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THE CONTROLLING FACTOR IN BIOLOGICAL COMMUNITIES

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Abstract. Through the use of qualitative models (loop models and time averaging), factors controlling biological communities are examined. The traditional approaches, choosing one factor over another, insisting on a strict null hypothesis as opposed to alternative hypotheses, and generally omitting the study of interactions themselves are unproductive, if not misleading. Five examples are examined: density dependent and independent factors; simple predator-prey relations with self-damping; resource - herbivore - predator or parasite correlations; controlling factors in a two predator and one prey system in which one predator is self-damped; controlling species in two resources, two consumer systems in which one consumer switches.

1. Introduction

Theoretical discussion in ecology is often hampered by the posing of dichotomous choices: Are populations regulated by density independent or density dependent factors? Do physical or biotic factors predominate? Are the observed variations in space and time deterministic or stochastic? Is nature Clementsian (that is, consisting of tightly coupled communities endowed with super-organismic properties) or Gleasonian (individualistic independently distributed and fluctuating species associated by the capricious correlations of independently evolved biologies)? The arguments are further impaired by common sense expectations of how a particular kind of relationship would be observed. Thus the absence of statistical correlation between a pair of species is often taken as evidence that there is no major interaction between them. Simberloff (1980) has contributed to the clarification of issues by insisting on a rigorously defined null hypothesis (no interaction) with well specified expectations of what should be observed. However, insufficient attention has been paid to the expected consequences of the alternative hypotheses.

Another view of nature neither Clementsian nor Gleasonian, super-organismic, nor individualistic - is dialectical. In this view, the interesting questions are not what relative weights to assign the different kinds of factors, but rather to elucidate how they interpenetrate. The argument that follows falls into what May (1983) defined as strategic modeling. The models are chosen not to represent any particular community or population but rather to grasp an essential type of relation. The conclusions are not directly conclusions about nature but about interactions, dynamics and models. They show that the factors confronting each other in dichotomous choices can interact in interesting and unexpected ways, that common sense is often a poor guide for determining expectations, and that the appropriate locus of explanation is often not in the variables or factors themselves but in the structure of their interactions.

Method

The methods used to explore these problems, signed digraphs (1) and time averaging, are described in Puccia and Levins (1985). In the digraph representation, each variable is represented by a vertex. These are connected by edges (lines) that have direction and sign. The first figure (Fig. 1) represents a predator-prey relation in which the prey X has a direct positive effect on its predator Y, denoted by the arrow (→) while Y has a direct negative effect on X, indicated by the line with the small circle (—0). The assignment of edges and their signs is usually straight-forward. However, ambiguities arise, especially in relation to the effect of a variable on itself. These can be resolved by observing that the link from X_j to X_i is defined by

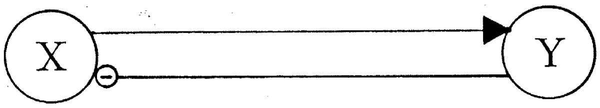

Fig. 1. A predator (Y), prey (X) relation. See explanations in the text.

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(1) In a review of Puccia and Levins (1985), Schonemann (1987) pointed out that we introduced an idiosyncratic terminology for objects that were already defined and named in graph theory such as "loop" for cycles. This came about as a result of our own ignorance of graph theory while the methods were being developed, and the inertia of habit later on. With this note we begin a process of rectification.

$$\alpha_{ij} = \frac{\partial}{\partial X_j} \quad \frac{dX_i}{dt}$$

evaluated at equilibrium. Therefore, if a variable exhibits simple reproduction with

$$\frac{dX}{dt} = rX$$

where r can depend on other variables in the system but not on X, then at the non-trivial equilibrium $r = 0$ and $\alpha_{XX} = 0$. But if r decreases with X (density dependence) or individuals enter the system by migration as well as reproduction,

$$\frac{dX}{dt} = rX + m$$

and $\alpha_{XX} < 0$, while if X is harvested,

$$\frac{dX}{dt} = rX - h$$

and at equilibrium r must be positive and $\alpha_{XX} > 0$. These migration and harvest rates, m and h, are independent of population size.

The method of time averaging uses a series of descriptive measures such as expected values (average), variance and covariance of variables in the system. If a variable is bounded, then in the long run its derivative has an average value of zero. Furthermore, if f(X) is any bounded function of X, then $f(X) \frac{dX}{dt}$ is the derivative of a bounded function, which also has a zero expected value.

The digraph method applies rigorously to systems near equilibrium. In practice, its results usually are consistent with only minor modifications with the time averaging results for non-equilibrium systems.

Examples

Example 1. Is regulation density dependent or independent? Consider the pair of alternative equations

$$\frac{dX}{dt} = X\,(f - m_1) \qquad (1a)$$

and

$$\frac{dX}{dt} = X\,(f - m_1 - m_2 X) \qquad (1b)$$

where f and m_1 are frequently fecundity and mortality parameters influenced by any factors, physical or biological, that are not directly functions of the population size X. In case 1 (equation 1a), unless $f - m_1 = 0$ the population will either crash or explode, but if $|f - m_1|$ is small enough this may take a very long time. If there is a random component, then log X (t) will have a normal distribution with mean $(f - m_1)\,t$ and a variance increasing with t that depends on the autocorrelation of $f - m_1$. In case 2 (equation 1b), the population will fluctuate around an average

$$m_2 \bar{X} = \bar{f} - \bar{m}_1$$

where the bars indicate averages. The distribution will therefore differ in the two cases.

The mortality due to density independent factors in both cases in $m_1 \bar{X}$. But $\bar{X}$ is determined by the form of the equation. And there is an additional component of mortality in case 2: $m_2 X^2$, which has an average value

$$E\,[m_2 X^2] = m_2\,(\bar{X}^2 + \mathrm{Var}\,(X))$$

$$= \frac{(\bar{f} - \bar{m}_1)^2}{m_2} + m_2\,\mathrm{Var}\,(X).$$

Therefore the relative mortality assignable to density dependent, compared to independent factors is

$$\frac{\dfrac{(\bar{f} - \bar{m}_1)^2}{m_2} + m_2\,\mathrm{Var}\,(X)}{(\bar{f} - \bar{m}_1\,\bar{m}_1)} = \frac{\bar{f} - \bar{m}_1}{\bar{m}_1\,\bar{m}_2} + \frac{m_2^2\,\mathrm{Var}\,(X)}{(\bar{f} - \bar{m}_1)\,\bar{m}_1}$$

This ratio clearly increases with Var (X) and m_2 but has a more complex relationship to f and m_1. The important point is that it may be quite small, the two cases being indistinguishable most of the time on the basis of causes of mortality, and yet their distributions are clearly different. Furthermore,

$$E\left[X \frac{dX}{dt}\right] = \mathrm{Cov}\,(X, \frac{dX}{dt}) = \bar{X}\,E\left[\frac{dX}{dt}\right]$$

with the right hand term always zero, so

$$E\left[X \frac{dX}{dt}\right] = \mathrm{Cov}\,(X, \frac{dX}{dt})$$

Because

$$X \frac{dX}{dt} = \frac{1}{2} \quad \frac{dX^2}{dt},$$

is also a derivative of a bounded variable, its expectation is zero. Moreover, the covariance of X with $\frac{dX}{dt}$ is always zero in the limit, regardless of whether or not there is density dependence (see Puccia and Levins 1985).

If f is constant in equation 1b so that variation is driven by the mortality term, $m_1 = m_1(t)$, then

$$\mathrm{Cov}(X, \text{mortality rate}) = \mathrm{Cov}(X, m_1) + m_2 \mathrm{Var}(X).$$

Dividing equation 1b by X before averaging gives

$$\frac{1}{X}\frac{dX}{dt} = f - m_1 - m_2 X.$$

Because the left hand side is $\frac{d \log X}{dt}$, its average is also zero. Since $\mathrm{Var}(X) > 0$, $\mathrm{Cov}(X, m_1) < 0$. If we could identify m_1 related deaths we would conclude that these are ameliorated by crowding. If not, total mortality is variable but uncorrelated with population size. But if m_1 were constant and fecundity variable, then

$$\mathrm{Cov}(X, f) = m_2 \mathrm{Var}(X) > 0$$

and fecundity would appear to increase with population! A strange way to detect density limitation.

Although fecundity and mortality would both appear to be positively correlated with population in a counterintuitive way, fecundity would also show a positive correlation with the rates of population change. Multiplying both sides of equation 1b by $\frac{1}{X}\frac{dX}{dt}$, we have

$$\frac{1}{X}\left(\frac{dX}{dt}\right)^2 = f\frac{dX}{dt} - (m_1 + m_2 X)\frac{dX}{dt}.$$

The expected value of the left hand side is always positive. On the right, $(m_1 + m_2 X)\frac{dX}{dt}$ is the derivative of a bounded function of X and has an average of zero, so that

$$E\left[f\frac{dX}{dt}\right] > 0.$$

A similar argument will show that if m_1 is time-dependent, then it will be negatively correlated with $\frac{dX}{dt}$

Example 2. A simple predator-prey model with self-damping. We can offer equally plausible arguments for reaching opposite conclusions about the geographic correlation between predator and prey species; the more prey, the more predators. Therefore, we expect a positive correlation. But the more predator, the less prey, generating a negative correlation. This situation arises whenever there is negative feedback. But when plausible common sense arguments lead to opposite conclusions, this indicates the problem is poorly posed. We have to distinguish between points of entry of the external influences that drive the spatial variation. The table shows the effects on both species of positive environmental impacts entering at either species. The same argument would also apply to genetic differences affecting one or the other.

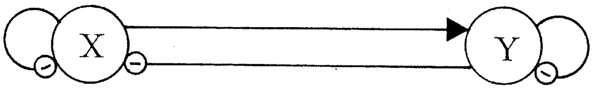

Fig. 2. A predator (Y), pray (X) system with self-damping. Explanations are in the text.

Point Impact	Effect on X (prey)	Y (predator)
X	+	+
Y	−	+

Thus, if most of the variation enters by way of conditions affecting the prey, a positive correlation is generated. But if the major environmental influences impinge directly on the predator, a negative correlations results. Further, if the environment affects both species in the same direction, the predator will show more variation because the direct impact on itself and the indirect impact through the prey cause the predator's abundance to change in the same direction, have opposite effects on the prey's. In a range where environmental changes affect the two species in opposite directions, the prey will change more than the predator. Finally, since a genetic change acting on the effectiveness of predation or predator-avoidance affects the two species oppositely, such genetic variation will be manifest mostly in variability of prey populations. Time average methods lead to similar conclusions for temporal variation.

Example 3. Resource - herbivore - predator or parasite correlations. This model, given by the equations 2a-e, is derived from consideration of such herbivores as scale insects, mites or aphids feeding on the photosynthate of a host plant. Resource, R, is either consumed by the herbivore or translocated and transformed into inedible plant substance at rate c. Therefore,

$$\frac{dR}{dt} = a - R(pX + c) \qquad (2a)$$

$$\frac{dX}{dt} = X(pR - m_1 - qY) \qquad (2b$$

or, alternatively,

$$\frac{dX}{dt} = X\,(pR - m_1 - qY - X) \qquad (2c)$$

$$\frac{dY}{dt} = Y\,(qX - m_2) \qquad (2d)$$

or, alternatively,

$$\frac{dY}{dt} = Y\,(qX - m_2 - Y). \qquad (2e)$$

The alternative forms for $\frac{dX}{dt}$ and $\frac{dY}{dt}$ (equations 2c,e) allow for direct density dependence either of herbivore or predator. The results depend on where the main external influence enters the system, and the loci of self-damping. Unnecessary constants are omitted.

The correlation pattern can be found by examining first those equations that lack external variables. Therefore, if variability enters the system through a, (i.e., $a = a\,(t)$ in equation 2a), then the equation for $\frac{dY}{dt}$ gives $\mathrm{Cov}\,(X,Y) > 0$ in equation 2e with self-damping, and $\mathrm{Cov}\,(X, Y) = 0$ without self-damping in equation 2d. If Y is self-damped or if X is self-damped, then $\mathrm{Cov}\,(X, R) > 0$. Otherwise $\mathrm{Cov}\,(X, R) = 0$. If variation enters the system through variable mortality of Y, then the analysis at the equation for R becomes:

$$a = \bar{R}\,(p\bar{X} + c) + p\,\mathrm{Cov}\,(R, X), \text{ or} \qquad (3a)$$

$$\frac{a}{R} \equiv \frac{a}{E\,[R]} = p\,\bar{X} + c + \frac{p\,\mathrm{Cov}\,(R, X)}{\bar{R}} \qquad (3b)$$

Dividing equation 2a by R, then averaging yields

$$aE\left[\frac{1}{R}\right] = p\bar{X} + c.$$

But for $R > 0$ and not constant,

$$E\left[\frac{1}{R}\right] > \frac{1}{E\,[R]}.$$

Therefore,

$$p\bar{X} + c > p\bar{X} + c + \frac{\mathrm{Cov}\,(X, R)}{R}$$

and $\mathrm{Cov}\,(X, R) < 0$. This relationship is substituted into the equation 2b or 2c, giving $\mathrm{Cov}\,(X, Y) < 0$; and finally into equation 2d or e, giving $\mathrm{Cov}\,(Y, m) < 0$.

Table 1. Covariance* Among Resource (R), Herbivore (X) and Predator or Parasite (Y) with self-damping and entry point of external variation.

self-damped variables	point of entry	Cov (X, R)	Cov (X, Y)
R	R	0	0
	X	—	0
	Y	—	—
R, X	R	+	0
	X	—	0
	Y	—	—
R, Y	R	+	+
	X	—	+
	Y	—	—
R, X, Y	R	+	+
	X	—	+
	Y	—	—

* 0, no covariance; +, positive covariance; —, negative covariance

The results, summarized in Table 1, may be interpreted as follows: 1. The correlation between a herbivore and its predator and resource depend on the locations of external influence and self-damping. 2. In systems driven from above (from the predator end of the chain) there will be negative correlations; the predator may be rare when its prey are abundant. This does not preclude a major role in regulation. 3. A positive correlation between a consumer and a particular state of its resource does not imply that the resource condition is optimal for the consumer. In particular, the correlation of young leaves with mite populations in citrus does not imply that they prefer or develop best on young leaves. 4. A positive correlation between resource and consumer implies self-damping higher systems driven from the resource level. 5. The economic value of the crop may depend on the amount of resource R transformed into usable yield. Because

$$\bar{R} = E\left[\frac{a}{pX + c}\right]$$

the economic return increases with reduced average herbivore level X and increased variance. Further, because

$$\bar{R} = \frac{a - p\,\mathrm{Cov}\,(R, X)}{p\bar{X} + c},$$

a negative covariance of R with X improves yield. This comes about when the system is driven in part from above; that is, with environmentally sensitive herbivores and parasites.

As will be shown below, a second predator may have no effect on the average herbivore level, but could still contribute to increased R and therefore yield.

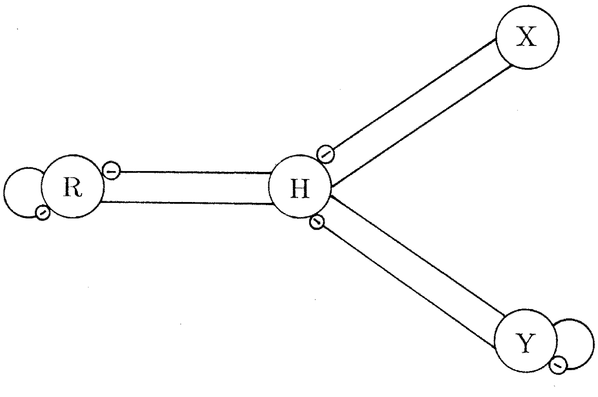

Fig. 3. A two-predator (X, Y), one pray (H) system. R = resource. See explanations in the text.

Example 4. Controlling factors in a two predator, one prey system in which one predator is self damped. Fig. 3 and the table below are relevant. Note that

Point of Impact	Change in Equilibrium Level R	H	X	Y
R	+	0	+	0
H	0	0	+	0
X	+	—	+	—
Y	0	0	—	+

the herbivore level is insensitive to any parameters entering the system through Y. In a time averaging model,

$$\frac{dR}{dt} = a - R\,(pX + c)$$

$$\frac{dH}{dt} = H\,(pR - m_1 - q_1X - q_2\,Y)$$

$$\frac{dX}{dt} = X\,(q_1H - m_2)$$

$$\frac{dY}{dt} = Y\,(q_2H - m_3 - Y)$$

The average herbivore level is $\bar{H} = \dfrac{m_2}{q_1}$ regardless of what Y does. But the mortality due to Y is

$$q_2\,E\,[YH] = q_2\,(\bar{Y}\,\bar{H} + \mathrm{Cov}\,(Y, H)\,)$$

This covariance will be positive if the system is driven from R, H or X. Therefore, in general, the more variable the system the greater the mortality of H that can be attributed to Y. Y still does not influence the average level of H. Even improved conditions for Y, which reduce X, do not alter H. It is therefore incorrect to argue that if X is responsible for only a small part of the mortality, it is not a controlling factor.

It is rigorously true for equilibrium models of single prey and many predators that the impact of a predator is proportional to its predation rate and inversely proportional to its self-damping. (If there is no self-damping, it exercises complete control, and two predators that lack direct or indirect self-damping could not coexist).

Example 5. The controlling species in two resource, two consumer systems in which one consumer switches. Fig. 4 and the table below are relevant. When two consumers share the same resource, the resource abundance varies inversely with its main consumer and directly with the consumer that switches on another resource. The generalist consumer Y uses both resources R_1 and R_2, while X specializes on R_1. For the marine intertidal, the behavior of X is seen as obligate feeding, or preferential feeding in the extreme. This single resource used by a species might be inferred as the controlling factor. No matter how much the environment shifts to alter the grazing capability of Y, it does not affect the resource R_1. Only through changes in X will R_1 levels alter. Nevertheless, increases in the population size of Y will reduce the abundance of X. The common resource R_1 does not affect the generalist consumer Y.

Point of Impact	Change in Equilibrium Level R_1	R_2	X	Y
R_1	0	0	+	0
R_2	0	0	—	+
X	—	+	+	—
Y	0	—	—	+

The community equations with a nonlinearity in the growth equation of Y from the first resource R_1 are:

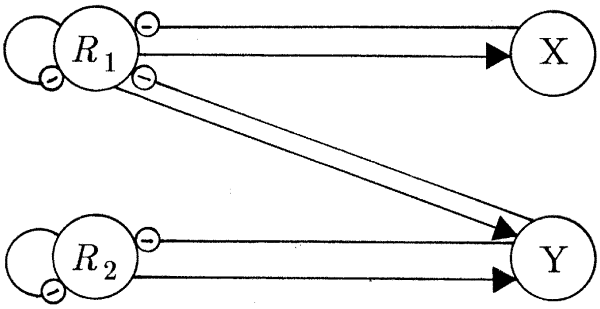

Fig. 4. A two-resource (R_1, R_2), two-consumer system. X = specialist, Y = generalist consumer. See explanations in the text.

$$\frac{dR_1}{dt} = R_1 (k_1 - pX - q_1 Y - R_1) \quad (4)$$

$$\frac{dR_2}{dt} = R_2 (k_2 - q_2 Y - R_2) \quad (5)$$

$$\frac{dX}{dt} = X (pR_1 - d_1) \quad (6)$$

$$\frac{dY}{dt} = Y (q_1 R_1^2 - q_2 R_2 - d_2) \quad (7)$$

As the abundance of R_1 increases, the generalist consumer enhances its own growth rate, although it does not shift its feeding behavior. The nonlinearity, however, does not change the fact that the generalist consumer Y has no influence on the abundance of R_1 (see Puccia and Levins 1985), but it does affect the outcome of the other predictions in the table.

When the natural mortality d_1 of X is an environmentally sensitive parameter, (i.e., $d_1 = d_1(t)$), then equation 6 averaged before and after dividing by X yields

$$p \operatorname{Cov}(X, R_1) = \operatorname{Cov}(X, d_1) \quad (8)$$

From equations 5 and 7,

$$q_2 \operatorname{Cov}(Y, R_2) = - \operatorname{Var}(R_2) < 0$$

$$q_1 \operatorname{Cov}(Y, R_1^2) + q_2 \operatorname{Cov}(Y, R_2) = 0$$

and $\operatorname{Cov}(Y, R_1^2) > 0$. For small values of R_1 or for small variation in R_1, it is plausible to assume that $\operatorname{Cov}(Y, R_2) > 0$. This will not be true, for example, in the case of a parabolic relation between Y and R_1 with variation clustered around the higher values of R_1; the results are sensitive to the distribution and variation pattern. Using equation 4,

$$p \operatorname{Cov}(X, R_1) + q_1 \operatorname{Cov}(Y, R_1) = - \operatorname{Var}(R_1) < 0.$$

For a positive covariance between Y and R_1, $\operatorname{Cov}(X, R_1) < 0$, and $\operatorname{Cov}(X, d_1) < 0$ from equation 8. In the intertidal, the main consumer of an alga would be rare when the food supply was abundant. The covariance pattern predicted by the nonlinear, nonequilibrium analysis repeats that found for the corresponding loop analysis of the signed digraph. However, it becomes sensitive to the location of the nonlinearity and distributional pattern between the generalist consumer and resource R_2. There is no meaning to "the controlling factor" or the "controlling species" in this example. We can identify the single species X as a satellite (Puccia and Levins, 1985) of R_1, which acts as a buffer for the resource.

Conclusions

The focus in the ecological literature of the controlling factor in biological communities is based on the correlation between abundance levels between populations. The search for shifts in population levels of one species accompany the population changes in another. We suggest a shift in focus, from population abundance to the parameters that regulate growth. A change in the feeding rate, reproductive rate, or mortality rate are examples of parameters changes that produce shifts in the population levels in a community. The "controlling" factors are inputs to particular population parameter changes, either from the outside or as a result of evolutionary change.

A population level may not change, but the functional contribution of the species may be important to community stability and resilience. There are system level characteristics such as satellite variables which serve as sinks that protect their principals (2) from changes entering anywhere else in the system and restrict the impact of inputs at the principal variable to the satellite.

The lack of change in a population abundance does not mean that the population has remained unaffected. In a population with an increase in reproductive rate and predation, the overall population size may not change but the turn-over rate will increase. Furthermore, the absence of correlation between population abundances can not be construed as a lack of interaction between them. A negative correlation between a predator and its prey can be caused by impacts entering at the predator end of the food chain; the fact that the predator is rare when the prey is abundant does not negate its role. The locus of control in ecological communities is diffuse, with different components playing different roles for different aspects of the system, and conditioning the roles of other components. In the last analysis, the behavior of the system depends on its structure as a network of interactions.

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(2) The term principal carries no connotation of dominant. It denotes the variable interacting with the satellite variable. Every variable may have one and only one satellite (Puccia and Levins 1985).