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Source: *BioScience*, Vol. 39, No. 9 (Oct., 1989), pp. 600-605
Published by: Oxford University Press on behalf of the American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/1311089
Accessed: 14/11/2014 08:23

Inferring Process from Pattern in Natural Communities

Can we understand what we see?

William G. Cale, Geoffrey M. Henebry, and J. Alan Yeakley

A basic assumption of scientific investigation is that observed phenomena have underlying physical causes (Beck 1982). Understanding causes—the biotic and abiotic processes of nature—can explain why the world is the way it appears and how it can change. Biologists use the word *pattern* to describe the observable traits of a system and their configuration. Pattern is what is seen, whether using an electron microscope or a satellite imaging system. Biologists and other scientists apply logic, experience, and statistical analysis to explain a pattern in terms of the processes believed to underlie it. But to what extent do these patterns mirror the processes that created them?

This article examines the relationship between pattern and process in ecology. The general conclusions are applicable to other aspects of complex living systems. We present a hypothetical system as a model of two natural processes. This system is used to examine the intricate relationships between pattern and process. Often processes are not deducible from pattern. Therefore, understanding and predictions must derive from analysis not of patterns but of fundamental processes themselves.

Predictions must derive from analysis not of patterns but of fundamental processes themselves

Pattern in ecological theory

Much ecological theory attempts to explain community patterns, commonly measured in terms of the distribution or abundance of individuals of different species, and the changes they undergo. But ecologists, past and present, have disagreed on what processes create pattern in communities. Because it is impossible to conduct controlled experiments in nature, ecological data are subject to a greater breadth of interpretation than are data from the laboratory of, for example, a physical chemist. Darwin's success in observing patterns of change within species and inferring the underlying process led later biologists to attempt an inductive approach to theory. But inductive methods do not necessarily converge on the truth.

Succession provides a familiar example of ecological controversy. Clements (1916, 1936), Gleason (1926), Whittaker (1953), Odum (1969), and Drury and Nisbet (1973) each explained an observed pattern differently, although they all based their explanations on natural biotic and abiotic processes.

Another example of attempts to explain pattern by process is the spirited debate in the 1960s, in which ecologists argued about the mechanisms responsible for the abundance of populations (Ehrlich and Birch 1967, Hairston et al. 1960, Murdoch 1966, Slobodkin et al. 1967). Ecologists have also analyzed patterns of diversity, complexity, and trophic structure (Connell 1978, Goodman 1975, Hurlbert 1971, Paine 1966, Pimm 1984, Whittaker 1965, Wilhm and Dorris 1968); these important areas of ecological inquiry (May 1986) form the basis for much theoretical conjecture.

Ecological competition

The role of ecological competition in creating community pattern has been the subject of considerable debate. For this article, we have modeled ecological competition as an example of the role of process in determining pattern. Competition between two organisms in nature occurs whenever a resource required by both is in short supply. Competition can occur over, for example, nesting sites, mates, territories, and food. Due to genetic heterogeneity, individuals in a species are not equally able to secure resources. There are also differences between species in ability to obtain resources. These intraspecific and interspecific differences may determine which species are found in a particular ecosys-

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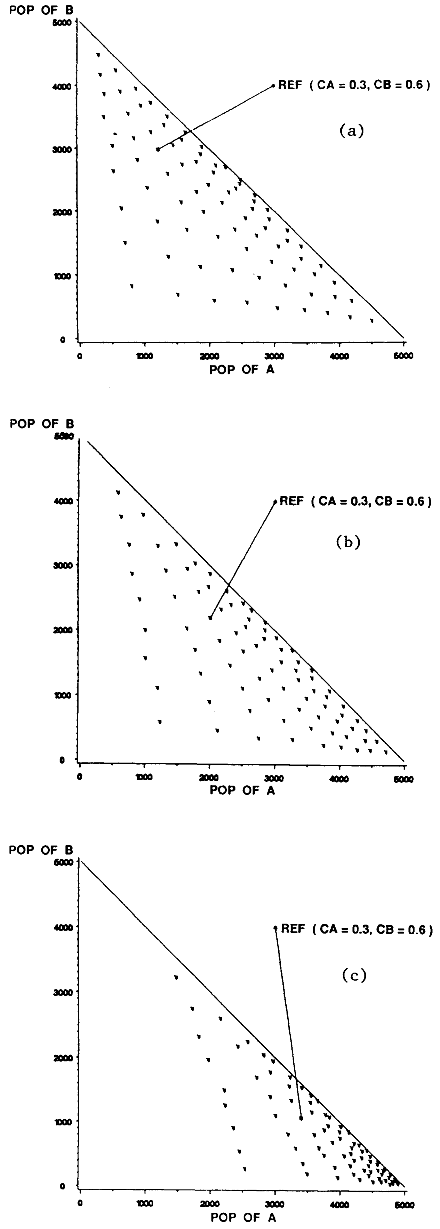

Figure 1. Each graph plots the 81 equilibrium solutions that result from individually varying competition parameters C_A and C_B over the range 0.1–0.9 (10:10, 10:20. . . 20:10, 20:20. . . 90:80, 90:90, giving 81 combinations) while holding reproduction ratios constant at 50:50 in (**a**), 70:30 in (**b**), and 90:10 in (**c**).

tem and which individuals in those species successfully reproduce.

Hutchinson's (1959) classic essay set forth the ideas that spawned what is now known as competition theory. Its claims were bolstered by a wide array of empirical observations (Cody 1975, Diamond 1975, Gilpin and Justice 1972, Schoener 1974, 1983). By the end of the 1970s, competition was widely regarded as the most important biological process shaping the pattern of natural communities (Cody and Diamond 1975). Wiens (1977) remarked, "The conventional wisdom of competition theory also dictates that competition is *the* major selective force acting upon the resource-utilization traits or determining the distributions of species" (emphasis in original).

Although the tenets of competition theory had been questioned much earlier (Ayala 1969, Miller 1967), the end of the 1970s began a period of intense scrutiny (Connell 1978, Connor and Simberloff 1979, Simberloff and Connor 1981, Strong et al. 1979). Examination ultimately focused on questions of methodology, especially hypothesis testing, and whether the empirical evidence supported the predictions of theory. These challenges provoked responses in the literature (Diamond and Gilpin 1982, Gilpin and Diamond 1982, Grant and Abbott 1980, Grant and Schluter 1984, Roughgarden 1983, Rummel and Roughgarden 1983, Tilman 1982), but the issue was not resolved. Writing in *Science,* Lewin (1983) brought the matter to international attention. Further volumes presented multiple points of view (Salt 1984, Strong et al. 1984). Different scientists often analyzed the same data sets; different conclusions came out of the same patterns of species distribution and abundance.

Two distinct, fundamental questions are central to the competition controversy. First, does community pattern reflect competition? If so, competition's effect should be detectable through analysis of empirical data on species distribution and/or abundance. If, however, the analysis indicates a pattern statistically indistinguishable from random distribution, is it appropriate to infer that competition is absent, that is, can competition be an important force shaping community pattern, even if it is not detected through observation of pattern? If competition is important but not easily detected, its analysis may require new and improved methods of observation. Simulation modeling can be used to examine whether the analysis of pattern can reveal the qualitative or quantitative nature of underlying generative processes.

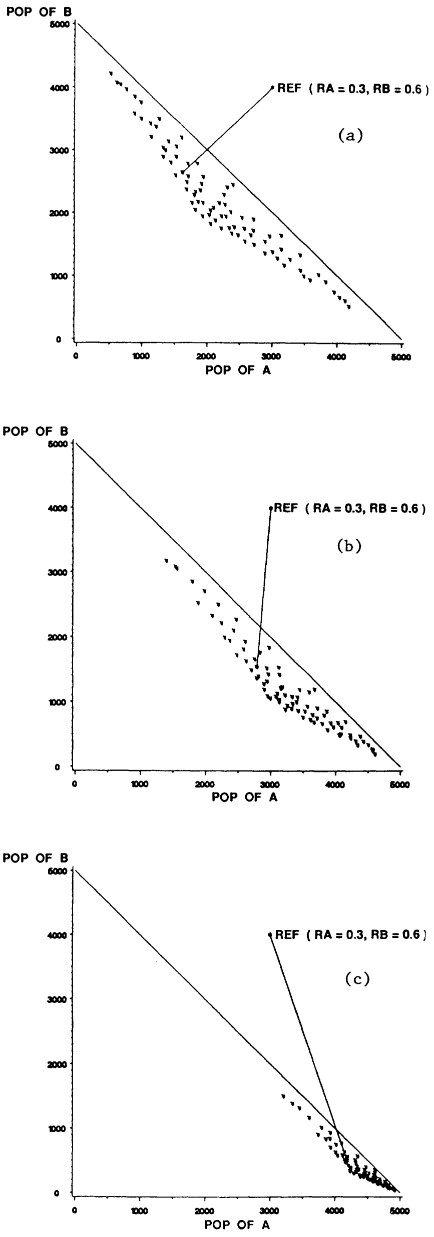

Figure 2. Each graph plots the 81 equilibrium solutions that result from individually varying reproduction parameters R_A and R_B over the range 0.1–0.9 (10:10, 10:20. . . 20:10, 20:20. . . 90:80, 90:90, giving 81 combinations) while holding competition ratios constant at 50:50 in (**a**), 70:30 in (**b**), and 90:10 in (**c**).

Stochastic model

Justification. Simulation methods are often useful in the analysis of models that describe only a small number of processes. In the case of natural systems, the advantage of this approach lies not so much in creating a model that imitates a particular system but rather in analyzing the model to yield ecological insights. Using models as surrogate systems—analogous to nature but not nature itself—has proven a powerful technique in theoretical ecology (Gardner et al. 1982). In this article, we model processes analogous to competition and reproduction to resolve the epistemological question of whether, in nature, pattern is a window to process.

To be useful in the investigation of pattern and process, a model should permit development of hypothetical populations of a size sufficient to produce significant statistical results; our model can include as many as 5000 organisms. The model uses two species so that their abundances may be compared. The model allows simultaneous analysis of two ecological processes—reproductive success and resource competition—that act together. Finally, the representation is stochastic: no single individual is assured of either successful reproduction or acquisition of sufficient resources.

Our objective was to generate a pattern of species' abundances from the two processes. Our strategy was to examine whether model output can be used to infer known processes that create the observed patterns.

Development. For this study, the universe consists of 5000 cells, each holding one unit of a renewable resource. To survive and have the opportunity to reproduce, an individual of either species requires one unit of resource during each iteration (considered a generation or a cycle) of the model. The generations do not overlap, so there are no age-class distinctions. Both species are capable of reproducing each generation, and the resource base is renewed each cycle.

Identifying the two species as A and B, the following definitions describe the two processes involved in the simulation:

C_A, C_B: the respective probabilities that individuals of species A and B successfully obtain a unit of resource in a given cycle.

R_A, R_B: the respective probabilities that individuals of species A and B successfully reproduce in a given cycle.

These four probabilities are assigned by the investigator and remain constant during one simulation. They are used in the simulation to determine which cells are occupied by individuals of species A or B.

After an initial census for species A and B, the program sequentially examines each of the 5000 cells. Whenever an occupied cell is encountered, a reproduction test is made by selecting a uniformly distributed random number between zero and one. The cell remains occupied (i.e., successful reproduction occurs) if the random number is less than or equal to the R value of the occupant's species. Otherwise, the cell becomes available for later capture by either species.

Next, the grid is sequentially reexamined to simulate competition. Whenever an unoccupied cell is encountered, an organism of either species may capture a unit of resource and occupy the cell. To avoid bias, the first opportunity to capture the next available resource unit is alternated between the two species. For example, a random number between zero and one is drawn at the next available resource unit; if that number is less than C_A, the cell becomes occupied by species A. Otherwise, the comparison is made against C_B and either B takes the cell or it stays blank. At the next encountered blank cell, the procedure is repeated with species B given first chance. After the entire grid is covered with this capture procedure, the next cycle begins with the reproduction tests. Because the process of resource acquisition is stochastic, some resources are not used, and those cells remain available for capture by an individual of either species during the next competition cycle. These procedures are repeated until the abundances of A and B stabilize; 40 cycles of competition and reproduction are usually sufficient.

To test whether the results are sensitive to initial conditions, we conducted multiple simulations of the same probability configurations with different initial conditions. We tested all pairwise combinations of the extreme values of $R_{A,B}$ and $C_{A,B}$ (16 combinations × 10 trials for each) first by starting the system with zero abundance for each species and then by filling the grid randomly with each species having a 0.5 chance of occupying a cell. Pairwise comparisons of A and B expressed as proportions of the total population differed by an average of 0.25% (maximal deviation: 4.05%). In all results reported here, the system was initiated using the random, equal opportunity method.[1]

The model thus has two interacting, stochastic processes that are much simpler but nevertheless analogous to processes in nature. Most important is the analogy to multiple processes acting together to produce a pattern. The model becomes a tool to ask what can be learned about underlying processes from a study of emergent pattern.

Behavior. Simulation trial results are shown in Figures 1–4. In each graph, a plotted point represents the final abundance of both species for a particular combination of the four parameters R_A, R_B, C_A, and C_B. The line connecting the end of each axis is the locus of all points:

$$A + B = 5000$$

Because simulations are stochastic, the resource grid is never completely filled, and final values always fall below the line of maximal abundance.

To facilitate further discussion, parameter combinations will be written as probability ratios (×100), with species A appearing first. For example, Figure 1a displays the results of variation in competition ratios under a fixed reproduction ratio of 50:50. In Figure 2, competition ratios are constant in each plot and equal in magnitude to the reproduction ratios used in the first series. Figure 3 shows the broad range of patterns that the model can generate. Figure 4 plots the points bounded by the diverging lines of Figure 3.

Patterns and processes

Successful reproduction implies acquisition of resources. In these simulations, reproduction can occur only after resources have been obtained. Thus, comparison of Figures 1 and 2 demonstrates that competition exerts greater influence than reproduction. Variation in $C_{A,B}$ (Figure 1) for a

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[1] The most efficient computer implementation translates the easily visualized matrix description into its equivalent finite difference representation. Write to G. M. Henebry for a brief description of these equations.

fixed reproduction ratio covers more of the potential solution space than fixing competition and altering $R_{A,B}$ over the same range (Figure 2). That is, abundance is more sensitive to changes in competition than to changes in reproductive potential. Reproduction implies maintenance of the current population; competition enables the species to expand its population through acquisition of additional resources. But solutions exist and overlap greatly in both diagrams.

Consider points in the lower right-hand portions of Figures 1c and 2c. The probabilities of successful competition and reproduction are interchanged between the two, yet the patterns appear almost indistinguishable. Other regions of extensive overlap exist; thus, pattern appears the same but generating processes are distinctly different.

Figure 3 is a thorough examination of the solution-space that the algorithm can create. It is interesting to use this diagram to illustrate how two processes acting together can mask one another. A no-effects or neutral model (Caswell 1976) would test the hypothesis of equal abundance versus populations significantly different from those expected by chance. This test is equivalent to a null hypothesis of equal proportions of each population. A normal approximation to the confidence limits for a test of proportions is given by Zar (1984). If $\hat{p}$ is the proportion from a sample of size N, $s\hat{p}$ is the standard deviation $(=\sqrt{\hat{p}(1-\hat{p})/(N-1)})$, α is the significance level, and the null hypothesis is that $\hat{p} = p$, then the $(1 - \alpha)$ confidence limits are given by

$$p = \hat{p} \pm (Z_\alpha \cdot s\hat{p} + 1/2N).$$

Setting $N = 200$, $p = 0.5$, and $Z_\alpha = \pm 1.96$ (the 95% confidence level), the boundary of acceptance of the hypothesis $\hat{p} = p$ is $0.428 \leq \hat{p} \leq 0.572$. Multiplying these limits by possible population sizes (A + B) yields the bounded interior region shown in Figure 3. Similar calculations for other values of p would produce different enclosures. The arbitrarily chosen sample size of 200 represents 4% of the total resource space. Such a large sample safely permits a valid assumption of sample normality (Zar 1984).

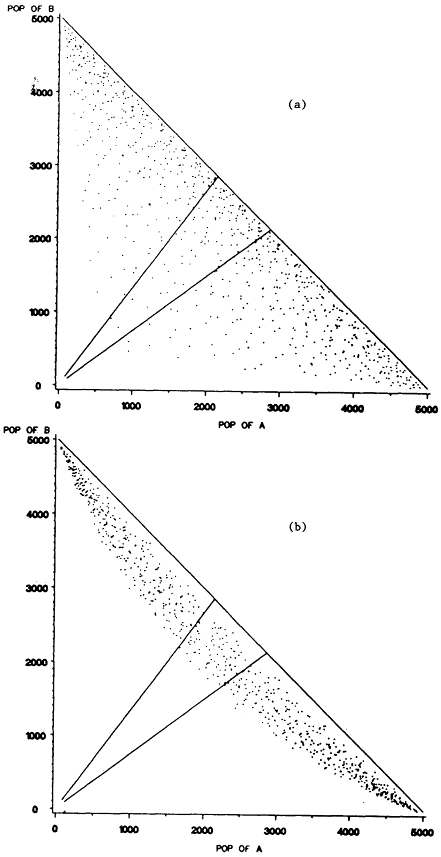

Figure 3. Range of solutions generated by the model when (**a**) each of nine reproduction ratios (10:90, 20:80. . . 90:10) is simulated with each of 81 competition ratios (10:10, 10:20. . . 20:10, 20:20. . . 90:80, 90:90) and (**b**) each of nine competition ratios (10:90, 20:80. . . 90:10) is simulated with each of 81 reproduction ratios (10:10, 10:20. . . 20:10, 20:20. . . 90:80, 90:90). Diverging lines arising at the origin are the 95% confidence limits for a sample size of 200 when the null hypothesis is equal proportions of both populations.

Figures 1–4 illustrate that the location of a simulation result on the graph (or, analogously, knowledge of the abundance of species) is not sufficient to deduce the process configuration that produced it. Most of the points within the acceptance region of Figure 3 have unequal parameter pairs ($R_A \neq R_B$ and $C_A \neq C_B$) and parameter ratios as high as nine. Highly ordered processes can produce final abundances that are indistinguishable from random assembly. In other regions of the solution space, rejection of the random assembly hypothesis cannot lead with assurance to a conclusion about which process or processes were responsible for the observed pattern.

Significance for ecology

Understanding the causes that produce pattern in natural communities is one of the central challenges in ecology. Our investigation leads to three ideas for consideration regarding the interaction of processes to create pattern in ecosystems.

First, pattern is not isomorphic to generative process. The same structure is possible from multiple expressions of process. Furthermore, well-defined nonrandom processes can produce patterns indistinguishable from random assembly. The possibility of apparent random assembly emerging from structured processes was also noted by Rummel and Roughgarden (1983) in the analysis of their island invasion model and by Case and Sidell (1983) in their analysis of the Galapagos finch data. In a theoretical study examining whether competition could be detected on idealized islands inhabited by arbitrary numbers of species, Hastings (1987) concluded that rejecting the null hypothesis of random assortment of species is difficult even when competition is strong.

Masking of underlying cause may become worse in more complex systems. In Figure 3, suppose that a third process (e.g., predation) were included. Points currently outside the bounds of seeming randomness could easily be transported to within bounds by adjustment of the ability to escape predation. Additional processes could affect abundances in ways that could not be detected from the resultant pattern.

That process may not be deducible from pattern can be interpreted in terms of ecological aggregation theory (Cale et al. 1983, Cohen 1985, Gardner et al. 1982). Aggregation theory deals primarily with the loss of information that results when several components are lumped together into a single state-variable in a model. In nature, processes are aggregated to produce a pattern that conceals its origins. Yet this phenomenon may be amenable to mathematical analysis. For example, if pattern changes, as it frequently does along a cline, what are the constraints on the various

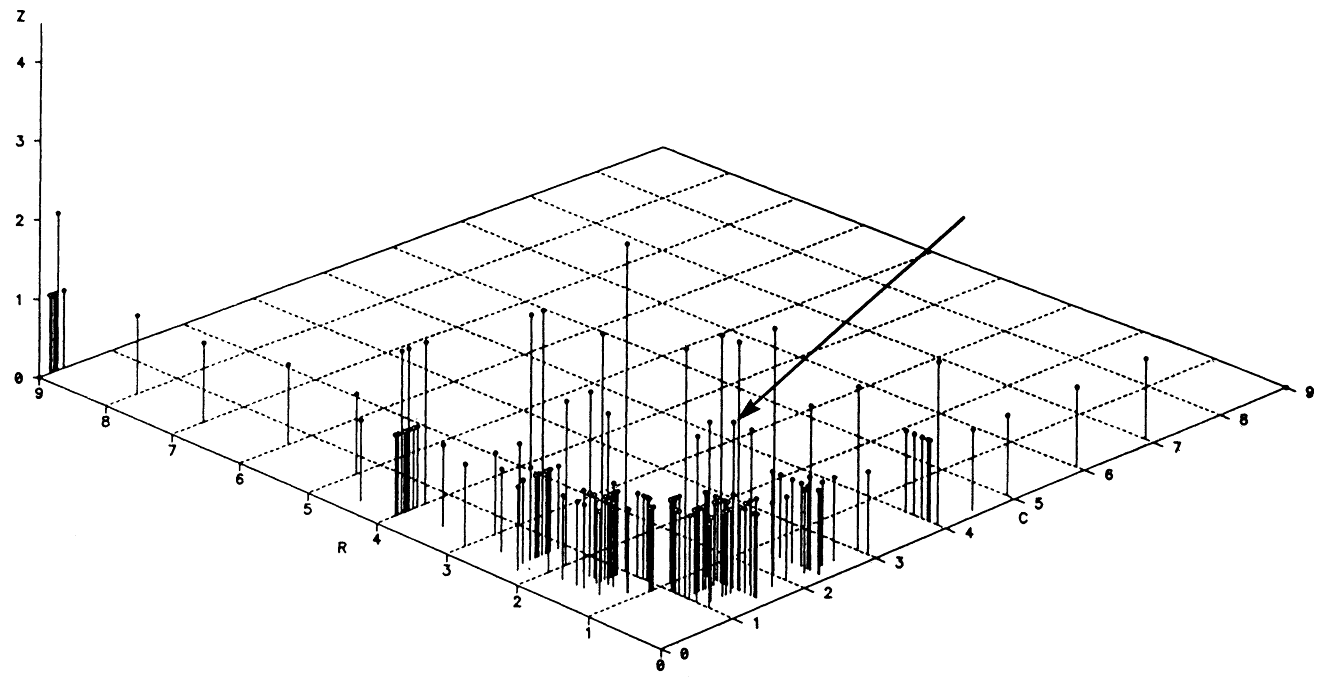

Figure 4. Points within the null regions of Figures 3a and 3b plotted with respect to their process ratios. The horizontal axis C is the ratio C_A/C_B; the horizontal axis R is the ratio R_A/R_B. The vertical axis Z is the number of occurrences observed of a given ratio within the null region. Cases where $R_A = R_B$ and $C_A = C_B$ are not plotted. Reference arrow: $R_A = 0.3$, $R_B = 0.6$, $C_A = 0.6$, and $C_B = 0.4$.

interacting processes that are consistent with the observed change?

The other ideas are more speculative. The second is that competition may not be a ghost (Connell 1980) of past events. Competition may well be acting intensely in situations where it is masked by other processes. In our simulations, competition turned out to be the more important of the two processes, although the resultant pattern often made it invisible. Stable assemblages may be subject to continuous, highly competitive interactions that produce the appearance of peaceful coexistence.

The role of hypothesis testing and deductive reasoning can be examined in light of this finding. Acceptance or rejection of statistical hypotheses can have meaning only in the context of expectation from underlying process. Communities represent a continuum of potential abundances. Some of those abundances fall into regions predicted by nonecological models, most notably the random-assembly model. When that happens in a real community, it would be wrong to conclude, on that basis alone, that ecological processes are not at work.

For example, the reference arrow in Figure 4 identifies a result created when $R_A = 0.3$, $R_B = 0.6$, $C_A = 0.6$, and $C_B = 0.4$. The final abundances were A = 2142 and B = 2124, values indistinguishable on the basis of statistical sampling. The problem of appropriate model selection is the subject of a recent work in the statistics literature (Linhart and Zucchini 1986).

The third idea is that the absence or low abundance of a species in a place where it once lived (or potentially could live) does not in itself provide evidence for the significance or insignificance of competition or any other process. Miller (1967) attributes Gilbert et al. (1952) with the first discussion of this problem for competitive exclusion. Competitive adults relatively unable to reproduce will almost certainly decline in numbers. However, differential potentials in distinct processes may compensate in unexpected ways. In our simulations, the maintenance of qualitatively large abundances due to increased competitiveness (Figure 1c) was an unexpected result that permitted survival in the presence of low reproductive potentials.

In a recent note (May 1989), May says, "Using computers to generate pseudodata for imaginary worlds whose rules are known, and then testing conventional methods of data analysis for their efficiency in revealing these known rules, seems to me to be a useful approach." It is in this spirit that we developed our model. The important result from this study is that a straightforward, fully understood system can produce patterns that mask the processes which created them. Nature, in comparison to our algorithms, is infinitely more complex and capable of myriad dynamic interactions. Caution is therefore advised.

The study of pattern, isolated from the biological processes that generate it, is not likely to advance ecosystem theory. Because multiple process configurations can produce the same pattern, understanding and predictive capability must evolve from analysis of fundamental ecological processes.

Acknowledgments

The authors thank Bruce Milne, Robert O'Neill, and John Wiens for help-

ful comments on an earlier draft of this manuscript.

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