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Interspecific interactions: constructing a general neutral model for interaction type

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Experiments have not been devised to provide unbiased estimates of the relative co-occurrence of all different interaction types in communities. Thus, we have no idea what types of interspecific interactions to expect if we randomly sample species from an environment. The probability that a unidirectional, non-zero interaction is negative (P_-) or positive (P_+) has a direct effect on the expected types of reciprocal interspecific interactions. Analysis of field studies where strengths and signs of interactions between seven or more species were documented (large studies were selected to avoid bias from choosing species known to interact) suggests that $P_+ = P_- = 0.5$. Data also suggest that the proportion of non-zero interactions (C) is generally less than 0.6 when 10 or more interactions are considered. The proportion of expected reciprocal interspecific interactions can be calculated given the proportion of direct interactions that are not significantly different from zero and assuming that non-zero interactions are equally likely to be positive or negative. In general, this neutral model predicts that if species are chosen from an environment randomly, non-interaction (0/0), commensalism (+/0), or amensalism (−/0) will be most common when $C < 0.6$. Predation and functionally similar interactions (+/−), competition (−/−), and mutualism (+/+) should be relatively rare when there are less than 10 species with $C < 0.6$. Predation should be twice as common as competition or mutualism, and mutualism as common as competition. The neutral model suggests that community ecologists place undue emphasis on competition and predation.

How organisms interact is a fundamental ecological question. However, were organisms of different species chosen randomly in the field without regard to size or taxonomic status, what interactions should we expect between them? No estimates exist of the relative importance of all different interaction types in ecological communities to answer this question. Communities are not randomly connected associations of species, but how they diverge from random assemblages is not clear since a neutral model of community structure has not been clearly delineated.

If only large animals and plants are sampled, particularly when only a few species are considered, discerning which species are eating others is relatively easy, hence

the wealth of information on food webs (e.g., Pimm 1982, Cohen et al. 1990). It is not possible to use these data to calculate the predominance of most specific direct interaction types because the only interactions described are predator/prey. Such food webs have been used to estimate competition (e.g. Cohen 1978), but these indirect interactions are based upon predator/prey dynamics alone. Even less is known about many of the smaller, less obvious species and how they interact with others. What interactions do we expect among a group of bacteria isolated from a single environment? How do we expect these organisms to interact with multicellular organisms from the same environment? A general expectation about the numbers of different types of interactions in communities could provide a basis for comparing different types of community structures.

Constructs such as food webs and competition communities explain subsets of ecological communities, but how well they represent community dynamics is uncertain. Take for example the comprehensive interaction matrices reported for the rocky intertidal zone by Menge (1995). These webs are dominated by predator/prey and competitive interactions. No direct mutualistic and few commensal interactions are reported. In contrast, Bertness and coworkers describe saltmarsh communities where facilitative interactions are common (Bertness 1984, 1985, Bertness and Shumway 1993, Bertness and Callaway 1994, Bertness and Hacker 1994). In yet another approach, plant communities are described as being dominated by competitive interactions (Aarssen 1988). How do we reconcile these vastly different views of community organization? A neutral model may provide a basis for comparing and contrasting such views.

An estimate of what interactions might occur could provide a starting point for extracting useful generalities from nature (e.g. what is the relative importance of competition), forming expectations about poorly

studied communities or inter-habitat community comparisons (e.g. aquatic versus terrestrial). An estimate of the relative importance of different reciprocal interactions may be important in contrasting community models; for example, how can we determine the causal relationships between diversity and stability if we do not know how species interact? Here, I propose a neutral model that yields general expectations of the types of interactions encountered in communities. An approach with very few assumptions is used to construct a general model with a minimum of bias. The model is calibrated with and compared to available community interaction matrices.

Methods

If one randomly selects two species from an environment, each unidirectional interaction between them can be significantly greater than zero, significantly less than zero, or not significantly different from zero. The combination of these unidirectional interactions leads to six possible reciprocal interactions: no interaction $(0/0)$, amensalism $(-/0)$, commensalism $(+/0)$, competition $(-/-)$, mutualism $(+/+)$, and exploitation $(+/-)$. Here, exploitation includes predation, parasitism, successional facilitation, and any other $+/-$ interaction. For the model I present, the interactions are static in each community matrix (i.e. an interaction can not be both $+/-$ and $+/+$ over time). If the proportion of each type of unidirectional interaction is known, the expected proportion of each type of reciprocal interaction can be calculated.

The following relationships serve as the basis for a neutral model for species interactions. The probability that any unidirectional interspecific interaction is non-zero is given by the connectance (C, or the proportion of non-zero interactions to all interactions, Pimm 1982). This is similar to "directed connectance" used by Martinez (1991), except that I exclude intraspecific interaction so:

$$C = \frac{\text{total non-zero unidirectional interactions}}{s \cdot (s-1)} \quad (1)$$

The probability that any non-zero interaction is positive is P_+ and the probability that it is negative is P_-.

$$P_+ + P_- = 1 \quad (2)$$

The probability that any unidirectional interaction is positive is:

proportion of positive interactions $= P_+ \cdot C$ (3)

Conversely, the probability that it is negative is:

proportion of negative interactions $= P_- \cdot C$ (4)

And the probability that it is zero is:

proportion of zero interactions $= 1 - C$ (5)

Then we can construct expected probabilities for each interaction type by multiplying probabilities. For example, the expected proportion of $+/-$ is the probability that the first interaction is positive (eq. 3), multiplied by the probability that the reciprocal interaction is negative (eq. 4), plus the probability that the first is negative (eq. 4), multiplied by the probability that the second is positive (eq. 3). This yields the following expectation:

$$\text{expected } (+/- \text{ and } -/+) = 2 \cdot P_+ \cdot P_- \cdot (C)^2 \quad (6)$$

The equations for expected commensal and amensal interactions are similar in that the $0/+$ and $+/0$ or $0/-$ and $-/0$ possibilities both need to be summed. This yields the following equations:

$$\text{expected } (0/+ \text{ and } +/0) = 2 \cdot P_+ \cdot C \cdot (1-C) \quad (7)$$

$$\text{expected } (0/- \text{ and } -/0) = 2 \cdot P_- \cdot C \cdot (1-C) \quad (8)$$

The $0/0$, $+/+$ and $-/-$ equations are simply the squares of the expectations of the unidirectional interactions:

$$\text{expected } (+/+) = (P_+ \cdot C)^2 \quad (9)$$

$$\text{expected } (-/-) = (P_- \cdot C)^2 \quad (10)$$

$$\text{expected } (0/0) = (1-C)^2 \quad (11)$$

Eqs (6–11) sum to 1. Given eq. (2), all that is needed to calculate a value for any of the relationships in eqs (6–11) are values for C and one for P_+ or P_-. I now review experimental data to estimate these values.

Results and discussion

Finding values for P_+, P_- and connectance

The initial step in determining values for P_+ and P_- is to establish if the distributions of interaction strengths and signs center on zero or tend toward positive or negative interactions. I consider only experiments that tested seven or more interactions. The rationale for this is that investigators might consider preferentially organisms that display a certain interaction type when only a few interactions are selected for study. This effect of finding more significant interactions when fewer species are considered has been demonstrated clearly for competition experiments by Connell (1983) but has been disputed by Gurevitch et al. (1992). The criteria I used to select experiments were: (1) interaction strengths and signs were determined, (2) seven or more interactions must have been determined among organisms from the same environment, and (3) experiments were conducted under similar conditions within the

Table 1. Tests for distribution of mean interaction strength.

System	Test method	Reference	Species or strains	Interac-tions	t	P	(V)	$<p$
Plants, old field, upper	species removal	Allen and Forman 1976	6	30	−0.523	0.599	192	0.5
Plants, old field, middle	species removal	Allen and Forman 1976	6	30	3.193	0.0034	75	0.001
Plants, old field. lower	species removal	Allen and Forman 1976	5	20	0.9816	0.3386	80	0.36
Insects, *Heliconia wagneriana*	growth w diff. combin. of insects	Seifert and Seifert 1976	4	12	−0.226	0.825	26	0.34
Insects, *Heliconia imbricaota*	growth w diff. combin. of insects	Seifert and Seifert 1976	4	12	−0.090	0.930	30	>0.5
Plants, old field 1977	2 spec. & 4 spec. mix	Aarssen 1988	4	16	−7.091	$1.0e^{-7}$	0	0.004
Plants, old field, 1958	2 spec. & 4 spec. mix	Aarssen 1988	4	16	−6.406	$4.0e^{-7}$	0	0.004
Plants, old field, 1939	2 spec. & 4 spec. mix	Aarssen 1988	4	16	−4.319	$2.4e^{-5}$	0	0.004
Plants, wetland	pairwise growth relative to pure stand	Johansson and Keddy 1991	6	30	−0.0362	0.971	143	0.1
Intertidal inverte-brates	path anal. (modelw recip-rocal loop include.)	Wooton 1994	5	9	−0.163	0.8743	18	0.65
Plants, shoreline	pairwise growth	Wilson and Keddy 1986	7	42	2.5756	0.0137	265	0.02
Plants, grassland, April	species removal	Fowler 1981	9	30	1.9706	0.058	128	0.05
Plants, grassland, September	species removal	Fowler 1981	10	47	3.532	0.00095	245	0.001
Intertidal inverte-brates, algal sporelings	grazer exclusions	Paine 1992	7	8	6.46	0.888	17	>0.5
Planktonic *Nostoc* bacterial strains	pairwise growth	Gantar 1985	49	49	−1.5046	0.1397	601	>0.5

A negative t value means an excess of negative interactions (the mean is less than zero). Results also are reported for Wilcoxon Signed Rank test (V), and the p values for this test were determined from Lehmann and D'Abrera (1975) or Zar (1984). Both tests report 2-tailed probabilities. See text for description of criteria used to choose studies.

study. Since interactions were determined or reported in different ways among studies (e.g., path analysis, biomass response, per capita interaction strength). I used meta-analytic techniques to combine the results of the dissimilar studies. The benefits and drawbacks of meta-analysis in ecological research have been discussed previously (e.g. Gurevitch and Hedges 1993, Arnqvist and Wooster 1995).

The studies included ten distinct tests of interactions strengths and signs with terrestrial plant communities. two with insect communities, two with intertidal inver-tebrates, and one with planktonic *Nostoc* and bacteria (Table 1). For each individual group, all of the uni-directional interspecific interactions were used. Results were log transformed in some studies where they were scaled relative to 1, which represented growth in unispecific stands. Each group of interactions from a set of species in one habitat was tested for a distribu-tion significantly different from zero (i.e. an excess of

positive or negative interactions) with a 2-tailed t-test. For this procedure a negative t value represented a distribution of interactions less than zero. Because dis-tributions may not be normal, the Wilcoxon Signed Rank Test (Lehmann and D'Abrera 1975) also was used to calculate values for V. This procedure resulted in slightly higher p values than the parametric t-tests. but generally yielded results similar to those of the t-tests.

Meta-analysis of the p values for the t-tests in Table 1 showed no evidence to reject the neutral hypothesis that species interactions are distributed evenly around zero. The inverse normal method for combining the results of dissimilar studies using the summary statistics (Hedges and Olkin 1985) was used. This method is appropriate for combining the results when the direc-tion of deviations from the null hypothesis is not known in advance. The analysis resulted in a combined z score (the z statistic that describes effects across

Table 2. Reviews establishing the relative proportion of positive, negative and non-interactions.

Source	Study sites	Organism	Proportion of each unidirectional interaction type			P_-
			$-$	0	$+$	
Goldberg and Barton 1992	89 studies reviewed	plant competition	55.9	32.9	11.2	0.83
Menge 1995	23 webs reported	intertidal interactions	25.3	60.0	14.6	0.63
Connell 1983	72 studies reviewed	plant and animal competition	62.5	37.4	1.1	0.98
Hutchinson 1967 (after Hartman 1960)	119 comparisons reported	phytoplankton	71.0	20.2	8.8	0.90
Schoener (1983)	150 studies reviewed	plant and animal competition	76.0	?	?	>0.76

The reviews by Hutchinson (1967), Connell (1983), Schoener (1983) and Goldberg and Barton (1992) include many studies in which interactions among only a few species were tested.

studies) for the 15 individual studies of -0.17, which leads to a p value of 0.567. Thus, I cannot conclude from this analysis that negative interactions are generally more or less prevalent than positive interactions. However, some communities have significantly more negative interactions, and some have more positive interactions.

A potential problem with the experiments analyzed in Table 1 is that species additions or removals in complex communities do not allow investigators to distinguish between direct and indirect interactions (Yodzis 1988). Pairwise growth experiments and path analysis (Gantar 1985, Johansson and Keddy 1991) are less likely to suffer from this problem. When these four experiments alone are considered, only one (Wilson and Keddy 1986) shows a significant trend toward an excess of negative interactions.

Many of the studies cited in Table 1 evaluated competition. The investigators were interested in competitive interactions and likely chose species that they thought would be competitors. Even with this potential bias, the neutral hypothesis that $P_+ = P_- = 0.5$ is not rejected overall. The studies considered were generally of organisms of one trophic level. This should not affect the conclusions because including predator/prey interactions introduces a positive interaction for every negative interaction, a situation where $P_+ = P_-$. Thus, including trophic interactions in this analysis would only tend to mask any imbalance between P_+ and P_-.

Previously, several papers have reviewed competition studies (Hutchinson 1967, Connell 1983, Schoener 1983, Goldberg and Barton 1992). The results from those reviews suggest that negative interactions are more prevalent than positive interactions (Table 2). When trophic interactions are also considered (Menge 1995), the $+/-$ pairs bring down estimates of P_-. The competition analyses looked at large numbers of interaction tests, but many of the individual studies reported only a few interactions, thus we expect a strong bias toward choosing organisms likely to be competitors (Connell 1983). Even so, the proportion of positive interactions found was significant in some of these studies. The overall proportion of negative interactions

in these studies was 0.82, setting what may be an upper approximate bound on P_- given the potential bias toward competitive interactions in these studies.

If $P_+ = P_-$, as indicated when only considering larger studies, then the relative importance of different types of interactions expected in communities is a function of C (Fig. 1 top panel). This figure illustrates that, at all connectances, competition and mutualisms are equally likely and exploitation is twice as likely as either of these two interactions. Commensalism and amensalism become most important when connectance is below
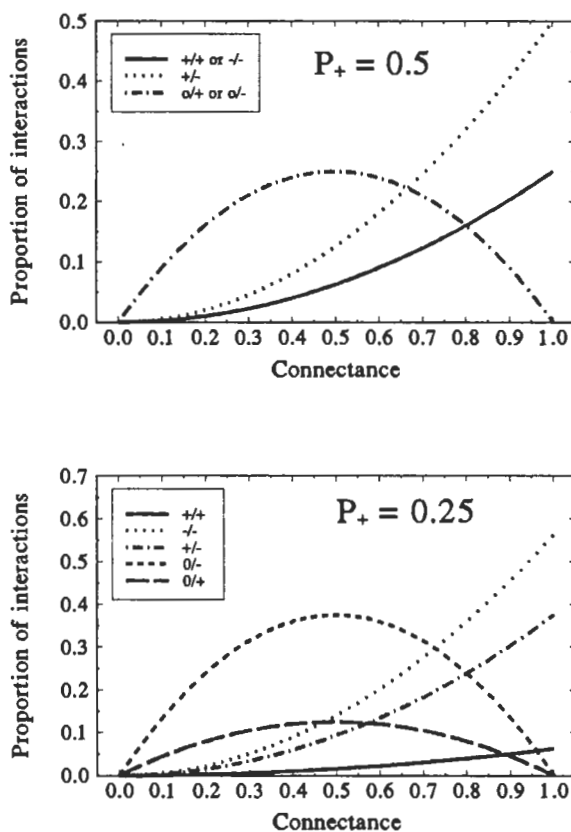

Fig. 1. Expected occurrence of different species interactions as a function of connectance when $P_+ = 0.5$ (top) and when $P_+ = 0.25$ (bottom).
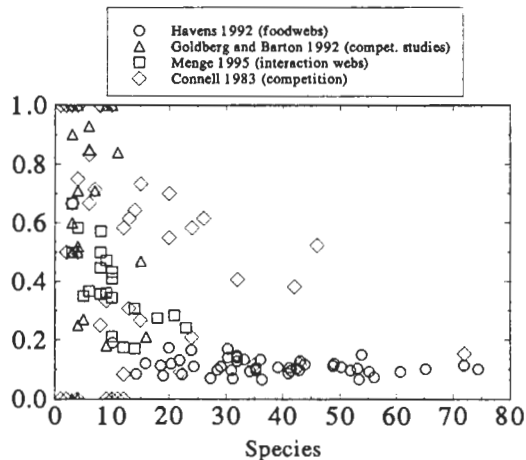
Fig. 2. Connectance values from a variety of food web, interaction web, and competition studies. There is some overlap in the studies reviewed by Connell and those by Goldberg and Barton.

about 0.6. Interestingly, even when $P_- = 0.75$ ($P_+ = 0.25$), some mutualism is expected (Fig. 1 bottom panel). Commensal and amensal interactions are more common than competition or predation when C is less than 0.45. This raises the question: what is C in real communities?

Connectance has been determined for a large number of food webs (e.g. Pimm 1982, Paine 1988, Sugihara et al. 1989, Martinez 1991, Polis 1991, Havens 1992, Warren 1995, Tavares-Cromar and Williams 1996). Those estimates of C ignore all but predator-prey interactions. On the one hand, this bias leads to low connectance by ignoring other types of links between organisms in the food web; on the other hand, high connectance may result because species in each web are only included because they are known to interact with other species (they are chosen because they are linked to the other species). It is currently impossible to know which of these biases are more important.

Connectance of some food webs, and competition and interaction web studies can be used to obtain a general feel for connectance expected in ecological communities (Fig. 2). This is obviously an "apples and oranges" type of graph, and interpretation of trends with some of these data may be controversial (Havens 1993, Martinez 1993), but the important point is that connectance is generally below 0.6 for communities of more than 10 species. This point is consistent with results from all of the food web analyses referred to in the previous paragraph. Therefore, amensal and commensal interactions are likely to occur at the highest frequencies, assuming that my neutral model applies to ecological systems.

Expected and observed proportions of interspecific interactions in interaction matrices

Interaction matrices can be inspected directly and the relative occurrence of each reciprocal interaction type described. This is important because, even if $P_+ = P_-$, the two-way interactions may not be distributed according to eqs (6–11). For example, in a food web, P_+ must be 0.5. This is because for every positive direct interaction, there is by definition a negative direct interaction (a + effect on each predator for a − effect on each prey). Such food web communities conform to my analysis so far in that $P_+ = P_-$, but there will be no other direct interaction types (e.g. mutualism, competition) that are expected by my neutral model. Slightly different criteria are required for the analysis of occurrence of reciprocal interactions in generalized community matrices than for the analysis of distribution of interaction strengths. It is only necessary to know if each of the individual direct interactions in a community matrix are significantly different from zero (no interaction) and the interaction sign for all non-zero interactions to establish the relative occurrence of all reciprocal interactions. If we assume that $P_+ = 0.5$ and set connectance according to eq. 1, then the proportion of each expected interaction can be calculated from eqs (6–11).

All but commensal and amensal interactions are expected to be rare in the small communities that are most studied (six species or fewer, Table 3) given the neutral model described here. These data (Table 3) suggest a tendency toward amensal interactions over commensal interactions with exploitation about as common as commensal interactions overall. If trophic interactions and the pollinators in these mainly plant studies were considered, +/− and +/+ interactions would become more important. Obviously, it is still imprudent to ignore either commensal or amensal interactions. Ecologists studying "competition" in plant communities may take amensal interactions into account; many of these scientists operationally define competition as any unidirectional negative interaction (Goldberg and Barton 1992).

It is possible that community ecologists emphasize competition and predation over other types of interactions. To investigate this possibility I conducted a search of Biological Abstracts from 1993–1995 using the keywords "community" and "ecology" to establish an initial subset of the database. Wildcards were used to generalize terms. For example, all words that start with "predat" are indicated by predat*. I read all of the abstracts found to insure that they fit the search profile. The search revealed 139 abstracts that referred to predation or food web. Competition and antagonism were found in 119 abstracts. Mutualism (sometimes called symbiosis) appeared in 13 abstracts, amensalism in one and commensalism in none. This analysis of the ecolog-

Table 3. Observed and expected numbers of species interactions generated from field interaction experiments.

Study	Observed and (expected) interactions					
	0/0	0/−	0/+	−/+	−/−	+/+
Fowler 4/81	2 (2.1)	1 (0.4)	0 (0.4)	0 (0.0)	0 (0.0)	0 (0.0)
Fowler 9/81	6 (6.4)	3 (1.6)	0 (1.6)	0 (0.2)	0 (0.1)	0 (0.1)
Seifert and Seifert 1976 (*Heliconia wageriana*)	3 (3.4)	1 (1.1)	2 (1.1)	0 (0.2)	0 (0.1)	0 (0.1)
Seifert and Seifert 1976 (*Heliconia imbricata*)	1 (1.0)	1 (1.5)	2 (1.5)	1 (1.0)	1 (0.5)	0 (0.5)
Aarssen 1988; 1977 field	2 (2.7)	4 (1.3)	0 (1.3)	0 (0.3)	0 (0.2)	0 (0.2)
Aarssen 1988; 1958 field	2 (2.7)	4 (1.3)	0 (1.3)	0 (0.3)	0 (0.2)	0 (0.2)
Aarssen 1988; 1939 field	1 (2.0)	5 (1.5)	0 (1.5)	0 (0.5)	0 (0.3)	0 (0.3)
Allen and Forman 1976, upper	18 (13.1)	1 (0.9)	1 (0.9)	0 (0.0)	0 (0.0)	0 (0.0)
Allen and Forman 1976, middle	11 (11.3)	4 (1.7)	0 (1.7)	0 (0.1)	0 (0.1)	0 (0.1)
Allen and Forman 1976, lower	8 (8.1)	2 (0.9)	0 (0.9)	0 (0.0)	0 (0.0)	0 (0.0)
Johannsson and Keddy 1991	4 (1.4)	0 (3.2)	1 (3.2)	9 (3.7)	0 (1.8)	1 (1.8)
Total numbers observed	58	26	7	10	1	1

The expected rate was computed from eqs (6–11) assuming $P_+ = P_-$, and C was set as non-zero interactions total possible interactions for each set of species studied.

ical literature shows that ecologists emphasize species interactions in a radically different fashion than my neutral model.

The disparity between my model and published abstracts may be due to several factors. Perhaps the simplistic approach of my model misses key features of ecological communities. If this is true, I do not know what the missing features are. Another possibility is that investigators are biased toward the organisms and interactions that they study. It is unlikely that amensalism and commensalism are only 1% as common as competition and predation in communities.

Conclusions

The data reviewed suggest that the neutral model for one-way interactions between species should be based on the idea that a positive interaction is as likely as a negative interaction. I reach this conclusion even though the studies with seven or more interactions that were found to estimate a value for P_+ are possibly biased toward finding negative interactions. If small competition studies (fewer than seven interactions tested) are included, then the occurrence of negative interactions is greater than positive interactions overall. Given an expected proportion of negative (or positive) interactions and the connectance, an expected frequency can be calculated for each two-way interaction. Data from a variety of field studies suggest that connectance is often below 0.6 when communities contain more than 5–10 species. Thus, under the neutral model, the most likely reciprocal interactions are no interaction, amensalism and commensalism. The few published interaction matrices analyzed here support this prediction. Furthermore, with a six-species assemblage, even though 15 reciprocal interactions are possi-

ble, it is unlikely to find many competitions, mutualisms, or even exploitations (+/−).

The approach presented here provides the most basic expectations of community structure. Addition of other constraints may alter model predictions. For example, +/− interactions in food webs involve transfer of energy and may be obligate interactions for the predators. In contrast, +/− interactions between plants may be more conditional. The approach presented here provides a framework against which to identify such varied influences.

As ecologists, we are apparently good at finding, testing, and publishing descriptions of interactions, such as competition and predation, that could represent a small subset of the total possible interactions in communities. Such interactions may be extremely important in structuring communities, but their relative importance cannot be established without testing the importance of the other types of interspecific interactions.

The neutral model presented here explicitly provides for a more rigorous approach to the study of all possible direct interspecific interactions. The neutral model has been used implicitly in previous community simulations (Dodds 1988, Dodds and Henebry 1995, in press). As more data are collected, perhaps the neutral model presented here will prove indefensible. However, it may be useful for community ecologists to keep the simple predictions presented in Fig. 1 in mind. In particular, the data presented here suggest that the importance of other interactions, in addition to predation and competition should be considered.

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