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FORUM

Interaction strengths in food webs: issues and opportunities

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Summary

1. Recent efforts to understand how the patterning of interaction strength affects both structure and dynamics in food webs have highlighted several obstacles to productive synthesis. Issues arise with respect to goals and driving questions, methods and approaches, and placing results in the context of broader ecological theory.

2. Much confusion stems from lack of clarity about whether the questions posed relate to community-level patterns or to species dynamics, and to what authors actually mean by the term 'interaction strength'. Here, we describe the various ways in which this term has been applied and discuss the implications of loose terminology and definition for the development of this field.

3. Of particular concern is the clear gap between theoretical and empirical investigations of interaction strengths and food web dynamics. The ecological community urgently needs to explore new ways to estimate biologically reasonable model coefficients from empirical data, such as foraging rates, body size, metabolic rate, biomass distribution and other species traits.

4. Combining numerical and analytical modelling approaches should allow exploration of the conditions under which different interaction strengths metrics are interchangeable with regard to relative magnitude, system responses, and species identity.

5. Finally, the prime focus on predator–prey links in much of the research to date on interaction strengths in food webs has meant that the potential significance of non-trophic interactions, such as competition, facilitation and biotic disturbance, has been largely ignored by the food web community. Such interactions may be important dynamically and should be routinely included in future food web research programmes.

Key-words: allometry, body size, ecological networks, interaction strength, keystone species, population dynamics, stability.

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Introduction

Food webs have long been a central concept in ecology and are useful because they provide tractable abstractions of the complexity and interconnectedness of natural communities that potentially transcend system-specific detail. While potentially unifying, the food web concept has proved scientifically divisive over the past three decades. Those interested in predicting species population dynamics have suggested that the structure of unweighted links alone tells little about the outcome of a species perturbation (Levine 1976; Holt 1977; Paine 1980; Vandermeer 1980; Abrams 1987; Paine 1988; Polis 1991), while others claim that generalities in unweighted link structure transcend the spatially and temporally variable details of individual species dynamics (Cohen 1978; Briand & Cohen 1987; Sugihara *et al.* 1989; Cohen *et al.* 1990; Martinez 1994).

The discovery of keystone predation was among the first empirical examples that demonstrated dramatically how unweighted link structure by itself is not a good predictor of species and population dynamics (Paine 1969, 1974, 1980). Ironically, this example is also one of the first to illustrate the critical *dependence* of dynamics on web structure. Keystone predation is not a single strong predator–prey interaction, but rather a particular configuration or structural organization of strong and weak links: strong predation, relative to other predators of that guild, on a competitively dominant prey species. It demonstrates how a combined knowledge of both web structure and interaction strengths is a key to understanding how ecological communities function. Characterizing and abstracting this relationship between web structure, interaction strengths and population dynamics allowed others to identify the presence (or predictable absence) of keystone effects in other sites and communities (Estes & Palmisano 1974; Lubchenco 1978; Castilla & Duran 1985; Paine *et al.* 1985; Carpenter & Kitchell 1993).

General patterns of food web structure also appear to be an emergent property of dynamical constraints on species interactions (e.g. Bastolla *et al.* 2001; Drossel *et al.* 2001; Fox & McGrady-Steed 2002; Montoya & Solé 2003). With interaction strengths assigned at random from a specified distribution, early theoretical work suggested that weak interactions are necessary for diverse systems to be stable under certain mathematical conditions (May 1972, 1974; Cohen & Newman 1984, 1985). More recent work suggests that non-random patterning of strong and weak links can be critical for the stability or persistence of theoretical and empirically observed complex communities (de Ruiter *et al.* 1995; Polis & Strong 1996; Haydon 2000; Kokkoris *et al.* 2002; Neutel *et al.* 2002). Additionally, not only stability but also ecosystem functions might be strongly mediated by the arrangement of interaction strengths (Mikola & Setälä 1998; Duffy 2002; Montoya *et al.* 2003).

Together these advances suggest that understanding the causes and consequences of interaction strength structure in ecological networks may help bridge the gap between food web patterns and dynamics. However, recent efforts to do so have also raised issues that pose obstacles to productive synthesis. Here we articulate potential issues that have arisen at each general stage of scientific inquiry: (1) goals and driving questions; (2) methods and approaches; and (3) placing results in the context of broader ecological theory. We use illustrative examples to identify opportunities for progress.

Issue and opportunities

GOALS AND DRIVING QUESTIONS

Issues

An important underpinning of the historic gap between studies of structural food web patterns and those of population dynamics lies in different basic goals and levels of questioning. The former identify general community-level attributes that characterize natural systems or systematic variation among habitats (e.g. Pimm *et al.* 1991; Martinez 1992; Hairston & Hairston 1993; Schmid-Araya *et al.* 2002a; Williams *et al.* 2002). The latter seek to understand what underlies the relative importance of different links and processes that determine the population variation within and among communities (e.g. Menge & Sutherland 1976, 1987; Polis & Strong 1996; Ives *et al.* 1999a; Petchey 1987; Carpenter *et al.* 1987). Confusion and miscommunication arise from the fact that different kinds of questions are being asked by the two approaches, as illustrated by the two different categories of questions asked about interaction strengths in food webs:

1. *Questions about community-level patterns.* For example: (a) Are natural systems characterized by a predictable non-random patterning of interaction strengths? (b) What are the underlying mechanisms that generate non-random patterns of interaction strengths? (c) What are the consequences of this patterning for community-level functions, such as stability and persistence?

2. *Questions about species-specific dynamics.* For example: (a) What is the minimum detail necessary to predict the effects of a change in abundance or extinction of one species on other species abundances or extinctions in the web? (b) Which particular species have disproportionately large effects on community structure and species' population dynamics? (c) Which species are particularly vulnerable to extinction?

Opportunities

The debate about the best way to characterize species interactions is often a debate about what questions are more interesting. Often, however, one approach cannot answer all questions, and each approach must be evaluated in light of the type of question it addresses. For example, if the goal is to predict community changes resulting from a species removal, statistical Markov models may be a useful approach even though they do not clearly shed light on the patterning of interaction strengths or the exact mechanisms of change (e.g. Wootton 2001).

Being clear about driving questions and their underlying assumptions facilitates communication among different research programmes (Austin 1999). This awareness is a critical first step for identifying synthetic opportunities where apparently divergent lines of research are actually two sides of the same coin. It encourages additional lines of inquiry into how these different questions are related. For instance, when does one level of questioning provide insights into another? Is there a third line of questioning that could provide a unifying framework for all? Thus, in the case of interaction strengths, recent integrative studies have shown that body size, temperature and stoichiometry are critical determinants of rate processes in organisms, including the most fundamental process underlying trophic interactions, metabolism (West *et al*. 1997; West *et al*. 1999; Belgrano *et al*. 2002; Sterner & Elser 2002). Understanding how the distribution of body sizes, population abundances and predator–prey body size ratios constrain trophic links and interaction strengths may provide a foundation that could simultaneously explain community-wide patterns of interaction strength structure, predict species-specific deletion effects and identify dynamically important species (e.g. Yodzis & Innes 1992; Sala & Graham 2002; Cohen *et al*. 2003; Emmerson & Raffaelli 2004).

METHODS AND APPROACHES

What is meant by 'strong' and 'weak' interactions?

Issues. A number of studies have observed that weak interactions prevail in natural communities (Power *et al*. 1996; Paine 1992; Fagan & Hurd 1994; de Ruiter *et al*. 1995; Raffaelli & Hall 1995; Wootton 1997; Sala & Graham 2002; Navarrete & Castilla 2003). This pattern has been observed in field experiments, matrix analyses of food webs and numerical simulations of random and evolved food webs and competitive communities (De Ruiter *et al*. 1995; Ives *et al*. 1999a; Kokkoris *et al*. 1999; Quince *et al*. 2003). Similarly, the importance of weak interactions for dynamic stability and species coexistence has been suggested from matrix analyses of soil food webs, numerical simulations of small and large webs and experimental manipulations (McCann *et al*. 1998; Polis 1998; Berlow 1999; McCann 2000; Neutel *et al*. 2002; Montoya & Solé 2003). However, these studies actually measure different things with the most, or only, consistent aspect being the use of the words 'interaction strength'. Laska & Wootton (1998) clearly articulated one aspect of this problem: what theoreticians call interaction strength is generally not what empiricists measure in the field. However, even *within* theoretical or empirical investigations there exists a diversity of measures of link weight, or interaction strength (Table 1). These include: (1) elements of the interaction matrix; (2) elements of the community, or Jacobian, matrix; (3) elements of the inverse Jacobian matrix; (4) biomass flux; (5) relative prey preference; (6) maximum consumption rate; (7) consumption frequency; (8) non-linear functional response of consumption with respect to prey and/or predator abundance; (9) link density; (10) perturbation effects on population abundances, variability or secondary extinctions; and (11) statistical correlations among population abundances (Table 1). Appendix I summarizes some important characteristics of commonly used theoretical measures of interaction strength. A critical problem with using a common word for these different aspects of link weighting is that it may generate unnecessarily false or misleading predictions about the effects of strong or weak interactions in a community. For example, strong consumption intensity by a predator, or large energy flow from prey to predator, is not necessarily a good predictor of large dynamical effects on prey abundance (e.g. Paine 1980; Paine 1988; Lawton 1990; Raffaelli 2000; Navarrete & Castilla 2003), nor is it necessarily a good predictor of strong interaction coefficients in the community matrix (e.g. de Ruiter *et al*. 1995). Similarly, strong interaction coefficients in the community matrix, which are defined by small perturbations, may not necessarily predict strong effects of a large perturbation such as a species addition or removal (e.g. Yodzis 1988; Abrams *et al*. 1996; Woodward & Hildrew 2001).

Opportunities. Differences among studies in what they measure as interaction strength highlight differences between the two classes of questions described above. In this respect, the various kinds of interaction strengths can be distinguished into two categories: (1) interaction strengths that refer to the property of an individual link (e.g. the Jacobian matrix element, specific maximum feeding rates, biomass flow along on e link, etc.); and (2) interaction strengths that refer to the impact of a change in the properties of one link or of a set of links (e.g. all links to and from a given species) on the dynamics of other species or on the functioning of the whole system (Table 1). The second category includes the majority of field and microcosm perturbation experiments. It is important to remember that even if studies are focused on a single interaction, the outcome of small press perturbations will always be a whole system response (e.g. Bender *et al.* 1984; Yodzis 1988). Thus, in the first category individual interaction strengths are independent of the network, in the second category they are in theory inseparable from their network context. Given this distinction, it is important to understand whether and how these different kinds of interaction strengths are related. Previous attempts to translate pertubation interaction strengths into individual link properties have proved problematic (see

Table 1. Multiple theoretical and empirical metrics of interaction strength in food webs

Interaction strength metric	What it measures	Level of measurement	Advantages	Disadvantages	Example references
Interaction matrix	Interaction coefficients (α_{ij}) in a Lotka–Volterra multispecies competition model Can be generalized to the partial derivative of one species' per capita growth rate with respect to small changes in another species' abundance (see Appendix I) Units: ($n^{-1}t^{-1}$)	Property of individual link	Can be explicit coefficients in a L–V equation Includes non-trophic interactions Simple relationship with the community matrix under some circumstances Facilitates cross-system comparison because the coefficients are independent of population size	The distribution of elements in the interaction matrix does not necessarily predict the distribution of elements in the 'community matrix' Assumes linear functional response or constant interaction strength for each directed link Measures effects of very small perturbations, and thus may not always apply to large perturbations typical of most empirical studies	Kokkoris *et al.* (2002)
Community (Jacobian) matrix	See Appendix I Partial derivative of one species' growth rate with respect to small changes in another species' abundance Units: (t^{-1})	Property of individual link	Includes non–trophic interactions Analytically tractable At equilibrium, it gives information about local stability Can be measured at any state, although may not give information about stability at a non-equilibrium one	Only valid in a small vicinity of the state where it is calculated Local stability analysis at equilibrium may not inform global stability in response to large perturbations and non-equilibrium situations Values depend on species' population size Assumes linear functional response or constant interaction strength for each directed link Measures effects of very small perturbations, and thus may not always apply to large perturbations typical of most empirical studies	de Ruiter *et al.* (1995) Schmitz (1997) Ives *et al.* (1999a)
Inverse interaction matrix	Change in the equilibrium density of one species in response to a change in the carrying capacity of another species (see Appendix I) Units: (nt) Total direct and indirect effects of one species on another	Whole system response	Similar to a typical 'press' perturbation experiment	Similar to the interaction matrix	Bender *et al.* (1984) Yodzis (1988)
Non-linear functional response	Number of prey consumed as a function of prey density and predator density or predator–prey ratios 'Top-down' measure of consumption intensity Various units	Property of individual link	Interaction strength more realistically varies with prey and predator density Critical for parameterizing dynamic models	Real form in nature unknown Non-linear function makes analytical solutions difficult unless clear equilibrium exists Does not measure prey response Difficult to measure for all but a few interactions, and difficult to measure in an uncontrived (or natural) setting	Beddington (1975) Abrams & Ginzburg (2000) Ruesink (1998)
Relative prey preference	Fraction of a predator's maximum consumption rate that is targeted to a specific prey item Top-down measure of consumption intensity	Property of individual link when assigned a value in a model Whole system property when measured empirically	Easy to tune in a dynamic model Standardizes all IS relative to maximum Empirically tractable	Limited to numerical simulation Difficult to interpret simulations because strengthening one link simultaneously weakens another Does not measure prey response Snapshot in time, will probably vary with the presence/abundance of alternate prey	Yodzis & Innes (1992) McCann *et al.* (1998)
Maximum consumption rate	Measures maximum consumption per unit time on fixed abundance of prey Measures 'top-down' potential consumption intensity	Property of individual link	Isolates potential direct effect on prey A model parameter that is empirically tractable in field or laboratory	Ignores functional response Does not measure prey response	Sala & Graham (2002)

Table 1. *Continued*

Interaction strength metric	What it measures	Level of measurement	Advantages	Disadvantages	Example references
Biomass flux	Absolute or relative magnitude of biomass flowing from prey to predator per unit time	Property of individual link	Common currency Potentially can be derived from first principles (body size, abundance, metabolic rates)	Does not measure either prey or predator response magnitude	Benke *et al.* (2001) Bersier *et al.* (2002) Cohen *et al.* (2003)
Change in population variability	Effect of changing the abundance of one species on the pattern of population variability of another species	Whole system response	Stability measured as population variability is empirically tractable	Not analytically tractable Difficult to explore parameter space if investigated with numerical simulations	McCann *et al.* (1998) Ives *et al.* (2003)?
Link density	Measures the number of ingoing and/or outgoing links to/from a species Deletion 'experiments' focus on 'bottom-up' effects of prey on predator	Whole system response Node property rather than link property	Identifies boundary conditions for secondary extinctions (e.g. predator loses all its prey) Identifies easily isolated species Easy to measure	Assumes links are temporally constant, and no prey switching if predator loses all prey species Difficult to estimate effects of predator on prey Cannot estimate effects of changes in prey or predator density	Solé & Montoya (2001) Dunne *et al.* (2002)
Secondary extinctions	Number of species that go extinct as a result of perturbing a given species	Whole system response	For extreme cases, bottom-up effects of prey on predator can be measured from topology of links alone Theoretical results are empirically testable	To include all cases, can only be measured with numerical simulation of population dynamics	Borrvall *et al.* (2000) Solé & Montoya (2001) Dunne *et al.* (2002)
Absolute prey response	Absolute changes in one species' abundance or biomass in response to typically large changes in another species' abundance (e.g. species removal) Measured either as a *per capita* effect or a species-level effect	Whole system response	Characterizes visually dominant effects Highlights effects on dominant species	Difficult to compare across sites of varying productivity or spp . density Snapshot in time/space (e.g. ignores functional response) Difficult to separate direct and indirect effects	Many field experiments where response variables are untransformed
'Paine's Index'	'Absolute prey response' standardized by some measure of prey abundance Measured either as a *per capita* effect or a species-level effect	Whole system response	Comparable across sites of varying productivity Highlights effects on rare species	Snapshot in time/space (e.g. ignores functional response) Difficult to separate direct and indirect effects	Paine (1992)
Log response ratio	Log of the ratio of prey abundance 'with' vs. 'without' predators Measured either as a *per capita* effect or a species-level effect	Whole system response	Comparable across sites of varying productivity Does not depend on equilibrium conditions Works well for short-term experiments	Snapshot in time/space (e.g. ignores functional response) Difficult to separate direct and indirect effects IS approaches zero at equilibrium	Berlow *et al.* (1999) Laska & Wootton (1998)
Statistical correlation	Measures magnitude of correlation between change in one species and change in another	Whole system response	Can estimate from observational data Includes non–trophic interactions	Can be difficult to interpret mechanisms Difficult to separate direct and indirect effects Snapshot in time (e.g. ignores functional responses)	Wootton (1994) Pfister (1995) Ives *et al.* (1999a)
Frequency of consumption	Frequency of hosts that are parasitized (e.g. parasite prevalence)	Whole system property	Easy to measure Can estimate key parameters in discrete-time host–parasite models Measures host response as the abundance of hosts in the next generation	Cannot estimate host response magnitude when other forms of predation are an important source of host mortality Snapshot in time (e.g. ignores functional responses)	Hawkins & Cornell (1994) Müller *et al.* (1999) Montoya *et al.* (2003)

below; Laska & Wootton 1998; Abrams & Ginzburg 2000; Sarnelle 2003). A different line of synthesis is to explore how the patterns and structure of strengths of individual system components/links can help predict whole system responses to individual perturbations (Ives *et al.* 1999a).

One intriguing pattern that emerges despite this unrigorous terminology is that so many different measures of trophic link weighting point to the same, a few strong and many weak, pattern. This pattern presents an opportunity for exploring whether there are underlying mechanisms responsible for this consistency across different attributes of link weight. For example, constraints on predator-prey body size ratios (Cohen *et al.* 1993; Warren 1996), self-similar species area relationships (Harte *et al.* 1999), hierarchical constraints on feeding relationships (e.g. Cohen 1989; Williams & Martinez 2000; Neutel *et al.* 2002; Emmerson & Raffaelli 2004), metabolic scaling relationships (West *et al.* 1997), body size vs. home range size relationships (e.g. Schoener 1968), etc. may independently or interactively constrain the configuration of links and link weights to a skewed distribution. Investigating fundamental mechanisms and scaling relationships that limit the number of possible interactions to a subset of probable ones may provide a holistic framework for understanding the links between food web structure and dynamics. A critical question here is to what degree species (or populations) can be abstracted into key traits that determine probable feeding relationships, preferences and magnitudes (Cohen 1989; Warren 1996; Williams & Martinez 2000; Jennings *et al.* 2001; Hooper *et al.* 2002; Petchey & Gaston 2002; Woodward & Hildrew 2002; Brown & Gillooly 2003; Cohen *et al.* 2003). At the same time, it is important to test the null hypothesis that these patterns are to be expected at random. For example, the log-normal distribution arises as the product of an increasing number of independent identically distributed positive random variables, even if those variables are distributed symmetrically (Johnson & Kotz 1970).

Identifying consistencies in a community-level pattern of interaction strengths does not necessarily provide information about the identity of key species or particularly vulnerable species. Similar community-level patterns of a few strong and many weak interactions for two different interaction strength metrics do not necessarily mean that the same species will be identified as strong players in each case. A highly connected topological keystone may not be the same species as the population dynamics keystone or the biomass flow keystone. These differences should encourage us to be explicit about what we are measuring and to be cautious about inferring that a species identified as a weak player based on one metric is generally unimportant across all metrics (e.g. Paine 1980; McCann *et al.* 1998; Berlow 1999; McCann 2000). At the same time, the differences encourage us to explore other potentially more synthetic lines of inquiry that may simultaneously explain both emergent community-level patterns and species-specific dynamics.

Theory vs. experiment

Issues. Laska & Wootton (1998) pointed out that what theoreticians use as coefficients of interaction strength are not what empiricists typically measure. These authors, with Osenberg *et al.* (1997) and Navarrete & Menge (1996), proposed independently an empirical metric that could potentially bridge this gap. However, this metric measures only the interaction coefficient of the simplest possible formulation of a Lotka–Voltera competition model (Berlow *et al.* 1999). Because non-linear predator functional responses and predator interference make empirical interaction strengths contingent on prey and predator density as well as prey productivity (Ruesink 1998; Berlow *et al.* 1999; Abrams & Ginzburg 2000), it remains a challenge to translate easily the results of perturbation experiments into interaction coefficients for more complex and realistic models of species interactions (Sarnelle 2003). This problem is complicated by the difference between interaction strengths measured as individual system components vs. those that are whole system responses, as discussed above.

Many theoretical investigations have focused on stability of model communities (e.g. Levins 1968; May 1971, 1972, 1974; Hutchinson 1978; Cohen & Newman 1984; Cohen & Newman 1985; Case 1990; Logofet 1993; McCann & Hastings 1997; McCann 2000; Kokkoris *et al.* 2002; Jansen & Kokkoris 2003; Logofet 2004). Multiple definitions of stability have been proposed, with some designed to have closer ties to empirical data (e.g. Lewontin 1969; Pimm 1979, 1984; Law & Morton 1996; Grimm & Wissel 1997; Dambacher *et al.* 2002, 2003; Loreau *et al.* 2002). Despite these developments, many current analytical studies evaluate linear stability of a community at equilibrium in the face of small perturbations (realistically, a change of one individual). Empirical investigations, on the other hand, rarely measure stability in this formal sense, but rather focus on community changes (with no assumed equilibrium) in response to comparatively large perturbations, such as species removals, species additions and physical disturbance (Ives *et al.* 1999a; Woodward & Hildrew 2001; Woodward *et al.* 2002). Thus, one disconnect between theory and experiment arises from the fact that many theoretical analyses make predictions that are logistically difficult to test empirically (Ives *et al.* 2003). For example, the effects of small pulse perturbations, such as removing one individual, are unlikely to be statistically detectable in most field situations (but see Law & Morton 1996).

Opportunities. Combining field experiments with statistical analyses of detailed population time-series data offers one promising approach for the estimation of community-wide patterns of direct interaction coefficients (e.g. Pfister 1995; Ives *et al.* 1999a, 2003). Where the results of field and microcosm experiments may not be translatable easily into model coefficients, they can serve as critical independent tests of food web models that are parameterized with other types of empirical data (Morin & Lawler 1995; Sarnelle 2003). Exploring ways to estimate or derive biologically reasonable model coefficients from other easily obtained empirical data, such as foraging rates, body size, metabolic rate, biomass distribution and other species traits, is likely to enhance greatly the link between theory and experiments (e.g. Yodzis & Innes 1992; Moore *et al.* 1996; Wootton 1997; Williams & Martinez 2001; Drossel & McKane 2003). These approaches will facilitate empirical contributions to model development (e.g. Peters 1983; Yodzis 2000). Theoretical contributions to empirical work will be greatly enhanced if the former focuses on response variables that are empirically tractable, such as permanence, invasion resistance, the number of secondary extinctions and patterns of population variation (Pimm 1979, 1980; Case 1990; Law & Morton 1996; McCann *et al.* 1998; Borvall *et al.* 2000; Ives *et al.* 2003).

New approaches to numerically simulating realistically large webs will also allow computer-based perturbation experiments to be tested directly against field and microcosm experiments (Caldarelli *et al.* 1998; Drossel *et al.* 2001; Williams & Martinez 2001; Quince *et al.* 2002; Montoya & Solé 2003). Until recently, most published dynamic food web models were limited to relatively few species (e.g. McCann *et al.* 1998). For example, using a typical Lotka–Volterra framework, the systems assembled by Law & Morton (1996) from a pool of 50–75 species have invasion-resistant endpoints of 4–6 species, although this seems to depend critically on the strength of interactions among species in the pool and connectance (Kokkoris *et al.* 2002; Jansen & Kokkoris 2003). For both this framework and the non-linear bioenergetic model developed by Yodzis & Innes (1992) and used by McCann & Hastings 1997) and McCann *et al.* (1998), persistent dynamics for systems beyond six species are difficult to generate without using biologically unrealistic species and interaction parameter values (Chen & Cohen 2001a,b; Williams & Martinez 2001).

Both numerical simulation and analytical approaches have different benefits and limitations and thus shed different but complementary light on food web dynamics. Simulations can provide information about food webs constructed using realistic population dynamics and other processes known to be present in real ecosystems (e.g. Drossel & McKane 2003). Ideally, they can allow for multiple metrics of interaction strength, including both measures of individual link properties as well as those of whole system responses, to be calculated simultaneously and compared. The power of complex simulations comes at the price of difficulty in interpreting model output or in determining the exact consequences of individual assumptions. With many parameters, numerical simulations quickly experience the curse of dimensionality, making it difficult to explore parameter space or conduct sensitivity analysis. Clearly, a simulation that is as complex as the reality it is trying to describe is unlikely to be very insightful. Analytical approaches to studying model food webs have the advantage of being elegant, simple and precise. They can offer clear heuristic insight into the consequences of individual assumptions. However, analytical solutions for food webs are limited currently to those that make many unrealistic assumptions. One hope is that numerical simulations of larger webs can facilitate the development of new analytical approaches to more realistic systems. Combining numerical simulations with community matrix analyses may help specify the conditions under which analytical solutions based on simplifying assumptions are reliable predictors of more realistic dynamical models. For example, when is local stability in the face of small perturbations a good predictor of stability or persistence in the face of more realistic large perturbations (Chen & Cohen 2001a,b)? Combining numerical and analytical approaches should allow more thorough explorations of the conditions under which different interaction strengths metrics are interchangeable with regard to relative magnitude, system responses, and species identity.

INTERPRETING RESULTS IN A BROADER ECOLOGICAL CONTEXT

Predation in context

Issues. Because food web models focus by definition exclusively on trophic interactions, they implicitly assume that predation is the most important process regulating community structure and dynamics. A long history of experimental and theoretical ecology has elucidated how predation interacts with other non-trophic processes, such as interference competition, facilitation, disturbance, environmental stress, productivity and recruitment, to regulate species distribution and abundance (e.g. Dayton 1971; Menge 1976; Bertness & Callaway 1994; Holt & Lawton 1994; Leibold 1996; Dodds 1997; Chase *et al*. 2002; Post 2002). While models of complex food webs implicitly incorporate exploitative competition among most species, they generally ignore any form of resource competition among the basal species (Lockwood *et al*. 1997; Borvall *et al*. 2000; Williams & Martinez 2001; Drossel & McKane 2003). Food webs lacking competition among basal species implicitly ignore extensive theoretical and empirical research on keystone predation and the role of resource competition in structuring assemblages of plants and other basal species (e.g. Grime 1979; Tilman 1982; Connell 1983; Schoener 1983; Goldberg & Barton 1992; Gurevitch *et al*. 1992; Menge *et al*. 1994; Leibold 1996; Power *et al*. 1996; Hooper 1998; Tilman *et al*. 1998; Huisman & Weissing 1999; Jansen & Mulder 1999).

Opportunities. Embracing this broader context opens the door to fruitful interactions with other ecological research programmes in order to integrate multiple processes that potentially regulate both food web structure and dynamics. Theoretical development must always find a balance between abstraction and relevant detail. It is easy to make a laundry list of processes known to *potentially* influence diversity, population dynamics and stability that should be incorporated into an emerging synthetic theory of food web structure and dynamics (e.g. non-trophic species interactions, disturbance, productivity, environmental stress, resource subsidies and dispersal). The critical challenge is to develop a rigorous framework for addressing the consequences of incorporating them or not. This framework will require both modifying food web models to include non-trophic processes as well as integrating these models thoroughly with empirical data.

A research programme that addresses both trophic *and* non-trophic processes is not necessarily one doomed to be plagued by detail; rather, it is an opportunity to explore more thoroughly the minimum detail required to explain the widest variety of observed food web patterns and dynamics. In the extreme case, it may identify conditions under which unweighted link structure alone is a reliable predictor of community stability, population dynamics, and/or system responses to a perturbation (e.g. Albert *et al.* 2000; Sole & Montoya 2001; Dunne *et al.* 2002). One challenge to incorporating non-trophic links (e.g. pollination, habitat provisioning and ecosystem engineering) in community models is that their broad patterns and prevalence are not as easy to specify as are feeding links. Toward this end, theoretical explorations that include non-trophic links will benefit greatly from empirical work that documents the subset of potential non-trophic interactions that are observed most commonly (e.g. Menge 1995), and how they vary with environmental conditions (e.g. Choler *et al.* 2001; Callaway *et al.* 2002). At the same time, if theoretical results suggest that certain patterns of non-trophic link placement have disproportionately strong effects on community dynamics, they can motivate empirical investigations into their prevalence in real systems.

Webs in space and time

Issues. Many of the data on food web structure and patterns of interaction strengths are snapshots in time and space (Lawton 1990), yet in reality both feeding links and interaction strengths vary over time and space, at the very minimum due to non-linear functional responses, predator interference and predator switching, variation in prey productivity and environmental conditions (e.g. Schoenly & Cohen 1991; Menge *et al*. 1994; Polis *et al*. 1995; Schoenly *et al*. 1995, 1996; Spiller & Schoener 1995; Tavares-Cromar & Williams 1996; Menge *et al*. 1997; Robles 1997; Sanford 1999; Woodward & Hildrew 2001; Schmid-Araya *et al*. 2002b; Navarrete & Castilla 2003). Most webs occur in a spatial context with potentially critical dynamic linkages across systems (Holt 1996, 2002; Polis & Hurd 1996; Menge *et al*. 1997; Polis *et al*. 1997; Menge 2000; Nankano & Murakami 2001; Finlay *et al*. 2003; Sabo & Power 2003a,b). Differences in the spatial grain of investigation also hinder productive links between food web models and experiments (e.g. Martinez & Dunne 1998). For example, in many small-scale predator exclusion experiments, prey effects on predators may be governed by predator immigration rather than population growth (Navarrete 1996; Navarrete *et al*. 2000). Ignoring the spatial context of food webs and the role of temporal and spatial variability may inhibit productive communication with other areas of ecology.

Opportunities. Incorporating spatial scale, external subsidies and open population dynamics into an emerging synthesis of food web structure and dynamics creates new opportunities for integrating basic and applied ecology, such as designing effective marine reserves to protect adjacent harvested food webs (e.g. Botsford *et al.* 2003; Carr *et al.* 2003; Lubchenco *et al.* 2003). The fact that multiple empirical snapshots of interaction strengths have yielded similar patterns of a few strong and many weak links may point to underlying space- and time-invariant constraints on this community-level property, even though the identity of the strongest links may vary. A better understanding of the relationship between spatial and temporal variation in individual link properties and spatial and temporal consistency in system-level properties may help to predict the potential for compensatory responses to buffer community level changes from perturbations of individual species (e.g. Walker 1992; Chapin *et al.* 1995; Frost *et al.* 1995; Tilman 1996; Ives *et al.* 1999b; Yachi & Loreau 1999).

Conclusions

Recent approaches to using interaction strengths as a focal point for integrating food web structure and dynamics have raised issues due to: (1) confusion about questions of interest; (2) confusion over the meaning of interaction strength; (3) a disconnect between theory and experiments; and (4) a lack of integration with other ecological research programmes. A common source of confusion lies in a lack of effective communication among research programmes that are driven by different questions and objectives. Converting these problematic issues into opportunities for progress requires: (1) clearly defining the questions addressed and identifying points of synthesis where apparently divergent questions emerge as two sides of the same coin; (2) recognizing fundamental differences among the variety of interaction strength metrics and searching for new approaches to relate the complementary insights they provide; and (3) actively making connections to existing ecological theory. This approach can help to reconcile variation in results, prevent false debates, guide new approaches to linking theory and experiments and identify avenues of potential synthesis. Throughout, it is critical to avoid confusing the ultimate goal with the assumed means to achieve it. If the goal is to integrate food web structure and dynamics, interactions strengths may be a useful conduit for discussion but not an endpoint.

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Appendix I

COMMON THEORETICAL MEASURES OF INTERACTION STRENGTH

Theoreticians commonly use a number of measures to quantify interaction strength. Originally these measures were based to the interaction coefficients of the Lotka–Volterra (L–V) interaction model, a_{ij} (e.g. Levins 1968). These interaction coefficients can generally be described without having to invoke a L–V model, as the change in the *per capita* growth rate of species i under a small change in the density of species j. Formally, this can be performed as follows. The change in the population density of species i over time is written as $\frac{dN_i}{dt} = N_i f_i(N_1, \ldots, N_n)$ where N_i is the density of species i and $f_i(N_1, \ldots, N_n)$ is the per capita growth rate of species i. We can now formally define the interaction coefficient as the partial derivative of the *per capita* growth rate of species i with respect to the density of species j, i.e.

$$a_{ij} = \partial \frac{1}{N_i}\frac{dN_i}{dt} \Big/ \partial N_j = \frac{\partial f_i(N_1, \ldots, N_n)}{\partial N_j} \qquad \text{eqn 1·1}$$

This measures the *per capita* level direct effect of species j on the *per capita* growth rate of species i (Laska & Wootton 1998). The interaction coefficients together form a matrix, to which we will refer generally as the *interaction matrix*, $A = [a_{ij}]$. For the L–V model the assumption is made that the interaction coefficients are constants. There is no a priori reason why this should be the case. Often it will be more appropriate to consider interaction strengths as functions of densities rather than as constants (see e.g. Hernandez 1998).

An alternative way of quantifying interaction strength is by measuring the change in the growth rate of the population of species i under a small change in the density of species j (the partial derivative of the *species* growth rate of species i with respect to the density of species j), i.e:

$$\partial \frac{dN_i}{dt} \Big/ \partial N_j = \frac{\partial [N_i f_i(N_1, \ldots, N_n)]}{\partial N_j} \qquad \text{eqn 1·2}$$

This equals $N_i a_{ij}$ if $i \neq j$ and $f_1(N_i, \ldots, N_n) + N_i a_{ii}$ if $i = j$. This measures the *per capita* level direct effect of species j on the population level growth rate of species i. These elements together form what we call the *community matrix*.

The notion of ‘community matrix’ in ecology was first articulated by Levins (1968), who used the interaction coefficients in an L–V interaction model scaled such that the diagonal entries were unity. Without this scaling, the community matrix coincides with the *Jacobi matrix* of the L–V system linearized at N^* (May 1974):

$$J = \mathrm{diag}\left\{ \dots , N_i^*, \dots \right\} A \qquad \text{eqn 1·3}$$

where diag{…} represents a diagonal matrix by listing its diagonal elements and $N^* = [\dots , N_i^*, \dots]^{\mathrm{T}} > 0$ is a (column) vector representing a feasible equilibrium. This provides a simple relationship between these two measures of interaction strength, but only at equilibrium. The *Jacobi matrix* can be used to analyse (at least, local) stability of the community at equilibrium (N^*). In this special case, it combines community structure and stability into a single analytically tractable formulation:

$$J \equiv [\partial(dN_i/dt)/\partial N_j \mid_{N^*}]. \qquad \text{eqn 1·4}$$

As in the case of the interaction matrix, this formulation can be generalized to non-L–V cases where the right sides of population equations admit formal differentiation. Although the Jacobi matrix is determined traditionally at an equilibrium point, it can be formally calculated at any point N, thus bearing a potential to describe, without the former stability sense, the state-specific pattern of interactions in the non-equilibrium community.

Since the time of May's formulation, the above matrices have often been referred to as the 'community matrix' or 'interaction matrix' (Clark & Hallam 1982; DeAngelis *et al*. 1986; Logofet 1994), leading to much confusion in the literature. The long persistence of various definitions is due partly to the fact the congeneric matrices differ only by multiplication with a positive diagonal matrix. This leaves the sign pattern invariant under any one of the above definitions. Unfortunately, this consistency among different formulations is not true for the stability analysis: it is only within *D-stable* matrices, a proper subset of the mere stable ones, that the interaction matrix, A, and the community matrix, J, always yield the same stability or instability result (Logofet 1993, 2004). Therefore, one can easily find an example of a stable yet not D-stable matrix (*ibidem*), so that a stable community matrix calculated by one definition would not be stable when calculated by a congeneric one. A further reason to be careful to distinguish between the two measures of interaction strength is that a weak (*per capita*) interaction coefficient of species j upon species i, a_{ij}, can still result in a sizeable interaction strength at the population level, $N_i a_{ij}$, if species i is abundant. This somewhat counterintuitive result is a direct consequence of the species-level definition of interaction strength that considers the per capita effect of species j on the population-level growth of species i. In the absence of a generally accepted nomenclature we urge authors to include clear definitions in future papers.

A third theoretical measure of interaction strength that has been proposed is the inverse of the *per capita* measured interaction matrix, A^{-1} (Bender *et al*. 1984). In Bender *et al*.'s model, elements of the inverse interaction matrix represent the change in the equilibrium density of species i in response to a change in the carrying capacity of species j. This measure represents the sum of the direct and indirect effects of the interaction.