

Chapter 16

Simple and Complex Interactions

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16.1 Introduction

While the role of abiotic factors in governing species interactions is dealt with in various chapters of this book (e.g. Chap. 7 by Terlizzi and Schiel, Chap. 9 by Benedetti-Cecchi and Chap. 13 by Gili and Petraitis), we will focus here on the biotic factors that affect species interactions. Due to the large number of examples on biotic interactions, we can not and do not attempt to give a complete overview on this topic. Rather, we will present selected examples, mainly from competitive and trophic interactions among macroscopic individuals, describing the principal mechanisms that turn simple into complex interactions. One gradient of complexity concerns the number of interacting species. In this regard, we define the simplest level of species interactions as (1) among conspecific individuals and populations (intraspecific level), followed by interactions (2) between species (interspecific level), and how this reflects on (3) larger sets of species (community level), as the highest level of complexity. Orthogonal to this cline of complexity based on the number of participating species, a number of non-mutually exclusive factors further affect and complicate species interactions, including (1) context specificity, (2) variability, (3) modulation and (4) simultaneous action of several interactions (Fig. 16.1).

16.2 Intraspecific Interactions

Interference competition among conspecifics may represent one of the simplest forms of biotic interaction. Here, individuals of the same species directly affect each other. Antagonistic behaviours between conspecifics represent a commonly observed mechanism of intraspecific interference competition, which may lead to mortality rates as high as 10% of production (Cerda and Wolff 1993). From an ecological and evolutionary perspective, it is favourable to reduce injury or mortality rates among conspecific competitors, as this increases survival and fitness of each antagonist and, thus, benefits the species as a whole. An elaborated example of avoiding conspecific rivals to reduce aggressive encounters has been observed in

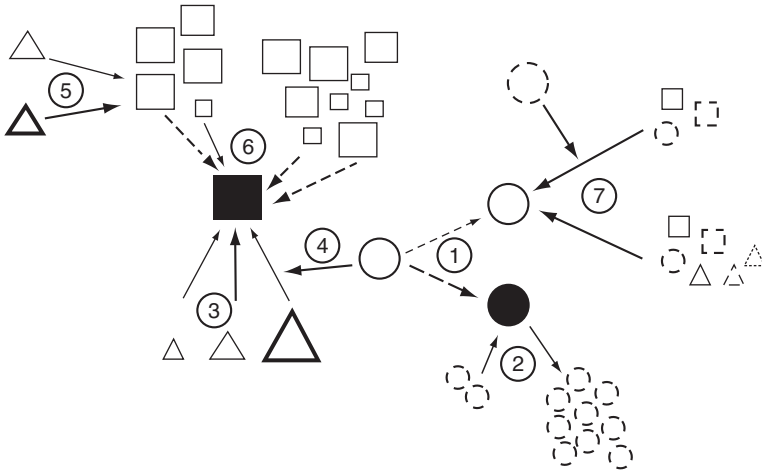


Fig. 16.1 Schematic interaction web showing different types of context-specific interaction (sex-dependent cannibalism (1), density-dependent predator–prey reversal (2), size-dependent optimal foraging (3)), modulation of interaction (trait-mediated indirect effects on, e.g. trophic interaction (4) and community structure (7)), variability of interaction (inducible responses (5)), and simultaneous actions of multiple interactions (size- and density-dependent effects (6)). *Circled numbers* refer to studies presented in the text. *Triangle* photoautotrophs, *square* herbivores, *circle* predators, *black* females, *white* males. Different line patterns of symbols indicate different species, thickness of symbol contours indicates different physiological or phenotypic states, thickness and direction of arrows indicate strength of interaction and flow of energy/competitive superiority respectively, and stippled and solid arrows indicate intra- and interspecific interactions respectively

populations of the sea anemone *Anthopleura elegantissima* (Ayre and Grosberg 2005). Clonal aggregations of this species expand and encounter other clones, among which distinctive anemone-free bands several centimetres wide are formed. These bands are a demarcation line, reflecting the current status of intraspecific interference competition between two clones. Competing clones exist of morphologically distinct casts of polyps, including scouts, warriors and reproductive individuals. Scout polyps explore the border area and, depending on their fate (death or repulsion), the scout-sending clone can organize heavily armed warrior polyps to coordinate the next attack, with the aim to repress the antagonistic clone.

Intraspecific interactions gain complexity if they are context-specific—e.g. by the density-dependency of effects. Positive density-dependent effects can result from beneficial effects under gregarious conditions, like protection against abiotic stress. For instance, crowding of barnacles (*Chthamalus anisopoma*) increased survivorship, due to increased resistance to desiccation (Lively and Raimondi 1987). In contrast, in several furoid algae an increase in density showed detrimental effects on plant growth (Choi and Norton 2005), with the result that intraspecific competition led to the death of conspecifics (self-thinning). Species traits may modify intraspecific interactions. For instance, sex can determine competitive superiority. The intensity of cannibalism is higher in male than in female crabs (Cerdeira and Wolff 1993).

Moreover, success of cannibals depends on age, with older individuals of *Carcinus maenas* foraging more effectively on conspecifics than do younger individuals (Moksnes et al. 1998).

Multiple context-specific interactions may simultaneously drive intraspecific interactions. For instance, Shuster and Wade (1991) demonstrated that species traits may interact with density-dependent effects in intraspecific competition (see 6 in Fig. 16.1). In their study, equal male mating success among three differently sized (=trait) morphs of the isopod *Paracerceis sculpta* was dependent on their relative densities. Large males defend harems within intertidal sponges and ensure paternity at low densities of conspecific males. However, by mimicking female behaviour and morphology, medium-sized males successfully enter harems and mate. Invasion of the dwarf males further increases male densities in sponges and alters the relative share to sire. Thus, within one species alternating density-dependent effects may occur, suggesting high context specificity in species responses that make predictions about their population structure and dynamics ultimately difficult.

16.3 Interspecific Interactions

Competition and consumption are direct and, therefore, relatively simple ways in which individuals of different species can interact. Exploitation competition is one form of competition in which detrimental effects on one organism are caused by the depletion of a resource through another organism that also requires this resource. The differential success of species in the depletion of a shared resource will cause asymmetrical competition. For this to happen, the superior competitor must use a limiting resource more effectively than does the other species. The competitive outcome may, however, vary with environmental conditions (Dudgeon et al. 1990) and, ultimately, with the physiological status of rivals, making predictions on the outcome in biotic interactions more difficult. Besides resource depletion, exploitation competition may also occur as a result of antagonistic behaviours. For instance, species may display antagonistic behaviours when competing for access to resources, like suitable substratum for settlement, which is often the most limiting resource for sessile organisms on rocky shores. Antagonistic behaviours among competitors may result in hierarchical competition webs if competitive abilities are fixed. However, the variability in interactions makes interspecific interactions more complex. For instance, competitive superiority may alternate between rivals, if the physiological status of opponents is variable. The stony coral *Oculina patagonica* is the superior competitor for space in the interaction with the bryozoan *Watersipora* sp. between bleaching events but becomes inferior during bleaching events (Fine and Loya 2003).

The study by Raimondi and Lively (1986) provides an example of how simultaneous positive and negative direct effects in species interactions complicate interspecific interactions. In their study, the herbivorous gastropod *Nerita funiculata* adversely affects the distribution of the hermit crab *Clibanarius digueti* by removal of hermit crab food. While this exploitation competition has a negative effect on the distribution

of hermit crabs, gastropods were disproportionately more beneficial to hermit crabs, as they are the only source of small-sized shells that small hermit crabs need for successful recruitment. Consequently, negative effects at the level of individuals are not reflected at the population level, strongly indicating that the outcome of interspecific competition is dependent on the relative importance of different resources that competitors require, like food and habitat (=shells) in the case of hermit crabs.

Relatively simple interspecific interactions are also known from trophic interactions. The direct effect of consumers on their prey leads to a sometimes dramatic removal of prey biomass. For instance, labrid fish consumed up to 95% of mussel recruits from experimental plots within 1 day (Rilov and Schiel 2006), and sea urchins are known to deforest kelp beds (Scheibling et al. 1999). The pronounced removal of habitat-forming species can have an important influence on the structure and functioning of benthic food webs at the level of seascapes (see Sect. 16.4). Besides the effects of larger consumers like fish and urchins, the smaller (<2.5 cm) meso-herbivores may also severely affect prey population structure when, for instance, early life stages are consumed (Chapman 1990).

Context specificity also occurs in trophic interspecific interactions, which depend on a large number of traits of the interacting species, for which we present here five examples, starting with size-dependent effects. The Optimal Foraging Theory predicts that consumers will prefer prey that maximises the ratio of energy uptake relative to energy used for foraging, handling and feeding (Stephens and Krebs 1986). Besides the identity, morphology or behaviour of the predator, prey characteristics like shell thickness (Brousseau et al. 2001), epibiosis (Laudien and Wahl 1999), induction of byssus thread production (Cote 1995) or the presence of shell-boring species (Buschbaum et al. 2006) can further complicate prey size selections by predators in opposing directions and with different magnitudes.

Additional traits known to complicate interspecific interactions include age, sex, dietary status and defensive status of interacting species. The age of prey has been shown to alter trophic interactions. For instance, juvenile dogwhelks (*Nucella lapillus*) take fewer risks when foraging in the presence of predatory cues (*Carcinus maenas*) than do adults (Vadas et al. 1994). Presumably, this behavioural trait change reflects the higher susceptibility of thin-shelled juveniles to crab predation. This effect was further dependent on the dietary status of the juveniles, with hungry whelks being less risk-sensitive than fed conspecifics (Vadas et al. 1994). A predator-induced reduction in grazing may have strong indirect effects on other parts of the food web (this chapter, 'trait-mediated indirect effects'). Finally, the defensive status of an organism will affect species interactions. An extensive theory on defensive species responses exists (summarized in Cronin 2001), like the Optimal Defence Theory, which predicts a positive correlation between the level of defence and the fitness value of an algal part (Rhoades 1979).

Besides species traits, numerical responses can complicate interspecific interactions in quite different ways. In benthic invertebrate and macroalgal populations, density-dependent effects are likely to occur at early life stages as a result of mass spawning. The importance of density-dependent effects includes (1) modification of competitive hierarchies among species (e.g. macroalgal seed banks; Worm et al. 2001),

(2) establishment of negative feedback loops in species interactions (Zabin and Altieri 2007), (3) simultaneous alteration of intra- and interspecific interactions (Clark et al. 1999) and (4) reversal in predator-prey relationships (Barkai and McQuaid 1988).

The mechanisms and processes we have considered thus far assume constancy in the responses of individuals, at least for a given life stage. Yet, formal models have been developed (Karban et al. 1999) and experimental evidence gathered that demonstrate that species traits change not only among life stages but also 'on demand' within one life stage. This temporal variability in species traits will ultimately modulate species interactions because patterns that might exist today may not be valid tomorrow, e.g. when defences have been switched on in response to increased consumption pressure and/or risk of consumption (Yun et al. 2007, see 5 in Fig. 16.1). Phenotypic plasticity in the responses of individuals from rocky shores, mainly alga/meso-herbivore interactions, have received increasing attention over the last 15 years (Toth and Pavia 2007). In this regard, benthic ecologists lag behind terrestrial colleagues, where more information exists on the biological responses, mechanisms and responsible chemical substances that trigger induced responses (Karban and Baldwin 1997).

Induced responses may concern morphological, behavioural and/or chemical traits, with many studies investigating the induction of chemical traits in several species of algae (Toth and Pavia 2007). The production of secondary metabolites may be induced to serve directly as anti-herbivory defences or these may be used as waterborne infochemicals to warn adjacent conspecific algae about actual or even potential grazer attacks (Yun et al. 2007). As an intrinsic part of inducible defence theory, defences can be switched off when threat-related cues diminish, thereby further complicating species interactions (Rohde et al. 2004). The ability of an organism to induce, rather than permanently exhibit defences carries several important ecological consequences for its bearer. First, Molis et al. (2006) observed consumer specificity in the induction of defences, indicating an ability of the defender to discriminate between the magnitude of consumption pressure exerted by different consumer species and, thus, optimise resource allocation (Cronin 2001). Second, inducible responses increase trait variability. For instance, the palatability of macroalgae in which anti-herbivory defences have been induced is variable in space and time, resulting in increased feeding dispersal (Borell et al. 2004) that, in turn, may lead to an as yet to be experimentally tested increased visibility of grazers to their predators. Third, intraspecific variation in palatability of seaweed species can lower herbivore fitness and, thus, indirectly reduce grazing impact (Toth et al. 2005). Finally, induced responses may affect indirect interactions with consequences on community structure (see Sect. 16.4).

The addition of a third species makes indirect effects possible, adding a new quality to interspecific interactions, which strongly complicates even the simplest interaction web. Indirect effects occur when the interaction between two species depends on the presence of a third species. Associative defences (bodyguard hypothesis) are an example of mutualistic indirect effects that may be generated by epibionts (Enderlein et al. 2003) or occur at larger spatial scales (Pfister and Hay 1988). The latter study demonstrated that mutualistic indirect effects may even occur between competitors

but also revealed the conditional nature of mutualisms. Indirect effects are highly context-dependent. The study by Coleman et al. (2007) of predator-mediated consumption of *Ascophyllum nodosum* by the herbivorous snail *Littorina obtusata* provides a clear example. In this tri-trophic interaction, crabs function as bodyguards. The release of waterborne cues by grazed algae is perceived by green crabs and used as infochemicals, guiding these organisms to their prey, i.e. *L. obtusata*. This effect is predator-specific, in that crabs responded to all cues, while fish responded only to cues released from snail-damaged but not from artificially damaged algae. Thus, the bodyguard function was tailored by and dependent on the quality of the 'emergency call' of grazer-attacked seaweeds. Informing the enemy of one's own enemy may be an effective way to foster indirect species interactions, as this may maximise predation success of higher-ranked consumers, especially if signals serve as guides to preferred, inconspicuous prey (Hay et al. 2004).

Between-species associations may also result in negative indirect effects in species interactions (shared doom, sensu Wahl and Hay 1995). For example, barnacle-fouled mussels share a higher predation risk than do clean conspecifics (Enderlein et al. 2003). This pattern was also displayed when barnacle mimics were used, suggesting that improved handling to open mussels, rather than additional food gain may drive crab predation. Furthermore, the Enderlein et al. (2003) study enabled a relative weighing of the ecological importance of indirect effects against other theoretical aspects in trophic interactions. Prey size was the primary control of mussel selection by crabs, corroborating the predictions of the Optimal Foraging Theory, while the indirect effects of epibionts were responsible for the fine tuning of predation success by crabs for a given prey size class.

Jormalainen et al. (2001) demonstrate that indirect effects in species interactions may be sex-dependent. Their study revealed within-alga (*Fucus vesiculosus*) differences in consumption according to gender in isopods (*Idotea baltica*), with males and females grazing apical and basal tissues respectively. As both tissue types exhibit different predation risks for isopods, males face a higher risk of being consumed by predators than do females. This ecological configuration may also pose evolutionary constraints, as males performed better on apical tissues—which pose a higher risk of predation—than on basal algal tissues, while performance (weight gain, intermoult duration) of females was comparable when reared on apical and basal tissues. Because size is more important for mating success of males than of females, males fed in a high predation-risk microhabitat to increase fitness, whereas females adapted to utilise the low-quality food of the safer basal microhabitat as efficiently as the high-quality food of the apical plant parts.

Indirect effects can be classified as density- or trait-mediated (Abrams et al. 1996). The former is a function of a numerical response of the intermediary species, while the latter involves the modification of the interaction between two species by a third species. This interaction modification can arise in two ways. First, indirect effects can result from an environment-mediated modification of interactions. Here, one species changes the environmental context that affects the interaction between two other species. For example, the brown seaweed *Dictyota menstrualis* chemically deters omnivorous fish, providing shelter from fish predation to the amphipod

Ampithoe longimana, which resists the fish-detering secondary metabolites of the alga (Duffy and Hay 1994). Second, indirect effects may occur from 'trait-mediated indirect interactions' (TMII; Abrams et al. 1996). The principal mechanism in TMII results from the non-lethal effect of species C on a trait of species A from an interaction pair A–B. Due to the altered trait of species A, the outcome of its interaction with species B will change (see 4 in Fig. 16.1). TMII seem to be more important in aquatic than terrestrial ecosystems (Preisser et al. 2005). Studies addressing TMII in rocky shore communities have emerged recently, with a strong emphasis on trophic interactions. Field studies by Trussell et al. (2002) indicated that the mere presence of crabs (*Carcinus maenas*) can reduce the activity level of their prey, the periwinkle *Littorina littorea*, which in turn relaxes grazing pressure on *Fucus* recruits. Interestingly, this *Fucus*–*Littorina*–*Carcinus* food chain has been a classical textbook example of a density-mediated indirect interaction (DMII). Furthermore, the sign and magnitude of TMII effects may change between safe and risky habitats, and the magnitude of TMII effects being comparable with or higher than that of DMII (Trussell et al. 2006). There are several reasons why the ecological relevance of TMII should exceed that of DMII (Peacor and Werner 2001; Preisser et al. 2005). First, TMII have immediate effects as soon as a modifying species enters a community, while DMII will not be immediately effective. Second, TMII affect entire populations. For instance, waterborne cues from green crabs influenced the behaviour of nearby snails; further assuming an even distribution of crabs in a given habitat, TMII should operate across a broad spatial scale (Trussell et al. 2002). In contrast, DMII will affect only that part of a snail population that falls prey to crabs. Third, TMII act over the entire period when cues are present. The disappearance of differences in snail density after green crabs were removed from experimental plots in the study by Trussell et al. (2002) clearly shows this immediate function of TMII. In contrast, DMII operate only at times when crabs kill prey. Finally, DMII attenuate through food chains, while TMII continue to be strong, as indicated by a more pronounced contrast in effect size between DMII and TMII when trophic cascades were considered in the meta-analysis by Preisser et al. (2005).

16.4 Community Interactions

The above examples from competitive and trophic interactions among up to three species form the basis for even more complex interactions, when these relatively simple interaction webs merge with each other at the community level. The review by Worm and Duffy (2003) highlights the importance of joining food web theory with biodiversity research, as consumers can modify the directionality of biodiversity–productivity–stability relationships that are derived from isolated studies of simple species interactions. Present empirical and theoretical knowledge of the effects of more species, adding trophic links to a community, has been reviewed by Duffy et al. (2007). These authors emphasise the role of multi-trophic interactions across trophic levels, rather than within one trophic level, as an important driver increasing

the variety of diversity-functioning relationships in ecosystems. Such multi-trophic interactions will partly depend on (1) the numbers of consumer and prey, (2) food chain length, (3) relative importance of top-down vs. bottom-up effects within a food web and (4) the level of plasticity of individual species-species interactions within a food web.

16.4.1 Multiple Predator and Prey Effects

Predation is one of the key factors governing patterns in natural communities but is usually understood from the perspective of a single predator species, rather than from a multi-species perspective. However, in nature each prey species is usually exposed to multiple predators, rather than to a single specialized one. Recent studies demonstrated that predator richness can have a strong effect on the efficiency of resource capture and, thus, ecosystem functioning (Griffin et al. 2008). This is particularly important in marine hard-bottom communities, where feeding specialization rarely—if ever—occurs (Hay 1992), in contrast to terrestrial habitats.

Although many trait-mediated indirect interactions (TMIIIs) are caused by changes in prey behaviour, less is known about the effects of changes in predator behaviour, such as prey switching, or multiple predator effects (MPEs) on indirect interactions, especially in marine systems. Thus, understanding emergent MPEs is a critical issue for marine community ecology. Few works have studied MPEs in marine communities (reviewed by Sih et al. 1998). Siddon and Witman (2004) tested for the presence of behaviourally mediated indirect effects in a multi-predator system. Here, the effects of crab (*Cancer borealis*) as well as crab and lobster (*Homarus americanus*) predation (=MPE treatment) on sea urchins (*Strongylocentrotus droebachiensis*) were quantified in three habitats (algal beds dominated by the green seaweed *Codium fragile*, barrens, and mussel beds), representing differing combinations of food and shelter, to examine the effects of prey switching by crabs. The study revealed that the presence of lobsters modifies crab behaviour, thereby dampening changes in community structure. These results illustrate the importance of predator behaviour and habitat context in modifying consumer pressure and community structure, and argue for the consideration of these factors in other multi-predator systems where habitats represent food and/or shelter.

The diversity of prey can also influence consumer impact. Hillebrand and Cardinale (2004) conducted a meta-analysis of 172 laboratory and field experiments that manipulated consumer presence to assess their effects on freshwater and marine periphyton, and concluded that grazer effects on algal biomass tend to decrease as algal diversity increases, indicating that periphyton communities characterized by higher species diversity are less prone to consumption by grazers. Diversity of prey may enhance the probability of inedibility and/or of positive interactions. The presence of non-edible prey is generally expected to reduce the efficiency of consumer–prey interactions. Less known, however, are the effects of prey defences on predator–predator interactions. When prey have non-specific defences

(i.e. those that can be moderately effective against more than one predator), the addition of a second predator is expected to result in an increase in anti-predator behaviour (or perhaps in chemical defences) and a reduction in predation by both predators, i.e. risk reduction (Sih et al. 1998).

Consumers may also have pervasive indirect impacts on community organization when prey strongly interact with other species in the community. Depending on the timing of the interaction, the carnivorous whelk *Acanthina angelica* kills the barnacle *Chthamalus anisopoma* or induces a predation-resistant morph, which resulted in strong differences in species composition of intertidal communities between sites where the predation-induced morph was present or absent (Raimondi et al. 2000). Indirect effects can thus extend well beyond the particular prey taxa consumed. One classic demonstration of this phenomenon is the fundamental change in community structure after the removal of the starfish *Pisaster ochraceous* from a northeast Pacific rocky intertidal habitat (Paine 1974). Despite its relatively low abundance, *Pisaster* removal resulted in a dramatic reduction in species diversity because its main prey, the mussel *Mytilus edulis*, was competitively dominant and excluded other species when released from predation.

By linking two or more direct interactions together via intermediate species involved in two interactions, 'trophic cascades' emerge in which, e.g. the impact of a top predator indirectly affects the biomass of photoautotrophs. Perhaps the best documented example of a trophic cascade, ranging over four trophic levels, comes from the northeast Pacific and includes killer whales (*Orcinus orca*), sea otters, urchins and kelp (*Macrocystis*) beds (Estes and Duggins 1995). Sudden increases in killer whale predation on otters were correlated with pronounced decreases in otter densities, increases in sea urchin biomass and grazing intensity, and dramatic declines in kelp abundance. In fact, humans may have long been causing periodic shifts between urchin barrens and kelp communities by acting as top predators in the role played by killer whales, by overharvesting sea otters and then allowing these to recover, resulting in what Simenstad et al. (1978) called alternate stable state communities.

In contrast, if prey have conflicting predator-specific defences, then predators would have mutualistic effects on each other (reviewed by Sih et al. 1998). Complex interactions such as these are poorly known in the marine environment but are expected to occur. Many benthic marine invertebrates and algae have physical (i.e. sclerites, spicules, spines, hard exoskeletons, tunicae, etc.) and chemical adaptations against predators, generally as non-specific defences (e.g. Amsler 2008). We do know whether these defences can, in some cases, have conflicting effects, on one hand protecting against generalist predators but, on the other hand, exposing the organisms to more specialized consumers that may even use defences as cues signalling the presence of prey (Avila 2006). These defences can even be sequestered and employed by consumers as a defence against their own predators by a variety of consumers, such as molluscs and some crustaceans.

However, the effects of defences against predators at the community level are hardly known in marine communities, although they have long been postulated to be important in maintaining high species diversity in marine benthic communities.

An example given to illustrate this is associational defence in communities dominated by one or more chemically defended macroalga species. Hay (1986) shows that increasing abundance of one or a few species does not necessarily lead to decreased species richness within the community. In seasons with higher fish abundance, the in situ frequency of species associated with *Sargassum filipendula* and *Padina vickersiae* increased. Similar patterns occurred in microcosm experiments. In fish-inclusion treatments, a significant positive correlation between the cover of *Sargassum* and *Padina* and the number of other species present was found, so that species richness increased as the community became dominated by *Sargassum* and *Padina*. This seemed to result from the unpalatable species creating microhabitats of lowered herbivory that then facilitated the invasion of palatable species, which were excluded by herbivores if these refuges were not available. TMIs may also be considered in this context, as changes in the density of one species that are caused by induced changes in one or more traits of an intervening species can affect community structure by altering the nature of indirect effects that are mediated through intervening species (e.g. Raimondi et al. 2000). The role of environmentally induced polymorphisms on species interactions and, ultimately, on the structure of hard-bottom communities will be one logical next step in community ecology studies.

In conclusion, we emphasised in this chapter that, in addition to the number of interacting species, context specificity, variability, modulation and simultaneous actions of multiple interactions complicate interactions among individuals. Furthermore, phenotypic plasticity within individuals generates temporal variation in environmentally triggered species traits, and the only recently recognized role of trait-mediated indirect interactions in ecological systems suggests ubiquity of and far-ranging effects on species interactions due to this plasticity. Single experiments may be of limited help in assessing species interactions, as they can sample only a subset of possible species configurations. Thus, the resulting evidence on species interactions from one site or season does not enable extraction of generalities about a studied phenomenon. Due to the strong context dependency of species interactions, future studies should strive for replication in space and time to better understand and predict the causes and consequences of simple and complex species interactions for the functioning of ecological systems.

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