

Box 8.3 Interaction strengths and mutualism

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The strengths of interactions among species are key to understanding the structure and dynamics of ecological communities. Interaction strength is a diffuse concept, however, so care must be taken to identify precisely what it means in any given study, how it relates to ecological theory, and what motivates its empirical quantification. Recent reviews of the study of interaction strengths (Laska and Wootton 1998, Wootton and Emmerson 2005) identify four theoretical concepts that are aligned with most ecological studies: (1) the per capita effect of an individual of one species on an individual of another species; (2) the effect of one individual of one species on the population of another species near equilibrium; (3) the effect of a sustained input of individuals of one species on the equilibrium abundance of another; and (4) the effect of removing one species on the abundance of another. The first concept, which is often treated as a constant but can also be a nonlinear function that may include other species in the community, describes the parameters of functions in ecological models that govern changes in species abundances. Because of this strong link to theory, and its underlying influence on all other measures of interaction strength, it is often the most desirable to estimate empirically. The second concept estimates the direct effect of an individual of one species on the population of another, which is important in considering stability properties of communities. The third incorporates both direct and indirect effects of a species. The fourth includes both direct and indirect effects of a species, but also accounts for changes in the interaction network generated by a species. The latter measure has related to the most common experimental studies of species interactions. In general, generating empirical indices of interaction strength is most useful when explicitly linked to mathematical theory (Laska and Wootton 1998, Novak and Wootton 2008).

Quantifying interaction strengths has been largely targeted toward consumer–resource interactions of predation and competition (Wootton and Emmerson 2005). Estimating interaction strengths of consumer–resource interactions has included analysis of experimental manipulations of consumer density, observing consumption rates of individual consumers, inference based on fitting models to the dynamics of consumer and resource populations through time, and estimates based on energetic constraints and relationships with body size. In general, generating empirical estimates of interaction strengths in ecological communities has proven

to be challenging, with many approaches needing further experimental tests and validation.

For the study of interaction strengths of mutualistic interactions between species, two key questions arise: (1) Can methods designed for consumer–resource interactions be extended to mutualism? (2) Are alternative approaches better suited to mutualism? One complicating factor in transferring these methods to mutualism is that consumer–resource interactions have a very well-defined functional basis—the transfer of energy and/or nutrients from one organism to another. While most mutualisms involve the movement of energy and nutrients, mutualisms also involve other underlying mechanisms, ranging from ant defense against herbivores to propagule and gamete dispersal. Some of these components share key elements with consumer–resource interactions, notably the provision and consumption of food rewards, so commonalities exist (Holland and DeAngelis 2010), but in some other cases new empirical approaches may be required. Furthermore, some mutualisms turn out to be indirect interactions arising from linked consumer–resource interactions, so common approaches may well apply here as well (Holland and DeAngelis 2010).

Although still rare, studies of mutualism have begun to estimate interaction strength involving a number of species pairs. The focus has largely been on plant–pollinator (Vázquez et al. 2006, 2012) and plant–seed disperser interactions (Jordano 1987, Bascompte et al. 2006). These interactions involve active mobile species, sessile species, and often strong signaling among them, features that in combination facilitate direct observation of interactions and their longer-term consequences. Commensurate with this advantage, investigators have used an observational approach based on estimates of the (relative) frequency of recorded interactions (flower visits, fruits removed) among species pairs. In general, the ratio of interactions of species i to total interactions observed (i.e., relative frequency) has served as an index of the interaction strength of species i , although Vázquez et al. (2012) used independent data on reproductive output to generate indices of both per visit and estimated impacts of all visits to flowers to generate metrics in the spirit of per capita and total impact interaction strengths.

Relative frequency of observed interactions seems a reasonable first index to get a handle on relative interaction strengths among mutualistic species, as it likely contributes to net impacts of species on one another, and interesting patterns in the distribution of this metric across species pairs

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Box 8.3 *Continued*

and networks have arisen. For example, relative frequencies of species interactions exhibit skewed distributions (Bascompte et al. 2006, Vázquez et al. 2012), similar to those of consumer–resource interactions (Wootton and Emmerson 2005). Nevertheless, we ultimately want to compare interaction strengths of mutualism with other species interactions, and to use them in dynamic models of ecological communities. In this regard, further advances are needed to measure strengths of mutualism in the currency of population size or biomass. Pollination and seed dispersal involve only part of the plant life cycle, and these components of reproduction may not correspond, at least linearly, with plant population dynamics when stage- and density-dependent survival play important roles. The demographic consequences of dispersal and gene flow are poorly known. Hence, studies integrating these mutualistic effects within full demographic models may provide more insights. Relative frequencies also contain no information on the population size or biomass of interacting species, and as a result may not yield per capita effects and may well vary with population sizes. For example, a species with a high frequency of interaction may have traits that make each individual more effective at an interaction, or alternatively may simply have a high population size. Additionally, observed interactions could each involve a different individual, or could be the same individual returning to a plant multiple times, so per interaction effects may not mirror per capita effects. For species receiving food resources, the impact of the interaction will depend on the contribution of alternative food resources, which may not be quantified in the context of studies of mutualisms. Including more information on population sizes of interacting species and the dependence of population growth on the target life stages will be useful in future work. Despite these limitations, there is some evidence that relative frequencies of interactions sometimes, but not always, correspond to important demographic components (Vázquez et al. 2012).

Experimental approaches have also been used to study mutualism, although they have generally not quantified interaction strength for the purpose of modeling, and they have been limited to small modules of interacting species (Stanton and Palmer 2011). Conceivably, these could be expanded to estimate interaction strength more explicitly, although logistical issues limit the number of interactions that can be handled. These studies also usually focus on a portion of the life cycle of species, so efforts to incorporate these into a full demographic analysis are also needed.

Other approaches used in consumer–resource studies, such as energetic constraint approaches and community dynamics modeling, have not been widely applied to the study of mutualism. The former might be especially applicable to components of mutualistic interactions involving energetic resource transfer (Holland and DeAngelis 2010), although it needs more rigorous field experimental testing. The latter may also be powerful because it is a fairly flexible approach that can address multiple mechanisms of mutualism, though it will be necessary to generate detailed time series of mutualists' densities in communities to implement it. In any event, there appears to be substantial scope for transfer of methods from traditional studies of consumer–resource interactions to studies of mutualism, just as food-web studies have inspired new insights into networks of mutualistic interactions (Bascompte et al. 2006).

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