

Interaction strength is a characteristic of ecological systems, most often used in studies of stability and robustness. There are about as many measures of interaction strength as there are studies on interaction strength and robustness, and they give different results. What makes a network stable? A particular pattern of interaction strengths (defined how?) The presence of “key” species (those that have the most or strongest interactions?)... The list goes on.

Interaction strengths can be approached either as a property of the individual links between species or as a property of a network as a whole. Here are some measures that have been used.

### **For individual relations:**

Coefficients in the Lotka-Volterra interaction matrices,  $\alpha_{ij}$

- can include non predator-prey interactions
- scaled

Assumptions:

- dependence, linearity, perturbations are small

Relative Prey Preference

$f \sim \frac{\text{(consumption of } i\text{th prey species)}}{\text{total consumption}}$

- easier to measure than Lotka-Volterra coefficients
- difficult to account for time evolution: doesn't allow prey preference (or interaction strength) to depend on prey abundance
- difficult to get an analytic result for the entire system

Total Biomass Flow:

- weight each interaction (represented by a matrix) by total amount of biomass flowing between links
- this technique is described in detail in the paper by Bersier et al.

### **For entire systems or networks:**

Link Density

- average # of links per node
- also assumes no time or density dependence
- system-wide measure (rather than individual measure)

Cluster Coefficient:

- likelihood of nodes being connected to the nearby nodes
- large CC ~ strongly interacting network

Shortest mean path length:

- average shortest path length between any two nodes
- small SMPL ~ stronger interactions

There's a great list with descriptions of different ways of looking at interaction strengths in Berlow et al. Here I've copied it and pointed out the particular strategies I looked at in more detail:

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 ( $\alpha_{ij}$ ) 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: ( $r^{-1}r^2$ )	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 <i>et al.</i> (2002)
Community (Jacobian) matrix	See Appendix I Partial derivative of one species' growth rate with respect to small changes in another species' abundance Units: ( $r^{-1}$ )	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 <i>et al.</i> (1995) Schmitz (1997) Ives <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (2001) Bersier <i>et al.</i> (2002) Cohen <i>et al.</i> (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 <i>et al.</i> (1998) Ives <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (2000) Solé & Montoya (2001) Dunne <i>et al.</i> (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 <i>per capita</i> 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 <i>per capita</i> 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 <i>per capita</i> 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 <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (1999) Montoya <i>et al.</i> (2003)

Here are the references I used, which give a more detailed picture of particular methods.

Berlow, Eric, et al. "Interaction strengths in food webs: issues and opportunities." *Journal of Animal Ecology*. 2004. **73**, pp. 585-98.

This paper is a great overview of the methodology, uses, and limitations of the various characterizations of interaction strength. It includes the summary table I inserted above, plus lots more explanation and discussion.

Bersier, Louis-Felix, Carolin Banasek-Richter, and Marie-France Cattin. "Quantitative descriptors of food-web matrices." *Ecology*, 83(9), 2002, pp. 2394-2407.

This paper uses experimental food web data to compare methods weighting the network by biomass flow.

De Ruiter, Peter C, Anje-Margriet Neutel, and John C. Moore. "Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems." *Science*. Vol. 269. 1 September 1995, pp. 1257-60.

This paper investigates patterns of interaction strength (top down vs bottom up) and their effect on ecosystem stability.

Sole, Richard V. and Jose M. Montoya. "Complexity and fragility in ecological networks." *Proc. R. Soc. Lond. B*. **268**. 2001, pp. 2039-2045.

This paper looks at patterns in ecological networks and relates them to network and ecosystem stability.