

REVIEW AND SYNTHESIS

How context dependent are species interactions?

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Abstract

The net effects of interspecific species interactions on individuals and populations vary in both sign (–, 0, +) and magnitude (strong to weak). Interaction outcomes are context-dependent when the sign and/or magnitude change as a function of the biotic or abiotic context. While context dependency appears to be common, its distribution in nature is poorly described. Here, we used meta-analysis to quantify variation in species interaction outcomes (competition, mutualism, or predation) for 247 published articles. Contrary to our expectations, variation in the magnitude of effect sizes did not differ among species interactions, and while mutualism was most likely to change sign across contexts (and predation least likely), mutualism did not strongly differ from competition. Both the magnitude and sign of species interactions varied the most along spatial and abiotic gradients, and least as a function of the presence/absence of a third species. However, the degree of context dependency across these context types was not consistent among mutualism, competition and predation studies. Surprisingly, study location and ecosystem type varied in the degree of context dependency, with laboratory studies showing the highest variation in outcomes. We urge that studying context dependency *per se*, rather than focusing only on mean outcomes, can provide a general method for describing patterns of variation in nature.

Keywords

Coefficient of variation, community context, conditionality, distributed outcomes, interaction strength, meta-analysis.

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INTRODUCTION

Variation in the outcome of interspecific interactions is common in nature. This variation is commonly described as context dependency: the sign or magnitude of the effect on fitness changes as a function of the biotic or abiotic context in which the interaction occurs. Many studies have documented variation in the outcomes of species interactions (Appendix S1). For example, interspecific interactions between plant species varied with elevation in a global study: competition dominated at low elevations where abiotic stress was relatively low, but facilitation dominated at high elevations where abiotic stress was higher (Callaway *et al.* 2002). Similarly, interaction strengths between predatory *Pisaster* seastars and *Mytilus* mussels varied more in space than in time, and species abundances were important drivers of this variation in interaction strength (Menge *et al.* 1994).

On ecological time scales, variation in interaction outcomes can generate variation in population growth as well as in community properties, such as food web structure and stability. For example, insect herbivory on cholla cactus in the Chihuahuan Desert varies among populations along an altitudinal gradient: stronger herbivory at low elevation slows cactus population growth rates, while weaker herbivory at high elevation allows faster population growth rates (Miller *et al.* 2009). At the community scale, when species interactions are more variable, interactions that form links in food web compartments may stray outside these compartments, decreas-

ing compartmentalisation of the web (Miller & Travis 1996; Travis 1996) and food web stability (Kokkoris *et al.* 2002; Stouffer & Bascompte 2011). On evolutionary time scales, variation in the outcomes of species interactions influences natural selection on species traits (Thompson 2005). For example, variation in the strength of protection conferred by ants resulted in different selection pressures on extrafloral nectary traits that attract ants to wild cotton plants in the Sonoran Desert (Rudgers & Strauss 2004).

Despite substantial evidence that the magnitude and sign of species interactions vary with context, the extent of context dependency and the drivers of this variation have not been well characterised (Benedetti-Cecchi 2000; Inouye 2005; Agrawal *et al.* 2007; Fraterrigo & Rusak 2008). Thompson (1988) was among the first to review the evidence for variation in interspecific interactions, and many studies since then have examined context dependency in individual cases (Appendix S1). However, a quantitative meta-analysis comparing context dependency across different class of species interactions has been mostly lacking. Morris *et al.* (2007) conducted a meta-analysis of 160 studies of plant performance in which the presence of putative plant mutualists and plant enemies were crossed factorially, and tested for context dependency via interactive effects. In another study, Larimer *et al.* (2010) compared plant performance with single symbiont species to the interactive effects of multiple symbiont types. As in other prior meta-analyses, these studies examined *mean outcomes* within each species interaction (or study). Here, we consider

context dependency *sensu stricto* by quantifying variation in the outcomes of species interactions, rather than focusing on mean outcomes.

Although the study of context dependency has been a major theme in mutualism for two decades (Thompson 1988; Bronstein 1994), context dependency has received less formal attention in other classes of species interactions. A key question is whether certain species interactions vary in outcome more than others. The mutualism–parasitism continuum hypothesis (Johnson *et al.* 1997; Karst *et al.* 2008) proposes that mutualisms commonly grade into parasitism as contexts vary, suggesting that context dependency in mutualistic interactions is particularly likely. Mutualisms may show greater context dependency than antagonisms if weaker mean interaction strengths indicate greater variation. While some biological phenomena display increasing variance with larger means (Taylor 1961), empirical evidence suggests that species interactions with weaker average effect sizes are weaker precisely because they are highly variable in magnitude across contexts (Berlow 1999). Previous reviews have found that mean interaction strengths are largest for predation, intermediate for competition and the smallest for mutualism (Sih *et al.* 1985; Gurevitch *et al.* 1992; Morris *et al.* 2007), consistent with a hypothesis that mutualisms will show the greatest context dependency. An alternative mechanism that leads to the same prediction involves energy transfers: predation results in more direct, one-way flows of energy between species than does competition, which often relies on indirect transfers of energy via an external resource (e.g. exploitative competition for prey or nutrients; Wootton 1994). Mutualisms can have even more complex energy transfers than competition because they can require bidirectional energy transfers (e.g. carbon transfers to mycorrhizal fungi and nutrient transfers to plant) or the presence of additional species (e.g. natural enemies are required for benefits to accrue in protection mutualisms), thus opening up these interactions to greater opportunities for variable outcomes. Thus, we predicted that mutualisms would show the greatest context dependency, followed by competition, then predation.

Variation in interaction outcomes often occurs along gradients, for example, shifting abiotic conditions (e.g. temperature; Daskin & Alford 2012), seasonality and phenology, or variation in the abundance of a third-party species (i.e. one that modifies a focal interaction between two other species, Wootton 1994). For example, competition between two plant species can be altered in the presence of an herbivore (e.g. Schädler *et al.* 2007). Often context dependency is studied along simple gradients in space and/or time, which likely encompass a number of changes in context. Although much research has documented variation in the net effects of species interactions (Thompson 1988; Menge *et al.* 1994), the relative importance of different kinds of gradients for generating this variation remains largely unresolved.

Using meta-analysis, we compared the magnitude and sign of variation in species interaction outcomes among three major classes of species interactions: competition, predation and mutualism. For each context, we first quantified the magnitude of the effect of each species interaction on the fitness of the target species using an effect size metric (Armas *et al.*

2004). For each study, we then quantified context dependency using two response variables: the coefficient of variation (*CV*) of the effect size among contexts (e.g. years or sites); and the sign change of the interaction outcome (+, 0, –) across contexts within a study. *CV* measures the amount of total variation with respect to the mean outcome. For example, a study for which the effect size of competition on the fitness of a target competitor species was similar across levels of nitrogen availability would have a low *CV*, whereas a study that showed a competitive response was very strong under low nitrogen but very weak under high nitrogen would have a high *CV*. In contrast, sign change reports only whether an interaction outcome significantly changed in sign between positive (+), neutral (0), or negative (–) outcomes, without incorporating the magnitude (i.e. effect size) of the interaction. To be clear, a change in sign does not necessarily imply a change in the mechanism of the interaction. For example, an interaction between aphid-tending ants and aphids in the presence vs. absence of aphid enemies (e.g. parasitoids) may vary in outcome from positive to neutral, but ants still gather honeydew from aphids in both cases.

We used meta-analysis of the *CV* and sign change from 247 published articles to address three questions: (1) Do classes of species interactions (competition, predation, or mutualism) or types of context gradients (abiotic, spatial, temporal, third party) differ in the magnitude of variation in effect size across contexts, as measured by the coefficient of variation? (2) Do classes of species interactions or context gradients differ in their propensity for the interaction to change sign? (3) Does the magnitude of variation or the propensity for sign change differ among study locations or ecosystem types?

MATERIALS AND METHODS

Literature search and data set description

We aimed to locate studies that altered a species interaction across more than one context and that measured correlates of fitness for a target responder species. We searched for relevant studies using two general methods. First, we searched for studies in previous meta-analyses examining interspecific competition, predation, or mutualism (Gurevitch *et al.* 1992; Chase *et al.* 2002; Kaplan & Denno 2007; Holt *et al.* 2008; Chamberlain & Holland 2009). We focused on these three types of species interactions because appropriate studies are well represented in the literature and they have contrasting interaction signs for each partner (–/–, +/–, and +/+ respectively). Second, we searched Web of Science for experimental studies of predation [keywords: ‘(pred* and prey) AND experiment*’], competition (‘competition AND experiment*’) and mutualism [‘(mutualis* OR pollinat* OR mycorrhiza* OR rhizobi* OR endophyte) AND experiment*’], refined to include ‘ecology’ articles only. We then applied the following selection criteria: (1) The study measured the responses of individual organisms to experimental manipulation of one of the following interaction classes: interspecific competition, predation, or mutualism. Observational studies that performed natural or uncontrolled experiments were not included; while this excludes many studies, only manipulations can determine

Table 1 Summary of the independent variables examined in the meta-analysis

Variables	Description	Levels of variable
Species interaction class	Categorical fixed-effect variable	Competition Predation Mutualism
Context-dependency gradient	Categorical fixed-effect variable The gradient along which variation in the species interaction outcome in question varied	Abiotic (nutrients, etc. manipulated) Spatial (multiple sites) Temporal (data collected over time) Third-party presence (third party, e.g. predator in a competition study)
Location	Categorical fixed-effect variable Location of study	Laboratory Greenhouse Field Outdoor mesocosm (aquatic or terrestrial)
Ecosystem	Categorical fixed-effect variable Ecosystem in which study was conducted	Freshwater Marine Terrestrial

causality. (2) The study measured response variables under more than one context (e.g. in multiple years or sites); this restricted our set to studies informative on context dependency. (3) The study provided estimates of the mean response, sampling dispersion around the mean (e.g. standard deviation, standard error) and sample sizes for each treatment. Appendix S1 provides references for all publications used in the analyses.

When multiple response variables (e.g. growth rate and fecundity) were reported for the same individuals, we calculated the effect size for each response variable separately (see Effect size calculations). We then took the mean effect size across different types of response variables to obtain the average response. When data were available for multiple dates, we collected all data and averaged the effect size over time, except in cases for which we explicitly examined temporal variation as a context gradient. When data were replicated over multiple factors, we recorded all data and averaged across the other factors other than the context of interest. For predation studies, we excluded all studies ($n = 3$) from the final data set that measured the response only in the predator; thus, all predation studies reported here measured the prey response.

Independent variables

Data on several independent variables were collected at the scale of each study (Table 1). Species interaction classes had one of three values: competition, predation, or mutualism. Data were categorised into one of four gradients of context dependency: abiotic, spatial, temporal, or third party presence (Table 1). *Abiotic variation* occurred when outcomes were measured across either a well-documented environmental gradient or in specific habitat types that varied in a known abiotic factor (e.g. sand vs. mud habitat; Bonsdorff *et al.* 1995). *Spatial variation* included studies for which outcomes were simply measured across different geographic sites, with no *a priori* inclusion of abiotic gradients, and thus may represent biotic and/or abiotic spatial variation. *Temporal variation* occurred when outcomes were measured at multiple points in

time, ranging from hours to years depending on the system (e.g. Barnes & Archer 1999). *Third-party variation* captured studies of the same pairwise interaction most typically in the presence vs. absence of an additional species (e.g. competition between plant species in the presence/absence of aphids; Schadler *et al.* 2007). There were too few studies (generally < 10 per interaction class) spanning gradients of intraspecific variation (e.g. body size, developmental stage) or in the abundance of one species to permit analysis of these context gradients, highlighting these as potential contexts worth exploring in future work.

Study location and ecosystem type

We collected data on both study location and ecosystem type (Table 1). We categorised study *location* as one of four values: laboratory, greenhouse, mesocosm (aquatic or terrestrial enclosed containers), or field (natural setting, not in containers), and *ecosystem type* as one of three values: marine, freshwater, or terrestrial. We expected greater variation in effect sizes in field studies than in greenhouse studies, and the least variation in laboratory studies, reflecting differences in the degree of experimenter control over variables that could generate context dependency. Previous studies have documented that species interactions do (predation; Preisser *et al.* 2005) or do not (herbivory; Hillebrand 2009) vary in their mean effect sizes among ecosystems. We tested here, for the first time, whether ecosystems differed in how variable their effect sizes were across contexts. Analyses of less biologically relevant variables, including study duration, sample size, the year the study was published and journal impact factor are presented in Appendix S2.

Effect size calculations

We calculated effect sizes as the relative interaction intensity:

$$RII = (\bar{x}_C - \bar{x}_E) / (\bar{x}_C + \bar{x}_E),$$

and variance of *RII* following Armas *et al.* (2004). For a given response variable, *RII* is the difference in the means of

the control treatment (*C*) vs. the experimental treatment (*E*, here, in the absence of the species interaction), standardised by the summed means. We chose *RII* because of its excellent statistical properties. It is bounded between 1 and -1, is symmetrical around zero, and is negative for species interactions that negatively affect the focal species and positive for mutualisms. The symmetry was particularly important as it allowed us to compare the effect sizes of positive and negative interactions on the same scale by taking the absolute value of *RII*. Hedges' *d* was not useful for this study because of its unbounded range.

We calculated the coefficient of variation (*CV*) for *RII* among records within a study as: $CV_{RII} = (\sigma_{RII} / \bar{x}_{RII}) \times 100$, where σ_{RII} is the standard deviation of *RII* across all contexts within a study, and \bar{x}_{RII} is the mean of *RII* across all contexts within a study. We then calculated the unbiased estimator of CV_{RII} as $CV^*_{RII} = (1 + 1/4n)CV_{RII}$, which corrects for small numbers of contexts (Haldane 1955), an important correction because studies varied widely in the number of contexts examined (mean ± 1 SEM = 3.86 ± 0.18 , range = 2–31). CV^*_{RII} has a variance of $v_{CV^*} = ((1 + 1/4n)_{SCV})^2$ (Sokal & Rohlf 1969), where *n* is the number of independent contexts used to calculate the CV^*_{RII} for each study. For meta-analysis on CV^*_{RII} , we used the inverse of the product of the sample size per treatment combination and the number of contexts examined to estimate the within study variance, which gave the smallest variance estimates to studies with high replication both within treatments and across contexts (Hedges & Olkin 1985). When specifying variances in all models described below, we used fixed variance estimates (PARMS statement specifying EQCONS in SAS, following Van Houwelingen *et al.* 2002). We considered using the variance of CV^*_{RII} , but this resulted in a bias, with the largest CV^*_{RII} always having the largest variance estimate because the response variable (CV^*_{RII}) is part of the variance calculation.

We determined whether the interaction significantly changed sign (hereafter 'sign change'), either between zero (0) and negative (-), zero (0) and positive (+), or negative (-) and positive (+). Sign change differs from CV^*_{RII} in that it explicitly quantifies whether the interaction changed in direction, not just in magnitude. For each context within a study, we first calculated the sign of the interaction (-1, 0, 1) from the effect size. Effect sizes that did not significantly differ from zero (using a 95% confidence limit, as $RII \pm 1.96(\sigma_{RII}/\sqrt{n})$, where σ_{RII} is the standard deviation of *RII* and *n* is the sum of replicates from each record) were considered neutral (0) for the focal species. Then, we determined whether the sign significantly changed across contexts (no sign change in any response variable = 0, sign change in at least one response variable = 1).

Statistical analyses

Because some studies explored multiple gradients of context dependency (e.g. variation in both time and space), we maximised representation across the types of context gradients by using an algorithm to pick data for the least represented context for any study that examined multiple types, resulting in one record per publication in our final data set. Thus, analyses are not confounded by non-independence due to multiple

records from the same study. Five studies were excluded from the analyses due to extremely high weights resulting from very low variance or high sample sizes. The following are descriptions of analyses for the questions posed in the Introduction.

(1) *Do classes of species interactions or context gradients differ in the magnitude of variation in effect size?* Data were analysed with a generalised linear model that included the fixed effects of context gradient (Table 1) and species interaction class (competition, predation, or mutualism), as well as their interaction (SAS v. 9.2, SAS Institute, Cary, NC, USA). In all models, we included a random intercept using PROC MIXED (SAS v. 9.2). CV^*_{RII} was log transformed to achieve normality of residuals and homogeneity of variances. When the species interaction class \times context gradient term was significant, we decomposed differences among classes of species interactions with *post hoc* Tukey HSD tests within each context gradient.

(2) *Do classes of species interactions or context gradients differ in their propensity for the interaction to change sign?* For sign change (binary response variable) we used a logit function, following the same workflow and within study variances as for Question 1.

(3) *Does the magnitude of variation or the propensity for sign change differ among study locations or ecosystem types?* We were interested in whether study location and ecosystem type had a main effect on context dependency and whether such an effect differed among species interaction classes or context gradients, suggesting that the locations and system studied influenced the ability to detect context dependency. We included study location and ecosystem type individually in models testing for statistical interactions with the species interaction class and the context gradient. Interaction terms tested whether differences in context dependency among the three classes of species interactions (or four context gradients) varied with study location or ecosystem type (Table 1). If factors interacted with species interaction class and/or context gradient, we used Tukey HSD tests to decompose interactions.

RESULTS

Magnitude of variation in effect size

CV^*_{RII} spanned six orders of magnitude (range: 0.4–18,227), but on average, there were no significant differences among species interaction classes in the magnitude of variation in interaction outcome magnitude, as quantified by CV^*_{RII} (Fig. 1a, Table 2). This result leads us to reject the prediction that *on average*, mutualisms are more variable in magnitude than competition and predation interactions. However, this measure of context dependency did vary among context gradient types. CV^*_{RII} was the smallest for studies of third-party presence [mean (95% CL), different letters indicate significant differences = 0.52 (0.44–0.61)*a*], followed by temporal [0.67 (0.60–0.74)*b*], spatial [0.75 (0.65–0.87)*b*] and abiotic gradients [0.81 (0.71–0.93)*b*], which showed the greatest CV^*_{RII} . In addition, species interactions differed in their degree of context dependency along all four context gradients (Fig. 2, interaction class \times context gradient, $P < 0.0001$, Table 2). Along

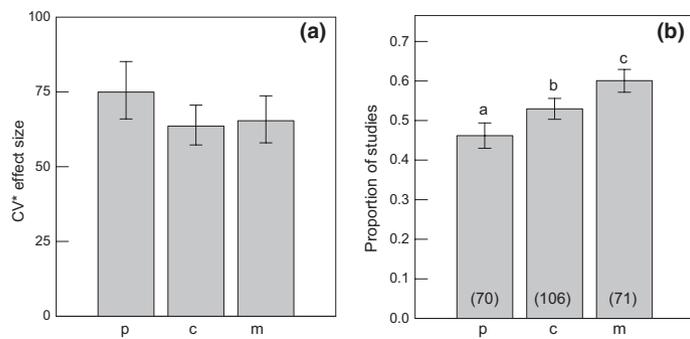


Figure 1 Differences among classes of species interactions (p = predation, c = competition, m = mutualism) in (a) the CV^*_{RII} , and (b) the proportion of studies showing a change in the sign of the interaction (among -, 0, and + outcomes). Bars show back-transformed least squares means \pm 95% confidence intervals. Different letters indicate significant differences between classes of species interactions ($P < 0.05$) according to *post hoc* Tukey HSD tests. Sample sizes for each interaction class are provided on bars.

Table 2 Summary statistics for the analyses of CV^*_{RII} of the effect size and for the change in the sign of the interaction (binary: 0 = no change, 1 = changed)

Effect	df	CV^*_{RII}		Interaction sign change	
		F	P	F	P
Species interaction class	2, 235	2.06	0.1295	19.67	<0.0001
Context gradient	3, 235	6.82	0.0002	86.17	<0.0001
Interaction \times Context	6, 235	12.80	<0.0001	17.21	<0.0001

abiotic gradients, CV^*_{RII} was 45% greater for predation than competition, and neither differed from mutualism which had an intermediate value of CV^*_{RII} (Fig. 2). As an example for predation, the magnitude of the effect of trout on prey abundance was extremely variable ($CV^*_{RII} = 4582$) across six different substrates, with a strong negative effect on prey on sand substrates, but a positive effect on prey abundance on a pondweed substrate (see Fig. 3 in MacNeil *et al.* 1999). In contrast, belowground plant competition for the mustard *Rorippa austriaca* varied little ($CV^*_{RII} = 6$) across nutrient levels (see Fig. 2 in Dietz *et al.* 2002). Spatial gradients showed the same rank order as abiotic gradients: CV^*_{RII} was 72% greater for predation than competition, with mutualism, again, intermediate (Fig. 2). Along temporal gradients, CV^*_{RII} was 139% greater for competition than mutualism, and 68% greater for competition than predation (Fig. 2). Finally, along third-party gradients, CV^*_{RII} was 92% greater for mutualism than competition (Fig. 2). Two representative studies highlight this difference. In a study of plant-fungal endophyte mutualism, growth of the grass *Festuca rubra* was quite variable in response to the presence/absence of a third-party herbivore ($CV^*_{RII} = 562$) (see Fig. 1 in Clay *et al.* 1993). In contrast, a plant competition study found that competition outcomes between *Medicago polymorpha* and *Lotus wrangelianus* were not nearly as variable with herbivore presence ($CV^*_{RII} = 1.9$) (see Fig. 5 in Lau & Strauss 2005).

One possible confounding factor influencing the ability to detect differences among species interaction classes is the number of contexts examined for each interaction class. However, we found no significant differences in the number of contexts examined among the classes of species interactions [mean number of contexts \pm SE [range], competi-

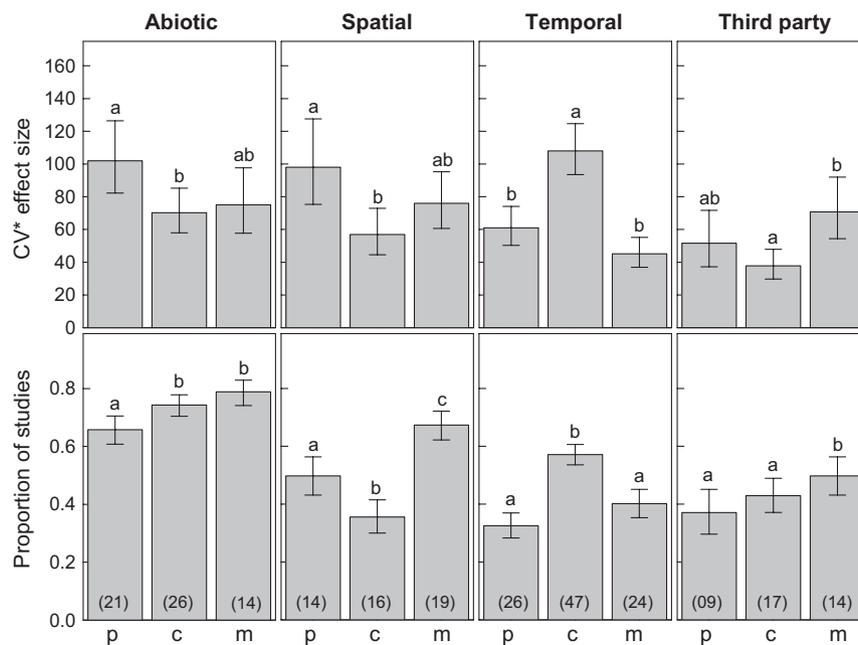


Figure 2 Differences in the CV^*_{RII} of the effect size, and the proportion of studies showing a change in the sign of the interaction among classes of species interactions (p = predation, c = competition, m = mutualism) and contexts: abiotic, spatial, temporal and third-party presence. Bars show back-transformed, weighted least squares means \pm 95% confidence intervals. Within each context gradient, different letters indicate significant differences between classes of species interactions ($P < 0.05$) according to a Bonferroni-corrected pairwise test within each context type. Sample sizes are provided below labels on bars.

tion = 2.9 ± 0.25 (2–31); mutualism = 2.9 ± 0.23 (2–18); predation = 2.8 ± 0.32 (2–24); $F_{2,235} = 0.18$, $P = 0.83$). Some context gradients were more frequently studied than others ($F_{3,235} = 18.2$, $P < 0.0001$). Specifically, studies on third-party effects had the fewest contexts examined (often just two: presence vs. absence of the third-party species), significantly fewer than for temporal gradients. Abiotic gradients had the next fewest number of contexts studied, followed by studies of spatial variation (Table 1). Studies of temporal variation had the most contexts examined, significantly more than studies of abiotic, spatial or third-party gradients (see also Appendix S3).

Propensity for interactions to change sign

On average, the likelihood that an interaction changed in sign across contexts was highest for mutualism, intermediate for competition and lowest for predation (Fig. 1b, Table 2). This result was consistent with our prediction that mutualism would be the most variable class of species interaction, and predation the least variable. However, the difference between mutualism and competition, although significant, was small in magnitude, at only 7% (Fig. 1b). In contrast, the proportion of mutualism studies showing a change in sign was 14% higher than for studies on predation. It may be surprising that studies of predation showed evidence of a change in sign at all; however, this effect occurs when the predator manipulation has no significant effect on prey under one context, but a significantly negative effect on prey under another context (see also Appendix S3). It is also possible for predation to have a positive effect on prey individuals that remain in a population after a predation event (e.g. prey may benefit from the removal of intraspecific competitors by the predator). Contrasting studies serve to illustrate these results. The sign changed in an interaction between an arbuscular mycorrhizal fungus species (*Scutellospora dipurpurens*; Gigasporaceae) associated with a plant species (*Teucrium scorodonia*; Lamiaceae) over three nutrient (phosphorous, P) levels. Specifically, *S. dipurpurens* positively increased plant biomass only at the highest P level, while outcomes were neutral at low and intermediate P levels (Helgason *et al.* 2002). In a competition study, the sign of the interaction between two *Daphnia* species (*D. pulicaria*, *D. galeata mendotae*; Branchiopoda: Diplostraca) did not change over the course of 3 months (Hu & Tessier 1995).

Like CV^*_{RII} , the sign change varied significantly among context gradients (Table 2). Mean sign change was the smallest for studies of third-party presence [mean (95% CL), different letters indicate significant differences = 0.43 (0.39–0.47)a], followed by temporal [0.43 (0.40–0.46)a] and spatial context gradients 0.51 (0.47–0.55)b], with the greatest propensity to change sign for abiotic gradients [0.73 (0.71–0.76)c]. This result, combined with patterns observed for CV^*_{RII} , suggests that regardless of the class of species interaction, variation in third-party species is the least likely (of the mechanisms that we investigated) to generate context dependency, and abiotic gradients are the most important source of context dependency.

Also like CV^*_{RII} , the sign change responded to the combined influence of species interaction class \times context gradient

(Fig. 2, Table 2). However, results for the change in the sign of the interaction did not necessarily correspond to results for variation in the magnitude of the effect size, as captured by CV^*_{RII} (compare rows in Fig. 2). Under variable abiotic conditions, a change in the sign of the interaction was more likely for mutualism, less so for competition, and the least likely for predation. Under spatial variation, a change in the sign of the interaction was most likely for mutualism, less so for predation, and the least likely for competition. Under temporal gradients, there was a greater propensity for sign change in studies of competition than in studies of predation and mutualism, a pattern that matched the results for CV^*_{RII} . Finally, under third-party contexts, there was a greater propensity for sign change in mutualism than either competition or predation.

Variation due to study location or ecosystem type

We expected that experiments conducted under more controlled conditions would show less variable species interaction outcomes. Testing the location effect across species interaction classes, we in fact found the opposite pattern, with the highest CV^*_{RII} in laboratory conditions [mean CV^*_{RII} (95% C.I.) = 264 (198–351)a], and the second highest CV^*_{RII} in the greenhouse [86 (73–101)b]. The other two environments [mesocosm = 68 (53–88)bc and field = 64 (59–68)c] did not differ significantly from one another (location effect: $F_{3,243} = 32.3$, $P < 0.0001$, different letters indicate significant differences from Tukey HSD). Interestingly, the greatest propensity for sign change was also found under laboratory conditions [mean% of studies (95% CI) = 82% (78–86%)a], followed by greenhouse [74% (70–77%)b], then field [48% (47–50%)c], and finally mesocosm studies [42% (36–48%)c; location effect: $F_{3,243} = 81.6$, $P < 0.001$].

CV^*_{RII} showed divergence among ecosystems ($F_{2,228} = 6.7$, $P = 0.002$), with the highest CV^*_{RII} in non-marine, aquatic ecosystems [mean CV^*_{RII} (95% CI) = 85 (70–104)a] and terrestrial ecosystems [74 (67–82)a] and a significantly lower CV^*_{RII} in marine ecosystems [45 (33–60)b]; different letters indicate significance from Tukey HSD], indicative of less variable interaction outcomes. Ecosystems also differed in this measure of context dependency for particular species interactions (species interaction \times ecosystem, $F_{5,228} = 3.2$, $P = 0.008$) and context gradients (context gradient \times ecosystem, $F_{9,228} = 5.3$, $P < 0.0001$). Notably, terrestrial ecosystems were the only ones to show variation among species interaction types, with predation outcomes significantly more variable [93 (73–118)a] than mutualisms [61 (54–69)b], and competition falling in the middle [71 (64–79)ab]. The propensity for changes in the sign of the interaction varied among ecosystem types differently than for CV ($F_{2,228} = 6.6$, $P = 0.0016$), with a sign change more likely in marine [mean% of studies (95% CI) = 69% (62–75%)a] and terrestrial ecosystems [63% (60–65%)a], and least likely in non-marine, aquatic studies [55% (50–59%)b]. The propensity for sign change also depended on the class of interaction (species interaction \times ecosystem, $F_{5,228} = 66.5$, $P < 0.001$). In terrestrial ecosystems, mutualisms were the least likely to change sign relative to both competition and predation, thus showing the same pattern as for CV .

In aquatic ecosystems, competition showed a marginally greater propensity to change sign than predation, whereas the opposite pattern occurred in marine ecosystems. The proportion of studies in each ecosystem that showed a sign change additionally depended on the context type (context gradient \times ecosystem, $F_{9,228} = 139.0$, $P < 0.001$). For terrestrial ecosystems, spatial and temporal contexts were the most important source of variation in both CV^*_{RII} and sign change, with no significant differences among the other context types, and relatively small differences among the context types overall. For aquatic ecosystems, spatial and abiotic conditions had similarly high CV and propensity for sign change, followed by temporal contexts, with the lowest variation observed for third-party contexts. For marine ecosystems, third-party presence and abiotic contexts were the most likely to change the sign of the interaction (89–95%), followed by temporal contexts (39%), with spatial contexts (16%) being the least variable in sign, perhaps due to the more spatially homogenous marine environment relative to terrestrial or freshwater aquatic (e.g. pond) ecosystems. However, patterns for marine environments differed for CV^*_{RII} , with the smallest variation observed under third-party contexts, illustrating that a change in sign of the interaction outcome does not necessarily generate the largest values of CV .

DISCUSSION

Variation in the outcomes of interspecific interactions can have substantial ecological and evolutionary significance. Our meta-analysis of 247 published studies revealed significant variation in the degree of context dependency among different classes of species interactions and among different types of context gradients. The results indicate that, as predicted, among all classes of interactions, mutualisms were most likely to change in sign under different ecological contexts. However, variation in interaction strength (measured by the CV) was not substantially greater for mutualism than for competition. Our results additionally suggest that indirect species interactions resulting from ‘third-party species’ are, on average, weak sources of variation in pairwise species interactions, whereas abiotic gradients (in resources or abiotic stress) are rich sources of variation in the outcomes of pairwise species interactions.

Why is mutualism the most variable species interaction and predation the least variable?

Mutualisms may show greater context dependency than antagonisms because they have on average weaker mean interaction strengths, which may lead to greater variation. In addition, mutualisms show greater complexity in energy transfers than antagonisms (see Introduction). While the magnitude of variation in interaction outcomes (CV^*_{RII}) did not differ overall among classes of species interactions, variation in the sign of interaction outcome was the greatest for mutualism, slightly (7%) lower for competition, and the least for predation, consistent with our initial hypotheses that mutualisms would be more variable than other classes of species interactions. While mutualism and competition did not strongly differ in either metric of context dependency, it was clear that

mutualisms were more likely than predation to show a change in the sign of the interaction across contexts. The simplest explanation may be that within a predation interaction there are only costs to prey, while there are benefits and costs to predators. Prey experience costs when killed (density-mediated) or when they give up resources due to behavioural modification in the presence of predators (trait-mediated; Preisser *et al.* 2005), and predators experience benefits (gain resources) and costs (e.g. search and handling time). While predators never benefit the individual prey they consume, the magnitude of the negative effect on prey populations may vary. In contrast, resource exchanges in mutualisms can carry costs and benefits for both partners (Jones *et al.* 2012). For example, in a pollination mutualism, the plant gains the service of pollination, while pollinators get food (i.e. both partners benefit); however, at the same time, plants invest resources in attraction and pollinators invest time and energy searching out and handling food (both partners experience costs). Under a wide range of circumstances, the costs of mutualism can outweigh the benefits for one or both partners (Bronstein 2001). Thus, we posit that interaction outcomes in mutualism may be more variable than in predation because the greater complexity of resource exchanges in mutualisms increases the number of possible outcomes and range of possible interaction strengths.

Additional factors may contribute to differences among species interaction classes. For example, differences among interaction classes could be confounded with study system if attributes of the study organism contribute to variation in interaction strengths and outcomes. In our meta-analysis, mutualism studies largely involved plants (81%), predation studies mostly involved invertebrates (76%), while competition studies involved a mix of species (including 54% plants and 35% invertebrates, Appendix S3). In addition, mobility differed among interaction classes: 14% of species were mobile in mutualism studies, 87% in predation and 41% in competition. We could not test for a taxonomic effect due to lack of sufficient replication; however, we did find that the degree of mobility had no effect on our results by testing for an effect of mobility on both CV and sign change (data not shown). Lifespan, behaviour and plasticity could also contribute to observed differences, and could be a focus of future research.

Context dependency among classes of species interactions depends on the type of context

Species interactions differed in how much they varied among context gradients. A few patterns stand out. First, for both third-party and spatial contexts, mutualism had a significantly higher propensity to change sign than did either predation or competition. In some mutualisms, such as ant–plant protection (Heil & McKey 2003), the presence of a third party is required for benefits to accrue (Bronstein & Barbosa 2002). In other cases, it has been well documented that a third party alters the magnitude of costs and benefits accrued. For example, in the *Greya* moth–*Lithophragma parviflorum* pollination mutualism, whether *Greya* is beneficial to the plant depends on the presence of other (less costly) pollinator species, whose abundance varies strongly among sites (Thompson & Cunn-

ingham 2002). It may be the variation in this third party that underlies the high context dependency of some mutualisms (including across spatial locations), since variation is responsive to the dynamics of not just two, but three species (Fedriani *et al.* 2004). However, some types of mutualism do not require a third party. Thus, we expect protection mutualisms to show greater context dependency than transport (e.g. pollination, seed dispersal) or nutritional (e.g. plant-rhizobial) mutualisms given the requirement for a third-party species. The observed rankings of species interactions were similar for spatial and third-party contexts, with mutualism showing greater variability than competition or predation, suggesting that variation in the presence of third-party species (i.e. the biotic context) may be an important source of the variation observed across sites in the landscape.

Second, under temporal variability, competition showed both higher magnitude of variation in effect size and had a higher likelihood to change sign than either predation or mutualism. Exploitative competition depends on underlying resource gradients (e.g. among plants competing for nutrients or water), and prior work has documented that competition can shift to facilitation when abiotic stress is particularly high. For example, seasonal changes between dry and wet seasons shifted competitive interactions between wild ungulates and cattle to facilitative outcomes (Odadi *et al.* 2011). Intra- and interseasonal shifts in abiotic resources may be likely to cause greater variation in competition than in other interaction types, although if temporal variation primarily reflects shifts in abiotic conditions, it is surprising that abiotic contexts do not show more similar patterns to the temporal contexts.

Last, although predation varied the least overall, it varied more in magnitude, but less in sign change, along abiotic gradients than did other interaction classes, suggesting that predation interactions can vary in interaction strength, but are more constrained (than other classes of interactions) against changing sign because the interaction rarely deviates from being beneficial to predators and detrimental to prey.

Patterns of context dependency among study approaches and ecosystems

The study approach can lead to differences in the *mean* outcomes of species interactions (Preisser *et al.* 2005; Hillebrand 2009), and may similarly influence the degree of *variation* in outcomes. Surprisingly, laboratory studies had the highest variation in magnitude of outcomes, and the greatest proportion of cases of sign change, despite the expectation that variation would be lowest in the most controlled studies, where 'noise' can be best eliminated. This unexpected result may stem from the ability of laboratory studies to control other (non-target) sources of variation, and thereby to more effectively isolate the effects of different contexts on interaction outcomes – thus, accentuating variation along the studied gradient.

In addition, we found studies in terrestrial and freshwater systems had greater magnitudes of variation than did studies in marine systems, but that terrestrial and freshwater studies did not differ in their degree of context dependency. Marine ecosystems may be more buffered from context dependency than terrestrial or freshwater systems if there is less spatial

and temporal variability in biotic and abiotic conditions. Certainly, ocean temperatures show much less seasonal variation than do land temperatures, and ocean environments can experience the homogenising influence of higher connectivity due to large-scale movements of ocean currents, than many terrestrial and freshwater (e.g. ponds, small streams) ecosystems. Evidence from other work supports our finding. For example, Thackeray *et al.* (2010) found that phenological shifts in response to climate change have been greater in freshwater and terrestrial species than in marine species, which could be a source of variability in species interaction outcomes. Another important pattern was that the type of context gradient that generates the most variation in outcomes varied among ecosystems. For example, spatial and temporal contexts were the greatest sources of variation in terrestrial ecosystems, but abiotic and spatial contexts were the most important in freshwater ecosystems. These general patterns beg the question: Why would major drivers of variation in interaction outcomes differ among ecosystems?

Methodological considerations for studies on context dependency

In general, studies of longer duration tended to show greater variation in interaction outcome (Appendix S2), which is not surprising because with time, outcomes deviating from the mean are more likely to happen purely by chance. We also found that more recently published studies showed greater variation in magnitude, but were less likely to show a change in sign of the interaction outcome. Declines in the degree of sign change may indicate increasing pressure to publish less variable results or increasingly refined experimental approaches designed to minimize variation. Journal impact factor also influenced our detection of context dependency. Due to the differential emphasis on context dependency for mutualism vs. antagonism, it may not be surprising that mutualism studies documenting high context dependency tended to be published in journals with higher impact factors than highly context-dependent results from studies of antagonism (Appendix S2). In addition, competition and predation showed weaker relationships with journal impact factor overall.

Species abundances and relative frequencies within communities are important sources of context dependency in species interactions (HilleRisLambers *et al.* 2012) that were not included in our review. Indeed, context dependency does not only occur across environmental gradients, but can occur within them due, for example, to variation in dispersal and recruitment, abundance, or size-structured interactions. As an example, Bishop *et al.* (2008) showed that interaction outcomes between a predatory snail (*Conuber sordidus*) and prey mud whelk (*Pyrazus ebeninus*) varied greatly depending on the body size of the prey, with the greatest effect of predator on prey with medium size prey, and no effect on large prey. Our initial data set included 28 studies that investigated some aspect of species' abundance as a source of context dependency, but this type of context lacked sufficient replication across species interaction types to be included in the final analysis, with particularly low representation of mutualism studies relative to those on predation and competition, highlighting a gap in current literature.

Future directions

Two questions are of particular importance to address: (1) What factors contribute to variation in interaction outcomes? and (2) What are the ecological and evolutionary consequences of variation in interaction outcomes? Directly manipulating variation in interaction outcomes empirically would be difficult, but empirical studies could pair experimental manipulations of gradients (e.g. nitrogen gradient) with data on species interaction outcomes along that gradient (e.g. outcome of plant–mycorrhizal interaction along the gradient), then examine further ecological or evolutionary responses (e.g. natural selection on traits as a function of variation in interaction outcomes). Modelling studies could explore consequences of variation in interaction outcomes for populations, communities and evolution by manipulating variance.

Studies are clearly needed that compare variation in interaction outcomes for other major interaction classes, including herbivory and parasitism. This research is essential to broadening our understanding of when and where species interactions are most variable. Both herbivory and parasitism are $+/-$ interactions like predation, so we predict similarity in their patterns of ecological outcome variation. However, many mutualisms grade into parasitism. Thus, parasitic interactions may more closely follow trends for mutualism. This study combined responses at the individual and population scales. Although individuals vary in their interaction outcomes, populations may be more buffered from fluctuations that occur at the individual scale and therefore less likely to show context dependency.

Summary

The study of context dependency has been a major theme in mutualism (Thompson 1988; Bronstein 1994; Kiers *et al.* 2010). In contrast, variation has not been a strong topic of interest in other interspecific interactions and may, in fact, interfere with the primary objective of the study. We urge that studying context dependency *per se* (rather than focusing only on mean outcomes) provides a general method for describing patterns of variation in nature. Incorporating context dependency may advance progress in ecological understanding.

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AUTHORSHIP

All authors designed the study; SC collected meta-analysis data sets and compiled data; SC and JR performed analyses; SC, JB and JR wrote the manuscript.

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