

MEASUREMENT OF INTERACTION STRENGTH IN NATURE

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Key Words allometry, energy flow, food web, modeling, scale

■ **Abstract** Understanding and predicting the dynamics of multispecies systems generally require estimates of interaction strength among species. Measuring interaction strength is difficult because of the large number of interactions in any natural system, long-term feedback, multiple pathways of effects between species pairs, and possible nonlinearities in interaction-strength functions. Presently, the few studies that extensively estimate interaction strength suggest that distributions of interaction strength tend to be skewed toward few strong and many weak interactions. Modeling studies indicate that such skewed patterns tend to promote system stability and arise during assembly of persistent communities. Methods for estimating interaction strength efficiently from traits of organisms, such as allometric relationships, show some promise. Methods for estimating community response to environmental perturbations without an estimate of interaction strength may also be of use. Spatial and temporal scale may affect patterns of interaction strength, but these effects require further investigation and new multispecies modeling frameworks. Future progress will be aided by development of long-term multispecies time series of natural communities, by experimental tests of different methods for estimating interaction strength, and by increased understanding of nonlinear functional forms.

INTRODUCTION

All living organisms interact with other species through a variety of mechanisms, and these interactions can strongly shape the structure and function of ecological communities and ecosystems (Elton 1927, Paine 1966). To quantify the strengths of species interactions, identify the patterns that occur between species, and determine the mechanisms that cause interactions to vary across space and time in natural ecosystems are challenging but important goals for several reasons. First, because species interactions can strongly affect ecosystems, being able to predict the consequences of changes in species composition in response to the ongoing processes of biodiversity change is desirable. Ecosystems provide a range of goods

and services that are important to human populations. An understanding of how the provision of these services is affected by extinctions and alien introductions is important to have because species interactions often mediate how changes in the physical and chemical environment, such as those expected from global change and human activity, play out through the ecosystem (Schindler et al. 1987, Wootton et al. 1996). Because species are directly and indirectly connected to each other through a complex web of interactions (Elton 1927, Paine 1966), impacts that affect one species in the system can ramify to other system components through multiple direct and indirect pathways that may be of different sign or strength (Holbrook & Schmitt 2004, Schoener 1993, Wootton 1992). If we make predictions about the consequences of environmental impacts without knowledge of the strengths of species interactions, our predictions become indeterminate for any ecosystem with a reasonable degree of complexity (Yodzis 1988). Second, development of a general understanding of how ecological communities are structured can benefit from an analysis of the general properties of multispecies models (May 1973, Pimm 1982). Knowledge of the pattern of interaction strengths in natural ecosystems can help to guide the development of appropriate multispecies models. Here, we review recent developments in our understanding of interaction strength, emphasizing the links to empirical studies.

INTERACTION-STRENGTH CONCEPTS

What is interaction strength? Although the concept seems intuitive, recent reviews highlight the wide diversity of definitions (Berlow et al. 2004, Laska & Wootton 1998), which are shaped by the interests and goals of individual investigators and, to some extent, by the empirical data available. Most studies of interaction strength have focused on consumer-resource interactions in food webs, although an estimate of the strengths of nontrophic interactions such as direct mutualism and interference competition is also needed.

The discovery from field experiments that local deletion of species from ecosystems can generate variable results both in the magnitude of the response and in the extent to which impacts ramify through the community (Paine 1980, Menge et al. 1994, Morin et al. 1988) has motivated recent interest in interaction strength. These results lead naturally to an interaction-strength concept based on the consequences of species deletion. Although intuitively appealing, this definition has shortcomings, because the results of deletion experiments are context dependent in several ways. Experimental results can be a function of experimental duration (Davidson et al. 1984, but see Menge 1997) because the consequences of interactions, particularly via indirect pathways of interaction (Abrams et al. 1996, Schoener 1993, Wootton 1994), take some time to establish. Second, the impacts depend on the density of the focal species, which could vary widely and further lead to variable interaction-strength estimates. Third, because indirect effects may be a component of the net effect of one species on another, estimates of the strength of interaction

among species are likely to be strongly dependent on species composition, which further generates highly variable estimates for the same interaction. Finally, estimates of the overall impact of a species over a period of time can involve multiple mechanisms, and recovery of the parameters that describe the mechanisms that underlie the net long-term effects of one species on another is often difficult.

Development of a precise definition of interaction strength may facilitate the linking of multispecies theoretical frameworks with empirical information, which requires indices that are compatible with the structure of theory. Building these links would constrain model behavior and, thereby, increase our predictive ability. Several indices have been derived from models of multiple interacting species. One is the per capita interaction strength, the short-term effect of one individual on an individual of another species. Several authors have advocated focusing on this concept because it a priori should be a more consistent measure than the aggregate response of the system to a species removal, because it is defined without reference to equilibrium conditions, and because all other metrics of interaction strength can be derived from this measure (Laska & Wootton 1998, Paine 1992). A second possible index, Jacobian matrix elements, contains the partial derivatives of the system, which describe responses to a small, pulsed perturbation of a single species from equilibrium (Bender et al. 1984, May 1973, Schoener 1993). In some cases, these elements are standardized by the self-limiting effect of the perturbed species [i.e., intraspecific interactions (May 1973)]. This index has played a prominent role in theoretical analyses of multispecies systems, largely because it determines the stability properties of multispecies models. Conceptually, it represents the direct effect of a single individual of a focal species on the total population of another species at equilibrium. A third theoretical index, elements of the inverted matrix of per capita interaction strengths, describes the predicted change in the equilibrium conditions of the system to a sustained addition of individuals of a focal species (Yodzis 1988). Hence, it incorporates the net effects of an individual of one species on another through both direct and indirect pathways. Although similar to empirical experiments that delete species from a system over an extended period, it differs because complete species deletion changes the structural properties of the system, which can lead to different outcomes (Dambacher et al. 2003a,b; Laska & Wootton 1998). A fourth theoretical measure, the removal matrix, therefore, compares changes in the abundance of a species at equilibrium before and after the removal of that species from the system. These interaction-strength concepts, each useful in various contexts, behave differently; sometimes they even change in opposite ways as per capita parameters change (Laska & Wootton 1998). Therefore, investigators must explicitly identify which theoretical interaction-strength concept they are considering in their work and understand its implications.

Other metrics of interaction strength have been considered on the basis of the types of information available in various empirical studies. These metrics include magnitudes of energy or elemental flow through ecosystems (e.g., Hall et al. 2000), the magnitudes of path coefficients in structural equation models (Gough & Grace 1999, Wootton 1994), and the transitions among sessile species in Markov chain

models (Wootton 2001). The latter two methods can identify strong interactions in a field context in some cases but do not generate the interaction-strength parameters in standard dynamical models; hence they will not be considered further here. Measures of energy flow through ecosystems, used extensively in ecosystem models, have been criticized as inaccurately portraying interaction strength (Paine 1980, Raffaelli & Hall 1996). Most energy-flow models are structured with flow magnitudes independent of consumer abundance or biomass (i.e., the models are donor controlled), which limits their applicability to many communities where consumers have an impact on prey. However, to discard energy-flow information in the assessment of interaction strength may be premature for two reasons. First, energy-flow magnitudes probably reflect the interaction strength of resources on consumers, whereas critics of energy-flow metrics are interested in effects of consumers on resources. Second, energy-flow patterns can be cast into per capita consumer impacts by scaling them to consumer densities (de Ruiter et al. 1995, Hall et al. 2000, Moore et al. 1993, Wootton 1997). Whether this approach works experimentally is not well tested, however.

Whether interaction strength is best represented as a constant or as a function has received periodic attention (Abrams 2001, Ruesink 1998, Sarnelle 2003). Many theoretical (May 1973) and empirical studies (Gause 1934, Paine 1992, Wootton 1997) implicitly treat interaction strength as a single number. This treatment is partly a consequence of the substantial role in ecology played by the generalized Lotka-Volterra equations, which assume constant per capita interaction strengths of one species on another. The use of a constant-interaction coefficient is further reinforced by other theoretical analyses focused on system behavior in proximity to an equilibrium point (May 1973, Yodzis 1988). Here, responses to small perturbations are likely to approximate linear behavior even in nonlinear systems. Theoretical arguments suggest that interaction strength can be a function that depends on the densities both of the interacting species and of other members of the ecological community (Abrams 1983, 2001). Functional responses of consumers on prey may be a nonlinear function of prey density because of handling time (Holling 1965, Ruesink 1998, Sarnelle 2003). Also, species may modify the per capita interaction between individuals of other species, either by changing the traits of the interacting species ("trait-mediated indirect interactions") (Abrams et al. 1996, Werner 1992) or by changing the environmental context in which an interaction occurs (Crowder & Cooper 1982, Wootton 1992).

Several approaches have been adopted in response to nonlinear interactions. One approach takes nonlinearities as given but only focuses on a single parameter within the interaction-strength function, such as maximum interaction strength (Berlow et al. 1999, Ruesink 1998). Although this approach provides some information about the system, a full parameterization of the interaction-strength function would be desirable (Abrams 2001), and interaction strength typically might be far from its maximum. Hence, a second approach would estimate all parameters in all plausible nonlinear functions that describe interaction strength in an ecosystem (Abrams 2001). Although conceptually ideal, this approach is

extremely difficult to implement at present for several reasons. First, we still have a rudimentary understanding of which of the infinite possible forms of nonlinear interaction-strength functions we should attempt to apply a priori, particularly for interaction modifications. Identification of the most appropriate functional forms requires more extensive empirical exploration. Second, this approach substantially increases the number of parameters to be estimated, which increases the difficulty of an already challenging task and expands the potential for error propagation in multispecies models (Ludwig & Walters 1985). An alternative approach starts with the simplest possible characterization of interaction strength and introduces additional complexity as empirical investigation warrants. Although logistically more feasible, it remains a huge challenge and carries the risk that unanticipated, abrupt changes in system behavior will arise after large perturbation to the system as a result of unidentified nonlinearities. This approach characterizes most recent empirical attempts to quantify interaction strength (Moore et al. 1993, Paine 1992, Raffaelli & Hall 1996, Wootton 1997). The debate over which approach is more effective remains open. For example, Abrams (2001) criticized many empirical studies for use of linear estimates of interaction strength, yet in some cases, linear estimates have predicted reasonably well the effects of independent experiments (Pfister 1995, Schmitz 1997, Wootton 1997, but see Ruesink 1998, Sarnelle 2003).

ISSUES AND APPROACHES FOR DIRECT MEASUREMENT OF INTERACTION STRENGTH

With the recent increased interest in estimation of interaction strength in natural communities, several authors have examined in some depth issues related to effective synthesis of field studies with established theoretical frameworks. Aside from the problem of variable definitions of interaction strength described above, several studies have explored the behavior of commonly used empirical interaction-strength metrics after they were applied to simulated data sets and have identified other key difficulties (Bender et al. 1984, Berlow et al. 1999, Laska & Wootton 1998). First, empirical indices that were not explicitly developed to interface with multispecies mathematical models rarely estimate actual per capita interaction strength (Berlow et al. 1999, Laska & Wootton 1998). Second, empirical data can only be taken over discrete time intervals, whereas most ecological theory is based on instantaneous changes; hence, a mismatch in timescale can develop. In particular, if empirical measurements are taken over too long a time interval, indirect effects and density-dependent feedbacks can develop, which influence estimates of interaction strength between directly interacting species (Bender et al. 1984, Berlow et al. 1999, Laska & Wootton 1998). Hence, interaction-strength measures must be made over short time intervals. This requirement can be problematic empirically because changes in populations over short intervals are likely to be slight and, therefore, can be strongly affected or obscured by measurement error and stochastic processes.

Third, Berlow et al. (1999) found that interaction-strength metrics derived from models with linear per capita interaction strengths (Osenberg et al. 1997, Wootton 1997) did not accurately estimate one component (maximum interaction strength) of models with nonlinear interaction-strength functions. One may view this result in two ways. Finding that methods explicitly designed for one theoretical framework fail to estimate a parameter in a different theoretical framework is not particularly surprising; hence, such an analysis may not be a fair test of the approach. A more appropriate test would first derive the proper interaction-strength metrics for the new model form and then implement the necessary experimental treatments to estimate it, as was originally done for the linear case. The alternative perspective is that we may not know a priori the correct functional form of interaction strength and, therefore, may use the metric that represents the simplest theoretical case by default. In this situation, knowing the biases of the metric when plausible alternative functions are in fact operating may be useful.

With these considerations in mind, we identify four basic strategies to estimate interaction strength: field experimentation, laboratory experimentation, observational approaches, and analysis of system dynamics.

Field Experiments

Field experiments have been advanced as the most accurate way to assess interaction strength (Bender et al. 1984, Berlow et al. 1999, Paine 1992). As noted above, such experiments must be short term to estimate interaction strength well. A key difficulty of this approach is the logistical challenge of fully implementing it, because doing so generally requires as many treatments as the number of parameters in a community model.

Paine (1992) applied field experiments to a guild of rocky intertidal grazers that feed on the kelp *Alaria marginata*. This author constructed arenas from which grazers were removed or that contained a single grazer species and measured the change in kelp population size after 8 months. By use of an interaction-strength metric that standardized the difference in kelp abundance between treatments and controls by grazer and kelp density, the author found a distribution of interaction strength skewed toward a few strong and many weak impacts. This study has stimulated many recent attempts to measure interaction strength in the field, but it illustrates several of the general pitfalls inherent in estimation of interaction strength. The interaction-strength metric used matches theoretical parameters only under the limited condition of a two-species system at equilibrium (Berlow et al. 1999, Laska & Wootton 1998), and whether equilibrium conditions were reached is uncertain. Additionally, statistically significant positive effects of putative grazers on the kelp were identified, which suggests that indirect interactions with other species over the duration of the experiment affected the per capita estimates; hence, the consistency of such measures is doubtful under different community configurations.

Raffaelli & Hall (1996) summarized results of field experiments for an estuarine food web that involved effects of large predators on invertebrate prey. Like

Paine (1992), they found a skewed distribution of consumer effects; most interaction strengths were weak and only a few effects were strong. They also found net positive effects for some putative consumers, which suggests that indirect interactions may have affected their estimates. Alternatively, sampling error coupled with small populations of consumers and prey may generate positive but statistically nonsignificant results. The authors also noted that interactions with high per capita effects did not necessarily translate into large overall impacts on the system because of predator rarity, which illustrates the difference in behavior of different interaction-strength metrics.

Laboratory Experiments

Short-term laboratory experiments may be used to provide estimates of interaction strength (Abrams 2001, Vandermeer 1969). Laboratory experiments have the advantage that species interactions can be examined in isolation from other species, and often treatments and conditions can be more easily replicated, which allows a more precise estimate of interaction strength between species pairs. These experiments are usually done over smaller scales, which increases the tractability, but whether estimates of interaction strength derived from these studies can be readily transferred to field conditions is unclear (Skelly 2002, Taylor et al. 2002). One compromise approach is to carry out small-scale mesocosm experiments in the field (e.g., Fagan & Hurd 1994, Reusink 1998, Sarnelle 2003, Wilbur & Fauth 1994).

Levitan (1987) used numerous laboratory experiments that estimated nutrient uptake and excretion, mortality, consumption rates, and resource-dependent reproduction to characterize a planktonic lake food web that encompassed two classes of phytoplankton, three zooplankton genera, and externally managed trout populations. The author then analyzed the resulting model for stability properties and the contributions of particular interactions to stability. The model, one of the most thorough to date that involves both competitive and consumer–resource interactions across a food web, suggested that the system was fairly stable. Resource differentiation by both the phytoplankton and the zooplankton were the most important interactions that affected stability. An analysis of the interaction-strength estimates illustrates (a) expected asymmetries between consumers and their resources, in which consumers have stronger effects on their prey, and (b) an overall skewed distribution in the magnitude of interactions. No field experiments are available to verify the model predictions and evaluate the approach, but the study illustrates the substantial effort required to parameterize a multispecies model with an experimental approach. The study still required an abstraction of the system to a minimum number of species suspected of being important.

Schmitz (1997) carried out an experimental study on an old-field assemblage to explore the ability of multispecies models to predict the consequences of chronic perturbations. This author estimated interaction strengths in a laboratory setting by measuring short-term feeding rates among grasshopper and plant species,

nutrient uptake rates of plant species, and competitive interactions among plants. He then carried out a longer-term field experiment by manipulation of nutrients and grazers to determine how well his parameterized model predicted net effects on other species. The author found good qualitative agreement between predicted and observed patterns but some deviations from quantitative predictions. Interestingly, a generally consistent pattern to the deviations occurred, such that predicted plant responses tended to be approximately an order of magnitude greater than observed responses in nutrient manipulations and grazer-exclusion experiments, which suggests that some key parameter was either missed or not estimated accurately. These differences may also have been affected because predictions were based on the inverse community matrix, whereas the experimental manipulation of grasshoppers involved a complete species deletion, which changes the structure of the system and makes analysis by use of the removal matrix more appropriate. One limitation of this study was the inability to evaluate dynamics over more than one generation, which is likely to be a general problem in the use of laboratory experiments.

Observational Approaches

Observational information, such as rates of feeding, abundance, body size, and life-history rates, when appropriately transformed, can be used to estimate interaction strength (Hall et al. 2000, Moore et al. 1993, Raffaelli & Hall 1996, Wootton 1997, Yodzis & Innes 1992). In some cases, this approach may be logistically easier because experiments are not necessarily required.

Wootton (1997) used a direct observational approach to estimate the strengths of interactions of bird consumers on intertidal invertebrate prey. Because of the moderate size of both predators and prey species, in this case, direct observation of rates of feeding, diet composition, and abundances of predators and prey was feasible. Data were combined to obtain metrics with units appropriate to per capita interaction strength and yielded a range of estimated consumer effects on resources. As in other studies, a skewed distribution of interaction strength showed many weak and few strong per capita effects. More surprising, when other metrics of interaction strength were derived, they also showed a skewed pattern of distribution, although the identity of species involved in strong effects changed as a result of varying densities. For a subset of the estimates, experimental manipulations were available and were consistent with observationally derived estimates, which suggests that the approach is valid. The analysis centered on a focal group of avian species and only evaluated consumer impacts on resources; consequently, the results do not necessarily reflect community-wide patterns of interaction strength in the system. Inferences about the general pattern of relative interaction strength of prey on consumers probably could be inferred from the data, when it is combined with estimates of shell-free biomass of individual prey items, because consumption rates are likely to scale reasonably well with per capita effects of prey on consumers. Finally, although the direct observation approach plausibly could be extended to additional

interactions that involve large prey and predators (e.g., whelks or seastars), this method would be much more difficult or impossible to apply to other interactions, such as limpets grazing on microalgae or sessile species competing for space.

A second observational approach incorporates energetics with diet-composition information. Moore et al. (1993) estimated per capita interaction strength of consumer–resource interactions in soil food webs by documentation of diets, body size, and biomass of component taxa. The authors then incorporated prior information on consumption efficiency of different taxa from laboratory studies and used size-specific metabolism relationships to estimate predicted energy demand by a population of a given biomass and body size, under the assumption that the community was at equilibrium. This approach yielded estimates of per capita (or per biomass) effects both of predators on prey and of prey on predators, and it potentially generated one of the most complete model parameterizations of a system to date. Subsequently, these data have been used to explore the distribution of interaction strength within the food web and its impacts on system stability (de Ruiter et al. 1995, Neutel et al. 2002). Key findings included differences in magnitude between reciprocal interaction strengths and nonrandom arrangement of interaction strengths within the food web that appear to stabilize the whole food web. As more comprehensive estimates become available, a comparison of these results with other systems to assess their generality will be interesting and informative (e.g., Levitan 1987).

Observational approaches tied to the structure of ecological theory can provide information on interaction strength in field situations without numerous experimental manipulations. The approach is limited by the researcher's ability to make direct observations of rates of interactions, by the way it ignores potentially important species differences when allometric relationships are used to estimate key physiological parameters, by the limited applicability of the approach to nontrophic species interactions (e.g., interference competition and mutualism), and by the assumption of equilibrium made in energetics models. Additionally, energetics approaches may be unable to estimate important nonlinearities in interaction-strength functions (but see Yodzis & Innes 1992). Finally, parameterizations that use the energetics approach have not been independently evaluated by experimental manipulations, and this prospect remains a ripe area for future research.

Analysis of System Dynamics

A fourth approach, which fits models to system dynamics over time, may provide an efficient method for estimating interaction strength (Elkinton et al. 1996; Ives et al. 1999, 2003; Laska & Wootton 1998; Pfister 1995; Seifert & Siefert 1976). Most ecological theory is based on changes in abundance or biomass over time; hence, fitting these models to system dynamics is a natural approach to estimation of model parameters.

Laska & Wootton (1998) evaluated this approach by use of simulation studies based partially on model fits to the dynamics of a rocky intertidal system.

They found good agreement between estimates of interaction strength generated from limited segments of the simulated time series and actual parameters. The accuracy of the approach increased when observations were made on time intervals sufficiently spaced that temporal correlation in the time series was low. Unlike experimental studies, which require an experiment for each parameter to be estimated, effective parameter estimation requires only zero to two pulsed experimental manipulations if a sufficiently long time series is available and if identifiable disturbance events are exploited. The analysis could be extended in several ways to better evaluate the effectiveness of the time-series approach. First, the authors only simulated linear models and, thus, did not explore the power to detect nonlinear dynamics. Second, their simulations did not investigate process and measurement error, which could reduce the power of the approach. For example, Pascual & Karieva (1996) used dynamic model fitting to analyze data from the seminal studies by Gause (1934) that estimated interaction strength and found that, with observation error, the parameter range that described competitive interactions among *Paramecium* species was very wide. These studies also highlighted that when the goal is estimation of dynamical parameters, incorporation of experimental treatments that cover a range of initial conditions is much more effective than implementation of the highly replicated experiments that involve the few treatment levels that experimental ecologists typically use.

Ives et al. (1999, 2003) used multispecies dynamic data describing planktonic communities in north temperate lakes to parameterize models of the system and evaluate the processes affecting system stability. They further developed the approach by illustrating appropriate maximum-likelihood model fitting, integrating environmental covariates into the approach, and considering the separate effects of process and measurement error. The authors estimated per capita interaction strengths and used them to identify key processes that affect stability and evaluated the role of various direct and indirect pathways involved in responses to manipulation of fish planktivory. Unlike in most studies, the magnitudes of interaction strengths estimated in this study were only weakly skewed. This result may have arisen for several reasons. First, interactions with phytoplankton were not directly modeled. Therefore, many interactions were abstract competitive effects among zooplankton, whereas most other studies examined consumer–resource interactions. Second, the form of model estimated by Ives et al. (1999, 2003) follows the Gompertz equation, where per capita rates of change are functions of natural logs of species densities, which implies multiplicative effects of species. This difference raises a key issue: What type of discrete time approximation should be used in modeling a system? Many other studies have used Ricker-type models, in which the per capita population change is related to initial abundances of species, following the assumption of additive species effects in Lotka-Volterra models. A third approach is to estimate instantaneous rates of change by fitting some arbitrary function, such as separate linear, polynomial, or exponential functions, to a small subset of points around a focal data point and calculating the average slope of the function at the focal data point (e.g., Ellner et al. 2002). More systematic

exploration of the functions that provide the best fit to empirical data and assessment of the implications that these functions have for community dynamics and stability are needed.

Treatment of error in development of multispecies models from time series also requires further attention. Measurement error can bias parameter estimates in many contexts but is particularly problematic in time series because it introduces serial correlation into the data set. Serial correlation can be easily misinterpreted as an important process, such as density dependence (Ives et al. 2003). Ives et al. (2003) and others (e.g., de Valpine & Hastings 2002, Pascual & Karieva 1996) present methods to incorporate measurement error into time series analyses. Measurement errors can be estimated from the data as free parameters with these approaches but, consequently, require substantial increases in the data needed to maintain the power of the approach. An easier and effective alternative is to directly estimate measurement error during the course of empirical studies and insert it into statistical models, but ecologists rarely do this (Carpenter et al. 1994).

Process error also needs further attention in development of the time-series approach. The ability to estimate process error with time-series methods is appealing because stochastic processes have potentially important impacts on ecological systems (e.g., Chesson & Huntly 1997). Most analyses of time-series models assume that process error is an additive source of noise in growth rates, usually normally distributed. This feature need not be the structure of process error, however. For example, variation in the environment might change interaction coefficients and lead to

$$dN_i/dt = N_i \left[r_i + \left(\sum_{j=1:s} [f_{ij}(N_1 \dots N_s) + e_{ij}] N_j \right) + e_i \right],$$

where e_{ij} is the process error associated with a particular interaction between species i and species j , f_{ij} is the function describing per capita interactions between species i and j , and N_i is the abundance of species i . Hence, the effects of process error might interact with species densities. Incorporation of such error structure is undesirable because it increases the number of parameters to estimate, but the point where process error enters the system might have important consequences. For example, the temporal storage-effect mechanism for coexisting competitors (Chesson & Huntly 1997) involves variation in both the abundance of competitors and the intensity of the competitive interaction. The implication of inserting process error in different positions on theoretical predictions needs further exploration.

The use of system dynamics to fit multispecies models is a promising approach that needs further empirical and theoretical evaluation, including a better integration of mechanistic and statistical theory. Aside from its natural links to theory, the approach may be more powerful than direct experimentation because it requires fewer experimental manipulations of the system and can more easily probe short-term dynamics to avoid contamination of the estimates by indirect effects. Probing dynamics works best for systems that explore a wide range of possible parameter space (e.g., starting away from equilibrium), such as when experimental

manipulations are imposed or when well-defined, pulsed disturbances have affected the system. In general, the approach also requires studies of longer duration to generate sufficient dynamical data. At present, the multispecies, multitrophic time series of sufficient length needed for this approach are very rare and may be hard to obtain for some systems. Development of such data sets should be an important priority for ecology to better explore these methods and related methods that exploit ecological dynamics.

ALLOMETRIC APPROACHES TO ESTIMATION OF INTERACTION STRENGTH

Given the difficulties of direct estimation of interaction strength in the field, identification of general relationships between interaction strength and more readily measured properties of species would be convenient. Because the field measurement of interaction strength is still in its infancy, the existence of useful generalizations is uncertain, but some recent results are tantalizing.

Body size is one general property of organisms that might scale with interaction strength (Elton 1927, Yodzis & Innes 1992); therefore, investigating allometric relationships with interaction strength may be profitable. Several allometric relationships relevant to various interaction-strength concepts or parameters in multispecies models in general are already well established. For example, metabolic rates and movement rates scale strongly with body size (Calder 1996, Harestad & Bunnell 1979, Peters 1983) and potentially affect organism death rates, encounter rates, and assimilation efficiencies. Foraging theory also suggests that consumption rate should be affected by the size of interacting species (e.g., Schluter 1982, Werner & Hall 1974). Several empirical data sets are available for a preliminary analysis of allometric relationships (Emmerson & Raffaelli 2004, Sala & Graham 2002, Wootton 1997). When data from all three studies are combined, they tend to fall around the same relationship (Figure 1), which suggests a generally predictable pattern of interaction strength. However, some inconsistencies are present in the pattern. Specifically, consumption rates of kelp grazers (Sala & Graham 2002) and crabs (Emmerson & Raffaelli 2004) decrease with prey:predator size ratio, whereas bird consumption rates (Wootton 1997) increase. Because bird predation involved a wider range of prey:predator size ratios, these interactions dominate the overall relationship. The basis for these discrepancies is unknown, but they could arise as a result of a unimodal function in combination with trait differences between consumer and prey classes, or from differences in how body-size gradients were established (experimentally in the lab versus naturally in the field; single-prey species versus the natural range of prey species).

The feasibility of allometrically derived interaction coefficients were assessed by Emmerson et al. (2005), who also used allometric relationships between body size and population density to estimate equilibrium population sizes in an estuary and a stream. Jacobian matrices were calculated by combination of the estimated

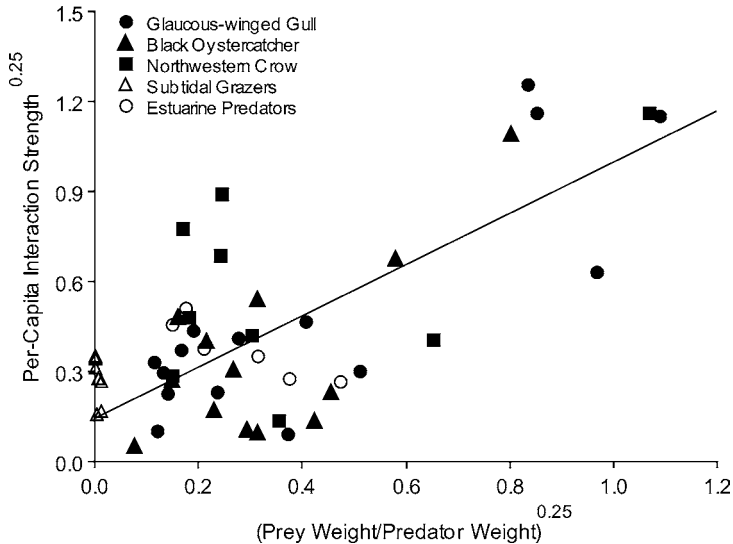


Figure 1 Relationship between per capita interaction strength and the ratio of prey to predator body size (fourth-root transformed data) from studies of avian rocky intertidal predators (Wootton 1997), subtidal grazers (Sala & Graham 2002), and estuarine predators (Emmerson & Raffaelli 2004). Points for estuarine predators illustrate the range of values observed in Emmerson & Raffaelli (2004), not specific data points in the experiment. The regression line presented is for intertidal bird predators only [$PCIS^{0.25} = 0.14 + 0.85 \times (\text{prey/predator mass})^{0.25}$, $R^2 = 0.50$].

interaction coefficients with estimated population densities and then assessed for stability. The resulting food-web parameterizations were stable, even though the webs contained 88 and 32 species, respectively.

INTERACTION STRENGTH-FREE APPROACHES

Several authors have suggested that studies focused on species-specific processes should be abandoned in favor of aggregate (macroecological) level properties of communities and ecosystems (Brown 1995, Lawton 1999), because of the difficulties associated with the estimation of interaction strength and the indeterminate predictions of models with species interactions. Such coarse description of ecological communities, however, may not be relevant in addressing many pressing questions, particularly those of importance to conservation. These questions usually concern the consequences of environmental impacts on, or extinction of, particular species, which requires consideration of the well-documented variation in responses and impacts by different species. Nevertheless, identification of ways

in which species-specific responses can be determined without resorting to estimation of interaction strengths would be very helpful. Several approaches have been advanced in which variation in interaction strength is ignored.

Neutral theories of biodiversity (Hubbell 2001) have recently been advanced that do not consider variation in species interaction strength. These theories posit that species in competition for a limiting resource are ecologically identical, and that variation in species abundances are primarily the result of random-walk processes, speciation rates, and the effects of dispersal limitation in a spatially structured system. These theories are appealing because they can generate realistic species-abundance and species-area distributions in ecological communities from first principles of population biology, and initial studies suggested that their predictions might apply to a wide range of communities (Hubbell 2001). A weakness of these analyses, however, is that the models are tuned to the data with several unmeasured parameters (McGill 2003). Stronger tests that use information on species identity have been developed, in which neutral models are tested against system dynamics in spatially distributed areas (Clark & McLachlan 2003) or parameterized with one data set and then tested against novel, independent data (Adler 2004, Wootton 2005). In these tests, the neutral models have not fared well, which indicates that, although their underlying mechanisms may play an important role in shaping community structure, accounting for variation in species interaction strength is crucial to making accurate predictions.

Analyses of linkage patterns in empirical food webs without reference to differences in the strength of the interactions that generate the links (e.g., Cohen & Briand 1984, Pimm et al. 1991) have been carried out extensively, but these studies generally have not attempted to make specific predictions about experimental or environmental impacts. Several recent approaches have revealed that topological characteristics of interaction webs can play a large role in the determination of ecosystem structure. Hence, perturbations that change these characteristics may generate predictable system responses.

Loop analysis does not account for interaction strength but predicts system response to perturbations near equilibrium on the basis of the qualitative patterns of species interactions in a community web (Levins 1975, Puccia & Levins 1985). Until recently, loop analysis received modest attention because its predictions quickly became indeterminate in the absence of additional information on per capita interaction strength. Advances, however, may substantially expand its scope in making useful predictions. Dambacher et al. (2003a,b) introduced methods for quantifying the strength and complexity of different feedback pathways in relatively complex systems and used simulation studies based on systems with empirically estimated interaction strengths to evaluate the performance of their methods. They found that by quantifying feedback patterns, they could gain substantial insight into the predictability of species response to system impacts. Therefore, even if all components of a complex system do not respond predictably to a perturbation, loop analysis may still provide valuable predictive information. This method has not been tested experimentally in the field, but may offer substantial promise if its

assumptions of approximately linear interaction strength and additivity of species interactions are not too badly violated.

Other analyses have also suggested that web architecture may have predictable effects (Pimm 1982). For example, Solé & Montoya (2001) investigated the effects of the loss of highly connected species from complex real food webs relative to the loss of species at random from these same webs. They found that food webs subject to random species loss tend to persist, but food webs that lose highly connected species become highly fragmented and experience many secondary extinctions. Empirical information may support this pattern. For example, in rocky intertidal systems of the northeastern Pacific, experimental deletion of the highly omnivorous starfish *Pisaster ochraceus* causes large responses in the rest of the system, whereas deletion of the specialist limpet *Acmaea mitra* has minor effects (Paine 1980). Whether the impact of a species generally correlates with its effect on overall linkage patterns remains to be determined, and to our knowledge, no one has undertaken a direct experimental test of this prediction. Montoya et al. (2005) used the inverse community matrix derived from estimates of Emmerson et al. (2005) to assess the relative importance of species connectance within food webs and found a negative relationship between linkage density of each species and the mean net indirect effect of that species on other species in the communities. The relative importance of specialist versus generalist species within food webs to other species could be tested experimentally in other systems to determine the validity of these findings.

INTERACTION-STRENGTH DISTRIBUTIONS: IMPLICATIONS AND ORIGINS

Empirical studies to date that have estimated per capita interaction strength among a number of species pairs have generally found distributions skewed toward many weak interactions and few strong interactions. This pattern is seen in the population-level interactions (Jacobian elements) documented by de Ruiter et al. (1995), which clearly show a strong skew toward weaker interactions for both the negative effects of predators on prey and the positive effects of prey on predators (Figure 2). This prevalent pattern is also seen for a range of studies that have quantified per capita effects in marine (Paine 1992, Raffaelli & Hall 1996, Sala & Graham 2002, Wootton 1997) (Figure 3A–D), freshwater (Levitan 1987) (Figure 3F), and terrestrial (Fagan & Hurd 1994) (Figure 3E) ecosystems. Interaction-strength distributions of non-trophic interactions have received less attention. Strengths of pollinator effects on plants seem to exhibit a skewed distribution on a per-interaction basis (Pettersson 1991, Schemske & Horvitz 1984), but whether these correspond to per capita interactions is unclear because pollinator abundance was unknown and indices of pollination success (pollen deposition, fruit set) may not translate directly to population dynamics. Despite the large amount of literature on interspecific competition, surprisingly few studies quantify the distribution of interaction strength

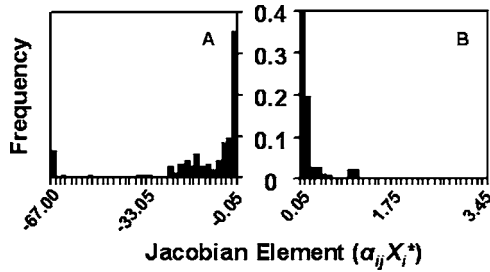


Figure 2 Frequency distribution of interaction strengths (Jacobian elements) from de Ruiter et al. (1995) soil food webs. (A) Negative effects of predators on prey. (B) Positive effects of prey on predators. Both positive and negative effects are skewed toward weak interaction strengths. Note difference in scale between consumer and resource effects.

among direct (nonexploitative) competitors in multispecies systems. Roxburgh & Wilson (2000) report the Jacobian matrix for a seven-species plant community, and the distribution of competitive interaction strengths exhibits a skewed distribution.

Such a regular pattern of skewed interaction strengths raises the question of how the shape of these distributions affects community dynamics and stability, and why such regular patterns might arise. Early theoretical studies of stability in multispecies webs assumed normal distributions of interaction strength and found that diverse webs tended to be unstable (May 1973, Pimm 1982), but recent work suggests that skewed interaction-strength distributions exhibit higher persistence under certain conditions, particularly when omnivory and multiprey satiation occur (Emmerson & Yearsley 2004, McCann et al. 1998). The relationship between the empirical and theoretical results is uncertain, however, because different interaction-strength units have generally been used: per capita interaction strengths (empirical) and Jacobian elements (theoretical). Hence, further studies exploring alternative interaction-strength metrics would be beneficial.

The effect of interaction strength on stability raises the question of how such interaction-strength distributions arise. One possibility is that community assembly processes favor interaction-strength distributions that convey stability. This proposition has been explored in several theoretical studies. In some cases, species interaction strengths were assigned at random, and simulations were carried out to determine the characteristics of interaction strength that lead to long-term persistence. Emmerson & Yearsley (2004) studied randomly parameterized Lotka-Volterra food webs with four species and found that the subset of locally stable communities had emergent skewed interaction-strength distributions, and weaker interactions were present in omnivorous loops. An alternative approach is to carry out simulations while continuously adding species with random characteristics. Kokkoris et al. (1999) studied Lotka-Volterra competition systems of

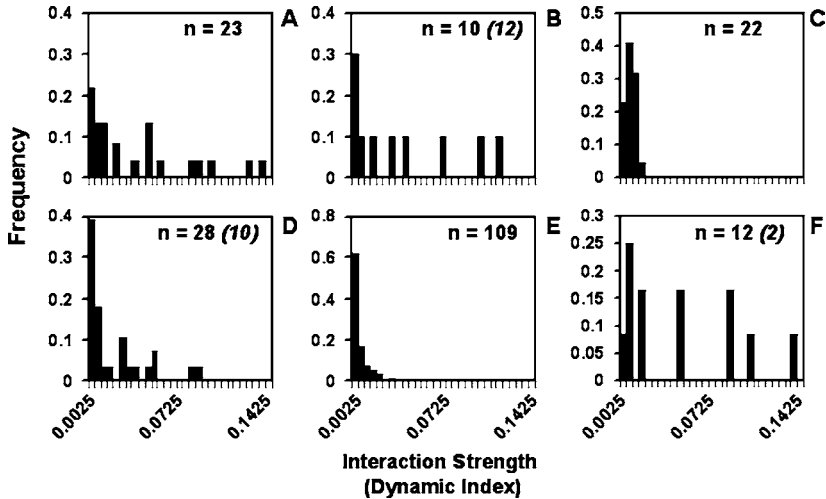


Figure 3 Frequency distribution of absolute per capita effects of consumers on their prey. Coefficients were calculated as $\ln(C/E \times P)$, where C and P are the abundance of prey and consumers, respectively, in control treatments, and E is the prey abundance in predator removal treatments (Osenberg et al. 1997, Wootton 1997). Each distribution was calculated using the raw data obtained from the studies detailed in (A) Paine (1992), (B) Raffaelli & Hall (1996), (C) Sala & Graham (2002), (D) Wootton (1997), (E) Fagan & Hurd (1994), and (F) Levitan (1987). These data represent some of the most comprehensive currently available in the literature. All distributions are skewed toward many weak interactions and few strong interactions, a pattern that is consistent across all of the systems studied. Numbers on the graph represent sample size (number of interactions) and numbers in parentheses indicate the number of interaction strengths found above the scale of the graphs.

40 species and found that skewed interaction-strength distributions developed over time. Drossel et al. (2004) studied assembly of food webs assuming a range of interaction-strength functional forms but placed no constraints on food-web configuration or species number. They found that resulting assembled communities exhibited skewed interaction-strength distributions. They also reported that food webs of realistic structure required mechanisms in which species focused on consuming the most profitable prey in the system. Further study of the outcome of community assembly processes would be beneficial to clarify the generality and causes of conflicting patterns of food-web structure. Such contrasting patterns occur in models with and without food-web constraints. However, the generality of the conclusion that stable communities exhibit distributions skewed toward weak interactions across studies suggests that it may be robust.

EFFECTS OF SCALE

Temporal and spatial scale may affect estimates of interaction strength in several ways, but their implications are only starting to be explored because of the difficulty of estimating interaction-strength functions at even a single scale. Indirect effects and density-dependent feedback can change interaction-strength estimates over long timescales of measurement. Disparate timescales among different species and different types of ecological processes may also affect interaction strength. For example, deaths, growth, and behavioral changes occur fairly continuously through time, whereas births are often seasonally pulsed. Such differences may affect key aspects of interaction strength, such as encounter rates among individuals of different species, and may favor biomass- rather than abundance-based approaches to species interactions. Similarly, different components of food webs have different generation times, which may affect the intensity of interactions through time. For example, in freshwater systems, algae may have generation times on the order of days, arthropod grazers have generation times on the order of weeks to months, and fish predators have generation times on the order of years. Hence, species operating on a fast timescale can quickly respond numerically to changes in the strength of species interactions, whereas species operating on longer timescales cannot. Asymmetries in timescales must be addressed by developing models that integrate fast processes over the timescale of slower processes or species, which can lead to nonlinear interactions. Additionally, integrating functions to account for disparate timescales can generate asymmetries in the functional form that describes the interaction for each of the interacting species (e.g., Nicholson & Bailey 1935).

One shortcut for dealing with disparate timescales of dynamically interacting entities is to assume that faster-scale processes quickly come to equilibrium (MacArthur 1972, Schaffer 1981), such that the interactions involving slower processes primarily experience these equilibrium conditions. MacArthur (1972) showed that resources generated locally under logistic growth at fast timescales produce logistic interaction-strength functions for consumers in which consumer dynamics are not explicitly linked to resource abundances, but are controlled by critical resource-rate parameters, which yield mechanistic interpretations of “intrinsic” population growth rate and carrying capacity. Similarly, for systems supported by nutrients derived outside the system, the effect of nutrients on plants generates a nonlinear, semi-ratio-dependent (DeAngelis et al. 1975) interaction-strength function, which is independent of nutrient concentrations but is controlled by critical nutrient-rate parameters. Because these functions collapse into equations involving a single trophic level in some cases, highly disparate timescales may allow abstraction to fewer component species, potentially simplifying the problem of dealing with all species in the system at once (Schaffer 1981). An understanding of how species operating at other timescales affect parameters within a population is essential, however, to predicting how a community will respond to environmental impacts. Additionally, when interaction strength is a nonlinear

function (e.g., a saturating type II functional response), multitimescale models generate much less tractable results.

Shifting the focus from abundance to biomass may help researchers to avoid disparate timescale issues (Hall et al. 2000, Moore et al. 1993, Reusink 2000, Wootton & Power 1993, Yodzis & Innes 1992). Pulsed reproductive bouts generate delayed changes in abundance that reflect integrated patterns of prior consumption, whereas energy is stored immediately as biomass at the same temporal scale as consumption. Modeling biomass dynamics rather than abundance dynamics typically requires several key assumptions, such as larger individuals will have equivalent consumption rates as several smaller individuals of equal biomass, and larger prey individuals will be encountered at rates as high as the encounter of several small individuals. These assumptions require careful empirical investigation. Chalcraft & Resitarits (2004) provided an initial assessment by varying size structure of predatory fish and frog tadpole prey and found that, although the assumptions were met qualitatively, the relationships were affected by density-dependent processes.

Spatial scale can also affect our perception of interaction strength in several ways. Spatial scale can affect interaction strength through changes in habitat heterogeneity. If the performance of interacting species is habitat dependent, then interaction strength may change with scale. For example, competing species often perform better in different habitats, which leads to habitat shifts and exclusion of each species by the other from its preferred habitat (e.g., Connell 1961, Grace & Wetzel 1981, Pacala & Roughgarden 1985). In this case, small-scale studies in one habitat would estimate strong interspecific interaction strengths among competitors consistent with competitive exclusion, but studies at larger scales that include multiple habitats would estimate lower interspecific interaction strengths, consistent with competitive coexistence. A similar situation would arise where habitats differ in structural cover, and habitat structure alters consumer–resource interactions (e.g., Werner et al. 1983). The way in which species perceive their physical environment and interact with it and other species depends on body size. As we already noted, the home range of a species is positively correlated with body size, and so size effects may also affect the way in which interactions are modified over varying spatial scales.

Spatial scale might also affect interaction strength because of localized interactions. Ultimately, all species impacts arise via interactions among individuals, and closer individuals are more likely to interact with each other than are distant individuals. Hence, as spatial scale increases, the mass action assumptions inherent in many models of communities may be violated, which affects interaction-strength parameters by generation of patchy population structure. In these situations, spatially explicit individual-based models may be required to adequately model multispecies systems. Pascual et al. (2001, 2002) explored this issue theoretically by use of an individual-based predator-prey system, and then examined how spatially explicit dynamics affected the form of mean field-population models at larger scales. Interestingly, they found that the individual-based models generated mean field dynamics with similar form to standard consumer–resource models. The per

capita interaction strengths in these models, however, depended on spatially relevant parameters such as individual dispersal distance; lower dispersal tended to weaken interspecific interaction strength. The generality of these results needs to be explored for other types of interactions and, more systematically, for changes in habitat scale, but may indicate that localized interactions can be adequately handled by standard interaction-strength functions.

Spatial-scale effects on interaction strength have been reported in several empirical studies. For example, Skelly (2002) and Taylor et al. (2002) compared per capita interaction strengths between species in small-scale mesocosms and large-scale plots imbedded in natural ecosystems and found variation between experimental venues. Wooster (1994) reported a meta-analysis of experiments that probed consumer–resource interactions and found changes in the magnitude of predator impacts with experimental plot size. Because manipulations were carried out by use of different methods, however, other differences in experimental venues than scale could have caused the documented differences. Experiments in which all aspects except scale remain constant are needed in future empirical evaluations of this question (e.g., Englund & Cooper 2003). In many cases, the scale-dependent patterns appear to arise because of variation in the openness of experimental arenas to migration: Larger arenas will tend to be less affected by populations outside the manipulated areas because of perimeter to area effects, and this may dilute or enhance the total effect of a manipulated species, depending on the relative mobility of the interacting species (Englund & Olsson 1996).

INTERACTION-STRENGTH LINKS TO ECOSYSTEM FUNCTION

Much interest has developed in understanding how biodiversity affects aggregate properties of ecosystems (Naeem et al. 1994, Petchey et al. 2004). Ultimately, the mechanisms by which species generate patterns in ecosystem properties depend in part on the characteristics of species interactions. To our knowledge no explicit experimental investigation has linked ecosystem function with quantified per capita effects of species interactions, even though niche overlap and complementary resource utilization among competitors are regularly invoked to explain increased ecosystem function with increased species richness.

Most studies that investigate biodiversity and ecosystem function only consider single trophic-level systems, whereas most natural ecosystems have multiple trophic levels. A few theoretical and empirical studies have been carried out to investigate the effects of diversity on the functioning of multitrophic ecosystems (Downing & Leibold 2002, Fox 2004, Petchey et al. 2004, Thébault & Loreau 2004). Uncertainty remains, however, in the role that interaction strength plays in the generation of the patterns in these studies. Thébault & Loreau (2004) investigated the effects of introduction of herbivorous consumers to a system of competing plants by use of linear per capita effects. Their models suggest that

both the strength and arrangement of interactions causes ecosystem-level effects within the community. Incorporating studies of species interactions into systems that probe the phenomenological association between biodiversity and ecosystem function would help clarify their relationship.

EVOLUTION AND INTERACTION STRENGTH

Interaction strengths depend in part on the traits of interacting organisms and represent potentially strong selective pressures; hence, they should evolve over time. Coevolution concerns itself with the evolution of interaction strength, and its literature is sufficiently large that we cannot adequately review it here (see Abrams 2000, Thompson 1998). One particularly exciting, and challenging, area of investigation is the link between coevolution and ecological dynamics. Although evolution is often assumed to proceed slowly, several studies show that it can proceed on an ecological timescale (e.g., Grant & Grant 1989, Lee 1999). Furthermore, adaptive phenotypic plasticity may evolve under some circumstances, which creates nonlinear interaction-strength functions and trait-mediated indirect effects when viewed at a species-wide level (Tollrain & Harvell 1999, Werner 1992). Such trait changes could affect ecological stability. For example, as consumer pressure increases, prey may evolve more resistant traits, which reduces interaction strength, but when consumer pressure is low, costs of resistance may favor susceptible genotypes. Such a situation could help stabilize ecological dynamics. Concurrent consumer evolution, however, might introduce cyclical time lags, thereby destabilizing systems. Although a challenge, some progress in modeling linked ecological and evolutionary dynamics has been made (Abrams & Matsuda 1996, Marrow et al. 1996, Saloniemi 1993), and it confirms some of these contingencies. Experimental studies with bacteria-phage systems demonstrate empirically that evolutionary changes in interaction strength can affect ecological dynamics (Bohannan & Lenski 2000).

CONCLUSIONS

Estimation of interaction strength in ecosystems and linkage of these estimates to theoretical frameworks remains a daunting challenge but is needed in many cases to aid in the understanding of ecological structure and function and the prediction of responses to environmental impacts. General rules, such as characteristic patterns of interaction-strength distributions across communities and within interaction webs, and relationships with species traits such as body size may be of use in the future, but their identification will require more extensive estimates from field systems. A key need is the development of comprehensive long-term, multispecies, multitrophic time series for a group of focal ecosystems. These data would allow more comprehensive analyses of system dynamics to estimate

interaction strength, as well as provide insight into other ecological questions and processes. Interaction strength-free approaches may also provide some insight as new methods become more available to analyze the effects of changing the structure of interaction webs. These methods, and several approaches, such as energetics, for estimating interaction strength also need to be experimentally tested in field situations. Empirical studies that incorporate interaction-strength estimates, body-size relationships, and ecosystem measures into highly resolved interaction webs will be valuable for clarifying the relative roles of interaction strength and web architecture on system behavior. The diverse approaches employed by ecologists illustrate the possibilities of bringing a range of techniques to bear on the challenging problems that society charges contemporary ecologists to address. Use of multiple approaches may enable us to distill some semblance of reality from natural complex systems.

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