

Redefining the community: a species-based approach

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We propose that effective community size can be defined on the basis of the web of indirect interactions experienced on average by each individual species. Indirect interaction chains are composed of links provided by direct interactions. We analyzed previously published data on 20 assemblages of species. Chain strengths were estimated by the weakest link and by the product of link strength. The average strength of the interaction chain decreased with increasing numbers of links with both models. Positive indirect interactions in chains with an even number of links offset negative direct interactions. We set the community size by the chain length where 95% of the indirect interactions are weaker than 10% of the mean of the absolute value of direct interaction strength. Using the multiplicative model, seven assemblages had a community size (web of interaction length) of three links, one of four links, and the remainder of communities were too small to set community size. The analysis suggests that communities of effective size are rarely investigated in ecological experiments.

Community ecologists have difficulty with the definition of community (Parker 2004). The boundaries of communities are elusive, as is agreement on which species to include in a "community". However, there are fundamental aspects of communities that do not depend upon a basic definition of community. Communities are structured by the interactions among species. These interactions often are described in terms of the interaction strength, which is the estimated magnitude of the effect of one species on growth of another (Laska and Wootton 1998). These interactions can be direct (e.g. predation), or indirect (mediated by other species).

Ultimately, evolution shapes the diversity and function of individual species. From an evolutionary-ecological point of view it is interesting to know if indirect interactions for individual organisms are predictable enough over time and space that they are agents of natural selection. Many species can have profound impacts on other species with which they do not interact directly (Wootton 1994a). However, indirect interactions can be difficult to quantify, leading to a fundamental question "do population interactions propagate significantly over long pathways through a food web, or are the only interactions worth taking into account those that pass through only a few links" (Yodzis 2000)? Thus, we

do not know if indirect interactions alter community dynamics in a predictable fashion, or whether general patterns of community structure can be used to manage communities (Wootton 1994b). If indirect interactions are predictable enough over space and time, then describing community structure and function over ecological time may be possible.

Abstractions of community structure such as food webs, or analyses of groups of competing species (community matrices), provide an avenue to analyze complex nets of interactions. However, these approaches of community analyses ignore the fact that species have a full range of interactions with other species, including not only predator prey and competition, but also mutualism, amensalism, commensalism, and neutralism. A comprehensive approach to community structure must consider all such interactions.

The problem of indirect interactions

To further complicate matters, a large number of indirect interaction chains potentially exist in any community, and ecological researchers are beginning to document this in nature. In this paper we use a definition of an indirect interaction after Strauss (1991). An indirect interaction is a unidirectional chain of linked direct interactions that involves no individual species twice. With this definition, an indirect interaction chain with four links would involve five species (Fig. 1a). Other examples are given in this figure as well. Theoretically, given a group of S species, there are $S \times (S-1)$ possible direct interactions, or interactions with one link. However, the number of possible indirect interaction chains with n links is $S \times (S-1) \times (S-2) \times \dots \times (S-n)$. The total number of indirect interaction chains increases much more quickly as species increase than does the number of direct interactions (Fig. 2). For example, in a group of seven species, there are only 42 direct interactions, but there are 5040 possible indirect interaction chains with

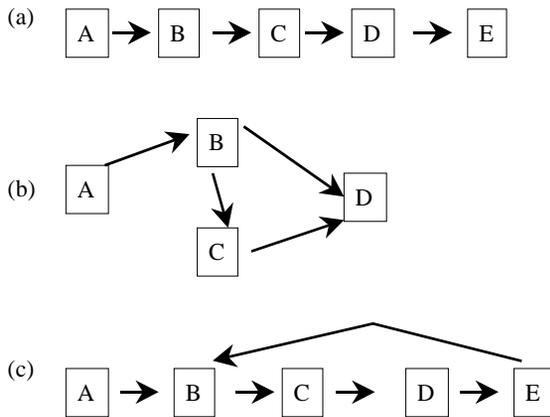


Fig. 1. Examples of indirect interaction paths allowed by the assumptions used in this paper. In (a), there is an indirect effect of A on E. There are five species and a chain of four links. In addition, there are four direct interactions with two links and two indirect interactions with three links in this diagram. In (b), A has two paths to effect D. A chain of two links mediated by B, and a chain of 3 links mediated by B and C. In (c), the effect of A on B mediated by C, D, and E is not allowed, because the chain uses B twice, however A effects C, D and E indirectly through B. Several indirect interaction chains with effects on B exist as a result of the effects of C and D mediated by E.

six links, and a total of 13 650 possible indirect interaction chains. Of course, the majority of species in most communities interact with far more than seven other species.

Given the huge number of potential indirect interactions, researchers (Pimm 1993, Schoener 1993) have asked the obvious question; is predictive community ecology possible? Some have suggested that doing short-term perturbation experiments is difficult because of indirect effects (Yodzis 1988), but others maintain that indirect effects manifest themselves quickly in experimental community ecology (Menge 1997). A general theoretical basis for how to cope with the tremendous

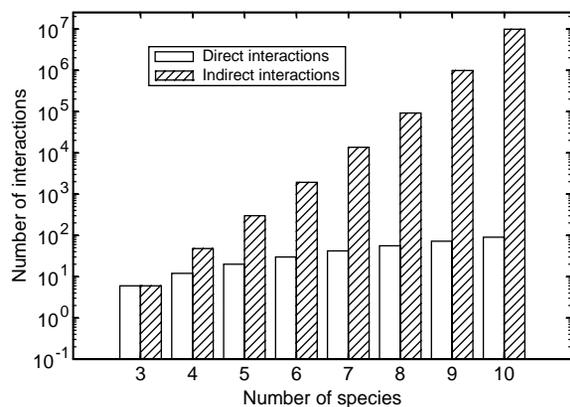


Fig. 2. Comparison of the number of potential direct interactions versus the total potential number of indirect interactions for groups of up to ten species.

complexity represented by indirect interactions is in the early stages of development.

One approach to dealing with community stability, and subsequently community structure, has been analyses of community matrices (May 1973, Wilson and Roxburgh 1992, Roxburgh and Wilson 2000). These approaches have two problems. First, they assign an artificial boundary to community interactions, so that their results may be altered by inclusion of a single species. Second, they assume that the community is at equilibrium, and spatially homogeneous. Only small perturbations are considered so the system is approximately linear. Such matrices have been used to estimate the importance of indirect effects by determining the inverse Jacobian matrix and subtracting out the direct effects implied by the Jacobian matrix. This approach is very sensitive to ignored species under some conditions, even in some cases where the ignored species do not interact very strongly with the focal species used in the community matrix (Bender et al. 1984). The limitations of the community matrix approach, particularly those associated with ignoring species, suggest that an approach that is less dependent upon arbitrary assemblage of species in a community is warranted.

This problem of indeterminate community size (scale) is recognized by theoretical community ecologists who have searched for scale-invariant properties of communities, mainly in food webs. Scale-invariant properties are useful because they allow for generalizations about communities independent of the size. However, there exists controversy about the existence of scale invariant properties and community sizes, such as the debate over community connectance and scale (Havens 1992, 1993, Martinez 1993).

There is some reason for hope that systems of indirect interactions will be tractable. Food webs tend to have weak links in long loops (Neutel et al. 2002). Small groups of strongly interacting species connected by weak interaction links have been proposed as a mechanism for stabilization of community structure (Tregonning and Roberts 1979). Thus, there may be some point at which indirect interactions can be ignored (i.e. not every species on earth must be considered simultaneously to successfully describe community structure).

If there is a general decrease in interaction strength with longer interaction chains, it may allow for characterization of interactions that influence, on average, an organism in a group of organisms. If the average length of strong interaction chains increases as the number of species in a community increases, then predicting the influence of indirect interactions on individual organisms is not likely to be possible (i.e. indirect interactions have no scale-invariant property). Likewise, evolution in response to community effects is unlikely with many strong, long interaction chains because of their diffuse nature and unpredictability. This problem is not limited

to ecological systems, and is generally covered in the study of small-world networks. Small-world networks have been studied with regard to establishment of scale-free networks in fields including cell biology, neural biology, epidemiology, business, and physics (Strogatz 2001). Describing behavior of complex networks is one of the next frontiers of science.

An alternate definition of community centered on individual species

We explore the consequences of assuming the interaction strength decreases as the length of indirect interaction chains increases. This specifically allows us to propose a definition of community size based on the web of influence of indirect interaction chains. We thus view a community not as a bounded group of species that all interact with each other. Instead, the community is based on the web of interactions that influences each single species. This definition is closely related to that proposed by Parker (2004). The key to this approach is to gauge the influence of indirect interactions, and this paper takes the conceptual framework proposed by Parker (2004) and relates it to empirical data on communities.

One view of interaction strength is guided by the concept that a chain is only as strong as its weakest link (Wootton 1994a). This approach makes perfect sense when an interaction strength of zero is considered; a zero link breaks the chain because it can propagate no effect. However, this approach does not capture the idea that a species with strong interactions on a weak link will have a greater influence on the affected species at the end of the chain than will a species with weak interactions on the weak link (Wootton, pers. comm.). In this view, a chain can be weaker than the weakest link but it cannot be stronger.

Alternatively, strength of interaction chains may be propagated multiplicatively (Neutel et al. 2002). This approach leads to short chains if weak links are a predominant feature of the interaction web (i.e. multiplication by direct interaction strengths less than one decrease strength of the indirect interaction). Work on very simple food webs suggests that interaction strength may not diminish as interactions are propagated through more reticulate food webs (Fox and Olsen 2000), but we will still investigate the implications of calculation of interaction chain strength via a multiplicative model.

In communities with many zero or weak interactions, a higher probability exists that long chains will contain a weak link or be broken by a zero interaction. It is possible that in such systems shorter chains are more common. Systems with more short chains should be more tractable (Schoener 1993). If the probability that long chains will be weak or broken increases more

rapidly than the number of chains, then a scale-invariant (not dependent upon community size), average, non-zero chain length could result.

We know that indirect effects occur in many natural communities (Wootton 1994a, Menge 1995). However, most prior research on indirect interactions has been limited in scope, not only because of the difficulty of designing and executing experiments with large numbers of species, but also because of conceptual difficulties in analyzing a large number of indirect interactions in multi-species groups. For example, most models given when discussing indirect interactions include only small groups of species (i.e. 3 or 4 species "communities").

Furthermore, quantifying direct interactions among species is often difficult, much less separating and quantifying the indirect effects among species (Laska and Wootton 1998). Most complete "community" matrices we found in the literature (complete in the sense that the strengths of all direct interactions were quantified) had only three or four species, and the largest had seven species. Food webs and interaction webs provide analyses of larger communities (Pimm 1982, Cohen et al. 1990, Menge 1995), but such webs are binary and include only the sign of the interactions and not the relative strengths (but see Raffaelli and Hall 1996, Berlow 1999, Neutel et al. 2002).

The purpose of this study was to analyze indirect interaction chains from community matrices where interaction strengths have been determined. We used published data for groups of up to seven species where signs and strengths were determined for interaction matrices. All indirect interaction chains were characterized.

Methods

Reports of interaction matrices of 20 groups of species from 12 studies were used in this study (Table 1). These investigators each used one of three basic methods to determine the interaction strengths: pairwise growth, species removal experiments, or multiple regression analysis (correlation). Because of differences in reporting the interaction strengths with the studies used, standardizing the matrices was necessary to facilitate generalizations across the analyses. Multiple regression analyses report interaction strengths as the coefficients in the regression analysis. Because these values are symmetric about zero, no transformations were performed on the matrices from these studies to separate positive from negative interactions. However, pairwise growth experiments and species removal experiments both report the interaction strengths as a ratio of relative yield of the plant grown in the presence of the competitor to the yield of the plant grown alone or as the percent change over control. These values are not

Table 1. Summary of the ecological system, method of interaction determination, number of species and potential direct interactions, normality for the studied groups of species.

System	Method	No. species	Interactions	Lilliefors' critical value*	Reference
1. Shoreline plants	Pairwise growth	7	42	<0.01	Wilson and Keddy 1986
2. Wetland plants	"	6	30	>0.20	Johansson and Keddy 1991
3. Old field plants, 1939	"	4	12	>0.20	Aarssen 1988
4. ", 1958	"	4	12	>0.20	Aarssen 1988
5. ", 1977	"	4	12	>0.20	Aarssen 1988
6. ", upper	Species removals - % cover change	6	30	<0.01	Allen and Forman 1976
7. ", middle	"	6	30	<0.01	Allen and Forman 1976
8. ", lower	"	5	20	<0.05	Allen and Forman 1976
9. ", April	"	3	6	<0.15	Fowler 1981
10. ", September	"	5	20	<0.10	Fowler 1981
11. Microtine rodents	Regression	3	6	<0.01	Dueser and Hallett 1980
12. "	"	3	6	<0.20	Crowell and Pimm 1976
13. "	"	3	6	>0.20	Hallett 1991
14. "	"	6	30	<0.10	Porter and Dueser 1982
15. ", July	"	4	12	<0.05	Hallett et al. 1983
16. ", September	"	3	6	>0.20	Hallett et al. 1983
17. ", 1972	"	3	6	>0.20	Hallett 1982
18. ", 1973	"	3	6	<0.05	Hallett 1982
19. Insects, <i>Heliconia imbricata</i>	"	4	12	>0.20	Seifert and Seifert 1976
20. ", <i>Heliconia wagnerii</i>	"	4	12	<0.05	Seifert and Seifert 1976

*Results of the Kolmogorov–Smirnov test for goodness of fit.

symmetric about zero, and so were transformed by taking the natural log of the matrix entries. After transformation inhibition by the test species was a negative interaction, and facilitation was a positive interaction. After all matrices were centered on zero, the interaction strengths in each matrix were scaled between + and -1 by dividing all direct interaction strengths by the maximum direct interaction strength within the interaction matrix. Because all the matrix values were less than one, this served to accentuate the differences in the relative strengths of the interaction chains, while allowing comparisons across studies. We recognize that this forces interaction strength to decrease with chain length when interaction strength is determined multiplicatively. Thus, our proposed community definition allows us to determine a minimum community size (make a conservative estimate of minimum size of community) using previously published data.

We also were interested in how interaction strengths were distributed in each interaction matrix (i.e. are species with strong interactions strengths more common than expected given a normal distribution, are negative interactions more likely than neutral or positive interactions). Normality is also important in determining if 95% confidence intervals of mean interaction strengths can be set for interaction chains. Thus, distributions of interaction strengths within matrices taken directly from the studies were tested for normality using the Kolmogorov–Smirnov test for goodness of fit (Sokal and Rohlf 1981). The test was performed on the interaction strengths prior to their transformation. Lilliefors' adjusted critical values were used because the

critical values of the Kolmogorov–Smirnov test are considered to be unnecessarily conservative. The null hypothesis, that the direct interaction strengths were not normal, was rejected at the 0.05 level of significance, but it is recognized that 20 consecutive tests for normality must be adjusted by Bonferroni's correction to avoid falsely inflating the number of significant results.

Several basic assumptions were used in the determination of average chain strength. The first assumption was that a chain includes no repetition (each species appears only once in a chain, and no loops or doubling back occur within a chain, Fig. 1). Although chains with repetition within them were not allowed, several chains with the same head and tail but different middle patterns were considered to be different chains (Fig. 1). We assumed these to be different chains because interactions between two species may be asymmetrical. Second, we assumed that the sign of the chain was negative if an odd number of negative direct interactions occurred in the chain and positive if an even number occurred (which comes from taking the product of the interaction strengths within the chain). Finally, we assumed that interaction strength of the chains was propagated in one of two ways. The first model was that the strength of a chain is equal to the product of the direct interaction strengths within the chain (the multiplicative model). The second model was that each chain is only as strong as its weakest link, the minimum direct interaction strength within the chain (weakest link model).

For each interaction matrix, we found all possible chains in an interaction matrix, and determined the strength of each chain using a computer program. Then

the average interaction strength was found by calculating the standard numerical mean from all chains of a given length. We calculated the standard error in the interaction strengths for each length of chain. In addition, we calculated the mean and standard error of the absolute value of the interaction strengths. The absolute value is important to know because in systems where approximately equal numbers of strong positive and negative chains occur, the mean interaction strength will be very low. These two calculation methods allow us to separate weak interaction strengths related to longer chains, from those resulting from averaging strong positive and negative interactions. Output of the program was checked against three and four species matrices that also were analyzed by hand and against simple seven species matrices with known characteristics, such as having all interaction strengths equal to -1 or containing only one long chain.

Results

The results of the normality tests showed that at least two-thirds of the interaction matrices had interaction strengths that were distributed normally (Table 1), if the Bonferroni correction for multiple statistical tests was applied, then at most 3 of the 22 systems had non-normal distributions. The non-normally distributed matrices usually appeared in the same published studies as normally distributed matrices. In one case, the interaction strengths of one particular group of species were not normal in one year but were normal when the same group was surveyed in the next year.

The signs of the average strength of indirect interaction chains alternated in matrices dominated by negative direct interactions. These results held even if the non-normally distributed matrices were deleted from the analysis, and for both the weakest link and the multiplicative models of interaction strength. The sign of the average interaction strength of chains was positive for chains with an even number of links (odd number of species) and negative for chains with an odd number of links (Fig. 3). The few exceptions to this pattern were matrices with mixed positive and negative interactions. In these matrices, the signs of the average interaction strength followed no obvious pattern because sign was dependent on the relative strengths of the positive and negative interactions and how they fit into the interaction chains.

There was a dramatic decrease in the average of the absolute value of the interaction strength as the links increased with both the weakest link and the multiplicative approaches (Fig. 4). The decrease in interaction strength was much stronger with the multiplicative model. Two studies exhibited a less pronounced decrease in average interaction strength than the rest with the

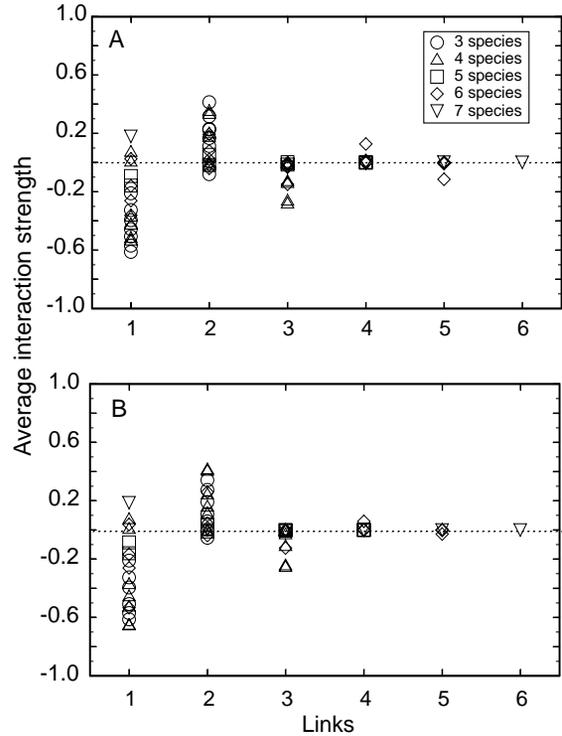


Fig. 3. The average interaction strength of the interaction chains within a group of organisms as a function of number of links for a weakest link model (A) and a multiplicative model (B).

weakest link model. These studies both had relatively strong interactions in the interaction matrix (i.e. interaction strength was distributed more evenly) and, therefore, did not decrease as dramatically. These matrices were composed entirely of negative interactions. In addition, we found a few instances where the average strength of shorter chains was slightly weaker than the average strength of a longer chain within the same matrix. This finding can be explained by the fact that these matrices had both positive and negative interactions, and the signs of the strengths of chains of the same length might cancel each other out. The phenomenon was not visible when the average of the absolute value of the chain strengths was considered instead of just the average of the chain strengths.

Discussion

Determining interaction strengths

Several different techniques were used in the various studies analyzed to produce the interaction matrices for this study. Regression correlation techniques, path analysis, and experiments where single species are removed from communities cannot separate indirect from direct effects. Thus, even though we used such

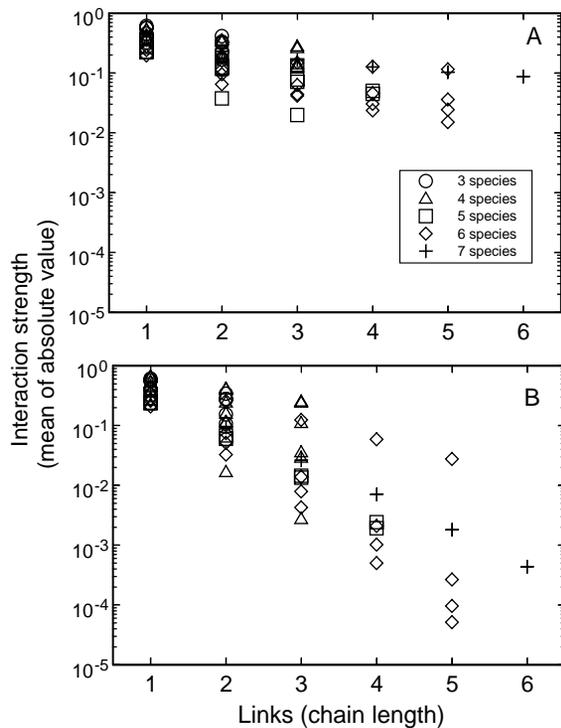


Fig. 4. The absolute value of the average interaction strength of a given chain length plotted on a logarithmic scale for a weakest link model (A) and a multiplicative model (B).

experiments to estimate the distribution of direct interaction strengths and signs, they might have included indirect effects. Given our results, inclusion of indirect effects should weaken estimated interaction strengths. The methods using regression and single species removals have the advantage of having been done under more realistic conditions than pairwise growth experiments, however, mesocosm experiments may show stronger interactions than field experiments (Skelly 2002). Thus, we expect that such experiments can at least reflect the possible distribution and type of interaction strengths.

Pairwise growth experiments clearly show only the direct effect of one species on another. However, these experiments may be artificial, because in nature two species do not appear in isolation from the other species in the community. Species were grown under the same conditions, so the results may approximate the distribution of direct interactions in an environment at one time. At the very least, these experiments allow for construction of a matrix of interaction strengths that is independent of the effects of indirect interactions. Results from studies using either method of determining interaction strengths were similar, however there is some evidence that experimental venue may affect the estimation of interaction strength (Skelly 2002).

The distribution of interactions in the studies we used in our analyses may have been more negative than that in many communities. Prior analysis of the distribution of interaction strengths suggests that positive interactions may be as likely as negative interactions in communities (Dodds 1997), but tests for normality were not included in the prior publication. We had no reason to expect interaction strengths would be distributed normally. Perhaps if only normal interaction distributions had been used in that prior analysis, the statistics would have suggested a greater tendency toward negative interactions. Between the prior analysis and those used for our study, only a handful of fairly small groups of species have been explored. The issues of positive versus negative interactions and the normality of distribution of interactions may be resolved as more and larger data sets become available. The distribution data analyzed here suggest that such an avenue of research may be profitable.

The distributions of interaction strengths can be used to comment on the relative commonness of strongly interacting species on a single trophic level. The normality tests are not sensitive to how interaction strength is scaled. They indicate that strongly interacting species (also referred to keystone species) should generally occur as expected by chance. Therefore, models of community interaction can assume that interaction strengths are distributed normally and capture the dynamics of many groups of interacting species.

Propagation of positive and negative interaction through communities

The concept of the positive effect of indirect interactions modifying the negative effects of direct interactions in community matrices has been described before. The idea of positive interactions dominating when entire systems are considered has been argued strenuously by Patten and his associates (Fath and Patten 1998). Likewise, a pattern of alternating signs and positive indirect effects in food chains has been described several times in the context of food webs since the earliest known published description in 1880 (Camerano 1994, Cohen 1994). Those descriptions were not based on quantified interaction strengths, though such a pattern has been cited as a reason for limits on numbers of trophic levels in food webs. More specifically, the pattern of decreased interaction strengths with longer chains has been used to explain the weakening of trophic cascades as more trophic levels are considered (Persson et al. 1996).

In communities with a balance of positive and negative interactions (e.g. food webs), the net effect of the indirect interactions also should balance around zero. If the probability that each additional link in a chain will be positive or negative is one half, then on

average, the number of positive and negative indirect interactions should be approximately the same. This approach is most likely to hold in larger systems. Organisms not at the top or bottom trophic level of large food webs, for example, should have an approximate balance between positive and negative interactions. The final case, a community made of positive interactions, is trivial. If all direct interactions are positive, all indirect interactions are positive as well. Our analyses explored matrices where most direct interactions were negative, but some were positive.

Can community size be defined with loop-length of indirect interactions?

We proposed a definition of community size based on the web of influence of indirect interaction chains in the introduction. To implement this definition, we arbitrarily set this web of influence using the variance in the average interaction chain strength of indirect interaction chains. Interaction chains were considered not to be important when they are weaker than 10% of the average of the absolute values of the direct interaction strengths. We considered the mean and variance of the absolute value of interaction strength for all chains of each number of links. The size of the web was set to the largest chain length where the upper value of the 95% confidence interval of interaction strength is less than 10% of the average direct interaction strength. Thus, community size is based on the number of links (chain length) where the strengths of most of the indirect interactions are low relative to direct interactions.

Our defining community size by web of influence shows promise using the multiplicative model, and gives inconclusive results using the weakest link model. Of the 20 species assemblages analyzed, only one had a defined community based on the 10% definition and the weakest link model (Table 2). However, using the multiplicative model yielded eight of 20 communities with a size of four or five species chains from each focal species. The multiplicative model gives a minimum potential community size because the interaction strengths were constrained to an absolute value ≤ 1 .

Even determining how interaction strengths should be set is a controversial issue. If the community matrix approach of May (1973) is used, then the interaction strengths represent the near-equilibrium size of the effects of species on each other's dynamics. In this case, the few foodwebs that have been characterized have a preponderance of values < 1 (Neutel et al. 2002), and the multiplicative model will lead to decreasing interaction strength with increasing chain length. It is not generally agreed on how to parameterize interaction strength (Miller 1996) given, among other considerations, the non-linear nature of many species interactions, the inability to distinguish between sublethal and lethal effects, and the fact that effects on growth may not translate into effects on reproductive success. Despite these issues, in any point in time, a zero interaction is unambiguous.

Seven of the groups of organisms analyzed were not large enough to determine if community size could be set at four or five species chains. The results are tantalizing, because they suggest (on the basis of fairly limited data) that a community size, or web of influence, based on indirect interaction chains could be about

Table 2. Potential community size using the multiplicative and the weakest link models of chain strength.

System**	No. species	Links in "community" weakest link model*	Links in "community" multiplicative model*
1. Shoreline plants	7	>7	5
2. Wetland plants	6	>6	4
3. Old field plants	4	>4	>4
4. "	4	>4	>4
5. "	4	>4	>4
6. "	6	>6	4
7. "	6	>6	4
8. "	5	>5	4
9. "	3	>3	>3
10. "	5	>5	4
11. Microtine rodents	3	>3	>3
12. "	3	>3	>3
13. "	3	>3	>3
14. "	6	5	4
15. "	4	>4	>4
16. "	3	>3	>3
17. "	3	>3	>3
18. "	3	>3	>3
19. Insects	4	>4	>4
20. "	4	>4	4

*The number of links lacks a ">" sign when the proposed criteria were met (upper 95% of confidence interval of mean absolute value of interaction lower than 10% of average of direct interaction strength)

**References for source of data are in Table 1

four or five species in the remaining cases, regardless of assemblage size.

Our data suggest that if a scale-invariant community size exists, it generally will be greater than three species. However, we have no data on larger groups of organisms to assess the possibility of scale-invariant community size from an organismic perspective. Our data analyses do suggest that "community" studies that consider few species are unlikely to capture true community dynamics unless most interaction chains longer than two links are too weak to matter. The data also suggest that interaction chains of moderate lengths (three-five links) may be important in many communities.

The effect of including food web data with such determinations is not clear. Food webs with interaction strengths are generally unavailable; most catalogued food webs are binary (Cohen et al. 1990). Interactions in food webs could be stronger than those analyzed here at single trophic levels. This is because the process of organisms eating other organisms or being eaten themselves suggests that a relatively strong interaction occurs. If strong chains are distributed evenly, our analysis suggests that indirect interactions should be relatively more important than in most of the studies analyzed here. Indirect interactions within trophic levels may be dilute compared to those found in food webs. If this were the case, it would be interesting to apply an analysis similar to that done here to trophic interaction webs where strengths are known. As interaction strengths for food webs and among species on each trophic level become available, such a comparison could be possible. An analysis of loop weights in a soil food web demonstrated sharp decreases in loop weight similar to those seen in our results (Neutel et al. 2002), where loop strength was propagated by multiplication, and interaction strength was not normalized to a maximum of one.

By defining community size on the basis of individual species, we avoid many of the problems associated with traditional definitions of communities. Because only strong chains from a single organism are considered at any one time, our definition allows investigators not to consider that all organisms are connected to all others on earth by interaction chains. Our definition could also have practical benefits; the Endangered Species Act in the United States and counterparts in other countries are written so individual species, not communities, are to be preserved. Thus, a species-based definition of communities may ultimately yield a legal definition that allows for preservation of unique groups of species in addition to individual species.

The basic weakness of our definition is lack of data, but what we have suggests that the idea is worth pursuing. Studies such as those analyzed here, but with 10-20 species, should allow for refining of the analyses and determining the possibility of emergence of scale-invariant community sizes. Results from such studies

would be more robust if spatial and temporal variation is also considered.

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