

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<br>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)<br>Units: ( $r^{-1}r^2$ ) | Property of individual link   | Can be explicit coefficients in a L–V equation<br>Includes non-trophic interactions<br>Simple relationship with the community matrix under some circumstances<br>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'<br>Assumes linear functional response or constant interaction strength for each directed link<br>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<br>Partial derivative of one species' growth rate with respect to small changes in another species' abundance<br>Units: ( $r^{-1}$ )   | Property of individual link   | Includes non-trophic interactions<br>Analytically tractable<br>At equilibrium, it gives information about local stability<br>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<br>Local stability analysis at equilibrium may not inform global stability in response to large perturbations and non-equilibrium situations<br>Values depend on species' population size<br>Assumes linear functional response or constant interaction strength for each directed link<br>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)<br>Schmitz (1997)<br>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)<br>Units: (nt)<br>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)<br>Yodzis (1988)                                   |
| Non-linear functional response | Number of prey consumed as a function of prey density and predator density or predator–prey ratios<br>'Top-down' measure of consumption intensity<br>Various units  | Property of individual link   | Interaction strength more realistically varies with prey and predator density<br>Critical for parameterizing dynamic models  | Real form in nature unknown<br>Non-linear function makes analytical solutions difficult unless clear equilibrium exists<br>Does not measure prey response<br>Difficult to measure for all but a few interactions, and difficult to measure in an uncontrived (or natural) setting  | Beddington (1975)<br>Abrams & Ginzburg (2000)<br>Ruesink (1998)                |
| Relative prey preference       | Fraction of a predator's maximum consumption rate that is targeted to a specific prey item<br>Top-down measure of consumption intensity   | Property of individual link when assigned a value in a model<br>Whole system property when measured empirically | Easy to tune in a dynamic model<br>Standardizes all IS relative to maximum<br>Empirically tractable  | Limited to numerical simulation<br>Difficult to interpret simulations because strengthening one link simultaneously weakens another<br>Does not measure prey response<br>Snapshot in time, will probably vary with the presence/abundance of alternate prey  | Yodzis & Innes (1992)<br>McCann <i>et al.</i> (1998)                           |
| Maximum consumption rate       | Measures maximum consumption per unit time on fixed abundance of prey<br>Measures 'top-down' potential consumption intensity  | Property of individual link   | Isolates potential direct effect on prey<br>A model parameter that is empirically tractable in field or laboratory   | Ignores functional response<br>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<br>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)<br>Bersier <i>et al.</i> (2002)<br>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<br>Difficult to explore parameter space if investigated with numerical simulations  | McCann <i>et al.</i> (1998)<br>Ives <i>et al.</i> (2003)?                                |
| Link density                     | Measures the number of ingoing and/or outgoing links to/from a species<br>Deletion 'experiments' focus on 'bottom-up' effects of prey on predator  | Whole system response<br>Node property rather than link property | Identifies boundary conditions for secondary extinctions (e.g. predator loses all its prey)<br>Identifies easily isolated species<br>Easy to measure            | Assumes links are temporally constant, and no prey switching if predator loses all prey species<br>Difficult to estimate effects of predator on prey<br>Cannot estimate effects of changes in prey or predator density | Solé & Montoya (2001)<br>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<br>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)<br>Solé & Montoya (2001)<br>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)<br>Measured either as a <i>per capita</i> effect or a species-level effect | Whole system response  | Characterizes visually dominant effects<br>Highlights effects on dominant species   | Difficult to compare across sites of varying productivity or spp. density<br>Snapshot in time/space (e.g. ignores functional response)<br>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<br>Measured either as a <i>per capita</i> effect or a species-level effect   | Whole system response  | Comparable across sites of varying productivity<br>Highlights effects on rare species   | Snapshot in time/space (e.g. ignores functional response)<br>Difficult to separate direct and indirect effects   | Paine (1992)   |
| Log response ratio               | Log of the ratio of prey abundance 'with' vs. 'without' predators<br>Measured either as a <i>per capita</i> effect or a species-level effect   | Whole system response  | Comparable across sites of varying productivity<br>Does not depend on equilibrium conditions<br>Works well for short-term experiments                           | Snapshot in time/space (e.g. ignores functional response)<br>Difficult to separate direct and indirect effects<br>IS approaches zero at equilibrium  | Berlow <i>et al.</i> (1999)<br>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<br>Includes non-trophic interactions   | Can be difficult to interpret mechanisms<br>Difficult to separate direct and indirect effects<br>Snapshot in time (e.g. ignores functional responses)  | Wootton (1994)<br>Pfister (1995)<br>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<br>Can estimate key parameters in discrete-time host-parasite models<br>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<br>Snapshot in time (e.g. ignores functional responses)  | Hawkins & Cornell (1994)<br>Müller <i>et al.</i> (1999)<br>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.