Apparent interactions in community models: A challenge for theoretical ecology

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Abstract
The primary aim of this working paper is to challenge theoretical ecologists to clarify the intended status of any simple model that they use. If we restrict our attention to a subcommunity and treat it as if it were the full community, we need to invoke apparent interactions that incorporate the effects of unspecified or hidden variables as well as direct interactions. This position resembles that of previous discussions of apparent competition (Holt 1977), indirect effects (Lawlor 1979), and ecological abstraction (Schaffer 1981), but my definition of apparent interactions differs from those stated or implied by these authors. I advance a method for calculating apparent interactions that incorporates the effects of hidden variables in a way that most closely generates the observed population trajectories. My method shows the apparent attractions can be counterintuitive, which points to some fundamental ambiguities in theoretical ecology. These ambiguities arise if we use simple models, that is, ones with few components, when we are actually concerned with naturally variable observations drawn from systems with more components than we have explicitly modeled. We need to clarify whether we intend simple models to represent the processes that generated those observations, or whether they are merely redescriptions or summaries of those observations or, a third possibility, whether they are mathematical systems which are used to suggest how ecological systems might operate.

In Vandermeer's (1969) study on the structure of a community of four competing ciliate protozoan populations he reported the interactions between populations summarized in Fig. 1. Three of the six pairs of interactions between the competitors were positive-negative—what we would expect of predator-prey relations. Were these interactions actually predator-prey? Further, were those pairs with negative-negative interactions actually competitors? How can we understand the parameter values Vandermeer derived and relate them to the actual ecological relationships among the protozoan populations?

The interpretation I present in this paper is that we should only talk about the species apparently interacting. If we restrict our attention to a subcommunity and treat it as if it were the full community we need to invoke apparent interactions. They incorporate the effects of unspecified or hidden variables as well as direct interactions. This position resembles that of earlier discussions of apparent competition (Holt 1977), indirect effects (Lawlor 1979), and ecological abstraction (Schaffer 1981), but my definition of apparent interaction differs from those stated or implied by these authors. I advance a method for calculating apparent interactions that incorporates the effects of hidden variables in a way that most closely generates the observed population trajectories.

I use my method to show that apparent interactions can be counter-intuitive. I do not, however, characterize the situations where
Figure 1. Community interactions reported by Vandermeer (1969). PA = Paramecium aurelia, PB = Paramecium bursaria, PC = Paramecium caudatum, BL = Blepharisma sp.
this is the case. It is sufficient simply that apparent-interactions exist and can be counter-intuitive to highlight some fundamental ambiguities in theoretical ecology. These ambiguities arise if we use simple models, that is, ones with few components, when we are actually concerned with naturally variable observations drawn from systems with more components than we have explicitly modeled (Schaffer 1985). We need to clarify whether we intend simple models to represent, albeit as a caricature, the processes that generated those observations, or whether they are merely redescriptions or summaries of those observations, or, a third possibility, whether they are mathematical systems which we use to suggest how ecological systems might operate. The primary aim of this paper is to challenge theoretical ecologists to clarify the intended status of any simple model they use. Only then can we appreciate the value and the limitations of simple models in helping us understand ecological relations and derive general ecological principles.

Simple models can also be confounded by aggregation of heterogeneous variables into synthetic variables (Lomnicki 1980). Current work on hierarchy theory in ecology (e.g. O'Neill et al. 1985) is an attempt to find coherent or natural levels of aggregation. Although I concentrate in this paper on the effects of hidden variables on simple models, my conclusions about the status of simple models and their use in developing general ecological principles are also relevant to modelers concerned with incoherent aggregations.
I. DIFFERENT DEFINITIONS OF THE TERM "INTERACTION"

What, for ecologists, is an interaction? Is it something we observe directly, for example, a predator consuming a prey? Or is an interaction something we infer from data on changes in population sizes? In practice ecologists use both direct observations and inferences from data and expect one to reinforce the other. Although inferences from data and observations are often consistent, they are not always, as I will indicate. It will assist my arguments if I keep the different meanings of interaction clear and so I will first distinguish four different types of interactions. I will refer to these as types 1 to 4. In addition, I distinguish between the "effect" of one species on another and the "interaction" of the two species, that is, the pair of effects.

1. Interactions directly observed

We might rely on direct observations to determine whether an interaction is occurring. In this case, direct observations of mutual interference or facilitation between individuals are sufficient for us to say there is competition or cooperation. Similarly, consumption signals a predator-prey interaction; the sharing of the same resource signals exploitative competition. We observe parasitism through the physiological effect of the parasite on the host, and so on.

There are problems in relying on direct observations of interactions between individuals. Our expectations may inhibit us from
noticing all the processes involved. For example, we expect a parasite
to be detrimental to its host, just as a predator is to its prey. Close
examination, however, has shown that parasites often contribute
facilitative metabolic compounds to their hosts (Lincicome 1971).
Another problem is that interactions between individuals do not
necessarily translate into equivalent interactions between populations.
To establish interactions between populations we need to make inferences
from data on population sizes. The remaining types of interactions
enable us to do so, but in different ways.

2. Interactions inferred from qualitative results

Suppose two species exploit a common resource and do not coexist in
a given area. We might infer from the qualitative outcome of
"non-coexistence" that the species compete. Such an inference invokes
the competitive exclusion principle, the theory that competing species
can only coexist under very special circumstances. There is controversy
over this inference (Diamond and Gilpin 1982). On the one hand there
are, in my terms, those who use a rule "if species compete, do not
allocate them to the same locality" to generate patterns of
(non-)coexistence across localities that match those observed. On the
other hand there are those who generate patterns using a rule "allocate
species at random" (Diamond and Gilpin 1982). The competitive rule
assumes that the competitive exclusion principle is correct and bypasses
any examination of the processes of competition. The random rule admits
no processes of interspecific interaction—even though we know that, at very least, animals feed!

Inferring interactions from qualitative results requires both a simple connection between the interaction and its outcome and a method of discriminating among alternative interactions which may generate the same outcome. This dual theoretical structure remains to be built. In its absence I will not discuss type 2 interactions any further.

3. Interactions among populations varying in size—conditions assumed constant

If population sizes are changing in a community operating under a given set of conditions, we can define the effect of population j on population i as being its contribution to altering the rate of change of i. In mathematical form, the effect \( e_{ij} \) is given by

\[
e_{ij}(N) = \frac{\dot{N}_i(N)}{\dot{N}_j} \quad i, j = 1, \ldots, m
\]

(1)

where \( N = (N_1, \ldots, N_m) \) = vector of population sizes

\( \dot{N}_i \) = rate of change of population i

m = number of species in the community

Because these effects may change as the population sizes change, \( e_{ij} \) and \( \dot{N}_i \) are expressed as functions of \( N \). With this definition of effects, competition occurs when both \( e_{ij} \) and \( e_{ji} \) are negative, a predator-prey interaction when they are of opposite sign, and cooperation when \( e_{ij} \) and \( e_{ji} \) are both positive.

In practice we estimate the \( e_{ij} \) values indirectly. First we fit a model relating population sizes to their rates of change and then
calculate \( e_{ij}(N) \) in terms of the fitted parameters and \( N \). We might assume, for example, that the population sizes are governed by the Generalized Lotka-Volterra (GLV) model:

\[
\dot{N}_i = N_i (b_i + \sum_{j=1}^{m} a_{ij} N_j) \quad i = 1, \ldots, m
\]

By fitting a set of observations of population size and their rates of change to this model, we can estimate the parameters \( b_i \) and \( a_{ij} \) and calculate \( e_{ij} \), indirectly, from them, using the following relations:

\[
e_{ij}(N) = N_i a_{ij} \quad (3a)
\]

\[
e_{ii}(N) = N_i a_{ii} + \sum_{j=1}^{m} a_{ij} (N_j - N_j^*) \quad (3b)
\]

where \( N_j^* \) is the equilibrium value of \( N_j \).

Notice that, apart from the small adjustment for \( e_{ii} \), the effects \( e_{ij} \) are linear functions of \( N_i \).

The values of \( e_{ij}(N) \) when the population sizes are close to a feasible equilibrium will be of particular interest in later sections. The effect \( e_{ij}(N) \) may then be approximated by a constant, \( \alpha_{ij} \). This is the \( \alpha \)-matrix formulation (Levins 1968) expanded to include non-competitive interactions:

\[
\alpha_{ij} = \frac{\partial N_j(N^*)}{\partial N_j} \quad i,j = 1, \ldots, m \quad (4)
\]

where \( N^* = (N_1^*, \ldots, N_m^*) \).

In theory, we could estimate these effects from data of population sizes changing over time by finding the best fit value for \( \alpha_{ij} \) in the equations

\[
\dot{N}_i = \sum_{j=1}^{m} \alpha_{ij} (N_j - N_j^*) \quad i,j = 1, \ldots, m \quad (5)
\]

The direct estimation of these \( \alpha_{ij} \)'s is not very reliable. Rates of change are small close to equilibrium, and both small inaccuracies in
estimating the equilibrium or small changes in conditions which change
the equilibrium can drastically change the estimates of deviations from
equilibrium. We can, however, estimate the $a_{ij}$'s indirectly if we make
an additional assumption about the form of the behavior away from
equilibrium.

For example, suppose we assume the behavior is governed by the GLV
(Eq. 2). Then, if we first find fitted values for $b_i$ and $a_{ij}$, we can
calculate $N_i^*$ and $a_{ij}$ indirectly from $b_i$ and $a_{ij}$ using the
following relations:

$$N_i^* = -A^{-1}b$$  \hspace{1cm} (6)

where $A$ is the matrix of $a_{ij}$ values

and $b = (b_1, \ldots, b_m)$

$$a_{ij} = N_i^* a_{ij}$$  \hspace{1cm} (7)

Any model relating population sizes to their rates of change could
be fitted and $e_{ij}$, $N^*$, or $a_{ij}$ estimated indirectly from the fitted
parameters. The value of such an estimation procedure is limited if
either the linearity assumption of the GLV model (or the assumptions of
any more general model) is inappropriate or if it is difficult to
collect a set of observations under the same conditions. The assumption
that conditions are changing is the starting point for the remaining
type of interaction.

4. Interactions among populations varying in size—conditions
assumed variable

Suppose that there is a change in some of the conditions under
which the community operates; the equilibrium population sizes may then
change. If we assume that our observations of population size are actually observations of population equilibria under different conditions we can define the effect of population j on population i in terms of the correlation between their equilibrium values. We can perform either a univariate regression of \( N_i^* \) or \( N_j^* \) or a multiple regression of \( N_i^* \) on \( N_1^*, \ldots, N_{i-1}^*, N_{i+1}^*, \ldots, N_m^* \) to generate regression coefficients \( d_{ij} \) (i\(\neq j\)). In this context we might define the effect of j on i to be the value of \( d_{ij} \). Notice that the univariate regression definition of effects, \( d_{ij} \), permits competition, mutualism and null interactions but not predator-prey interactions, because \( d_{ij} \) must be of the same sign as \( d_{ji} \). For this reason the multiple regression derivation is preferable to the univariate derivation.

A parallel conception of type 4 interactions begins with \( \alpha_{ij} \) values rather than observations of equilibrium. We attempt to derive from the \( \alpha_{ij} \) values the effect of (or correlation between) changes in the equilibrium population size of one species on another. Several methods of calculating these effects have been advanced (Levins 1975, Holt 1977, Lawlor 1979) but the earliest and most general comes from Levins's loop analysis (1975). Suppose the values of the \( \alpha_{ij} \)'s are known for a given feasible equilibrium. Now, if the change in conditions of the system can be expressed as a change in some parameter \( C \) that affects the values of \( N_i \), then the predicted change in equilibrium size, \( dN_i^*/dC \) is given by a complicated expression involving the entire \( \alpha \)-matrix and \( \frac{\partial N_i}{\partial C} \) values (Levins 1975:40). An alternative definition of effects, \( d_{ij} \), relates these predicted changes in equilibrium size to each other:
\[
\frac{d_{ij}}{dC} = \frac{dN_i^*}{dC} / \frac{dN_j^*}{dC}
\]

Given the difficulty of determining the \( \alpha \) values and the \( \partial N / \partial C \) values, Levins restricts his attention to qualitative results depending only on specification of the sign of these parameters, but the formulation is equally applicable to quantitative situations. Notice that \( d_{ij} \) values from loop analysis, as for \( d_{ij} \) values from univariate regressions, do not permit predator-prey interactions.

An inverse approach based on Levins's loop analysis enables us, in theory, to derive type 3 interactions from observations of population sizes taken as equilibria under different conditions. If we identify the locus of change in conditions we can attempt to find an \( \alpha \)-matrix which would be consistent both with the observed correlations between the equilibrium values and with biological intuition. This is, in fact, the customary rationale of loop analysis. However, the problems of using this method when there are multiple loci of perturbations in the community, and the problem of discriminating among alternative yet consistent \( \alpha \)-matrices have not yet been resolved.

In summary, interactions may be directly observed (type 1) but these are interactions between individuals. Alternatively, interactions between populations may be inferred from data. This requires either a theory tightly linking a qualitative outcome (non-coexistence) with the interaction (competition) (type 2), or quantitative data coupled with an assumption about whether the data are population sizes changing over time under one set of conditions (type 3) or equilibrium population sizes corresponding to conditions that change over time (type 4). The
estimation of type 3 interactions depends in general on fitting the parameters of a model postulated to govern the interacting populations. Type 4 interactions may be limited to competition, mutualism or null interactions in the case of the univariate regression or loop analysis definitions of type 4 interactions. With these preliminaries I will return to the problem of Vandermeer's predator-prey interactions.

II. APPARENT "TYPE 3" INTERACTIONS IN VANDERMEER'S PROTOZOA
COMMUNITY

In this section I begin to develop my reinterpretation of Vandermeer's protozoan community. In doing so I introduce a definition of apparent interactions that follows the third meaning (type 3) of interactions. (A complementary examination of Vandermeer's data is given more fully elsewhere.)

The interspecific effects derived by Vandermeer for his four protozoan species (Fig. 1) were derived so that after notational changes the GLV Model (Eq. 2) would fit the observed population trajectories:

\[ \dot{N}_i = N_i \left( b_i + \sum_j a_{ij} N_j \right) \quad i, j = 1, \ldots, m \]  

Vandermeer was clearly following the third meaning of interactions, and using the additional assumption of linearity of \( e_{ij} \) (Eq. 3).

Vandermeer constrains his fit to the four species community trajectories by measuring \( b_i \) and \( a_{ii} \) in isolated species experiments and his \( a_{ij} \)'s in two-species experiments. His fits are fairly good (but see this dissertation, Chap. 3) and give qualitatively correct predictions about coexistence of species (Vandermeer 1981).
Vandermeer did not specify all the components of the community. Each day he removed a sample from his experimental tubes and added an equal volume of culture medium with bacteria. The bacterial populations were alive and able to grow if not consumed by the protozoa. They had dynamics of their own not referred to in Eq. 2. Furthermore, it is possible that the protozoan species were affecting each other only through their shared prey species. If all the interactions had been competition (type 3) the missing components might not have caused us any concern. We would have considered that the experiments demonstrated exploitative competition. As I remarked at the beginning of the paper, they were not all competition (type 3). This anomaly demands an explanation but to my knowledge no previous author has given one.

Notice that the observed behavior of the protozoan sub-community—the full community minus the bacteria—was fitted with a GLV model containing interactions (type 3) only within the sub-community. Because there was no direct reference to the relationships with the hidden part of the community, the fitted interactions must have incorporated these other relationships, if they existed. I will call the fitted type 3 interactions apparent (type 3) interactions whenever modelers attempt to specify the system by restricting their attention to a sub-community and treating it as if it were the full community. In practice, type 3 interactions might always be apparent interactions, because there will always be variables we don't know about or have no data on—life stages lumped together, trophic components omitted and so on. In order to complete an interpretation of Vandermeer's apparent 'predator-prey' interactions we need first to ask whether apparent interactions should match our direct
observations of interactions in ecology, or our intuition about these. To answer this question I will advance a general method for deriving apparent interactions.

III. COUNTER-INTUITIVE APPARENT INTERACTIONS NEAR EQUILIBRIUM

Theoretical studies enable us to subject our intuition to scrutiny. We can specify the dynamics for a full community and with this omniscience examine the distorted picture gained by someone with lesser knowledge—someone aware only of part of the community if they modeled the behavior of their (apparent) community in terms of interactions only among its members. Schaffer (1981) also adopts the stance of omniscient theoretician in attempting to determine, in effect, whether the distinction between apparent and direct interactions matters. In order to provide my resolution to this issue, I introduce, in this section, a new method of calculating the apparent interactions near equilibrium—the $\alpha_{ij}$'s—so that they best fit trajectories over time near equilibrium. These apparent interactions are often counter-intuitive and different from the direct interactions. In Sect. IV I will compare my derivation with others, including that of Schaffer (1981).

Suppose that there are $m$ species in the full community with behavior governed by the equations

$$\dot{N}_i = f_i(N_1, \ldots, N_m) \quad i = 1, \ldots, m$$

(10)

where $f_i$ stands for a general time-independent functional relation. The GLV (Eq. 2) is a particular case of $f_i$. 

13
Suppose the community has a feasible equilibrium $N_i^*$, that is, $N_i^* > 0$ for all populations. Around this equilibrium the behavior can be approximated by the linear equations:

$$
\dot{n}_i = \sum_j \alpha_{ij} n_j \quad i, j = 1, \ldots, m
$$

(11)

where $n_i = N_i - N_i^*$

and

$$
\alpha_{ij} = \frac{\partial^2 N_i}{\partial N_j \partial N_i}
$$

(4)

If $\lambda_k$ and $u_k$ are the kth eigenvalues and (column) eigenvectors of the matrix $\alpha = (\alpha_{ij})$ then the linear equations (Eq. 11) can be replaced by a linear combination of the eigenvectors (Strang 1976:196 ff.), with dependency on time, $t$, made explicit:

$$
\dot{n}(t) = \sum_k c_k \exp(\lambda_k t) u_k
$$

(12)

where the initial conditions $n(0) = \sum_k c_k u_k$ define the values of the $c_k$'s through the equation

$$
\dot{n}(0) = \sum_k c_k u_k
$$

(13)

Now suppose we restrict our attention to $i, j \in R$--the apparent community--and want to find new values, $\alpha_{ij} \in R$ such that

$$
\dot{n}_i = \sum_{j \in R} \alpha_{ij} n_j \quad i, j \in R
$$

(14)

The superscript denotes that the effect $\alpha_{ij}$ is dependent on the choice of apparent community, $R$. Differentiating Eq. 12 and substituting it into Eq. 14 we have

$$
\sum_k \lambda_k c_k \exp(\lambda_k t) u_{ik} = \sum_{j \in R} \alpha_{ij} \sum_k c_k \exp(\lambda_k t) u_{jk}
$$

(15)

Separating Eq. 15 into the separate components (values of $k$):

$$
\lambda_k c_k \exp(\lambda_k t) u_{ik} = \sum_{j \in R} \alpha_{ij} u_k c_k \exp(\lambda_k t);
$$

$$
k = 1, \ldots, m
$$

(16)
In order to condense these expressions I will introduce the following notation:

\[ T_{ik} = \lambda_k c_k \exp(\lambda_k t) u_{ik} \]
\[ S_{jk} = c_k \exp(\lambda_k t) u_{jk} \]

Eq. 16 becomes in condensed notation:

\[ T_{ik} \approx \mathbf{a}_i^R S_k; \quad k = 1, \ldots, m \]
\[ \mathbf{a}_i^R = \text{row vector of } a_{ij}^R \]

and similarly for \( T_i, S_k \)

The value of \( \mathbf{a}_i^R \) which provides a least squares fit to Eq. 17 is

\[ \mathbf{a}_i^R = T_i S_H (SS_H)^{-1} \]

where \( H \) denotes Hermitian

and \( S = \text{matrix of } S_{jk} \) values.

Because \( T_{ik} \) and \( S_{jk} \) are functions both of initial population sizes, \( g(0) \) (through \( c_k \)), and time, \( t \), so are the \( a_{ij}^R \) values. I examine the dependency on initial population sizes and time below.

Before I employ this method I want to introduce, as a contrast, a more obvious method. We could have fitted Eq. 14 directly, inserting for \( \mathbf{a}_i^R \) values of \( \mathbf{a}_i \) (derived from Eq. 11) and \( n_i \). For a sample of points \((n_1, \ldots, n_m)\), we would be fitting \( \mathbf{a}_i = \sum_j a_{ij} n_j \) to \( \sum_{j \in R} a_{ij} n_j \). Over a large sample each \( n_j \) for \( j \not\in R \), that is, for the hidden variables, would be positive as often as negative, cancelling out the influence of \( a_{ij}, j \not\in R \), on \( n_i \). The \( a_{ij}^R \) values for \( j \in R \) would converge to the \( a_{ij} \) values as the sample size increased. That is, if the \( a_{ij} \) value is zero so will be the \( a_{ij}^R \) value. This will not, however, be the case if we restrict our attention to a small sample or constrain the hidden variables so that they are not equally likely to be positive as to be negative—a point I will return to in later
discussion. Having introduced this method of simply using the direct \( \alpha_{ij} \) values between members of the apparent community and ignoring interactions with the hidden variables, I will now use my method and show that it is both different and better.

First, I will show that this method works, that is, the apparent \( \alpha_{ij}^R \) values when inserted into Eq. 14 generate trajectories which mimic the correct ones, generated by Eq. 11.

I generated a model food web of eight species governed by GLV dynamics (Eq. 2) with parameter values given in Fig. 2 and Table 1. I then restricted my attention to the consumer (apparent) community, randomly generated one set of initial population sizes and calculated the apparent \( \alpha_{ij}^R \)'s at time, \( t = 0 \) (Table 2, Fig. 3). The trajectories for the five species as generated by the actual \( \alpha_{ij} \) values (using Eq. 11) are shown in Fig. 4 and the trajectories generated by the apparent \( \alpha_{ij}^R \)'s (using Eq. 14) in Fig. 5. Notice that these are very similar. Now compare the actual and the apparent interactions (compare Tables 2a and 2b or Figs. 3a and 3b). The apparent interactions include each consumer self-inhibiting, omnivore 6 and herbivore 4 both preying on top consumer 5, omnivore 2 competing with both 4 and 6, herbivore 4 competing with its predator 6 and being a prey of another herbivore, 8. In addition to these apparent interactions there are ones matching the direct predator-prey interactions of the actual food web. Whatever intuition we have about the effects of hidden resources it would not, surely, include a top consumer being a prey of lower consumers. Yet these are the apparent interactions that mimic the actual trajectories beginning from the given initial population sizes.
Figure 2. Eight species model food web. (Symbols as in Fig. 1.)
Figure 3. Interactions among the consumer community. A, apparent; B, direct. (See Table 2 for $\alpha_{ij}^R$ and $\alpha_{ij}$ values.)
Figure 4. Trajectories near equilibrium for the consumer community, as predicted by direct $a_{ij}$ values for the complete food web.

□, 2; *, 4; +, 5; -, 6; 9, 8.
Figure 5. Trajectories near equilibrium for the consumer community, as predicted by apparent $\alpha_{ij}^R$ values (given in Table 2).

(Symbols as in Fig. 4.)
Table 1. Parameters for eight species food web.

<table>
<thead>
<tr>
<th>Species</th>
<th>$b_i$</th>
<th>$j = 1$</th>
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<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
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<td>1</td>
<td>1.37</td>
<td>-1.00</td>
<td>-0.35</td>
<td>†</td>
<td></td>
<td></td>
<td>-0.02</td>
<td></td>
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<tr>
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<td>0.11</td>
<td></td>
<td>-0.36</td>
<td></td>
<td>0.17</td>
<td>0.14</td>
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</table>

*For all populations $N_i^* = 1$ so $a_{ij} = \alpha_{ij}^*$; † a blank entry corresponds to $a_{ij} = 0$. 
Table 2. Apparent* and direct† interactions for five species consumer (apparent-) community.

<table>
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<th>Species i</th>
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<th>5</th>
<th>6</th>
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<td><strong>a) Apparent interactions</strong></td>
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<td>-0.04</td>
<td>-0.13</td>
<td>-0.21</td>
<td>-0.01</td>
</tr>
<tr>
<td><strong>b) Direct interactions</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>-0.36</td>
<td></td>
<td></td>
<td>0.14</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td>-0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>0.18</td>
<td></td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>0.15</td>
<td></td>
<td></td>
<td>0.10</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>-0.28</td>
<td>-0.39</td>
<td>-0.11</td>
<td>-0.20</td>
</tr>
</tbody>
</table>

*Initial population sizes: 1, 0.34; 2, 1.69; 3, 0.58; 4, 1.75; 5, 0.75; 6, 0.02; 7, 1.28; 8, 1.65.
†Extracted from Table 1.
‡For all populations \( N_i^* = 1 \) so using \( a_{ij}^R = a_{ij}^R \) and \( b_i^R = \sum_j a_{ij}^R \) the apparent interactions can be inserted into a GLV model.
Now consider the consequences of using simply the direct interactions (Table 2b, Fig. 3b) between the consumers to generate the trajectories over time. They mimic the actual ones very poorly (compare Figs. 4 and 6). This point is reinforced by comparing the local stability as determined by the different \( \alpha \)-matrices. The dominant eigenvalue of the full food web has a real part of \(-0.0129\) and that of the apparent \( \alpha^R \)-matrix a real part of \(-0.0594\)—both indicating local stability. The matrix of direct interactions between consumers, however, has a real part of 0.016, indicating instability.

Next consider the dependency of apparent interactions on the sets of initial population sizes—the "starting points." I generated a sample of 20 starting points, calculated the apparent \( \alpha_{ij}^R \)'s for each at time, \( t=0 \), and then summarized this in a mean value and standard deviation for each \( \alpha_{ij}^R \) (Table 3a). The standard deviations are initially high relative to the means indicating that apparent \( \alpha_{ij}^R \)'s vary greatly with starting point. It is interesting to note that few of the effects are significantly different (at 5% significance level) from zero, and, with two exceptions (\( \alpha_{24}^R \) and \( \alpha_{44}^R \)), the significant \( \alpha_{ij}^R \)'s correspond to direct interactions in the full food web (Fig. 7). Nevertheless, as we have already seen, the direct interactions between the consumers alone, with the remainder kept at zero, cannot mimic the actual trajectories.

Although the mean apparent \( \alpha_{ij}^R \)'s are, in effect, a compromise over the range of starting points they do, in this case, give a reasonable fit for trajectories beginning at the particular starting point previously considered (compare Figs. 4 and 8). When more variables are hidden this becomes less so. As before I calculated the mean
Figure 6. Trajectories near equilibrium for consumer community, as predicted by the direct $a_{ij}$ for the consumers only.
Figure 7. Interactions among the consumer community. A, apparent; B, direct. (See Table 1 for $\alpha_{i,j}$ and Table 3a for $\alpha_{i,j}^R$ values. Symbols as in Fig. 3.)
Figure 8. Trajectories near equilibrium for the consumer community, as predicted by mean apparent $\alpha^{R}_{ij}$ values (given in Table 3a).
Table 3. Apparent interactions for five species consumer community. Means and standard deviations over 20 starting points.*

<table>
<thead>
<tr>
<th>Species i</th>
<th>j = 2</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) $t = 0$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>-0.30</td>
<td>-0.12</td>
<td>-0.45</td>
<td>-0.02</td>
<td>0.18</td>
</tr>
<tr>
<td>4</td>
<td>-0.21</td>
<td>-0.19</td>
<td>-0.21</td>
<td>-0.40</td>
<td>0.03</td>
</tr>
<tr>
<td>5</td>
<td>0.15</td>
<td>-0.02</td>
<td>-0.06</td>
<td>0.00</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>-0.09</td>
<td>0.06</td>
<td>-0.03</td>
<td>-0.08</td>
<td>0.16</td>
</tr>
<tr>
<td>8</td>
<td>-0.33</td>
<td>-0.04</td>
<td>-0.19</td>
<td>-0.19</td>
<td>-0.03</td>
</tr>
<tr>
<td>Standard deviation of $\alpha_i^R$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.20</td>
<td>0.03</td>
<td>0.13</td>
<td>0.17</td>
<td>0.06</td>
</tr>
<tr>
<td>4</td>
<td>0.15</td>
<td>0.09</td>
<td>0.34</td>
<td>0.14</td>
<td>0.05</td>
</tr>
<tr>
<td>5</td>
<td>0.02</td>
<td>0.01</td>
<td>0.07</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>6</td>
<td>0.07</td>
<td>0.05</td>
<td>0.12</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>8</td>
<td>0.05</td>
<td>0.02</td>
<td>0.10</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>b) $t = 0.923$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>-0.21</td>
<td>-0.11</td>
<td>-0.45</td>
<td>-0.06</td>
<td>0.16</td>
</tr>
<tr>
<td>4</td>
<td>-0.16</td>
<td>-0.15</td>
<td>-0.12</td>
<td>-0.40</td>
<td>0.00</td>
</tr>
<tr>
<td>5</td>
<td>0.16</td>
<td>-0.02</td>
<td>-0.03</td>
<td>-0.00</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>-0.07</td>
<td>0.09</td>
<td>-0.02</td>
<td>-0.07</td>
<td>0.13</td>
</tr>
<tr>
<td>8</td>
<td>-0.32</td>
<td>-0.04</td>
<td>-0.15</td>
<td>-0.20</td>
<td>-0.02</td>
</tr>
<tr>
<td>c) $t = 1.846$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>-0.15</td>
<td>-0.10</td>
<td>-0.43</td>
<td>-0.09</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>-0.11</td>
<td>-0.13</td>
<td>-0.06</td>
<td>-0.40</td>
<td>-0.01</td>
</tr>
<tr>
<td>5</td>
<td>0.17</td>
<td>0.02</td>
<td>-0.02</td>
<td>-0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>-0.05</td>
<td>-0.11</td>
<td>-0.01</td>
<td>-0.06</td>
<td>0.12</td>
</tr>
<tr>
<td>8</td>
<td>-0.31</td>
<td>-0.04</td>
<td>-0.13</td>
<td>-0.21</td>
<td>-0.02</td>
</tr>
<tr>
<td>d) $t = 2.769^+$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>-0.14</td>
<td>-0.10</td>
<td>-0.43</td>
<td>-0.09</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>-0.10</td>
<td>-0.13</td>
<td>-0.06</td>
<td>-0.40</td>
<td>-0.01</td>
</tr>
<tr>
<td>5</td>
<td>0.17</td>
<td>-0.02</td>
<td>-0.01</td>
<td>-0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>-0.05</td>
<td>0.11</td>
<td>-0.01</td>
<td>-0.06</td>
<td>0.12</td>
</tr>
<tr>
<td>8</td>
<td>-0.31</td>
<td>-0.04</td>
<td>-0.13</td>
<td>-0.21</td>
<td>-0.02</td>
</tr>
</tbody>
</table>

*Randomly allocated in the interval (0,2); †Standard deviations < .00005
apparent interactions among the higher-consumer community 2, 5 and 6 (Table 4, Fig. 9). In Fig. 10 we see that the trajectories generated by these apparent interactions do not reproduce the large initial oscillations in the actual trajectories (compare Figs. 4, 8 and 10). Nevertheless, although the fit is poor it is the best overall. We could improve the fit only by restricting our attention to a limited set of starting points.

Now consider the dependency of $\alpha_{ij}^R$ values on time. For each of the 20 starting points of the consumer community (2, 4, 5, 6, 8) I derived the apparent $\alpha_{ij}^R$ values at four different times and for each time calculated the means and standard deviations as before (Table 3a-d). The mean values change in magnitude and, very occasionally, in sign (e.g. $\alpha_{48}^R$); the standard deviations decline and all the apparent interactions become significantly different from zero. Initially the local stability as predicted by the mean apparent $\alpha$ matrix ($-0.0661$) overestimates the damping of the full community ($-0.0129$). As time increases the discrepancy decreases and at $t = 2.769$ the local stability is identical to that of the full community. This can be understood by considering Eq. 16. As time increases the components of Eq. 16 that correspond to the more negative eigenvalues decay until, in effect, there are only $M_R$ components (where $M_R$ = size of R) and the fit is exact. As time increases still further $SS^H$ becomes singular and the estimates become indeterminate. (In the case of an apparent community of size 1 $\alpha_{11}^R$ can be estimated directly from Eq. 16 even when $SS^H$ has become singular. It is exactly equal to the real part of the dominant eigenvalue.) Although the apparent interactions with zero standard deviation reproduce the actual local stability property the
Figure 9. Interactions among the higher-consumer community. A, apparent; B, direct. (See Table 1 for $\alpha_{ij}$ and Table 4 for $\alpha_{ij}^R$ values. Symbols as in Fig. 3.)
Figure 10. Trajectories near equilibrium for higher-consumer community, as predicted by mean apparent $a_{ij}^R$ values (given in Table 4).
Table 4. Apparent interaction for three species higher-consumer community. Means and standard deviations over 20 starting points at time $t = 0$.  

<table>
<thead>
<tr>
<th>Species $i$</th>
<th>$j = 2$</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_{ij}^R$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>-0.27</td>
<td>-0.44</td>
<td>0.03</td>
</tr>
<tr>
<td>5</td>
<td>0.15</td>
<td>-0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>6</td>
<td>-0.10</td>
<td>-0.37</td>
<td>-0.08</td>
</tr>
</tbody>
</table>

| Standard deviation of $\alpha_{ij}^R$ |         |   |   |
| 2                   | 0.15    | 0.16 | 0.11 |
| 5                   | 0.02    | 0.04 | 0.02 |
| 6                   | 0.12    | 0.15 | 0.04 |

Table 5. Parameter values, equilibrium and alpha matrix for chemostat model (Eq. 19).

- $d = 0.1 \text{ h}^{-1}$
- $i = 150$
- $k = 3$
- $m = 0.4 \text{ h}^{-1}$
- $y = 6.671 \times 10^{-4}$
- $N_1^* = 1.0$
- $N_2^* = 1.0$
- $\alpha = \begin{pmatrix} -112.45 & -149.9 \\ 0.07496 & 0 \end{pmatrix}$
time period over which this correspondence occurs depends on the relative size of the \( m_R \) and \( m_{R+1} \) th eigenvalues. If they are similar, the time period may be short and difficult to detect. From this point on I will, for consistency, restrict my attention to apparent \( \alpha_i^R \) 's derived at \( t=0 \).

How do apparent interactions compare with one's intuition about the interactions within the consumer community that are required to capture the effects of the hidden resources? It is true that when the apparent interactions were derived from a sample of 20 starting points (Table 3a, Fig. 7a) the most counter-intuitive apparent interactions derived for the case of a single starting point (Table 2a, Fig. 3a) disappeared. Nevertheless we still have a top consumer (5) competing with a herbivore (4) on another food chain, and two herbivores in a predator-prey relationship (4,8) (Fig. 7a). I doubt that these match anyone's intuition.

With this last observation we can interpret Vandermeer's "predator-prey" interactions between protozoa exploiting a common resource. Because he has specified only part of the community—the bacteria are hidden—his interactions are apparent interactions. They do not require biological interpretation—nor, similarly, do the apparent "competitive" interactions. Apparent interactions may match our intuitions but they do not necessarily. I will now present some simpler examples to reinforce this conclusion.
1. Bacterial growth in a chemostat.

A one stage chemostat is often modeled as follows where $N_1$ is the nutrient (e.g., glucose) and $N_2$ the cultured organism (e.g., bacteria) (see e.g. Segel 1984).

$$N_1 = 1 - dN_1 - mN_1N_2[y(k + N_1)]$$  \hspace{1cm} (19a)$$
$$N_2 = -dN_2 + mN_1N_2/(k + N_1)$$  \hspace{1cm} (19b)$$

where

$i =$ input rate of nutrient $d =$ dilution rate $m =$ maximum per capita rate of growth of $N_1$ or $N_2$ $k =$ "half-saturation" constant of uptake of $N_1$ by $N_2$ $y =$ "yield" or ratio of population increase to resource consumed.

Using the parameter values given in Table 5, the equilibrium values of $N_1^*, N_2^*$ are both 1.0 and the $\alpha$ matrix is as given in Table 4. The apparent $n_{22}^{R}$ value at $t=0$ for the one species community with the resource "hidden" is $-0.1516$. Although the direct self-interaction is zero, the apparent self-interaction is negative—a reasonable outcome in the case of one consumer on a hidden, renewed resource.

2. Two prey "sharing" a predator.

A simple model of a community in which two prey $(N_1, N_2)$ have the same predator $(N_3)$ is given in the following equations and Fig. 11.

$$\dot{N}_1 = N_1(b_1 + a_{11}N_1 + a_{13}N_3)$$  \hspace{1cm} (20a)$$
$$\dot{N}_2 = N_2(b_2 + a_{22}N_2 + a_{23}N_3)$$  \hspace{1cm} (20b)$$
$$\dot{N}_3 = N_3(b_3 + a_{31}N_1 + a_{32}N_2)$$  \hspace{1cm} (20c)$$
Figure 11. Two prey, one predator community. (Symbols as in Fig. 1.)
where \( b_1, b_2, a_{31}, a_{32} > 0 \)
\[ b_3, a_{11}, a_{22}, a_{13}, a_{23} < 0 \]
I calculated the apparent interactions at time \( t = 0 \) for a range of
different parameter values, both for species 1 and 2 with the predator
hidden, and for species 3 with its prey hidden. The results are
summarized in Table 6. The prey are, on average, apparent cooperators.
Holt (1977) examined the system and concluded that the prey were apparent
competitors. His definition of apparent interactions, however,
corresponds to type 4 interactions, a contrast I will discuss further in
the following section.

IV. APPARENT INTERACTIONS--A COMPARISON OF ALTERNATIVE DERIVATIONS

There are many references to apparent or indirect interactions in
the ecological literature (e.g. Holt 1977, Lawlor 1979, Schaffer 1981).
Some correspond to type 3 interactions; others to type 4 interactions.
My definition and derivation differ from others. A comparison will not
only make the differences clear but indicate some limitations of each of
the approaches.

A. Apparent type 3 interactions

There are various ways of mimicking the trajectories of members of
an apparent community. I will consider six different derivations of
apparent type 3 interactions, present a tabulated comparison of them
Table 6. Real and apparent $a_{ij}$'s for two prey, one predator community.

<table>
<thead>
<tr>
<th>Case</th>
<th>$\alpha_{22}$</th>
<th>$\alpha_{23}$</th>
<th>Mean $^2$ apparent community</th>
<th>Local stability (maximum real part)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\alpha^R$ matrix</td>
<td>s.d.</td>
<td>$\alpha^R_{33}$ value</td>
<td>s.d.</td>
</tr>
<tr>
<td>a)</td>
<td>-0.4 -0.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\begin{bmatrix} 0.27 &amp; 0.03 \ 0.27 &amp; -0.37 \end{bmatrix}$</td>
<td></td>
<td>$\begin{bmatrix} 0.22 &amp; 0.13 \end{bmatrix}$</td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td>-0.5 -0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\begin{bmatrix} -0.40 &amp; 0.15 \ 0.10 &amp; -0.35 \end{bmatrix}$</td>
<td></td>
<td>$\begin{bmatrix} 0.03 &amp; 0.04 \end{bmatrix}$</td>
<td></td>
</tr>
<tr>
<td>c)</td>
<td>-0.6 -0.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\begin{bmatrix} -0.40 &amp; 0.26 \ 0.08 &amp; -0.39 \end{bmatrix}$</td>
<td></td>
<td>$\begin{bmatrix} 0.12 &amp; 0.20 \end{bmatrix}$</td>
<td></td>
</tr>
<tr>
<td>d)</td>
<td>-0.7 -0.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\begin{bmatrix} -0.38 &amp; 0.32 \ 0.07 &amp; -0.51 \end{bmatrix}$</td>
<td></td>
<td>$\begin{bmatrix} 0.12 &amp; 0.35 \end{bmatrix}$</td>
<td></td>
</tr>
<tr>
<td>e)</td>
<td>-0.8 -0.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\begin{bmatrix} -0.33 &amp; 0.40 \ 0.07 &amp; -0.64 \end{bmatrix}$</td>
<td></td>
<td>$\begin{bmatrix} 0.15 &amp; 0.62 \end{bmatrix}$</td>
<td></td>
</tr>
</tbody>
</table>

$^1$For all the full communities $b_1 = b_2 = 1.; b_3 = -0.1$;

$\left( a_{ij} \right) = \begin{bmatrix} -0.5 & 0 & -0.5 \\ 0 & a_{22} & a_{23} \\ 0.04 & 0.06 & 0 \end{bmatrix}$

and $N_1^* = N_2^* = 1$ so $a_{ij} = a^R_{ij}$.

$^2$20 starting points, time = 0.

$^3$Local stability for apparent community with prey hidden is simply the $\alpha^R_{33}$ value.
(Table 7), and then apply each of them (with the exception of 4.) to the examples used in Sect.III (Tables 8 and 9a,b). The six derivations are as follows:

1. Apparent interactions near equilibrium, $a_{ij}^{R,s}$ (the method given in Sect.III).

2. Apparent interactions calculated as if the community were near equilibrium, but then extended to apply away from equilibrium by using a GLV model (Eq. 2) with the same $a_{ij}$ values, that is,

$$a_{ij} = \frac{a_{ij}^R}{N_i^*}, \quad b_i = -\sum_{j} a_{ij}^R \frac{N_j^*}{N_i^*}.$$

3. Apparent interactions away from equilibrium ($e_{ij}^{R,s}$) derived by fitting observed trajectories directly to the GLV model (see Sect.I.3).

4. Apparent interactions away from equilibrium ($e_{ij}^{R,s}$) derived by fitting observed trajectories directly to some model, other than the GLV, of the form $\dot{N}_i = f_i(N_1, \ldots, N_m)$.

5. A generalization of the method of MacArthur (1972:33 ff.). This method can be simply described. We take a general model (Eq. 10) to govern the full system but we consider the equation for $N_i$ (i R) and $\dot{N}_j$ (j R) separately. Setting $\dot{N}_j = 0$ we derive, if possible, expressions for $N_j^*$ as functions of the $N_i^*$'s. Finally, we replace $N_i^*$ by $N_i$ in these expressions and substitute them into the equations for $N_i$. These equations will now be in terms of the $N_i$'s only. MacArthur used this method only in the special case that the equations for $N_i$ could be factored out as $N_i g_i(N_1, \ldots, N_m)$.

6. A generalization of Schaffner's (1981) Abstracted Growth Equations. Schaffer proposed a method for deriving equations for the apparent community when we do not have knowledge of the full system. If
Table 7. A comparison of different derivations of apparent type 3 interactions.

<table>
<thead>
<tr>
<th>Method</th>
<th>Knowledge required</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Near equilibrium</td>
<td>Full system</td>
<td>Only holds close to the equilibrium. Counter-intuitive interactions common. Interaction estimates at t=0 vary greatly with starting points, but may settle down after time.</td>
</tr>
<tr>
<td>2. Near equilibrium</td>
<td>Full system</td>
<td>Fit away from the equilibrium may be poor, especially at N_i = 0.</td>
</tr>
<tr>
<td>extended</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Direct fit to GLV</td>
<td>Apparent community</td>
<td>Sensitive to starting points (including those of hidden variables). For any particular starting point fit is better than with method 2. Can be used to fit systems without a feasible equilibrium.</td>
</tr>
<tr>
<td>4. Direct fit to general model</td>
<td>Apparent community</td>
<td>As for method 3.</td>
</tr>
<tr>
<td>5. Generalized MacArthur</td>
<td>Full system</td>
<td>Cannot always be derived and may result in complex non-linear equations. Implicitly assumes that the time scale of the hidden variables is fast with respect to variables in the apparent community.</td>
</tr>
<tr>
<td>6. Generalized Schaffer</td>
<td>Apparent community</td>
<td>Fidelity of fit improves when a) time scale of hidden variables is fast with respect to variables in the apparent community and b) hidden variables have been allowed to equilibrate before observations are taken. Method of &quot;holding times&quot; to test these conditions (Schaffer 1981). Systematic method of derivation for special case of linearity only.</td>
</tr>
</tbody>
</table>

1See text for descriptions. 2Knowledge required to derive apparent interactions.
the system has a feasible equilibrium we construct, if possible, a GLV
model with two special features: a. The GLV model has the correct
equilibrium values for the apparent community; b. Per capita growth
rates when the $N_i$'s $= 0$ (ICR) as predicted by the model are identical
to those observed when the $N_j$'s ($j \neq i$) are at their equilibrium values
in the absence of the $N_i$'s. Schaffer applied this method to a special
case, similar to MacArthur's but where $g_i$ was a linear function of
$N_1, ..., N_m$. In this special case the methods of MacArthur and
Schaffer give identical results. Without that restriction on $g_i$
Schaffer's method is, in turn, a special case of method 3, in which
equilibrium values and initial per capita growth rate alone are used to
fit the GLV model.

I will highlight now some points from the comparison given in Table
7 and the supporting examples in Tables 8 and 9.

a. Time scales.

The derivations of MacArthur and Schaffer assume or require that
the time scales of the apparent community and the hidden variables are
disjunct. In contrast, when this is not known to be the case, apparent
$\alpha_{ij}^R$'s can be used to generate trajectories that mimic the observed
trajectories near equilibrium.

b. Restricted range of starting points.

Apparent $\alpha_{ij}^R$ values vary greatly with starting points. The
range of variation can be reduced by restricting the range of starting
points.
Table 8. Apparent dynamics for bacterial growth in a chemostat.\(^1\)

<table>
<thead>
<tr>
<th>Method</th>
<th>Apparent dynamics</th>
<th>Local stability(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>( \dot{n}_2 = -0.15 n_2 )</td>
<td>-0.15</td>
</tr>
<tr>
<td>2.</td>
<td>( \dot{N}_2 = N_2 (0.15 - 0.30 N_2) )</td>
<td>-0.15</td>
</tr>
<tr>
<td>3.(\dagger)</td>
<td>( \dot{N}_2 = N_2 (0.34 - 0.70 N_2) )</td>
<td>-0.34</td>
</tr>
<tr>
<td></td>
<td>( \dot{N}_2 = N_2 (0.48 - 0.89 N_2) )</td>
<td>-0.48</td>
</tr>
<tr>
<td>5.</td>
<td>( \dot{N}_2 = 0.5 - N_2 - 1./(8000 N_2 - 988) \approx 0.5 - N_2 )</td>
<td>-0.1</td>
</tr>
<tr>
<td>6.</td>
<td>( \dot{N}_2 = N_2 (0.3 - 0.6 N_2) )</td>
<td>-0.3</td>
</tr>
</tbody>
</table>

\(^1\)The full system has eigenvalues -.1 and -112.35. These correspond closely to the slow and fast time scales of bacterial growth and resource consumption respectively. The per capita growth rate of \( N_2 \) when \( N_2 = 0 \) lies between -.1 and .3 depending on the value of \( N_1 \).
\(^2\)Eigenvalue of linearization around equilibrium of .4997.
\(\dagger\)End-points selected from a range of starting points all having \( N_2(0) < N_2^{*} \).
<table>
<thead>
<tr>
<th>Method</th>
<th>Apparent dynamics</th>
<th>Local stability$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Two prey sharing hidden predator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. $^a$</td>
<td>$\dot{n}_1 = -.40 n_1 + .26 n_2$</td>
<td>-0.25</td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_2 = .08 n_1 - .39 n_2$</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td>$\dot{n}_1 = N_1 (.14 - .40 N_1 + .26 N_2)$</td>
<td>-0.25</td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_2 = N_2 (.31 + .08 N_1 - .39 N_2)$</td>
<td></td>
</tr>
<tr>
<td>3. $^b$</td>
<td>$\dot{n}_1 = N_1 (-2.5 - 5.1 N_1 + 7.6 N_2)$</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_2 = N_2 (-1.8 - 3.8 N_1 + 5.6 N_2)$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_1 = N_1 (-1.3 - 2.7 N_1 + 4.0 N_2)$</td>
<td>-0.006</td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_2 = N_2 (-0.9 - 1.8 N_1 + 2.7 N_2)$</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td></td>
<td>c</td>
</tr>
<tr>
<td>6.</td>
<td></td>
<td>c</td>
</tr>
<tr>
<td>b) Prey hidden</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. $^a$</td>
<td>$\dot{n}_3 = -.30 n_3$</td>
<td>-0.30</td>
</tr>
<tr>
<td>2.</td>
<td>$\dot{n}_3 = N_3 (.30 - .30 N_3)$</td>
<td>-0.30</td>
</tr>
<tr>
<td>3. $^b$</td>
<td>$\dot{n}_3 = N_3 (.075 - 0.73 N_3)$</td>
<td>-0.075</td>
</tr>
<tr>
<td></td>
<td>$\dot{n}_3 = N_3 (.082 - .082 N_3)$</td>
<td>-0.082</td>
</tr>
<tr>
<td>5.</td>
<td>$\dot{n}_3 = N_3 (.08 - .08 N_3)$</td>
<td>-0.08</td>
</tr>
<tr>
<td>6.</td>
<td>$\dot{n}_3 = N_3 (.08 - .08 N_3)$</td>
<td>-0.08</td>
</tr>
</tbody>
</table>

$^a_{22} = .6$, $a_{23} = -.4$ and the other parameters as given at the foot of Table 5. The full system has eigenvalues -.097, -.431, and -.472. There are no simple relationships among the time scales of the species.

$^b$Real parts of dominant eigenvalue after linearization around equilibrium (1,1). $^c$From Table 5 (20 starting points, t = 0). $^b$Samples from a range of different starting points all having $N_3(0) < N_3^*$. $^c$Indeterminate. Setting $\dot{n}_3 = 0$ does not yield an expression for $N_3^*$ because $a_{33} = 0$. 

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Methods 3 and 4 are also sensitive to variation of starting points. Consider fitting to observations generated by GLV dynamics a GLV model for the apparent community only, that is, fitting, for $i \in R$, over a set of starting points $(N_i, \ldots, N_m)$

$$N_i (b_i + \sum_{j \in R} a_{ij} N_j) \rightarrow N_i (b_i + \sum_{j = 1}^{m} a_{ij} N_j)$$

(21)

which is equivalent to fitting

$$N_i [\sum_{j \in R} a_{ij} R (N_j - N_j^*)] \rightarrow N_i [\sum_{j = 1}^{m} a_{ij} (N_j - N_j^*)]$$

(22)

Over a large sample of starting points in which the deviation from equilibrium of the hidden variables is equally likely to be positive as negative, the apparent $a_{ij}^R$'s will be, on average, simply the direct $a_{ij}$'s. That this is not the case in the examples of Tables 8 and 9 is simply an outcome of calculating the fit for one starting point at a time. The fitted model for the apparent community is thus applicable only for the starting point (or range of starting points) for which the fit was derived.

c. Counter-intuitive interactions.

From methods 1 to 3 both intuitive and counter-intuitive interactions can result; similarly for methods 5 and 6 if we designate the cases of indeterminate interactions shown in Table 9a as counter-intuitive. It is clear that this outcome is not peculiar to the particular method of deriving apparent $a_{ij}^R$'s that advanced in Sect.III. Notice that method 3, which fits the full trajectory and not simply the near equilibrium behavior, requires "self-enhancement" and local instability (Table 9a) in some cases. These unexpected parameter values require no biological interpretation, just as counter-intuitive apparent interactions in Vandermeer's protozoan community do not require
biological interpretation. Conversely, apparent interactions which fit our intuition (e.g. Table 9b) should not cause us to be satisfied with the model of the apparent community, a point I will return to in Sect.V.

B. Apparent type 4 interactions

What is the effect of specifying only a part of a community on type 4 interactions? That is, how do hidden variables affect the correlation between shifts in equilibrium of one variable and another (the others)? In Sect.I.4, I gave three derivations of type 4 interactions using univariate regression, multivariate regression or loop analysis. In the first case the interaction will be unchanged by omitting hidden variables. In effect, the interaction as defined is always an apparent interaction with all but two variables hidden (unless, of course, the community really has only two components.) In the second case omitting variables will make a difference to the outcome of the regression but not in any systematic fashion. In the case of loop analysis (or equivalent methods, e.g. Holt 1977) there are two ways of approaching the issue. The first is similar to the univariate regression case, that is, to consider that the interaction between two species derived by loop analysis is an apparent interaction—the remainder of the system invoked in the calculations are the hidden variables. The second approach is to use loop analysis to calculate the predicted changes when there really are hidden variables, that is, only the loops fully within the apparent community enter the formula.
I investigated the second approach to apparent (loop analysis) interactions. I compared the correct loop analysis predictions for the eight species food web (Fig. 2, Table 1) with those derived from the apparent consumer community. I assumed the parameter change affects the rate of change of one species only—the "node." (I have written a program in Fortran 77 to perform both quantitative and qualitative loop analysis. I will supply this on request.) First, I invoked the direct $\alpha_{ij}$ values for the apparent community. Because the predicted local stability is the opposite of the correct local stability (see Sect. III) the predictions are meaningless. Hoping to overcome this problem I followed conventional loop analysis protocol (Lane and Levins 1977) and added qualitative negative (self-inhibitory) $\alpha_{ii}$ values to represent the hidden resources. In this example the loop analysis predictions for these qualitatively specified interactions are indeterminate, that is, the sign of the determinant is ambiguous. Finally, I used the quantitative $a_{ij}^R$ values instead (Table 3a). The results are summarized in Tables 10a and 10b. The qualitative agreement is moderately good, but the quantitative agreement is poor.

This second approach to apparent (loop analysis) interactions needs further investigation. Nevertheless, it does suggest that apparent $a_{ij}^R$'s might give (qualitatively) reliable loop analysis predictions where direct interactions, even if supplemented with self-inhibitory interactions, do not. Loop analysis is, therefore, problematic. The loop analyst must either be sure that the complete set of direct (type 3) interactions has been specified or substitute apparent (type 3) interactions for direct interactions. Since apparent (type 3) interactions are not necessarily intuitive the loop analyst must adopt a
Table 10. Loop analysis predictions\(^1\) for five species consumer (apparent-) community.

<table>
<thead>
<tr>
<th>Node of parameter change</th>
<th>Predicted change in equilibrium size of species i</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>i = 2</td>
</tr>
<tr>
<td>a) Qualitative predictions</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>+</td>
</tr>
<tr>
<td>4</td>
<td>+</td>
</tr>
<tr>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>+</td>
</tr>
<tr>
<td>8</td>
<td>-</td>
</tr>
</tbody>
</table>

b) Quantitative predictions\(^2\)

<table>
<thead>
<tr>
<th>Node of parameter change</th>
<th>Predicted change in equilibrium size of species i</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>i = 2</td>
</tr>
<tr>
<td></td>
<td>3.71</td>
</tr>
<tr>
<td></td>
<td>(0.980)</td>
</tr>
<tr>
<td></td>
<td>4.96</td>
</tr>
<tr>
<td></td>
<td>(0.340)</td>
</tr>
<tr>
<td></td>
<td>-19.2</td>
</tr>
<tr>
<td></td>
<td>(-6.13)</td>
</tr>
<tr>
<td></td>
<td>.951</td>
</tr>
<tr>
<td></td>
<td>(.0426)</td>
</tr>
<tr>
<td></td>
<td>-10.1</td>
</tr>
<tr>
<td></td>
<td>(-.911)</td>
</tr>
</tbody>
</table>

\(^1\)Predicted change = \(\frac{\partial N_i^*}{\partial C}/(\partial N_j^*/\partial C)\). Figure in parentheses derived from apparent community using \(\alpha_{ij}\) values given in Table 3a. Shown only where different from correct value. By the definition of Sect.I.4 the effect of j on i is \(a_{ij} = \frac{\partial N_i^*}{\partial C}/(\partial N_j^*/\partial C)\).

\(^2\)Overall feedback of system = \(-7.06 \times 10^{-5}\) \((-5.98 \times 10^{-4}\)).
method for deriving them and address the limitations of the chosen method (see Sect.IV.A); limitations that include the fact that time scales might not be disjunct or that the full system might not be known. The conditions under which these limitations are negligible remain to be elucidated.

V. SOME IMPLICATIONS OF APPARENT INTERACTIONS

The method of Sect.III for calculating apparent interactions near equilibrium ($\alpha_{ij}^R$'s) is limited in its practical application. To calculate the best fit $\alpha^R$-matrix we require knowledge of the $\alpha$-matrix for the full community, but if this was known why not use it? I introduced the method for a different reason—to provide some clear examples to support the following conclusions about modeling. In order to contrast my conclusions with other views of modeling I will present them in the form of a rhetorical dialogue.

1. What information does a well-fitting model provide about actual ecological relationships?

We have seen that apparent interactions can generate trajectories that fit well those generated by the full dynamics (Figs. 5 and 8 vs. Fig. 4). We need, therefore, evidence, independent of the fit, that our model contains the full community. In the absence of such evidence the model is a summary or redescription of observations which need not correspond to actual ecological relationships. When we use a simple model we know that this is not the full community—we deliberately exclude certain variables, such as the resources of the consumers.
2. If the model fits well why not use it as a basis for predictions?

Suppose that we have fitted a model to observed trajectories and there is little variation in the estimates of the parameter values. If the observed trajectories begin over a large range of starting points it would be reasonable to apply the model widely, whether or not there are hidden variables. If, however, we have a narrow range of starting points (perhaps a single replicated starting point) then hidden variables can become important. We have seen that apparent interactions vary as the starting points of the trajectories vary (Table 3). The range of variation may be large compared to the mean values (Tables 3a and 4). So, in the case of the well-fitting model, if we observed trajectories beginning with different starting points, or if the hidden variables changed, the fitted parameter values would change, perhaps qualitatively. Conversely, the predictions for the changed circumstances based on the original parameter values could be poor. If we combine the first conclusion, that a model of an apparent community is a redescription, with the knowledge that apparent interactions are sensitive to starting points (and other changes in circumstances), then we should indicate the intended generality of the model. That is, we should specify the range of circumstances in which the fit was derived, and, in turn, might be expected to hold. Without this, a well-fitting model is an uncertain basis for predictions.

3. Is it not so that there will always be hidden variables? As a practical response to this fact, why not eliminate the distinction between actual and apparent ecological interactions, that is, simply define as the effect of one population on another the fitted $\alpha_{ij}$ value?
For example, exploitative competition is explicitly an apparent interaction with the shared resource implicit as the hidden variable.

We have seen, however, that apparent interactions can be counter-intuitive. If we adopt the pragmatic approach outlined we should not incorporate constraints on our parameter values to make the models appear biological. Vandermeer (1969), in contrast, insisted that $b_i$'s be positive and $a_{ij}$'s be negative—but not, paradoxically, that $a_{ij}$'s (the pairwise interactions between the protozoans) be negative. If, within the form of the GLV model, parameters are free to take any value and sign then a better fit to Vandermeer's data might be derived.

It follows, in addition, that we should not be satisfied with a model simply because it fits with parameter values that match our intuition. Similarly lack of fit should not be the only cause to make adjustments to a model. Counter-intuitive apparent interactions do not, in particular, require biological interpretation beyond recognizing that the community has not been fully specified (e.g. absence of the bacteria in Vandermeer's model).

Furthermore, even if we kept the parameters of our models "intuition-free" we could not expect the effects of hidden variables on these parameters to be constant over time or independent of the values of the hidden variables (see Table 3).

4. Aren't all models simplifications? We expect, therefore, the model to depart from reality and for these departures to guide us in subsequent improvement through the incorporation of additional biological detail. If we allowed concerns about hidden variables to inhibit our model formulation "there would be nothing to modify and we should get nowhere (Hutchinson 1978:40)." Is that not so?
We have seen, however, that a well-fitting model may require counter-intuitive parameter values. As a corollary we cannot translate our simple verbal models directly into mathematical terms. We cannot assume, for example, that exploiting a shared resource in a community is well represented by a negative-negative interaction in the apparent community consisting only of those "exploitative competitors." In this light, unless we knew the model contained the full community we cannot argue that lack of fit or counter-intuitive parameter values signify that some biological postulate is missing.

In summary, unless we know that the full community has been specified, a model is primarily a redescription of observations which does not necessarily, through either its fit or lack of fit, provide insight about actual ecological relationships. This conclusion, if accepted, requires us to review the strategy, common in community ecology, of building simple models referring to only two (or a few) species when those species are embedded in naturally variable and complex ecological situations. It is to such a review that I turn in the following section.

VI. SIMPLE MODELS, HIDDEN VARIABLES AND MACARTHURIAN ECOLOGY

When we use simple models we know there are unspecified or hidden variables. What allowance do we need to make for the variables left out of such mathematical models? This is a common concern which motivates the various derivations of apparent interactions compared in Sect.IV. In the previous section I concluded that we should consider the model to
be a redescription of observations and should not draw conclusions about actual ecological relationships. Where does that leave "MacArthurian" ecologists who readily employ simple mathematical models in the hope of deriving general ecological principles? To answer this question I will first distinguish the different roles, in addition to redescription, that we can ascribe to mathematical models, then interpret, in this light, some common approaches to using simple models and, in conclusion, comment on the prospect of using simple models to derive general ecological principles.

1. Different roles for models.

a. Models can be tools for exploration of the consequences of a system having the properties abstracted in the model. This exploration can proceed independently of establishing whether any real ecological situations have those properties or how special such situations are.

b. Models can be merely summaries or redescriptions of observations. In this instance, the only requirement is that the model fits the observations. If for another set of observations the form of the model is preserved but the parameter values are significantly different then it is, in effect, a different model. A redescription may provide a basis for us to predict and extrapolate but we do this on faith that past patterns continue into the future and not on knowledge of the underlying biological processes.

c. To establish that a model represents biological processes, that is, captures the relations that generate the observations in biology, requires more than redescription. In order to confirm that a model
represents generative relations, we must show that two criteria are fulfilled (Lloyd 1984). The first is that there is fit between the model and the observations. The second is that the assumptions or accessory conditions of the model have been established independently of that fit.

Accessory conditions arise as inevitable consequences of abstraction, for example, the assumption that all individuals in a species are equivalent in their response to the environment. Sometimes the accessory conditions are patently false but if they have a clear biological interpretation we can argue that they are, at least provisionally, unimportant. The equivalence of individuals is such a case. In contrast, the accessory conditions of simple models are difficult to characterize biologically. For example, in what circumstances can the effects of hidden variables be incorporated as a constant effect in the parameters of a simple model? The work in this paper has shown that, in general, these are special circumstances (limited range of initial conditions, separation of time scales and so on), and knowledge of the full system is required to characterize them. Confirmation of simple models is, therefore, difficult.

2. Common approaches to using simple models.

If a model is confirmed as a representation of generative relations we can do more than fit past observations—we can use the model to deduce the actual outcomes in situations not yet observed. The model subsumes explanation of the past and inference about the future into one form; the principles the model embodies stand as ecological laws. Yet hidden variables confound attempts to confirm simple models. For
unconfirmed models, the generality of a redescription is limited to the range of circumstances in which the model fits the observations, and the biological relevance of insights derived from exploration of the model—mathematical—system is unknown. How then can we use simple models? There are a variety of approaches (this is usually done), I will highlight the following:

a. Study controlled systems consisting of only a few components, isolated from their naturally variable context. Hidden variables are excluded or tightly controlled. Simple mathematical models are sometimes effective for laboratory microcosms (Williams 1972) and sometimes not (Hertz and McCauley 1980). In any case, this approach sidesteps the primary issue of models of non-laboratory ecological situations.

b. Concede that the mathematical model is a redescription of observations, applicable in the range of circumstances in which the model fits the observations. Perhaps use it as a basis for prediction and extrapolation, nevertheless.

c. Construct or select special circumstances of "quasi-independence" of modeled and hidden variables. For example, if the starting points of the full system are confined to a small domain, then hidden variables may have constant effects on the parameters of the simple model. Furthermore, if the time scales of the components of the apparent community are much longer than those of the hidden variables, the hidden variables may equilibrate quickly and their effects on the apparent community may be constant. This is the assumption behind the methods of MacArthur and Schaffer (see Sect.IV). Finally, sometimes the effects of the hidden variables may be overridden by the strength of the
interactions within the apparent community. It is important that ecologists do not reserve their interest for these special, quasi-independent ecological situations and thereby come to believe that they are general.

d. Generate hypotheses. Simple verbal models can stimulate ecologists to generate and investigate hypotheses in ecology. When we express a simple model in mathematical terms we enhance our facility for hypothesis generation by being able to explore systematically the possible behaviors of such a model. We should remember that this exploration is of the mathematical system; insights about the model are only hypotheses about biology. If we recognize the confounding effects of hidden variables we might be less interested in such hypotheses. At least, we might take them less seriously and not mistake the terms in a mathematical model for processes in ecology.


There are many ecologists who still hold MacArthur's (1972:169) words in mind: "Will the explanation of these facts degenerate into a tedious set of case histories, or is there some common pattern running through them all." They readily employ simple mathematical models in the hope of capturing these patterns (Roughgarden 1983). Although they recognize that the simplifications are gross, there are potential compensations, however, and these constitute the attraction of simple models. If a simple model is accepted as an explanation it reduces the complexity of nature to a level where it can be comprehended. Because a simple model is sparse in specification the model can be transferred to a range of situations and, perhaps, yield general theorems which unify
disparate facts. A simple model appears to require measurement of fewer quantities in order to assess the correspondence between the model and observations. And, finally, the model is more likely to be mathematically tractable and its range of behavior understandable.

A simple model will not, of course, correspond precisely to observations. When either the lack of correspondence becomes unacceptable or we want to refine the initially loose insight we invoke additional biological postulates and replace the model with another having greater detail. More refined theory builds on initially crude theory (a process of "factualization" (Haila and Jarvinen 1982)). For MacArthurian ecologists theory is general, that is, widely applicable. Loose, qualitative insights are to be preferred for their generality over more detailed, but only locally applicable, models (see e.g., Levins 1966; MacArthur 1972; May 1973; Hutchinson 1978).

In this strategy of model building and refinement a fundamental ambiguity has arisen: how can we think of the addition of detail as addition of biological postulates unless we show the initial simple model is a representation of generative biological relations? The obvious answer is that, at some loose level of specification, the simple model does represent biological relations, such as growth, resource limitation, competition, immigration and so on. This obvious answer breaks down, however, when we express our simple model in mathematical terms. In a mathematical form the simple model requires that the effects of the species in the community that are not referred to directly can be incorporated indirectly through the parameter values or the form of the simple model. Yet, as my analysis of apparent
interactions has shown, this requirement is problematic. Simple mathematical models are neither necessarily general nor realistic.

MacArthurian modeling has played an important role in stimulating ecology (Kingsland 1985:Chap. 8), but this effect may be attributed primarily to a quality independent to the mathematics, that is, the juxtaposition for our attention of particular biological processes. The mathematical elaboration of MacArthurian verbal models has compromised this primary role, by conflating, in my terms, exploration, redescription and representation of generative relations.

It is not surprising that simple models, which are difficult or impossible to confirm, have provoked strong reaction (Simberloff 1982; Strong et al. 1984). The thrust of this reaction is that modeling should be replaced by "investigation" (Simberloff, 1982). The argument goes as follows: There are many factors operating in nature and in any particular case at least some of these will be significant. A mathematical model cannot capture these and still have general application. Instead, we should investigate particular ecological situations and experimentally test specific hypotheses about these situations, guided by and adding to knowledge about similar cases. Although this "particularist" reaction is provocative, I do not want to dismiss models so readily.

I concede that the "particularist" ecologists may be correct; that investigation of particular ecological situations is more revealing than (premature) attempts to apply simple mathematical models to a range of ecological situations. This is especially so if the application of models entails the selection or construction of special "quasi-independent" cases. Notwithstanding my concession, however, I
believe both that there is scope for general theory in ecology and that the empirical categories which particularist ecologists use to frame and test their hypotheses also depend on abstractions (what, for example, is a stochastic process in ecology?). If MacArthurian ecologists are to withstand the vigorous challenge of particularism (Strong et al. 1984) they must continue to suggest fruitful and general ways of viewing ecological processes—ways which may be quite abstract and are not obvious to particularist, "investigative" ecologists. While mathematical models may be a tool in yielding such fruit they provide no shortcut to generality. If we appreciate the confounding effects of hidden variables (and incoherent aggregation) we should use mathematical models in a highly qualified, provisional or exploratory fashion. This is a challenge to the imagination and patience of theoretical ecologists.

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Literature Cited


