

Advantageous indirect interactions in systems of competition

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Abstract

Ecological foodwebs display complex networks of species interactions. Here we discuss how two species, whether directly interacting or not, can crucially affect each other ‘indirectly’ through their mutual associations with intermediary species. A technique is presented for quantifying these “indirect effects”, so that a simple measure emerges for the degree of overall harm or advantage that a particular species encounters from another in the context of a given foodweb. If the system is one of pure competition, the “direct” interaction between any two species is of course harmful to both. But when the method is applied to such systems it predicts that, if *all* interactions are allowed for including the indirect, in a large proportion of pair interactions at least one species will be deriving benefit from the other. Computer-generated samples confirm that this proportion is accurately predicted. The many pathways for indirect interaction can thus often reverse the direct connection, so that competing species achieve an interaction here called ‘Advantageous in A Community Context’ (ACC).

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1. Introduction

It is only under laboratory conditions that a pair of species can be isolated for study in an environment held constant, and an understanding of their “direct interaction” gained. In the real world, the entity presented to us is always a set, more or less numerous, of species interacting under physico-chemical conditions subject to slow or fast change. This remains true even if there is argument about the properties and especially the history of such entities. The dynamics of multi-species assemblages subject to change, are in the end largely influenced by the “chains” of direct interactions of which they are composed, making the interaction structure of communities a fundamental focus of foodweb theory today.

When two particular species are embedded in a larger community, the effect of one on the other will usually depend on the presence of intermediary or “associate” species (Strong, 1997). For example, two species not directly interacting may nevertheless influence each

other through a common species they are competing with. Such “indirect effects” or “indirect interactions” are now understood to be of enormous consequence in structuring ecological communities (Menge, 1995; Strauss, 1991; Wootton, 1994) and are believed to have important evolutionary effects through natural selection (Miller and Travis, 1996).

This paper concerns attempts to reckon with environmental change and the interaction structure in strategic multi-species models. Here, following May (1973), strategic modelling is taken as an approach, which ‘sacrifices precision in an effort to grasp at general principles’. In particular, it examines some work which allowed the competition coefficients to vary in the most commonly used model of competing species (Stone, 1988; Stone and Roberts, 1991, 1993), and which showed that a significantly different picture of species interaction can then emerge after indirect effects have been adequately recognized.

In this more realistic picture, a large proportion—often close to a third—of the “competing” species pairs were found to be benefiting each other, an interaction described there as Advantageous in a Community Context (ACC). This finding is remarkably close to others discussed in the literature where attempts have

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been made to quantify the influence of indirect effects. Connell (1983), for example, reviewed 72 competition studies, and found that in ~20% of these, the interactions were positive rather than negative. In a recent analysis of marine intertidal communities, Menge (1995) has noted that ~40–50% of community structure could be attributed to indirect effects. In his study of 23 different webs, he found the “apparent constancy of the level of change due to indirect effects ... intriguing. Why should the amount of changes due to indirect effects be approximately equal to that due to direct effects?” This and other puzzling and troubling questions expose many gaps in our knowledge concerning operational and theoretical aspects of indirect interactions.

Results of our earlier study on indirect effects in competition communities, while interesting and perhaps surprising, emerged from computer calculations—that is, not analytically but as a numerical result given by numerical samples. This implied that in an important sense it could not point to a way forward; resorting to the computer meant, as it often does, that the ‘effort to grasp at general principles’ could not be pursued further along these lines.

This could be taken as evidence that the prospects are severely limited, if one incorporates the variability of interactions in a strategic model that emphasizes, perhaps even starts from, the community context. The more usual models, based on the artificial concept of the isolated pair whose interactions are precisely defined for all time, might well strike us as unreal, but there would be little joy in securing greater realism at the expense of near-sterility. One should wait—it might be thought—for the mathematicians to create the necessary tools, as they have elsewhere done with chaos theory, for example.

This paper, however, shows that, at least in the case cited above, we should not be so discouraged, as the results can be derived from a theoretical perspective without resort, save for checking purposes, to the arithmetic of computer samples.

The model of multi-species competition in a varying environment is described in Section 2; Section 3 defines and derives an expression for the interaction in a community context—the ‘effective interaction’. This expression is examined in Section 4, noting how the community shapes it. This study leads us to question the utility of interpreting advantageous interactions in terms of the ‘enemy’s enemy’ effect. In Section 5, a resulting approximation for the number of ACC interactions is given, leading to an explicit formula for this quantity. The results given by this formula are compared here to the numbers given by Monte Carlo computer calculations, and found to give an excellent fit. Conclusions that can be drawn from the work are offered in Section 6.

2. The model used for a competition system

To make it easier to demonstrate the effects under study, we confine ourselves to the particularly simple generalized Lotka–Volterra (GLV) model with parameters specifying each interaction as competitive, although, as we have shown, some of the findings have a larger generality (Stone and Roberts, 1991). The most serious criticisms of this model (its dynamic shortcomings) are not of great concern in the present work which, as will appear, confines itself to studying system behaviour at equilibrium.

In this model the biomass N_j of the j th species S_j in an M -species community is given by

$$dN_j/dt = r_j N_j - \sum_{k=1}^M c_{jk} N_j N_k, \quad j = 1, \dots, M$$

with $c_{jk} > 0$, all j and k , and the mean of $c_{jk}(=c) > 0$.

Here the r_j are the intrinsic increase rates, and c_{jk} gives the strength of competition from S_k as felt by S_j . To simplify the work, we choose biomass units so that the auto-regulating coefficient is the same for all species:

$$c_{jj} = a > 0, \quad j = 1, \dots, M.$$

The equilibrium, where $dN_j/dt = 0$, is said to be feasible if the equilibrium populations N_k are all positive. They satisfy the equations

$$\sum_{j=1}^M c_{jk} N_k^* = r_j, \quad j = 1, \dots, M, \quad (1)$$

or, in an obvious matrix notation,

$$\mathbf{C}\mathbf{N}^* = \mathbf{r}, \quad \mathbf{N}^* = \mathbf{C}^{-1}\mathbf{r},$$

so that Eq. (1) can be rewritten as

$$N_j^* = \sum_{k \neq j} C_{jk}^{-1} r_k, \quad j = 1, \dots, M. \quad (2)$$

(Here and throughout, C_{jk}^{-1} denotes the (j,k) -th entry in the matrix inverse of \mathbf{C} .)

In the case where

$$C_{jk} = c \text{ (constant) for all } j, k, \quad j \neq k,$$

$$C_{jj} = a \text{ (constant) for all } j$$

and all increase rates are scaled to 1, we have the matrix \mathbf{C} of the ‘uniform model’, in which all species pairs compete with the same strength c . The equilibrium equations are then

$$\mathbf{C}\mathbf{N}^* = \mathbf{1}$$

with the solution

$$N_j^* = [a + (M - 1)c]^{-1}, \quad j = 1, \dots, M,$$

so that, with $a > 0$, $c > 0$, the uniform model is always feasible. The stability matrix \mathbf{S} of the competition system (recalling that its interaction matrix is $-\mathbf{C}$)

is thus

$-[a + (M - 1)c]^{-1} \mathbf{C}$, and its eigenvalues are readily found to be

$-(a - c)$, $(M - 1)$ -fold, and $-[a + (M - 1)c]$.

Thus each eigenvalue of \mathbf{S} has its real part negative, and the system is stable, iff $c < a$.

To incorporate stochasticity we write $c_{jk} = c + b_{jk}$, where c is a fixed positive constant and, for $j \neq k$, the b_{jk} are independent random variates all chosen from the same distribution of density $f(b)$; to keep the auto-regulation fixed at the value a , we take $b_{jj} = 0$. To ensure that the systems thus generated are indeed ones of competition with mean strength c , and that the degree of fluctuation is bounded, we require $f(b)$ to satisfy

$$\langle b \rangle = 0, \text{ var } b = \sigma^2, \text{ and } f(b) = 0 \text{ for } |b| > d, \quad (3)$$

where $0 < d < c$.

Note that if $\sigma = 0$ the equations reduce to the “uniform model” \mathbf{C} in which all competitive interactions between species are of exactly equal magnitude c . However, for $\sigma > 0$, the interaction strengths are free to vary about c as mean. The variability of the coefficients is understood as an indicator of disturbance. Thus two systems may have the same number of species and the same average interaction strength c , but the one which is the more violently disturbed will have its interaction coefficients varying more. In this model, then, greater disturbance is expressed by higher values of σ .

While different pairs of species will generally compete with different intensity in this model, we would also expect that even a given pair would change its relationship over time, given that resources vary in supply, the weather has its vagaries, and physico-chemical parameters fluctuate. We therefore consider a set of such sample matrices \mathbf{C} as giving a picture of the same ecosystem at different moments in time (Cohen and Newman, 1988; Stone, 1988). Here, we have again assumed that changing environmental and biological factors affect the strength of competition between species (Huston, 1979). This is certainly a crude way to deal with nature’s irregularities, but it is better than omitting it entirely as is often done, and as we shall see, leads to a picture radically different from that given by the “uniform model” where $\sigma = 0$.

3. How the community determines the effective interaction

In the model described in Section 2, the ‘nominal’ or ‘direct’ competition coefficient c_{jk} may be interpreted as follows (Laska and Wootton, 1998): in an isolated subsystem holding only the two species S_j and S_k , adding a small amount ΔN_k to the biomass of S_k would

decrease the per capita growth rate per unit time of S_j by an amount $c_{jk}\Delta N_k$.

We now leave this two-species abstraction and, while restricting the study to a near-equilibrium situation, consider the effect of S_k on S_j when both are situated in the M -species system under study. This requires us to consider not just the species’ pairwise direct interactions but also any indirect effects arising through “associated” species via interaction chains in the larger community. We ask: when this larger system is at equilibrium, what is the change in the equilibrium biomass of S_j if a small addition Δr_k is made to the increase rate r_k of S_k ?

Note that while such an addition is treated here as simply conceptual, it can in fact be experimentally achieved, by regularly importing—or, for a negative ‘addition’, culling—members of S_k . A very similar process has been termed, by Bender et al. (1984), a ‘press perturbation’; in which the population of a chosen species is experimentally maintained at a new level. The difference between the effect of this (their Eqs. (9) and (10)), and the formula below, arises from our taking the birth rate as varying rather than the population.

Looking at Eq. (2), we see that the change ΔN_j in the equilibrium biomass of S_j , that will be induced by this small increase Δr_k , is given by

$$\Delta N_j = \mathbf{C}_{jk}^{-1} \Delta r_k.$$

Thus, to find what S_j gains, we must multiply r_k ’s increase by \mathbf{C}_{jk}^{-1} —that is, by the (j,k) -th entry in the inverse of the system matrix \mathbf{C} . We emphasize that, while the direct interaction is the competition coefficient $(-c_{jk})$, the perceived interaction, which takes into account all indirect effects as well, is given by \mathbf{C}_{jk}^{-1} .

We therefore call this quantity \mathbf{C}_{jk}^{-1} the *effective interaction* with S_k as seen by S_j . Note that if it should happen that $\mathbf{C}_{jk}^{-1} > 0$, this means that S_j actually benefits from the presence of S_k , despite the fact that the two species are viewed as direct competitors in the traditional foodweb formulation. The interaction would therefore be viewed as Advantageous in a Community Context (ACC) (See Stone and Roberts, 1991). In the analysis that follows we are interested in finding how prevalent ACC interactions may be, in competition communities as they are traditionally modelled.

For the model described in Section 2, where the competition coefficients of the GLV equations include a component random in the interval $(-d, d)$, it is straightforward to write down expansions for these effective interactions to any required order in the “spread” d/c . For the first-order expression, which will be found adequate for present purposes, see Appendix A (Eq. (A.2)) and, in a different form, Eq. (5) below.

The process by which the community shapes the effective interaction becomes more transparent if we first

define the quantities

$$c' = c/(a - c), \quad T = a + (M - 1)c,$$

$$V = \sum_{p=1}^M \sum_{q=1}^M b_{pq}, \quad b'_{pq} = b_{pq}/(a - c). \quad (4)$$

They may be interpreted as follows: c' is an amplified interaction strength, sharply increasing as c approaches the self-regulation parameter a . T is the total strength of the interactions undergone by a species in the uniform ('unperturbed') case, and the expectation value of this quantity in the perturbed case. V is the total excess of interactions summed over all species in the system.

Then the effective interaction given by Eq. (A.2) may be re-written as

$$(C^{-1})_{jk} = -c'/T - (c'/T)^2 V + (c'^2/T) \left(\sum b'_{jq} + \sum b'_{pk} \right) - b'_{jk}/(a - c)$$

$$= U_{01} + U_{02} + U_1 + U_2, \text{ say.} \quad (5)$$

U_{01} and U_{02} may be called 'background' terms, since they are the same for all species pairs in the system; U_{01} arises from the regular model (all competition strengths c), and U_{02} allows for the excess actually present. The presence of the denominator T in these terms, as also in U_1 , indicates that here it is not the absolute value of the interaction which is operative, but rather its relative (or fractional) share of the total interaction T . This is patently a community effect, as is the remaining (parenthesized) factor of the term U_1 , which collects all the excess interactions undergone by S_j and all those inflicted by S_k , for all species in the system.

The direct two-species excess interaction b_{jk} asserts itself primarily through the term U_2 which, it will be noted, is amplified by the $1/(c-a)$ factor but not relativized, the denominator T being absent.

A conclusion of some interest follows from this examination: that the generalization often arrived at from analysing competition in the case of just three species, a case which is algebraically soluble, should be considered a guide of dubious utility when a larger number of competing species is involved.

This generalization, stressing the 'enemy's enemy' effect, correctly notes that, when $M = 3$, the condition for S_1 to gain advantage from the competition with S_2 is $c_{13}c_{32} > c_{12}$.

This is readily interpreted as implying that the 'enmity' of S_2 towards S_3 (as measured by c_{32}), which is the 'enemy' of S_1 (as measured by c_{13}), can outweigh the harm done by its 'direct' competition with S_1 (as measured by c_{12}). (See the exposition by Boucher et al., 1982; Stone and Roberts, 1991). In other words, this inequality guarantees that the effect of S_2 on S_1 will be ACC despite the fact that these species are direct competitors.

However, when there are more than three species ($M > 3$), this approach now involves an 'enmity chain' with more than one link; it is able to provide a far less transparent concept, and is considerably more difficult to sum and calculate. With $M-2$ species now able to intermediate between S_1 and S_2 , there are $\frac{1}{2}(M-2)!$ such chains, and it becomes problematic to interpret them in 'enmity' terms.

Even if the loop concept were developed into a mathematically exact condition for ACC interactions, it becomes forbiddingly complicated even for moderately sized $M > 3$. There seems little point in pursuing this mode of enquiry, then, when the essence of the ACC effect seems to be adequately captured (as will be shown below) by an approach which does not directly examine any loops at all.

4. The chance that a species is advantaged by competition

Consider now the effective interaction of S_k on S_j . The probability of an ACC interaction is

$$P_{ACC} = \text{prob}(C_{jk}^{-1} > 0).$$

This probability P_{ACC} is considered in Appendix A, starting from the expression found for the effective interaction (Eq. (A.2) or (5)), and a formula derived (Eq. (A.3)). The lines of development can be briefly outlined:

Looking at Eq. (5), we note (see Appendix A) that the 'excess' background term U_{02} is always small and may be neglected. We then see that, for the competition from S_k to benefit S_j , the sum of the other terms involving the random entries of \mathbf{B} (namely, U_1 and U_2) must be positive (i.e. reducing competition from its mean value), and exceed in magnitude the 'uniform' background term U_{01} . According to Eq. (5), P_{ACC} is therefore given by

$$P_{ACC} = \text{prob}(U_1 + U_2 > U_{01}).$$

To find the chance of this occurring, we approximate the distribution of the sums of the b 's by a normal distribution. The form of $f(b)$ has already been restricted by the conditions laid down to make it ecologically reasonable (Eq. (3)), which guarantee that these sums will indeed have the normal for their limit distribution.

To test the results given by this procedure, numerical data were obtained by generating sample systems of the model described in Section 2 and recording the mean value given for P_{ACC} by those that were feasible and locally stable. Without loss of generality, the autoregulation coefficient a was taken as unity; this is equivalent to finding the entries of the inverse for the matrix C/a , which have the same sign as those for C itself.

For such runs, a definite form had to be chosen for the probability density $f(b)$ of the random components. In the runs reported here, $f(b)$ was taken as a uniform

distribution, with all values in the interval $(-d,d)$ being equally likely. Mean values of P_{ACC} were got for various values of the ‘spread’ d/c in the interval $(0,1)$, a sample of 100 being run for each d .

(Note that if $f(b)$ were chosen to be a normal distribution, the sums of the b ’s would then be normal not just in their limit distribution but exactly. But this is not an allowable option, because the negative tail of $f(b)$ would give samples containing mutualist (positive) interactions and thus fail to model a pure competition system. If the normal were suitably truncated to avoid this, the reproductive property of a sum would no longer hold.)

For $f(b)$ thus uniform, Eq. (A.3) gives

$$P_{ACC} = \frac{1}{\sqrt{2}(\beta - \alpha)} \int_{\sqrt{2}\alpha}^{\sqrt{2}\beta} Q(x) dx,$$

where

$$\alpha = \sqrt{\frac{3}{2}} \frac{[1 - c - (T/c - 2)d]}{d\sqrt{2M - 4}},$$

$$\beta = \sqrt{\frac{3}{2}} \frac{[1 - c + (T/c - 2)d]}{d\sqrt{2M - 4}}$$

and $Q(x)$ denotes the area to the right of x in the standard normal distribution.

The integral can be evaluated in terms of the error function (see Abramowitz and Stegun, 1972, p.304), giving

$$P_{ACC} = \frac{1}{2} + \frac{1}{2(\beta - \alpha)} \left[\alpha \operatorname{erf}(\alpha) - \beta \operatorname{erf}(\beta) + \frac{1}{\sqrt{\pi}} (e^{-\alpha^2} - e^{-\beta^2}) \right]. \quad (6)$$

The right-hand side of Eq. (6) has been evaluated and compared with the numerical data obtained as just described, for a wide range of values of species number $M (\geq 5)$, mean competition coefficient c and disorder (‘spread’) d/c . Typical results for systems of 10 species are displayed in Fig. 1, as line curves for mean competition coefficients 0.1 to 0.5. Note that there is a rapid transition in which the number of ACC interactions increases rapidly to more than 40% as the variation in the competition coefficients, measured by d/c , increases.

It will be seen that the agreement is striking for $c < 0.5$. The analytic expression (Eq. (6)) in fact fits the data points to within the standard error of the Monte Carlo run, whose sample size would need to be extended well beyond 100 to reveal any error that may exist. In fact, it describes well systems in which M is as small as 5, as may be seen from Fig. 2. The accuracy of the normal approximation to the sum of $(2M - 4)$ independent variates of course improves for larger $M \gg 10$ (Fig. 3), but we have found indications that, when the spread

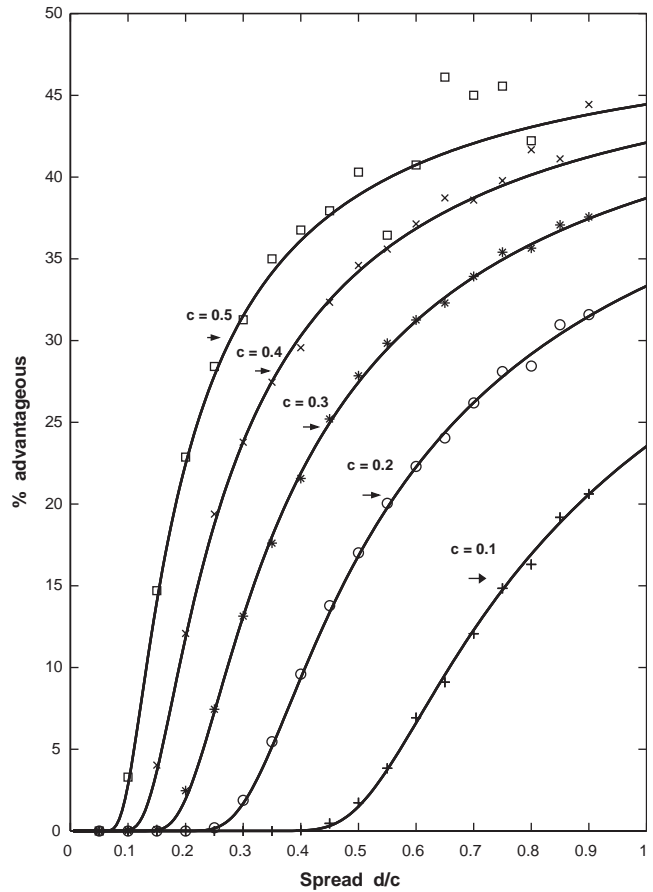


Fig. 1. Each point represents the average number of ACC interactions (as a percentage of all possible pairwise interactions) found in 100 model runs as a function of ‘spread’ (d/c). The continuous line graph indicates the theoretical prediction P_{ACC} found from evaluating Eq. (6). Model parameters: $M = 10$, for $c = 0.1, 0.2, 0.3, 0.4, 0.5$.

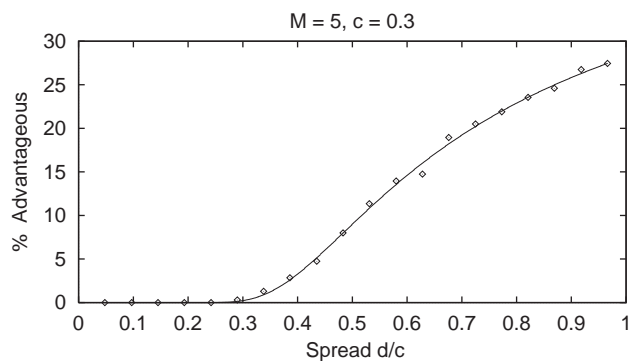


Fig. 2. As for Fig. 1. Model parameters: $M = 5, c = 0.3$.

$d/c \rightarrow 1$, for these larger M values the accuracy begins to deteriorate because of second order effects in the expansion in b .

How the competitive system’s behaviour depends on interaction strength and its degree of intrinsic variation is compactly illustrated by Fig. 1. It shows the percentage of advantageous interactions increasing with

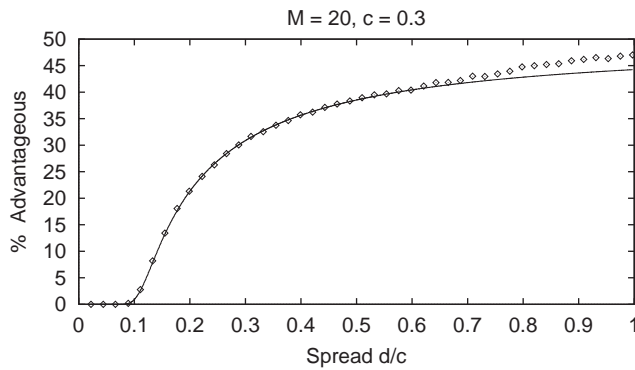


Fig. 3. As for Fig. 1. Model parameters: $M = 20$, $c = 0.3$.

both c and the spread d , in the Monte Carlo data and also in the theoretical expression of Eq. (6). The fluctuations of the data points about the predicted values, as seen in the upper right of the figure, have a simple explanation: the rarity of feasible, locally stable systems in this parameter region, the smaller numbers giving a greater sampling variance in the (mean) ACC percentage. (For $c = 0.4$, only 8% of the samples are feasible-stable for $d/c = 0.75$, while for $c = 0.5$ the fall to an 8% figure occurs even earlier, at $d/c = 0.5$.)

Here it is worth noting that, as a general phenomenon, the percentage of ACC interactions increases in precisely those regimes of parameter values in which persistence becomes rare—at least in the feasible, locally stable sense (Roberts, 1989). It would seem plausible, and even appealing, to interpret this increase in mutual benefit as the mechanism by which a few competitive systems are able to persist in difficult conditions. But unfortunately this view, however plausible, is simply not true. In surveying a large collection of Monte Carlo data, we have not been able to find any significant difference in the ACC figure of such persistent systems, when compared to those lacking such persistence. This observation is supported by the success of the theoretical expression offered here, which was derived without imposing any requirements for persistence. This suggests that a biological interpretation of the findings must be sought at a level lying somewhat lower, perhaps in the assumptions of the Lotka–Volterra model itself.

For M even smaller than 5, the predicted values can be corrected by using the exact distribution for the sum of the b 's rather than the normal approximation. This exact distribution is easy to find when $f(b)$ is uniform, and is given in Appendix A (Eq. (A.5)); it is used to derive the predicted line in Fig. 4, where $M = 3$. Comparing the line with the data points for a single run of 100, one might be inclined to think the fit poor, particularly for $d/c \rightarrow 1$, but closer study shows the fit is in fact excellent. To demonstrate this, the points for a second, independent run of 100 are also plotted in Fig. 4, and it may be seen that the line of predicted values falls

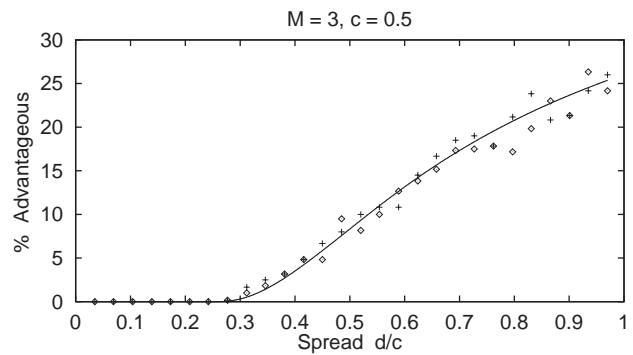


Fig. 4. As for Fig. 1. Model parameters: $M = 3$, $c = 0.5$. Each point represents the average number of ACC interactions found in 100 model runs as a function of “spread” (d/c). Two such runs of 100 are shown.

comfortably within the range of dispersion arising from the Monte Carlo error of the runs.

(This success seems less surprising when we note that the crucial parameter is not the species number (3), but the number of interactions (6).)

5. Conclusion

The expressions found for the effective interaction in a fluctuating community context (Eqs. (5) and (6)) have performed well in this study, when tested for its ability to predict advantageous interactions between nominally competing pairs of species. Moreover, the analysis helps understand why ACC interactions are so prevalent when there is variation in competition coefficients. For typical (possibly even conservative) levels of variation within the community's interaction matrix, the number of ACC interactions often falls in the range of some 30–40%.

It should be appreciated that these conclusions hold even when the competition coefficients inside one sample system have been allowed to differ greatly in size. When $d/c = 0.9$, for instance, the interval over which they can vary is $(0.1c, 1.9c)$, or by well over an order of magnitude. Thus the model is in no sense simply a ‘perturbation’ of the ‘hypercompetitive’ (uniform) competition system; such a perturbation treatment would involve only small changes from a constant strength of competition c . The random model thus incorporates a feature to be found in actual systems, where the strengths of competition can vary widely.

In general, it can be said that the approach used achieves, in agreeing so well with the Monte Carlo findings, a closer fit than we have a right to expect. This is always heartening, suggesting that it may contain hidden virtues not yet apparent to us. It encourages attempts to give it further trial on a broader range of problems—for instance, to test whether the restriction to

pure competition systems is indeed necessary. (See e.g. Jansen and Kokkoris, 2003.)

The findings may be seen from another aspect, however, which can lead us to query whether it is appropriate to make the ‘isolated-pair’ abstraction one’s starting point—i.e. to focus on the immediately observable interactions of a pair of species.

To illustrate this point, Fig. 5 shows the percentage of species pairs in which at least one member is advantaged by the interaction. To obtain this data, random systems of 10 species were generated, with the parameters c , d as described above, and the feasible, stable ones selected. The results are plotted only at parameter values for which at least 50% of the sample was feasible and stable. In order to carry greater conviction, no use was made of the analytic approximation in Eq. (6), though the latter gives entirely similar results.

The figure shows that systems with a comfortable preponderance of mutually disadvantaging pairs occur only for small competition strengths c that, moreover, are severely restricted in how much they can vary, as measured by the spread d . For the bulk of the systems, the set of advantaged pairs is far from negligible, lying in the region of 30–50% of all pairs.

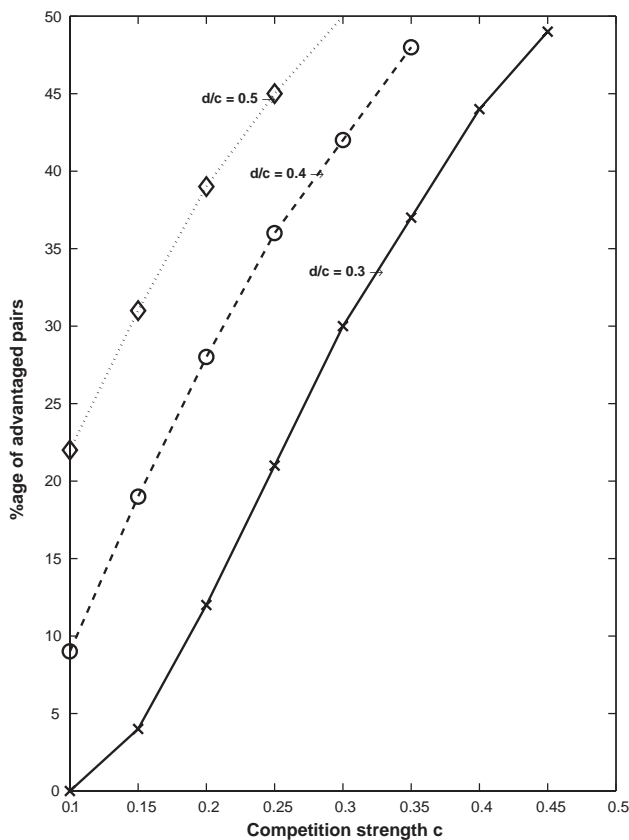


Fig. 5. Percentage of species pairs in which at least one member is advantaged by the interaction plotted as a function of competition strength c . $M = 10$.

If we look back to how a pair interaction is modelled in the GLV equations (part 2), we see that the increase rate of one species is assumed to diminish in proportion to the population of the other. Yet a simple mathematical step has shown that, in 30 to 50% of these pairs, at least one species will be advantaged—i.e., will gain in its number at equilibrium—if the other increases faster. While this cannot strictly be said to *contradict* the original assumption, it might well lead us to seek a different starting-point giving more insight into the way the system actually behaves.

It hardly seems an adequate explanation simply to refer to ‘indirect effects’ as responsible. It is the actual object of study—the community—which is the source of the behaviour that, if we continue to characterize it as a ‘competition system’, must now appear counter-intuitive. It is, of course, easier to note this deficiency than to construct a method that avoids it, but progress to this end seems most desirable, in attempting to grasp the broad structure of the system from the very beginning.

It cannot be pretended, however, that the model used here achieves any high degree of realism. Some of its shortcomings are worth pointing out:

1. It is based on the generalized Lotka–Volterra equations which, while acceptable as an approximation near equilibrium, do not satisfactorily handle more complicated (and more realistic) interactions in non-equilibrium situations.
2. In taking the competition coefficients as varying independently, it ignores the important sources of correlation we would expect from, for example, the ambient physico-chemical environment. On the other hand, it has already been found from computer runs that the results for the property examined do not vary greatly when such correlations are included (see Stone and Roberts, 1991), even if they need further study in enquiries with a different object (Jansen and Kokkoris, 2003; Kokkoris et al., 2002).
3. By confining itself to a system of pure competition, it has to deal with a particularly simple mathematical structure (in effect, a matrix of all-positive entries), and not with the more complex forms arising when several trophic levels need to be treated.
4. It has been shown to give excellent results in one particular study, seeking the chance of advantageous interactions, but its ability to perform well in other respects remains to be examined.

There seems no obvious reason to believe, however, that considerations such as these pose insuperable obstacles to further work on these lines. While the study of the ACC effect is a very special enquiry, and the model takes account of ambient variation only in a simplified way, the result should be considered encouraging for studies that focus on the entity actually presented to us in nature: a system composed of many

species whose interactions are community-dependent and vary over time.

Appendix A

A.1. Deriving and approximating the effective interaction

Let \underline{C} be the matrix of the regular case, which has a for each diagonal entry and c for each non-diagonal entry. Then

$$C = \underline{C} + B,$$

where the entries of B are described in Section 2. Then $C^{-1} = (\underline{C} + B)^{-1} = [\underline{C}(I + \underline{C}^{-1}B)]^{-1} = (I + \underline{C}^{-1}B)^{-1}\underline{C}^{-1}$.

From Gantmacher (1959, p. 113),

$$(I + \underline{C}^{-1}B)^{-1} = \sum_0^\infty (-\underline{C}^{-1}B)^k,$$

the expansion being valid for $|\lambda_q| < 1$, where λ_q is the eigenvalue of largest modulus of $\underline{C}^{-1}B$. Choosing the magnitude of the B entries sufficiently small to ensure validity and stopping after first order, we have

$$C^{-1} = \underline{C}^{-1} - \underline{C}^{-1}B\underline{C}^{-1} \dots, \tag{A.1}$$

where the further terms contain successively higher powers in the entries of B . As in Section 3, put

$$I = (M - 1)c + a, \quad V = \sum \sum b_{pq}.$$

It is easy to confirm that each diagonal entry of \underline{C}^{-1} is $(T - c)/[T(a - c)]$, and each non-diagonal entry is $-c/[T(a - c)]$. Straightforward multiplication then gives the result to first order in the entries of B , for $j \neq k$:

$$C_{jk}^{-1} = -W - W^2V - b_{jk}/(a - c)^2 + [W/(a - c)] \left[\sum b_{jp} + \sum b_{qk} \right], \tag{A.2}$$

where $W = c/[T(a - c)]$ as in Section 3.

A.2. Condition for an advantageous effective interaction

Neglecting the small background term W^2V , the condition $C_{jk}^{-1} > 0$ becomes, after multiplying Eq. (A.2) by $(a - c)/W (> 0)$ and transposing the term b_{jk} from each summation:

$$\sum_{p \neq k} b_{jp} + \sum_{q \neq j} b_{qk} > (a - c)(1 + wb_{jk}).$$

where $w = 1/[1/W - 2(a - c)]$.

The diagonal b 's being zero and the b_{jk} omitted, the left side is the sum of $(2M - 4)$ independent variates each with the p.d.f. $f(b)$ and finite variance σ^2 . Approximate to this sum's distribution by its limit for M large—normal with zero mean and variance $S^2 = (2M - 4)\sigma^2$.

Then, when b_{jk} has the value b , the probability of an ACC interaction is the area under the normal curve

$N(0, S)$ to the right of $(a - c)(1 + wb)$. Allowing for the p.d.f. $f(b)$, the probability P_{ACC} of an advantageous interaction is then

$$P_{ACC} = \int_{B_1}^{B_2} f(b)Q[(a - c)(1 + wb)/S] db, \tag{A.3}$$

where $f(b)$ has the range (B_1, B_2) , and we have used the notation of Abramowitz and Stegun (1972) in which, for the standard normal distribution, the area to the right of x is denoted by $Q(x)$.

A.3. Exact distribution of the sums for uniform b

With X the sum of n independent variates each uniform in $(-d, d)$, it is the cumulative density function $F(X)$ which is required in the work. This may be found straightforwardly, using (Kendall and Stuart, 1977, Chapter 4, Section 4.3, p. 97)

$$F(X) - F(0) = (1/2\pi) \int_{-\infty}^\infty \varphi(t)[1 - \exp(-iXt)] dt/it,$$

where $\varphi(t)$ is the characteristic function (c.f.) of the sum which, the variates being independent, is the product of the individual c.f.'s:

$$\varphi(t) = \sin^n(td)/(td)^n.$$

Then

$$F(X) - F(0) = (1/2\pi) \int [\sin^n(td)/(td)^n][1 - \exp(-iXt)] dt/it.$$

Since

$$\sin^n q = [\exp(niq)/(2i)^n] \sum_{j=0}^n (-1)^j {}^n C_j \exp(-2ijq),$$

$$F(X) - F(0) = (1/2\pi i)[1/(2i)^n] \sum \exp(niq)(-1)^{-j} {}^n C_j \exp(-2ijq) [1 - \exp(-iXq/d)] dq/q^{n+1}. \tag{A.4}$$

Using

$$\int_{-\infty}^\infty \frac{e^{i\beta\theta}}{\theta^n} d\theta = \frac{\pi i^n \beta^{n-1}}{(n-1)!} \operatorname{sgn} \beta, \quad \beta \neq 0, = 0, \beta = 0,$$

$$\int_{-\infty}^\infty e^{itu} u^{-n} du = \begin{cases} \pi i^n t^{n-1} \operatorname{sgn} t / (n-1)! & t \neq 0 \\ 0 & t = 0 \end{cases}$$

and substituting in Eq. (A.4), the c.d.f. is given by

$$F(X) - F(0) = [1/(n!2^{n+1})] \sum_{j=0}^n (-1)^{-jn} C_j \{ |n - 2j|^n \operatorname{sgn}(n - 2j) - |n - 2j - (X/d)|^n \operatorname{sgn}[n - 2j - (X/d)] \}. \tag{A.5}$$

A.4. Proof that P_{ACC} increases with d

Put $u = \sqrt{2\alpha}$, $v = \sqrt{2\beta}$. Let a prime superscript denote differentiation w.r.t. d . From the definitions of α and β ,

$$u' = -H/d^2 = v'$$

and, from (4),

$$v = u + K,$$

where, for $M > 2$, H and K are > 0 and independent of d . We then have

$$KP_{ACC} = \int_{u(d)}^{v(d)} Q(x) dx,$$

so that, differentiating and using $u' = v'$,

$$\begin{aligned} KP'_{ACC} &= [Q(v) - Q(u)]u' = -H[Q(v) - Q(u)]/d^2 \\ &= H[Q(u) - Q(v)]/d^2. \end{aligned}$$

From the definition of Q , and using $v > u$, the RHS > 0 , and thus P_{ACC} increases with d .

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