Quantitative synthesis of context dependency in ant–plant protection mutualisms

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Abstract. Context dependency, variation in the outcome of species interactions with biotic and abiotic conditions, is increasingly considered ubiquitous among mutualisms. Despite several qualitative reviews of many individual empirical studies, there has been little quantitative synthesis examining the generality of context dependency, or conditions that may promote it. We conducted a meta-analysis of ant–plant protection mutualisms to examine the generality of context-dependent effects of ants on herbivory and plant performance (growth, reproduction). Our results show that ant effects on plants are not generally context dependent, but instead are routinely positive and rarely neutral, as overall effect sizes of ants in reducing herbivory and increasing plant performance were positive and significantly greater than 0. The magnitude of these positive effects did vary, however. Variation in plant performance was not explained by the type of biotic or abiotic factor examined, including plant rewards (extrafloral nectar, food bodies, domatia), ant species richness, plant growth form, or latitude. With the exception of plant growth form, these factors did contribute to the effects of ants in reducing herbivory. Reductions in herbivory were greater for plants with than without domatia, and greatest for plants with both domatia and food bodies. Effect sizes of ants in reducing herbivory decreased, but remained positive, with latitude and ant species richness. Effect sizes in reducing herbivory were greater in tropical vs. temperate systems. Although ant–plant interactions have been pivotal in the study of context dependency of mutualisms, our results, along with other recent meta-analyses, indicate that context dependency may not be a general feature of mutualistic interactions. Rather, ant–plant protection mutualisms appear to be routinely positive for plants, and only occasionally neutral.

Key words: ant–plant interaction; conditionality; context dependency; domatia; extrafloral nectar; food body; herbivory; interaction strength; meta-analysis; protection.

Introduction

Although species interactions are often described by their outcomes, including predation (+, −), competition (−, −), mutualism (+, +), and commensalism (+, 0), they are not static, but vary along a continuum in which outcomes grade into one another. The causes and consequences of context dependency, or variation in interaction outcomes with biotic and abiotic factors, has attracted increasing attention (Bronstein 1994, Agrawal et al. 2007). Understanding whether interactions are generally context dependent, and what factors contribute to context dependency, can aid in our understanding of species interactions. Attention to context dependency is particularly widespread in the study of mutualistic interactions, which are now commonly thought to readily degrade into commensalism or parasitism under a variety of conditions. In keeping with empirical studies and qualitative reviews highlighting its importance (Bronstein 1994, Herre et al. 1999, Hay et al. 2004, Holland et al. 2005, Stadler and Dixon 2005, Bronstein

et al. 2006, Sachs and Simms 2006, Heath and Tiffin 2007, Rico-Gray and Oliveira 2007, Romero et al. 2008), context dependency has even been touted as one of the few generalizations that can be made of mutualism (Bronstein 1994, Holland and Bronstein 2008). Yet, the generality of context dependency of mutualism has not been examined quantitatively. In fact, a recent meta-analysis of plant–mycorrhizal mutualisms revealed routinely positive, rather than context-dependent effects of ectomycorrhizae on plant biomass and growth (Karst et al. 2008).

Ant–plant protection studies have contributed greatly to our perception that context dependency is a common feature of mutualistic interactions (Bronstein 1994, 1998). The effects of ants in reducing herbivory and increasing plant performance (growth, reproduction) may not always be positive (mutualism), but may also include neutral (commensalism) or negative (parasitism) effects. Moreover, given that ant–plant protection interactions involve a third party (herbivores), interaction outcomes between ants and plants may be more prone to context dependency than other mutualisms not involving a third party (e.g., pollination). Indeed, ant–plant protection interactions are not universally mutualistic, and may depend on local biotic and abiotic

conditions in which interactions occur (e.g., Gastreich 1999, Kersch and Fonseca 2005). For example, ant species identity and abundance were both important in determining variable plant benefits of ant protection in desert (*Gossypium hirsutum*) and tropical (*Dioscorea praehensilis*) plant species (Di Giusto et al. 2001, Rudgers and Strauss 2004). Several qualitative reviews have recently synthesized studies of ant–plant protection interactions, highlighting key progress in our understanding of them and their contributions to our knowledge of mutualism, including context dependency (Beattie 1985, Davidson and Epstein 1989, Huxley and Cutler 1991, Davidson and McKey 1993, Jolivet 1996, Bronstein 1998, Heil and McKey 2003, Bronstein et al. 2006, Rico-Gray and Oliveira 2007). Nonetheless, we currently have no quantitative synthesis of the generality of context dependency for ant–plant protection interactions or the biotic and abiotic factors contributing to it.

In this study, we examined the extent of context dependency in ant–plant protection mutualisms using meta-analysis, a technique that incorporates variation in the precision and statistical power of individual studies (Gurevitch and Hedges 1999, Gates 2002). If ant effects on herbivory and plant performance are routinely context dependent, then mean effect sizes (ratio of plant response with ants to that without ants) are predicted not to deviate from 0. Alternatively, if ant–plant interactions are regularly mutualistic, rather than context dependent, then mean effect sizes of ants in reducing herbivory and increasing plant performance are predicted to be positive and greater than 0. Although herbivory increasing with ant presence seems counterintuitive, ants are known to displace non-ant predators of herbivores (Mody and Linsenmair 2004, Izzo and Vasconcelos 2005), and are known to act as florivores (Yu and Pierce 1998). Thus, ant effects on both herbivory and plant performance can range from negative to positive. In addition to testing these predications for overall ant effects on plants, we also examined if these predictions for the effect sizes of ants on plants varied with several biotic and abiotic conditions. First, the effects of ants on plants may vary with the rewards supplied by plants (domatia, extrafloral nectar, and food bodies), which mediate their consumer–resource interactions with ants (Holland et al. 2005). Also, obligate interactions are often associated with domatia-bearing plants that house ant colonies (myrmecophytes), whereas non-domatia-bearing plants do not house interacting ants (myrmecophiles; Davidson and McKey 1993). Second, because plants that interact with ants range from herbaceous annuals to long-lived trees, the benefits of ants may vary with plant growth form (Bronstein 1994). Third, the number of ant species interacting with a plant may influence effect sizes of ants, possibly through interspecific competition among ants (Stanton 2003, Miller 2007). Fourth, variation in the effects of ants on plants may occur with latitude, given that ant–plant interactions span tropical, subtrop-

ical, desert, and temperate ecosystems. Last, we examined if herbivory and plant performance benefits varied with methodological practice and if our results were contingent upon the file drawer effect (the practice of not reporting negative results) for insignificant results. While a number of other important biotic and abiotic factors may be important to the context dependency of ant–plant interactions, we examined the above factors as they were most commonly reported among published studies (Appendix).

Methods

We surveyed the primary literature using Web of Science and citations within reviews of ant–plant protection interaction studies (Davidson and McKey 1993, Bronstein 1998, Heil and McKey 2003, Bronstein et al. 2006). We included studies that performed ant exclusion experiments (ants removed or prevented from accessing plants) and those that used the natural presence and absence of ants on plants. We assigned each study to one or both of two plant responses: herbivore damage and herbivore density (hereafter, herbivory), and plant growth and reproduction (hereafter, plant performance). For both herbivory and plant performance, we used mean values for records that were not independent (e.g., different years, populations, study sites, or multiple measures of the same response variable). We included each plant species when more than one was reported within a single paper. We combined records among studies of the same plant species. Importantly, we only incorporated studies into our data set that reported error estimates along with mean values. The data set includes 76 studies, representing 64 plant species in 28 families (Appendix).

We quantified the effect size of ants on herbivory and plant performance using the response ratio, as it assumes that effects are multiplicative, which is likely more biologically appropriate than assuming additive effects (e.g., Hedges' *d*; Sih et al. 1998). We performed statistical analyses, and graphically depicted results, using the ln-transformed response ratio, *L*, as it is less sensitive to errors in the denominator of the effect-size ratio denominator (Hedges et al. 1999). Although the response ratio is usually calculated as $L = \bar{X}_E / \bar{X}_C$, where $\bar{X}_E$ and $\bar{X}_C$ are means of experimental (ant exclusion) and control (ant access) groups, respectively, *L* was inverted and calculated as $\ln(\bar{X}_C / \bar{X}_E)$. In this way, the sign of the effect size reflects negative or positive effects of ants on plants. For herbivory, we reversed the sign of the effect of ants on herbivory prior to calculating the effect size to express the effect size in a consistent manner with that of ants on plant performance. Thus, when $L = 0$, ants had no effect on herbivory or plant performance; when $L > 0$, ants had a positive effect on plants by reducing herbivory or increasing plant performance; and when $L < 0$, ants had a negative effect on plants by increasing herbivory or reducing plant performance.

For each set of analyses described next, we estimated mean effect sizes ($\bar{L}$) and their 95% confidence intervals using resampling tests with 999 iterations (Rosenberg et al. 2000). We used a random-effects model that assumed the true effect size may vary among studies, which is a reasonable assumption given the variety of methods employed among the data sets included (Gurevitch and Hedges 2001). Confidence intervals not bracketing 0 differed significantly from 0 ($\alpha = 0.05$). We report weighted mean effect sizes ($\bar{L}$) among studies and confidence intervals as

$$\bar{L} = \sum_{i=1}^{n} w_i E_i \bigg/ \sum_{i=1}^{n} w_i$$

and $L \pm t_{\alpha/2(n-1)} \times S_L$, where $w_i = 1/S_L^2$ and E_i is the effect size for the ith study. S_L is the standard deviation of L:

$$S_L = \sqrt{\left\{ \left[S_E^2 / N_E (\bar{X}_E)^2 \right] + \left[S_C^2 / N_C (\bar{X}_C)^2 \right] \right\}}$$

where S_E and S_C and N_E and N_C are the standard deviations and sample sizes of experimental and control groups, respectively. When multiple measures of herbivory or plant performance were not independent for the same plant species within the same or different papers, we computed a mean L for those measures, as well as a mean standard deviation:

$$\bar{S}_L = \sqrt{\sum_{i=1}^{n} S^2 N_i \bigg/ \sum_{i=1}^{n} N_i - n}$$

where N_i is the sample size for the ith study. For all analyses described below, we used homogeneity statistics in MetaWin version 2.2 (Rosenberg et al. 2000). For categorical models, the among-group sum of squares (Q_B) was compared to the critical value ($\alpha = 0.05$) of the chi-square distribution (df $= n - 1$). For continuous models, we used weighted least squares regression, in which variation in effect sizes explained by the independent variable (Q_{reg}) was compared to the critical value ($\alpha = 0.05$) of the chi-square distribution (df $= 1$). Q_B and Q_{reg} were calculated as described by Rosenberg et al. (2000).

Using these protocols, we conducted a series of analyses to examine the effects of ants on herbivory and plant performance, and the contribution of multiple factors to such effects. First, we tested whether overall ant effects on herbivory and plant performance differed from 0 and whether the effect size of ants on herbivory differed from that on plant performance. Second, we tested whether effect sizes of reduced herbivory correlated with effect sizes of increased plant performance by calculating a P value based on comparing the observed Pearson correlation coefficient r (null hypothesis $r = 0$) to the distribution of r's from Monte Carlo randomizations (9999 iterations) of the data set. The data set for this analysis included studies with and without error estimates (Appendix) to obtain a larger sample size for

this analysis. In this analysis species are replicates, and a mean value was used for each species. Note that patterns from a within-species analysis may be quite different from our among-species analysis here, but the data are not available to conduct a within-species analysis.

Third, we conducted a series of analyses to examine the contributions of multiple biotic and abiotic factors to the effect sizes of ants on herbivory and plant performance. We examined whether effect sizes for herbivory and plant performance differed between plants with (myrmecophytes; Mt) and without (myrmecophiles; Ml) domatia. We also evaluated whether effect sizes of ants on plants varied with the type of plant reward supplied to ants. For this study, we refer to food, pearl, beltian, and mullerian bodies collectively as food bodies (F); to various types of nectaries outside of flowers as extrafloral nectaries (E); to shelter or housing provided by plants as domatia (D). We also include an "other" category (O) for trophobionts such as aphids which may attract ants to plants and aid in plant protection (Messina 1981). In total, we examined differences in effect sizes among six types or combinations of plant rewards (food bodies, extrafloral nectar, domatia, and trophobionts). Given different biologies of plants associated with their growth forms (Harper 1977), we examined the extent to which effect sizes varied with plant growth form (shrub [Sh], annual herb [Ah], succulent [Su], tree [Tr], liana [Li], and perennial herb [Ph]). We tested for differences in effect sizes among these plant groups using a random-effects model and Q_B, as described previously in this section. Alternatively, benefits of ant protection for herbivory and plant performance may vary with the number of ant species interacting with plants. We examined whether effect sizes for herbivory and plant performance varied with ant species richness using random-effects regression analyses as described here. Lastly, we examined whether effect sizes of ants on herbivory and plant performance varied with latitude, a reasonable proxy for large-scale variation in the environment. We used random-effects regression analysis with herbivory and plant performance as response variables and the absolute value of latitude (to 0.1 degrees) of each study as the explanatory variable. We asked if effect sizes varied across biomes (tropical systems [TR], temperate systems [TE], deserts [D], and savannas/grasslands [S]) using a random-effects model and Q_B, as described earlier in this section.

Fourth, we explored the influence of methodological variables on the effect sizes of ants on herbivory and plant performance. Specifically, we tested whether experimental (EX; ant exclusion, control) and nonexperimental (NE; natural presence/absence of ants) methods influenced effect sizes using a random-effects model and Q_B. Studies also varied in the use of plants (Pl), branches (Br), leaves (Lv), or reproductive parts (Rep) as the unit of replication. We tested whether these units of replication influenced effect sizes using a random-effects model and Q_B. The duration over which

individual studies occurred varied from one to three years. We performed a random-effects regression analysis, for both herbivory and plant performance, with effect sizes as a function of study duration, and calculated Q_{reg} as described above. Lastly, we investigated publication bias in the reporting of ant–plant protection studies using Rosenthal's method ($\alpha = 0.05$) to calculate fail-safe values for each of herbivory and plant performance.

Results

The overall effect size of ants on plants was positive and significantly different from 0 for both herbivory ($\bar{L} = 0.93$, 95% CI = 0.67–1.21; Fig. 1a) and plant performance ($\bar{L} = 0.25$, 95% CI = 0.06–0.46; Fig. 1b), though the mean effect size for herbivory was significantly greater than that of plant performance ($Q_B = 18.4$, df = 1, $P < 0.0001$). These overall effect sizes indicate that ants do generally reduce herbivory and increase plant performance, and thus ants are on average beneficial for plants. Over all possible influences that we examined, no single factor resulted in a significantly negative mean effect size, and most 95% CIs of positive effect sizes did not include 0. These results indicate that context-dependent outcomes are not common among ant–plant protection mutualisms. Nevertheless, five of 24 variables in Fig. 1 did have effect sizes that were not significantly positive (i.e., confidence intervals overlapped 0), suggesting some context-dependent commensalism. These five cases were limited to effect sizes for plant performance, for which sample sizes tended to be small, which could reduce statistical power.

For those studies reporting both herbivory and plant performance, the positive effects of ants on herbivory were not significantly correlated with the positive effects of ants on plant performance ($P = 0.09$, $n = 14$; Fig. 2). This insignificant result was unchanged by removing the outlier (top right data point, Fig. 2; $P = 0.245$, $n = 13$). Thus, ant effects on plant herbivory did not necessarily translate into proportional changes in plant performance, suggesting that it is best to measure both responses to accurately capture the effects of ants on plants.

Four factors contributed to effect sizes of ants on herbivory and plant performance. First, the effect size of ants in reducing herbivory was greater for plants with domatia (myrmecophytes, Mt) than without domatia (myrmecophiles, Ml) ($Q_B = 7.99$, df = 1, $P = 0.005$; Fig. 1a). No difference for plant performance effect sizes occurred between myrmecophytes and myrmecophiles ($Q_B = 1.13$, df = 1, $P = 0.287$; Fig. 1b), though only five records occurred for myrmecophytes. Second, plant rewards (domatia, food bodies, extrafloral nectar) provided to ants affected variation in the magnitude of the positive effect sizes of ants in reducing herbivory ($Q_B = 14.7$, df = 5, $P = 0.012$; Fig. 1a), but did not contribute to plant performance ($Q_B = 1.01$, df = 2, $P = 0.602$; Fig. 1b). In particular, the greatest effect size of
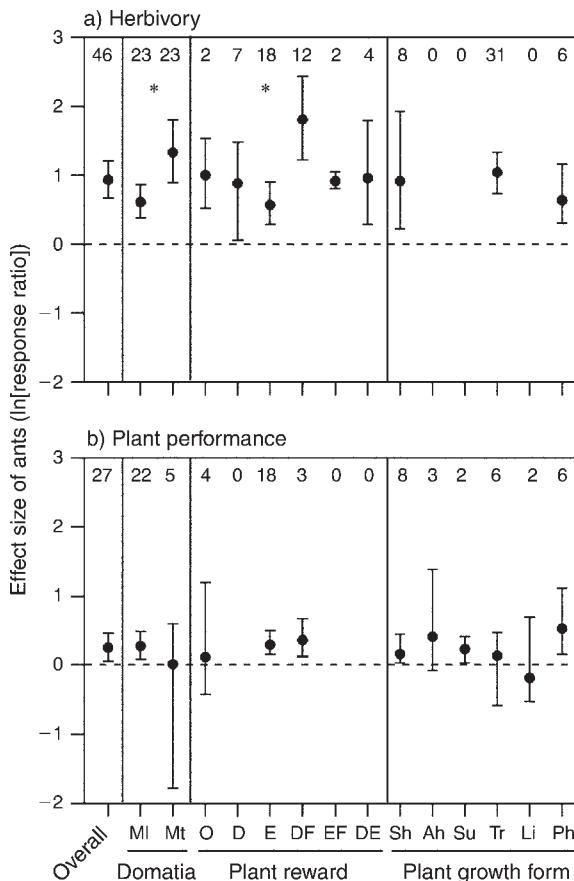
FIG. 1. Mean effect sizes and 95% confidence intervals (CI) of ants on (a) herbivory and (b) plant performance. Effect sizes are log-transformed response ratios ($\ln[\bar{X}_C/\bar{X}_E]$), where $\bar{X}_E$ and $\bar{X}_C$ are means of experimental (ant exclusion) and control (ant access) groups, respectively. When a 95% CI does not overlap 0, the effect size is significantly different from 0. Dashed lines show effect sizes of 0. Mean effect sizes >0 represent a reduction in herbivory or an increase in plant performance, whereas mean effect sizes <0 represent an increase in herbivory or a reduction in plant performance. Effect sizes are reported for four separate analyses: (1) "overall" ant effects combines all studies; (2) "domatia" compares plants with (myrmecophytes; Mt) and without domatia (myrmecophiles; Ml); (3) "plant reward" examines the plant rewards provided to ants, including domatia (D), extrafloral nectar (E), food bodies (F), domatia and food bodies (DF), extrafloral nectar and food bodies (EF), domatia and extrafloral nectar (DE), and other (O, hemipteran excretions); and (4) "plant growth form" consists of shrub (Sh), annual herb (Ah), succulent (Su), tree (Tr), liana (Li), and perennial herb (Ph). Sample sizes are reported in the top of each panel.
* $P < 0.05$ for the Q_B (among-group sum of squares) values of the four analyses.

ants in reducing herbivory occurred for plants that provisioned both domatia and food bodies, whereas those providing only extrafloral nectar tended to have the smallest, yet positive effect size (Fig. 1a). The only plant reward that did not provide a significant positive effect on plants was the "other" category (O) for plant performance. Plant growth form did not contribute to the magnitude of the positive effect sizes of ants on
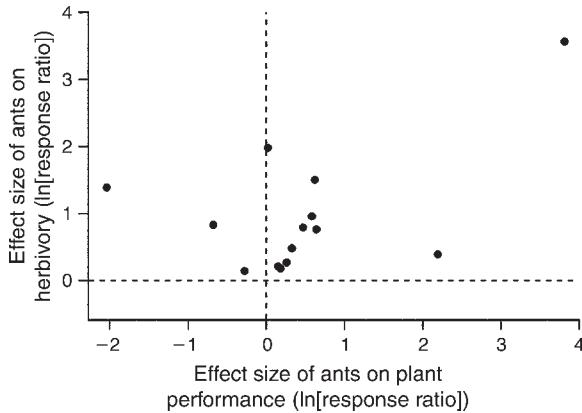
FIG. 2. Plot of effect sizes (response ratios, $\ln[\bar{X}_C/\bar{X}_E]$) of ants on herbivory vs. plant performance for studies in which both variables were measured. Dashed lines show effect sizes of 0.

reducing herbivory ($Q_B = 1.00$, df = 2, $P = 0.608$; Fig. 1a) or increasing plant performance ($Q_B = 5.77$, df = 5, $P = 0.329$; Fig. 1b). However, unlike effect sizes for herbivory, effect sizes on plant performance did not always differ from 0, including in particular those of

annual herbaceous plants (Ah), trees (Tr), and lianas (Li). Third, effect sizes of ants in reducing herbivory decreased, but remained positive, with increasing species richness of ants interacting with plants ($Q_{reg} = 4.86$, df = 1, $P = 0.027$; Fig. 3a). No such relationship was observed for plant performance ($Q_{reg} = 0.02$, df = 1, $P = 0.891$; Fig. 3b). Fourth, effect sizes of ants in reducing herbivory decreased, but remained positive with increasing latitude ($Q_{reg} = 9.42$, df = 1, $P = 0.003$; Fig. 4a), but showed no relationship with plant performance ($Q_{reg} = 1.01$, df = 1, $P = 0.316$; Fig. 4b). There is also a clear dichotomy between plants with domatia and without domatia, both for ant species richness and latitude. In other words, plants with domatia are associated with very few ant species, whereas plants without domatia tend to be associated with many ant species (Fig. 3). Plants with domatia also tend to be at more equatorial latitudes, with non-domatia-bearing plants at higher latitudes (Fig. 4). Effect sizes of ants in reducing herbivory remained positive across biomes and varied significantly among them ($Q_B = 7.02$, df = 2, $P = 0.029$; Fig. 5a). Plants in savannas/grasslands benefited more from ant protection than plants in tropical or temperate systems (Fig. 5a). Effect sizes of ants in increasing plant

FIG. 3. Effect sizes (response ratios, $\ln[\bar{X}_C/\bar{X}_E]$) of ants on (a) herbivory and (b) plant performance vs. ant species richness, for plants with (open circles) and without (crosses) domatia. Dashed lines show effect sizes of 0. Linear regression lines are shown for significant relationships (variation in effect sizes explained by the independent variable [Q_{reg}] compared to the critical value [$\alpha = 0.05$] of the chi-square distribution [df = 1]).

FIG. 4. Effect sizes (response ratios, $\ln[\bar{X}_C/\bar{X}_E]$) of ants on (a) herbivory and (b) plant performance vs. latitude (absolute value), for plants with (open circles) and without (crosses) domatia. Dashed lines show effect sizes of 0. Linear regression lines are shown for significant relationships (Q_{reg} is compared to the critical value [$\alpha = 0.05$] of the chi-square distribution [df = 1]).
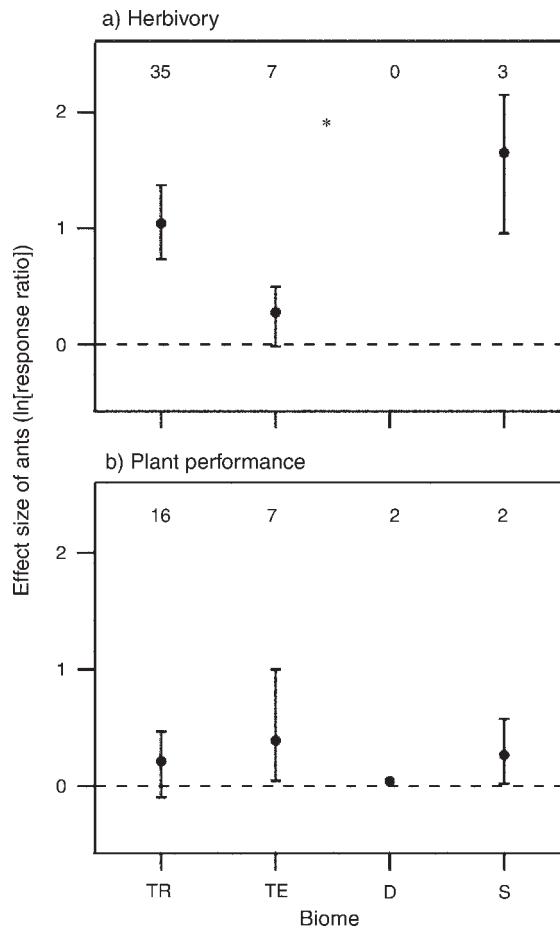
FIG. 5. Mean effect sizes and 95% CI (response ratios, $\ln[\bar{X}_C/\bar{X}_E]$) of ants on (a) herbivory and (b) plant performance for four major biomes of the world: tropical systems (TR), temperate systems (TE), deserts (D), and savannas/grasslands (S). Conventions follow Fig. 1.

performance did not vary significantly across biomes ($Q_B = 1.54$, df $= 3$, $P = 0.672$; Fig. 5b).

In addition to biotic and abiotic conditions, methodological biases may contribute to the effect sizes of ants in reducing herbivory and increasing plant performance. Effect sizes varied with the unit of replication (reproductive parts, leaves, branches, or plants) for herbivory ($Q_B = 90.3$, df $= 2$, $P < 0.0001$; Fig. 6a) and plant performance ($Q_B = 16.5$, df $= 2$, $P < 0.0001$; Fig. 6b), but sample sizes for reproductive parts, leaves, and branches were small ($n = 2$–5). Studies that excluded ants experimentally had smaller mean effect sizes than those relying on natural presence and absence of ants, for both herbivory ($Q_B = 3.94$, df $= 1$, $P = 0.047$; Fig. 6a) and plant performance ($Q_B = 5.64$, df $= 1$, $P = 0.018$; Fig. 6b). However, although sample sizes varied, nonexperimental studies showed greater variation around the mean effect size than did experimental studies for both herbivory (620% increase in CI between experimental and nonexperimental studies) and plant performance

(105% increase in CI). Studies varied in duration, ranging from one to three years, with 80% of studies occurring in only one year. Nevertheless, effect sizes did not vary with study duration for herbivory ($Q_{reg} = 0.08$, df $= 1$, $P = 0.779$) or plant performance ($Q_{reg} = 0.54$, df $= 1$, $P = 0.464$).

Last, the lack of context dependency and overwhelmingly positive effects of ants in reducing herbivory and increasing plant performance may simply arise from a publication bias toward those studies with positive
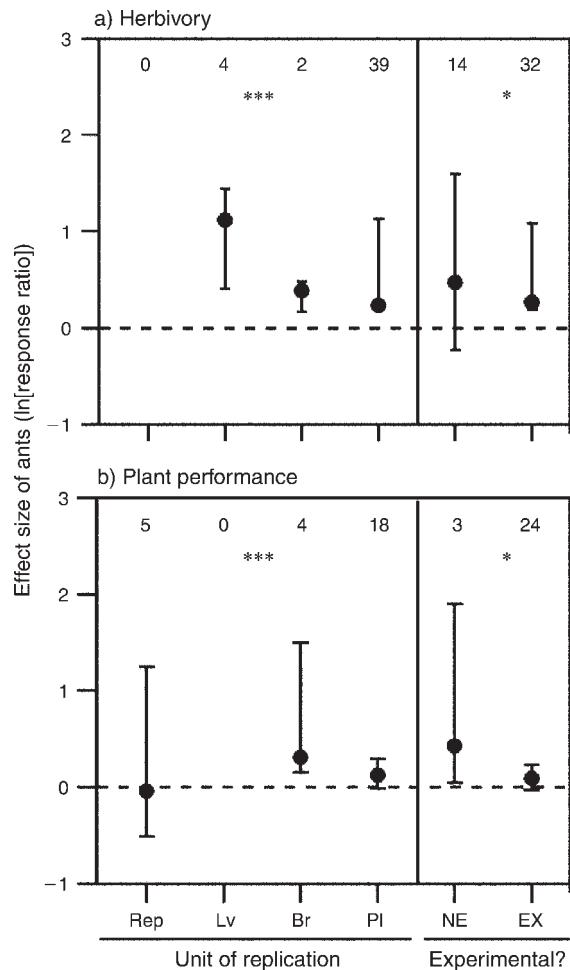
FIG. 6. Analyses of methodological influences on mean effect sizes (response ratios, $\ln[\bar{X}_C/\bar{X}_E]$) of ants on (a) herbivory and (b) plant performance with sample sizes reported in the top of each panel. Dashed lines show effect sizes of 0. When a 95% CI does not overlap with 0, the effect size is significantly different from 0. Mean effect sizes >0 represent a reduction in herbivory or an increase in plant performance, whereas mean effect sizes <0 represent an increase in herbivory or a reduction in plant performance. Mean effect sizes are reported for two separate analyses: (1) the unit of replication of the study being reproductive parts (flowers, fruits; Rep), leaves (Lv), branches (Br), or plants (Pl), and (2) natural presence and absence of ants (NE) vs. experimental manipulation (EX) of ant presence and absence. Significance of associated Q_B values is indicated by asterisks.

* $P < 0.05$; *** $P < 0.001$.

results. We used Rosenthal's method to calculate the number of nonsignificant studies necessary to change these results from significant to insignificant. The fail-safe value for the number of studies was 924 for herbivory and 109 for plant performance, suggesting that results are robust to the file-drawer effect for studies with insignificant results. Funnel plots (not shown) also showed little bias in the data set.

Discussion

We performed a meta-analysis to examine quantitatively the common perception that ant–plant protection mutualisms are typically context dependent, that is, their interaction outcomes routinely vary from mutualism to commensalism or parasitism depending on biotic and abiotic conditions. Our results demonstrate that, rather than context-dependent interactions, ants do generally interact mutualistically with plants by reducing herbivory and increasing plant performance (reproduction, growth). Nevertheless, we did identify some factors that affect the magnitude of the positive effect sizes of ants on plants, particularly for herbivory. We discuss implications of these results for the context dependency of mutualistic interactions in general, along with some potential directions for future research.

Our finding that ant–plant protection mutualisms are not generally context dependent is consistent with the few other quantitative analyses of mutualistic interactions. A recent meta-analysis of plant–mycorrhizal interactions showed that effect sizes of ectomycorrhizae on plant biomass and growth were generally positive and did not depend contextually on partner identity or abundance, duration of association, or phosphorus levels (Karst et al. 2008). In another recent meta-analysis, effect sizes of pollinators, ecto- and arbuscular mycorrhizae, and bacteria on plant performance were all significantly positive (Morris et al. 2007). It appears then that effects of a variety of mutualists on one another are not generally context dependent, as neutral and negative effects were not sufficiently frequent to shift mean effect sizes from significantly positive to neutral or negative. While ant–plant protection interactions can certainly be context dependent in individual cases, given local biotic and abiotic conditions within a species (e.g., Gastreich 1999, Kersch and Fonseca 2005, Chamberlain and Holland 2008), it appears that context-dependent shifts of mutualism to commensalism or parasitism are not the rule, but rather an exception.

We identified several factors that explained variation in the magnitude of the generally positive effects of ants on plants. First, as ant–plant protection mutualisms are mediated by the rewards (domatia, food bodies, extrafloral nectar) supplied by plants, it is not surprising that the type of plant reward influenced the magnitude of effects on herbivory. Plants that provide more energetic rewards (e.g., food bodies vs. extrafloral nectar) are likely to benefit more through reduced herbivory from ant protection. The most prominent difference was due

to domatia; plants providing housing for ants had a substantially larger reduction in herbivory than plants without them. This result is consistent with phytoecious ants that live on myrmecophytic plants being particularly aggressive in their defense of host plants (Heil and McKey 2003). Plant species supplying both domatia and food bodies (e.g., *Cecropia*, *Macaranga*, *Maieta*, *Piper*; Schupp 1986, Fiala et al. 1989, Vasconcelos 1991, Letourneau 1998) showed the greatest reduction in herbivory among the various types and combinations of rewards supplied by plants. Plants producing extrafloral nectaries and additional rewards such as food bodies or domatia experienced significantly greater reductions in herbivory than those producing extrafloral nectar alone. Plant rewards, which are a cost of mutualism (Bronstein 2001), contributed to variation in the magnitude of ant effects on plants. In this regard, further attention may need to be given to the role of such costs in understanding mutualistic interactions and the magnitude of their interaction strengths.

In addition to rewards supplied by plants, latitude, biome, and ant species richness contributed to the magnitude of the positive effects of ants on herbivory. Benefits via reduced herbivory declined from the equator to the poles. As plants with domatia (myrmecophytes) or extrafloral nectaries decrease from the equator to the poles (Fig. 4; Heil and McKey 2003, Rico-Gray and Oliveira 2007), it is difficult to separate abiotic and biotic mechanisms for this pattern in latitude. Ant species effects on plant benefits via reduced herbivory varied among biomes (Fig. 5), with benefits to plants greatest in tropical and least in temperate systems. Tropical systems are predicted to have higher diversity, productivity, and environmental stability relative to temperate systems (Reynolds et al. 2003, Thrall et al. 2007). Environmental stability in particular is thought to lead to increased interaction intimacy due to greater predictability of potential partners (Thrall et al. 2007), which may lead to increased plant benefits through time. Interacting with fewer ant species was associated with greater reductions in herbivory. Most of the plant species with low ant diversity have domatia (Fig. 3), and most plants with domatia form relatively specialized interactions with ants (Heil and McKey 2003). The decrease in benefit with both increasing latitude and ant species richness may appear contradictory, given that ant species richness generally declines with latitude in other studies (Cushman et al. 1993). However, in our data set, ant richness on plants increased at higher latitudes ($n = 56$ plant species, $\rho = 0.48$, $P = 0.0002$), and domatia mediated ant–plant interactions (which tend to include only one or a few ant species; Fig. 3) declined at higher latitudes (Fig. 4; Heil and McKey 2003). Latitude and ant species richness are proximate variables for some underlying factor that contributes to the magnitude of positive effects sizes of ants on plants. Whatever the cause, there is a trend for greater reductions in herbivory both at lower latitudes and lower ant species richness.

Although biotic and abiotic variables influence ant effects on plants, methods used to study ant–plant protection interactions can also influence conclusions about context dependency. Overall, the effect size of ants in reducing herbivory was 270% larger than for increased plant performance; this may reflect a real pattern, but is also likely influenced by fewer studies that measure plant performance (Fig. 1). Our results point to the need for more studies that quantify both herbivory and plant performance, as we identified only 14 species for which both responses were measured in the same study. Instead of methodological reasons, the lack of association between herbivory and plant performance may arise from biological factors, most notably that other direct and indirect interactions plants have with mutualists (e.g., pollinators) and antagonists (e.g., herbivores) may curtail individual effects of particular pairwise ant–plant interactions (Morris et al. 2007). The generality of conclusions from ant–plant protection studies will greatly benefit from more direct measures of plant fitness, including reproduction, growth, and per capita growth rates. The unit of replication and whether studies experimentally excluded ants also contributed to variation in effect sizes. Leaves and branches overestimated and reproductive parts underestimated (relative to whole plants) positive ant effects on plants. We suggest that future studies avoid fractional treatment application below the whole-plant level. Furthermore, studies that used natural presence and absence of ants inflated the positive effects of ants on plants relative to studies that experimentally excluded ants. Remedying these methodological issues will lead to a greater understanding of ant–plant protection mutualisms. Lastly, mutualisms are defined as net benefits to both sides. A holistic understanding of ant–plant protection interactions requires not only quantification of plant benefits and costs, but benefits and costs to ants of interacting with plants.

We have shown that ant effects on plants are consistently positive, and rarely neutral, suggesting that mutualisms may not be as context dependent as previously thought (Bronstein 1994, Holland and Bronstein 2008). Although context dependency does not appear common among species in ant–plant protection (this study) or plant–mycorrhizal interactions (Karst et al. 2008), it may be relatively more common among individuals or populations within a species. Past ant–plant protection studies have sought to understand if ant–plant interactions are on average mutualistic (Bronstein 1998). However, a greater understanding of the extent of context dependency in ant–plant protection interactions and mutualism in general, and the factors that contribute to it, will emerge from future studies explicitly studying interaction outcomes along gradients of abiotic (e.g., precipitation, nutrients) and biotic (e.g., partner identity, abundance, rewards) factors.

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APPENDIX

List of records used in the meta-analysis, followed by full citations (*Ecological Archives* E090-168-A1).