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A GENERAL TEST FOR INTERACTION MODIFICATION¹

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Abstract. How can measurements of population dynamics be used to deduce the mechanisms of interaction in an assemblage of species? We present a technique to use such measurements to distinguish among assemblages of species with no direct interactions, sets of species influenced predominantly by pairwise interactions, and communities with significant interaction modification. We define the interaction coefficients and show that their dependence on the population sizes of the various species reveals and pinpoints interactions. Our technique distinguishes non-additivity in the statistical sense from interaction modification in the biological sense.

Key words: higher order interactions; general tests for higher order interactions; non-additivity in species interactions; nonparametric regression tests.

INTRODUCTION

The population dynamics of a species can depend on many factors, including abiotic influences, resource levels, the population sizes of the species with which it interacts, and the mode of such interactions. When species interactions are important, they can take many forms, as described by Billick and Case (1994) and Wootton (1994). Of concern here are three types of interaction described in detail by Billick and Case (1994): indirect interactions mediated through known or unknown resources, a series of direct, pairwise interactions determined solely by population size, and direct pairwise interactions modified by the presence or density of other species (interaction modifications). To distinguish among these alternatives is to distinguish among very different views of communities, ranging from assemblages of species with no direct interactions, to sets of species involved only in pairwise interactions that operate more or less independently, to complex webs of action and reaction involving multiple species simultaneously. From a practical viewpoint, determining whether interaction modifications (IM) exist is a critical first step in teasing apart community dynamics: in their absence, a series of experiments that include all possible pairs of species in the community would in principle suffice to predict the trajectory of the entire species ensemble. However, when IM operate, experiments must determine not only

the rates of interactions between all species pairs, but how those rates are altered by additional species in the community.

Many interactions or processes that in theory could influence population dynamics in practice fail to produce measurable effects upon population dynamics. Consequently, while it may be easy to call attention to the theoretical importance of higher order interactions (HOI) (Abrams 1987), there remains an essential need for specific tests that can determine whether HOI are of sufficient magnitude to emerge above the din of multiple processes occurring simultaneously in real communities. If HOI are important, their neglect can lead to serious misunderstanding of particular communities. Conversely, if HOI are unimportant, research focused on them might distract us from other potential determinants of community dynamics.

Our purpose here is to discuss methods for testing whether interaction modifications lurk within a given ecological data set. We are particularly concerned with approaches that would enable the empiricist to distinguish simple non-additivity in the statistical sense from higher order interaction and interaction modification (IM) in the biological sense. Using explicit models, we propose a test for interaction modification that generalizes and reinterprets a criterion proposed by Abrams (1983), and discuss the advantages and limitations of applying this test to ecological data.

NON-ADDITIVITY DOES NOT IMPLY INTERACTION MODIFICATION

The simplest model of a community described by a sequence of pairwise interactions is one in which the per capita reproductive and death rates of individuals can be expressed as a sum of effects by other species. A non-additive model is, then, one which includes

¹ For reprints of this Special Feature, see footnote 1, page 1527.

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multiplicative terms that depend on more than one species. We here show that the presence of such multiplicative terms reveals nothing about the presence of IM.

We first discuss a model in which multiplicative terms do imply the existence of IM. Consider the three-trophic-level system described by Huang and Sih (1991), in which sunfish prey upon both isopods and isopod-eating larval salamanders. Addition of sunfish to a community consisting of isopods and salamanders could act additively to increase isopod mortality, or could diminish isopod mortality in two different ways: by depleting the salamander population through predation (an indirect effect), or by inducing salamanders to change behavior and become less efficient as isopod predators (IM).

Over the short times considered in their experiment, sunfish numbers remained constant, and there was no reproduction of salamanders or isopods (Huang and Sih 1991). A simple Lotka-Volterra model of the interaction in the context of this experiment (cf. Levin et al. 1977) needs to include only the three predation terms, and can be written

$$\begin{aligned} \frac{1}{L} \frac{dL}{dt} &= -aS \\ \frac{1}{I} \frac{dI}{dt} &= -bS - cL, \end{aligned} \tag{1}$$

where S , L , and I are the densities of sunfish, larval salamanders, and isopods. The left hand sides give net per capita death rates, where a represents the predation rate of sunfish on salamanders, b the predation rate of sunfish on isopods, and c the predation rate of salamanders on isopods. We assume there is no other source of mortality.

Any interaction modification in this system must be mediated through the various predation rates. For simplicity, we focus on the term c for predation of salamanders on isopods. If this rate is constant, or is a function only of L , the per capita death rate of isopods is an additive function of the densities of other species. In this case, the model would pass the test for the absence of HOI proposed by Case and Bender (1981) and further discussed by Billick and Case (1994), namely that the per capita growth rate of a species in a three-species mixture must equal the sum of that species' growth rate in the two possible two-species mixtures minus its growth rate in isolation. For example, from the perspective of isopods, the following equality holds:

$$\begin{aligned} &[\text{isopod death rate in 3 species mixture}] \\ &= [\text{isopod death in presence of sunfish only}] \\ &+ [\text{isopod death in presence of salamanders only}] \\ &- [\text{isopod death in isolation}] \end{aligned}$$

or

$$\begin{aligned} [-aS - cL] &= [-aS - c \times 0] \\ &+ [-a \times 0 - cL] - [0]. \end{aligned} \tag{2}$$

Now suppose that sunfish modify the interaction between salamanders and isopods. To model this situation, we replace c with $c_0 e^{-\gamma S}$ to indicate that the attack rate of salamanders on isopods declines as sunfish become more abundant and salamanders spend more time in refuges. In this case, Eq. 2 no longer holds, because

$$\begin{aligned} [-aS - c_0 e^{-\gamma S} L] &\neq [-aS - c_0 e^{-\gamma S} \times 0] \\ &+ [-a \times 0 - c_0 e^{-\gamma \times 0} L] - [0] \\ &= -aS - c_0 L. \end{aligned}$$

Because the reduction in salamander predation on isopods in the presence of sunfish introduces a non-additive term into an additive model, the Case and Bender test for higher order interactions was able to detect the interaction modification.

In contrast, consider a model in which species affect one another in a multiplicative fashion, but the rate of interaction between any pair of species is unaltered by the densities of other species in the community. Suppose a number of plant species compete for light, and that the species are numbered in order of increasing height, so that species j shades species i only if $j > i$. If plant species j allows only a proportion $e^{-a_j N_j}$ of available light to pass through its canopy, where N_j is the population size of species j , the proportion of light available to an average plant will be

$$\prod_{j>i} e^{-a_j N_j}$$

Assuming that L is the total incident light and that growth is proportional to available light, the per capita growth rate for each species will be

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i L \prod_{j>i} e^{-a_j N_j}, \tag{3}$$

where r_i is the amount of plant biomass produced by species i per unit of available light. Because all interactions are mediated through a single resource, and the rate at which each species utilizes that resource is independent of the densities of other species, there is no interaction modification. The Case and Bender test, however, fails, as

$$\begin{aligned} &[\text{growth rate of species 1 in competition with species 2 and 3}] \\ &\neq [\text{growth rate of species 1 in competition with species 2}] \\ &+ [\text{growth rate of species 1 in competition with species 3}] \\ &- [\text{growth rate of species 1 in isolation}] \end{aligned}$$

Instead, we have the equation:

$$\left[\begin{array}{l} \text{growth rate} \\ \text{of species} \\ \text{1 in} \\ \text{competition} \\ \text{with species} \\ \text{2 and 3} \end{array} \right] = \left[\begin{array}{l} \text{growth rate} \\ \text{of species} \\ \text{1 in} \\ \text{competition} \\ \text{with} \\ \text{species 2} \end{array} \right] \times \left[\begin{array}{l} \text{growth rate} \\ \text{of species} \\ \text{1 in} \\ \text{competition} \\ \text{with} \\ \text{species 3} \end{array} \right] \div \left[\begin{array}{l} \text{growth} \\ \text{rate of} \\ \text{species} \\ \text{1 in} \\ \text{isolation} \end{array} \right]$$

which is a multiplicative model of interaction.

These examples indicate that a test for IM must do more than test for non-additivity in per capita growth rates.

A GENERAL TEST FOR INTERACTION MODIFICATIONS

Competition coefficients (Schoener 1974) have been used to describe pairwise interactions in communities of competitors. Such coefficients are defined as the effect one species has on the per capita growth rate of a second species relative to the effect the second has on itself. Abrams (1983) equated higher order interactions with the presence of a functional dependence of these coefficients on the population size of a third species. Our test is similar, but is designed to identify interaction modifications.

Suppose we have a general system of equations

$$\frac{1}{N_i} \frac{dN_i}{dt} = F_i(N_1, \dots, N_m) \tag{4}$$

describing the dynamics of *m* interacting species. (Although we illustrate the test with a differential equation model, it applies equally well to difference equation formulations.) The effect of species *j* on species *i* can be described by what we term an "interaction coefficient" (denoted β_{ij}), defined as the effect an added individual of species *j* has on the per capita growth rate of species *i*. That is,

$$\begin{aligned} \beta_{ij} &= F_i(N_1, \dots, N_j + 1, \dots, N_m) \\ &\quad - F_i(N_1, \dots, N_j, \dots, N_m) \\ &\approx \frac{\partial F_i}{\partial N_j} \end{aligned} \tag{5}$$

Note that the usual competition coefficient α_{ij} is equal to β_{ij}/β_{ii} .

The absence of IM is characterized by the absence of dependence of the interaction coefficient β_{ij} on characteristics of species other than *i* and *j*. Formally, this means

$$\beta_{ij} = G_{ij}(F_i, N_i, N_j) \tag{6}$$

for each β_{ij} , where the function G_{ij} can take any form as long as the effect on species *i* of adding a new individual of species *j* depends only on the current growth rate and the population sizes of the two species under

consideration. This test generalizes those of Case and Bender (1981) and Abrams (1983), producing a more stringent criterion for the absence of IM. Case and Bender (1981) define the absence of higher order interactions as dependence of the interaction coefficient β_{ij} on *N_j* only, which is equivalent to the requirement that the per capita growth rate of each species be a sum of terms describing the effects of the other species. Billick and Case (1994) note that the Case and Bender test is based on a more general model in which the interaction coefficients can depend on both *N_i* and *N_j*. This parallels Abrams' (1983) definition of HOI in the competitive case as dependence of the competition coefficient α_{ij} on factors other than *N_i* and *N_j*. These criteria correspond to the broader class of population dynamic models in which the per capita growth rate of a species can be expressed as a sum of terms describing its pairwise interactions with other species.

As pointed out by Billick and Case (1994), population size may not provide a complete description of the state of a population, and apparent higher order effects may be due to unmeasured structure. In addition, they show that the dynamics of unmeasured resources can produce spurious positive results in tests for higher order effects. To partially obviate this problem, we allow the interaction coefficient to depend on the population growth rate. The growth rate can act as a surrogate for the level of a limiting resource in certain cases (Appendix). This additional functional dependence breaks the restriction to the additive model form, and the test is able to reject the presence of interaction modification in the multiplicative "competition for light" model, as we demonstrate below. Furthermore, the form of the functional dependence of the interaction coefficients on the growth rate identifies the structure of the interaction (see Appendix and Table 1).

This test can be used to examine each interaction in the system separately, because dependence of β_{ij} on *N_k* indicates that species *k* modifies the effect of species *j* on species *i*. The Case and Bender test, on the other hand, can only show that there is some higher order interaction affecting the per capita growth of species *i*, without pinpointing the specific interaction. For example, our test can identify when an intraspecific interaction involving species *i* is modified by species *k* by checking whether β_{ii} depends on *N_k*.

The general test we have proposed is able to detect the modification of the rates of interspecific interaction in both models discussed above. For the aquatic food web model (Eq. 1), the interaction coefficient describing the effect of salamanders on isopods is the term *c*. If *c* depends on isopod numbers (through a functional response by the salamanders), salamander numbers (through some direct interference among salamanders), or is constant, the test indicates the absence of inter-

TABLE 1. Some standard models and their analysis using the method of interaction coefficients.

Continuous-time models			
Model	Growth rate $F_N = \frac{1}{N} \frac{dN}{dt}$	Interaction coefficient	IM present?
Lotka-Volterra	$F_i = r_i \left(1 - \frac{\sum_j a_{ij} N_j}{K_i} \right)$	$\beta_{ij} = \frac{-r_i a_{ij}}{K_i} = \text{constant}$	no
Competition for light	$F_i = r_i L \prod_{j>i} e^{-a_j N_j}$	$\beta_{ij} = -a_j r_i L \prod_{j>i} e^{-a_j N_j} = -a_j F_i = G(F_i)$	no
One prey/two predators			
Prey (N)	$F_N = r - \frac{k_1 P_1}{N + D_1} - \frac{k_2 P_2}{N + D_2}$	$\beta_{N,P_i} = \frac{\partial F_N}{\partial P_i} = -\frac{k_i}{N + D_i} = G(N)$	no
Predators (P_1, P_2)	$F_{P_i} = \frac{m_i N}{N + D_i} - \delta_i$	$\beta_{P_i,N} = \frac{\partial F_{P_i}}{\partial N} = \frac{m_i D_i}{(N + D_i)^2} = G(N)$	no
		$\beta_{P_1,P_2} = \frac{\partial F_{P_1}}{\partial P_2} = 0$	no
Two prey/one predator			
Prey (N_1, N_2)	$F_{N_i} = r - \frac{k_i P}{N_1 + N_2 + D_i}$	$\beta_{N_i,P} = \frac{\partial F_{N_i}}{\partial P} = -\frac{k_i}{N_1 + N_2 + D_i} = \frac{F_{N_i} + r}{P} = G(F_{N_i}, P)$	no
		$\beta_{N_1,N_2} = \frac{\partial F_{N_1}}{\partial N_2} = -\frac{k_1 P}{(N_1 + N_2 + D_1)^2} = G(N_1, N_2, P)$	yes
		$\beta_{P,N_i} = \frac{\partial F_P}{\partial N_i} = G(N_1, N_2)$	yes
Predator (P)	$F_P = \frac{k_1 N_1}{N_1 + N_2 + D_1} + \frac{k_2 N_2}{N_1 + N_2 + D_2} - \delta$		
Discrete-time models			
Model	Growth rate $F_N = \frac{N(t+1)}{N(t)}$	Interaction coefficient	IM present?
Ricker competition	$F_i = r_i \exp(-\sum_j a_j N_j)$	$\beta_{ij} = -a_j r_i \exp(-\sum_j a_j N_j) = -a_j F_i = G(F_i)$	no
Hassell-Comins competition	$F_i = r_i (1 + \sum_j a_j N_j)^{-b_i}$	$\beta_{ij} = -b_i a_j r_i (1 + \sum_j a_j N_j)^{-b_i-1} = -b_i a_j r_i^{-1/b_i} F_i^{1+1/b_i} = G(F_i)$	no

action modification, because the interaction coefficient can be expressed in terms just of the population sizes of the interacting species. However, if the sunfish modify the interaction between salamanders and isopods, the interaction coefficient is equal to $c_0 e^{-\gamma S}$, which cannot be rewritten as a function of L, I , and the salamander growth rate alone.

In the "competition for light" model (Eq. 3), we have that

$$\beta_{ij} = -a_j r_i L \prod_{j>i} e^{-a_j N_j} = -a_j F_i \tag{7}$$

which satisfies our requirement for the absence of IM. However, unlike the aquatic food web model, the interaction coefficient is not constant, but depends linearly on the growth rate. This form is characteristic of multiplicative models of resource-mediated competi-

TESTING FOR INTERACTION MODIFICATIONS IN ECOLOGICAL DATA

While it is not difficult to see how the general test we have proposed can be applied to mathematical models of multi-species interactions (one takes a partial derivative), it is more difficult to see how it can be used to uncover interaction modifications in ecological data obtained from field or laboratory studies. We see three methods of testing for IM, each with its own strengths and weaknesses. We illustrate these three techniques using the data of Huang and Sih (1991), and simulation of two models of competition among three species.

1) *Direct observation of species interactions:* The most straightforward method of detecting interaction modifications is to directly observe the interaction between individuals of two species in the presence and absence of a third species and determine if that particular interaction is sensitive to the density of the third species. For example, Huang and Sih (1991) show directly that salamanders spend more time in refuges, and thus less time foraging for isopods, when they are exposed to predatory sunfish. The advantage of this approach is directness. The disadvantage is that direct observation may not be feasible or that the appropriate behaviors may not be evident a priori. For example, behavioral interactions whose rates are slow may not be compatible with the time scale of most observational studies. Other interactions may not be directly observable. Furthermore, behavioral observations must be carried out over a relatively short time interval to prevent indirect effects (changes in interactions mediated entirely through population size) from being confounded with IM (Billick and Case 1994). Huang and Sih (1991) addressed this problem by creating a third treatment that substituted the smell of fish for the fish themselves. The salamanders responded behaviorally to these chemicals in much the same way that they responded to fish, and the small decrease in isopod predation could be attributed entirely to this response. However, such experimental separation of the behavioral response (interaction modification) from the population dynamic response (indirect effect) may not always be possible.

2) *Guessing the right model form:* Our examples suggest a second way to establish the absence of IM in a given community. One could employ the partial derivative test to identify a model that lacks IM, and then ask whether it is able to predict the population data. We have argued that the Case and Bender test falls into this category, testing whether data deviate from a particular, though very general, additive form. The difficulty comes in choosing the right model structure. Failure of data to fit a model might erroneously suggest

the presence of IM, when in fact what was discovered was simply the choice of an inappropriate model.

With the data of Huang and Sih (1991) one plausible model is the Lotka-Volterra model presented in Eq. 1. In this case, the partial derivative test coincides with the Case and Bender test. For example, the effect of larval salamanders on isopods, can be estimated as

$$\beta_{IL}(I, 0, 0) \approx F_I(I, L, 0) - F_I(I, 0, 0)$$

in the absence of sunfish, and as

$$\beta_{IL}(I, 0, S) \approx F_I(I, L, S) - F_I(I, 0, S)$$

in the presence of sunfish. Then we have that β_{IL} is independent of S if

$$\beta_{IL}(I, 0, 0) = \beta_{IL}(I, 0, S),$$

or

$$F_I(I, L, 0) - F_I(I, 0, 0) = F_I(I, L, S) - F_I(I, 0, S),$$

which is precisely the Case and Bender test. For example, with the data in Huang and Sih (1991), we can estimate F_I as the average number of isopod deaths over the course of the experiment. They found that $F_I(I, 0, 0) = 10$, $F_I(I, L, 0) = 125$, $F_I(I, 0, S) = 60$, $F_I(I, L, S) = 70$, so β_{IL} is ≈ 115 in the absence of sunfish, and only 10 in their presence. That is, sunfish greatly decrease the effect of larval salamanders on isopods.

If the test proposed in Eq. 6 is to prove practical at detecting IM in real data sets, we must be confident that we can pick up the distinguishing signature of IM when a known underlying model operates against a stochastic background. To consider a case different from the additive case, we simulated three species in the competition for light model given in Eq. 3, and the Hassell and Comins competition model (Hassell and Comins 1976) given in Table 1, adding stochastic noise to the model parameters and the initial population sizes in both cases. In order to apply our test, more than two levels of some species must be considered. We consider four densities (0, 1, 2, and 3) of species 2 and 3, and focus on their effects on a single density (1) of species 1.

In the simulation of the competition for light model, we set all parameters (r and a) to be equal to 1.0, with normally distributed noise of standard deviation of 0.2 chosen independently in each of 5 replicates in the 16 treatments. Additionally, we assumed normally distributed measurement error of the initial sizes, with the same standard deviation. The simulation was run for a time of 0.2, which corresponds to $\approx 22\%$ growth. Growth rate was calculated as final size minus initial size. In the simulation of the Hassell and Comins discrete model, we set the growth parameter r to be 2.0, and the competition coefficients to be 0.5 with standard deviation of 0.2 chosen independently in each of 5

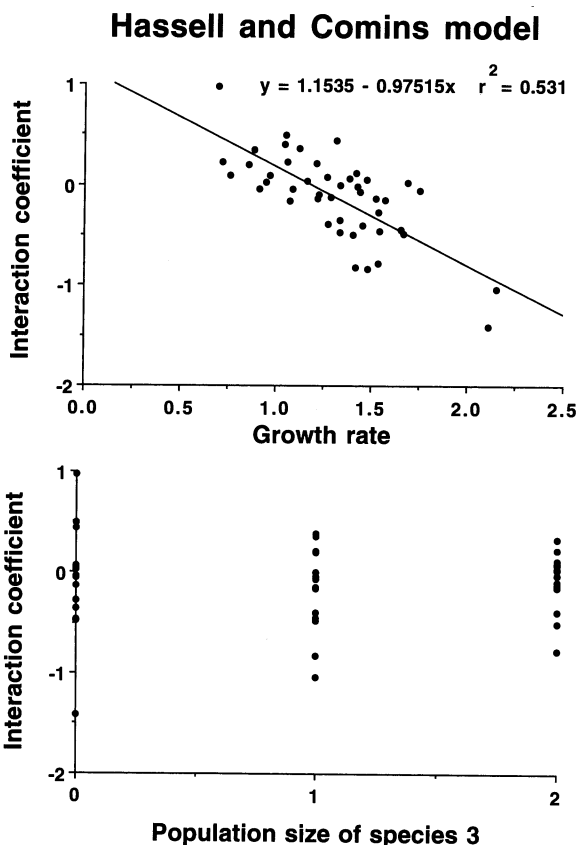


FIG. 1. Results of simulation of the competition for light model (Eq. 3). Parameter values are listed in *Testing for interaction modifications . . . : 2) Guessing the right model form*. The top panel shows the regression of the interaction coefficient β_{12} against the growth rate of species 1, and the bottom panel shows the relationship of the interaction coefficient β_{12} to the population size of species 3.

replicates in the 16 treatments. Measurement error was simulated as in the competition for light. The parameter b was set to 0.5, and we ran the model for a single interaction. Growth rate was calculated as final size divided by initial size.

In each case, we calculated the interaction coefficient as a finite difference between per capita growth rates; for example $\beta_{12}(1, 2, 2) = F_1(1, 3, 2) - F_1(1, 2, 2)$. We treated each replicate as a block. The results for β_{12} are shown in Figs. 1 and 2. In each case, the growth rate explains the majority of the variance, with the population size of species 3 showing little effect. Analysis of covariance shows that there is no effect of either species 2 or 3 on interaction coefficient when the growth rate is taken into account. This indicates that both models are effectively models for competition for a single resource (Appendix). However, the expected cubic relationship of the interaction coefficient to the growth rate for the Hassell-Comins model with $b = 0.5$

(see Table 1) cannot be discerned with the large amount of noise in the simulation. This suggests that our test may be relatively robust at detecting general relationships of the interaction coefficients, but may not be able to uncover the intricate details of an interaction as embodied in the exact functional form of a model.

3) *Using nonparametric regression:* Given the problems inherent in choosing an appropriate model, direct testing for dependence of the interaction coefficients on the population sizes of other species would be ideal. One more or less model-free approach would be to fit the interaction coefficients with a nonparametric regression using as predictors different subsets of the measured population sizes and growth rates (see Eubank [1988] for an introduction to nonparametric regression techniques). If no additional information were gained by using the population sizes of other species once the population sizes and growth rates of the in-

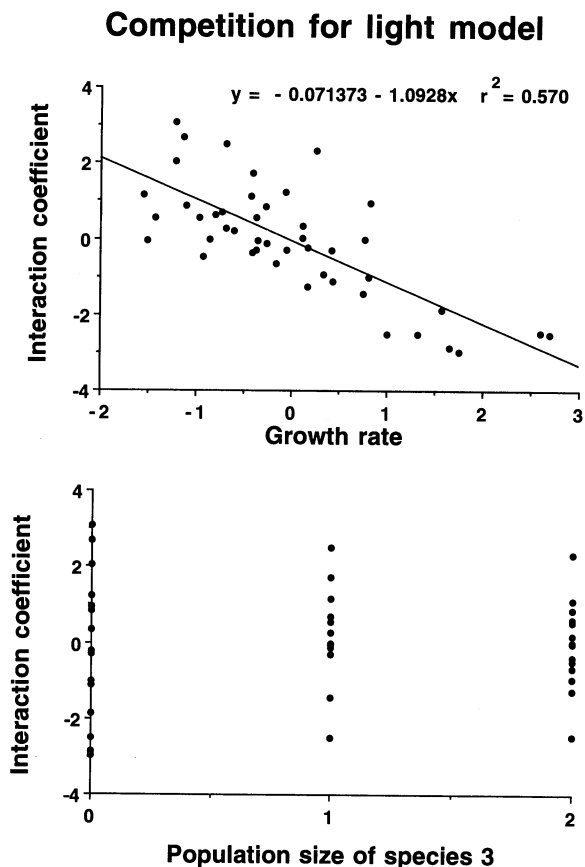


FIG. 2. Results of simulation of the Hassell-Comins competition model (Table 1). Parameter values are listed in *Testing for interaction modifications . . . : 2) Guessing the right model form*. The top panel shows the regression of the interaction coefficient β_{12} against the growth rate of species 1, and the bottom panel shows the relationship of the interaction coefficient β_{12} to the population size of species 3.

teracting species were used, a strong argument could be made for the absence of IM. Conversely, if the population size of some third species provided significant information about a particular pairwise interaction, one would have evidence for IM, and an indication of how a particular interaction had been modified. Not surprisingly, a test with this level of generality requires a very large data set, perhaps of the order of 1000 points. The theory of such tests is still preliminary, however, and the development of feasible tests with more limited goals might be possible.

WHY TEST FOR INTERACTION MODIFICATIONS WHEN WE KNOW THEY MUST BE COMMON?

Almost any realistic model of an ecological interaction includes interaction modifications. For example, the interaction between a predator and a particular prey species is modified by the presence of another prey species when the predator has any saturating functional response (Table 1; Abrams 1987), and numerous modifications of prey behavior in response to predation have been observed (Lima and Dill 1990). But how important should we expect these nearly ubiquitous effects to be for the actual dynamics of populations? Just as the dynamics of some species can be accurately predicted by ignoring all interactions and pretending that all processes are density independent, one can expect that population dynamics in many systems can be accurately predicted by ignoring HOI and pretending that all interactions are pairwise. Our more general test for interaction modification is more stringent than that of Case and Bender and can point the way in specific circumstances to a pairwise model suitable for describing data even when an additive model fails. Only by avoiding the unthinking use of familiar and mathematically convenient models and by having the discipline to ignore interesting but dynamically unimportant interactions, can we ever hope to develop predictive ecological theory.

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APPENDIX

We here show that the interaction coefficients produced by a competitive interaction mediated entirely through a single abiotic resource depend only on the growth rates of the competing species. An abiotic resource has been defined to be one which responds instantaneously to the abundances of the species eating it (Armstrong and McGehee 1980). Such resources cannot produce indirect effects because they have no "memory." Although it is not necessary, we simplify the computation by requiring the interaction to be "mechanistically resource-mediated" in the sense that resource depletion depends only on resource levels. This implies that the resource level must be a function of a weighted sum of the population sizes of the competing species (Adler 1990). Note that the Lotka-Volterra, competition for light, Ricker, and Hassell-Comins models all fall into this class.

We thus suppose that the per capita growth rate of species i depends only on the level of some resource R , or that

$$F_i(N_1, \dots, N_m) = h_i(R)$$

and

$$R = \sum_{j=1}^m a_j N_j.$$

That is, the growth rate of species i depends only on some resource, which can always be considered to be a weighted sum of population sizes. We assume that h_i is a decreasing function of R ; i.e., that this is a competitive interaction. In this case, we can write

$$R = h_i^{-1}(F_i).$$

The interaction coefficients then depend only on the growth rate, because

$$\beta_{ij} = \frac{\partial F_i}{\partial N_j} = a_j h'_i(R) = a_j h'_i(h_i^{-1}(F_i)),$$

where ' denotes differentiation.