium. Any consumer–resource pair sufficiently displaced from its equilibrium eventually sets off another round of transient dynamics. The probability that at least one pair is displaced increases as the dimensionality,  $m$ , rises. Increasing dimensionality shifts the control of the dynamics from local to spatial processes.



**Figure 3** Time series for the system with  $m = 4$  consumer–resource pairs. All other parameters and methods are the same as in Fig. 2.

## ACKNOWLEDGEMENTS

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## BIOSKETCH

Steven Frank studies specific recognition and polymorphism in host-parasite interactions, the evolution of social behavior, and conflict and cooperation in symbiotic relationships.

## IDEA

### Do Bertalanffy's growth curves result from optimal resource allocation?

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#### Abstract

Bertalanffy's equation is commonly used to model indeterminate growth. Bertalanffy claimed that this growth pattern results from growth potential decreasing with age. An alternative approach provided by life history theory predicts that indeterminate growth is optimal for organisms in a seasonal environment and results not from decreasing growth potential but from allocating increasingly less energy with age into growth, and more into reproduction. Bertalanffy's curves are the result of evolutionary optimization and should not be used in optimization models as an assumption, but they can be used as a tool to describe the indeterminate growth pattern phenomenologically.

#### Keywords

Bertalanffy's equation, growth curves, indeterminate growth, life history evolution, optimal resource allocation, optimization models, reproduction, seasonality, trade-off.

Many amphibians, reptiles, fishes, annelids, mollusks, crustaceans, and other animals continue to grow after maturation, slowing down their growth with age. Such an indeterminate growth pattern is often approximated by Bertalanffy's equation (Bertalanffy 1957; Beverton & Holt 1959; Sibly & Calow 1986; Charnov 1993; Weinberg & Helser 1996). Although growth curves generated this way fit the field data well, Kozłowski (1996), Day & Taylor (1997), and Kozłowski & Teriokhin (1998) warn that Bertalanffy's equation is misused in the theory of life history evolution.

In Bertalanffy's model, the rate of change in body weight is the difference between the rates of anabolism (tissue production) and catabolism (tissue dissipation), with anabolism proportional to the two-thirds power of body weight and catabolism directly proportional to body weight. According to Bertalanffy, the diminishing – with size – difference between anabolism and catabolism slows down growth with age; growth finally stops when