The strength of plant–pollinator interactions

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Abstract. Recent studies of plant–animal mutualistic networks have assumed that interaction frequency between mutualists predicts species impacts (population-level effects), and that field estimates of interaction strength (per-interaction effects) are unnecessary. Although existing evidence supports this assumption for the effect of animals on plants, no studies have evaluated it for the reciprocal effect of plants on animals. We evaluate this assumption using data on the reproductive effects of pollinators on plants and the reciprocal reproductive effects of plants on pollinators. The magnitude of species impacts of plants on pollinators, the reciprocal impacts of pollinators on plants, and their asymmetry were well predicted by interaction frequency. However, interaction strength was a key determinant of the sign of species impacts. These results underscore the importance of quantifying interaction strength in studies of mutualistic networks. We also show that the distributions of interaction strengths and species impacts are highly skewed, with few strong and many weak interactions. This skewed distribution matches the pattern observed in food webs, suggesting that the community-wide organization of species interactions is fundamentally similar between mutualistic and antagonistic interactions. Our results have profound ecological implications, given the key role of interaction strength for community stability.

Key words: asymmetry; ecological networks; interaction frequency; interaction strength; Monte desert; mutualism; plant–pollinator interactions; pollination; species impact.

INTRODUCTION

An inherent property of all interspecific interactions is that they consist of two distinct, population-level effects: the impact of a species on another and the reciprocal impact of the second species on the first. The meaning of these effects may be very different for each participating species, as epitomized by the life/dinner principle of evolutionary ecology (Dawkins 1976): the rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner. In other words, the impact of the fox population on the rabbit's mortality is very different from the impact of the rabbit population on the fox's nutrition. Similarly, an interaction in a plant–animal mutualism consists of the reproductive impact of the animal population on the plant population (pollination, seed dispersal), and the reciprocal nutritional impact of the plant's rewards (nectar, pollen, fruit pulp) on the animal population, which are likely to have different demographic consequences for the participating species. Quantifying these effects of interactions can be difficult because they require time-consuming observational and experimental field studies. Due to this difficulty, ecologists have often estimated ecological effects from only one side of the interaction, thus providing only a partial depiction of ecological effects. The goal of this study is to report quantitative field estimates of the reciprocal ecological effects between plants and their pollinators.

Studies of plant–animal mutualisms are increasingly using a network approach to understand the community-wide patterns of interaction, their underlying causes, and their ecological and evolutionary consequences (Bascompte and Jordano 2007, Vázquez et al. 2009). Although early studies focused on binary networks, more recent studies focus on weighted networks (i.e., those in which each link carries a numerical value measuring the strength of the connection; Bascompte and Jordano 2007). Studying these complex ecological networks requires estimating scores of ecological impacts between interacting species. Each species impact is a function of two components: interaction strength (the per interaction effect of one species on another, a measure of the quality of the interaction) and frequency of interaction (number of encounters) between species (Vázquez et al. 2005, Wootton and Emmerson 2005). In most systems, estimating interaction strengths for a whole network would be a monumental task, as it would typically involve conducting experimental evaluations of the magnitudes of scores of bidirectional interspecific interactions. For example, the 23 plant–pollinator networks analyzed by Vázquez and Stevens (2004) have an average of 258 pairs of interacting species (range 30–1202 pairs).

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Given this complexity, all past studies of weighted mutualistic networks have assumed that species impacts can be inferred from interaction frequencies, so that frequently interacting species have the greatest impacts on their mutualists (see, e.g., Bascompte et al. 2006, Vázquez et al. 2007). This is a crucial simplifying assumption, because it allows addressing some questions at the community level that require estimates of bidirectional ecological effects for all pairs of interacting species. Although evidence shows that species impacts of pollinators or seed dispersers on their plant mutualists can indeed be approximated by interaction frequency (Vázquez et al. 2005, Sahli and Conner 2006), the key unanswered question here is whether this approximation also holds for the reciprocal species impacts of plants on their animal mutualists. If it held, then all we would have to measure would be interaction frequency, which is relatively easy to do. However, if the approximation did not hold, the conclusions of past studies of weighted mutualistic networks may be invalid, and estimating species impact would require quantifying interaction strength for all pairs of interacting species, which would be unfeasible in most systems.

Here we report for the first time estimates of bidirectional interaction strengths and species impacts for interacting plants and pollinators, based on a field study in the Monte desert of Argentina. We use these data to address two questions. First, we evaluate whether quantifying interaction strength is needed to predict the species impact of pollinators on plants, the reciprocal species impact of plants on pollinators, and their asymmetry (i.e., the extent to which the impact of a plant on an animal matches the reciprocal effect of the animal on the plant; Bascompte et al. 2006). Second, we reevaluate a key finding of previous studies of weighted networks regarding the statistical distribution of interaction strengths and species impacts, an important community attribute with profound implications for community dynamics and stability (Yodzis 1981, McCann et al. 1998, Wootton and Emmerson 2005, Bascompte et al. 2006, Okuyama and Holland 2008). Food web studies have shown that in most communities interaction strengths and species impacts have a skewed distribution, so that few interactions are strong and most are weak (Wootton and Emmerson 2005); the same pattern has been described in weighted plant–animal mutualistic networks, when species impact was estimated using interaction frequency as a surrogate (Bascompte et al. 2006). We revisit this distribution with our improved measure of species impact; we also ask whether the same skewed pattern occurs for interaction strength, which had not been evaluated before for mutualistic networks.

MATERIALS AND METHODS

Study system.—The study area lies in the Monte desert of Villavicencio Nature Reserve (32°32′ S, 68°57′ W, 1270 m above sea level), Mendoza, Argentina.

Predominant vegetation is a tall shrubland dominated by *Larrea divaricata*, *Zuccagnia punctata*, *Prosopis flexuosa*, *Condalia microphylla*, *Acantholippia seriphioides*, and *Opuntia sulphurea* (Chacoff et al. 2012). Quantification of interaction strength of pollinators on plants was done at two 2-ha plots in the 2008 spring flowering season (October–December). Bee reproduction studies were conducted in the same two sites as the studies for plants plus another 12 sites in the same reserve in 2006–2008.

Description of the plant–pollinator visitation network.—In previous work (Chacoff et al. 2012), we described the plant–pollinator network, which includes 52 plant and 159 flower visitor species, and interactions between 727 pairs of species. In this ecological context, we quantified the interaction strengths and impacts of selected focal species of plants and flower visitors. Flower-visiting insects were observed on plant species in weekly surveys between September and January (2006) or between September and December (2007–2009). We attempted to sample plant–pollinator interactions in the whole community as comprehensively as possible. With these data, we constructed a quantitative plant–pollinator interaction matrix, with rows corresponding to plant species, columns to pollinator species, and cell entries to the number of floral visits by each pollinator species to each plant species. With the interaction matrix, we calculated pollinator visitation frequency to plants (I_{ij}, for pollinator species j and plant species i) and the asymmetry index (see *Calculation of asymmetry in species impacts*). This work was conducted in two sites between 2006 and 2009, and in two additional sites in 2006 (for further details, see Chacoff et al. 2012).

Defining interaction strength and species impact.—In the context of plant–pollinator interactions, we define interaction strength as the per-interaction contribution of a species to the reproductive output of another species, relative to the combined contribution of all species.

For plants, interaction strength p_{ij} is the contribution of a single visit of pollinator species j to some component of reproductive success of plant species i, relative to the contribution of all pollinator species, $p_{ij} = P_{ij}/P_{i.}$, where $P_{i.} = \sum_j |P_{ij}|$ is the added per-visit contribution of all pollinator species. In our study, we estimated P_{ij} as the number of pollen tubes resulting from pollen deposited by pollinator j on the stigma of plant species i in one visit (except for one species, for which we used proportion of flowers producing fruit; see *Quantification of interaction strength, interaction frequency, and species impact of pollinators on plants*), but it could also be the number of seeds produced. The absolute value of P_{ij} used in the denominator because effects of a single visit could range from positive (when the flower visitor contributes to reproduction) to negative (when the flower visitor impairs reproduction, e.g., because of nectar robbing, florivory, or removal of pollen previously deposited on the stigma; McCall and

Irwin 2006, Irwin et al. 2010, Morris et al. 2010). The species impact t_{ij} of a pollinator species j on a plant species i is defined as the total contribution of the population of pollinator species j to the reproductive success of the population of plant species i, relative to the contributions of other pollinators. Species impact is determined by the per interaction effect, P_{ij}, and the number of times the interaction takes place, I_{ij}, so that the total, population-level reproductive effect of pollinator species j on plant species i is $I_{ij}P_{ij}$. Hence, the relative contribution of pollinator species j to plant species i (the species impact) is $t_{ij} = I_{ij}P_{ij}/T_{i.}$, where $T_{i.} = \sum_j I_{ij}|P_{ij}|$ is the added population-level contribution of all pollinator species.

For pollinators, interaction strength p_{ji} is the relative contribution of a pollen grain of a plant species i to the production of offspring of pollinator species j, $p_{ji} = P_{ji}/P_{j.}$, where P_{ji} represents the reproductive effect of a pollen grain of plant species i on the reproductive success of the pollinator, and $P_{j.} = \sum_i |P_{ji}|$, as above. In our study, we estimated P_{ji} from the pollen of different plant species used to provision larvae of a given pollinator species. This allowed us to estimate the contribution of each plant species to pollinator reproduction. As above, we used the absolute value of P_{ji} in the denominator because the reproductive effect of a plant species on a pollinator species can go from positive (when it contributes to reproduction) to negative (when it impairs reproduction, e.g., because of secondary compounds of pollen; see Praz et al. [2008]). The total, population-level reproductive effect of plant species i on pollinator species j is then $I_{ji}P_{ji}$, and the relative contribution of plant species i to the reproduction of pollinator species j (the species impact) is $t_{ji} = I_{ji}P_{ji}/T_{j.}$, where $T_{j.} = \sum_i I_{ji}|P_{ji}|$.

Quantification of interaction strength, interaction frequency, and species impact of pollinators on plants.— We quantified interaction strength of pollinators on five focal plant species, *Capparis atamisquea* (Capparaceae), *Larrea divaricata* and *L. nitida* (Zygophyllaceae), *Opuntia sulphurea* (Cactaceae), and *Zuccagnia punctata* (Fabaceae). Although this is a small proportion of the plants in the network (5 out of 52 species), we believe it is a representative group in terms of phylogenetic diversity, degree of specialization, and time of flowering (Chacoff et al. 2012). First, it includes plants in four families, with diverse floral morphology and coloration. Second, the group includes three generalized species with a large number of recorded flower visitor species (*L. divaricata* and *Z. punctata* with 45 and *C. atamisquea* with 44), and two species with an intermediate number of flower visitors (*O. sulphurea*, 30 species, and *L. nitida*, 23 species). Third, the group includes a species flowering early in the flowering season (*L. nitida*), two flowering at the peak of the season (*L. divaricata* and *Z. punctata*), and another two flowering toward the end of the flowering season (*O. sulphurea* and *C. atamisquea*). We conducted these studies in the 2007 flowering season for

C. atamisquea and in 2008 for the other four species, in the same two sites studied between 2006 and 2009 for the visitation network.

We used the number of pollen tubes growing below the tip of the pistil as our measure of P_{ij}, except for one species (*C. atamisquea*), for which we used proportion of flowers producing fruit (data from Morris et al. 2010), as pollen tubes were not clearly seen for this species; this species produces only one seed per fruit, and thus our estimate represents seed set. We did not use number of pollen tubes at the base of the stigma (close to the ovary) because pollen tubes were more difficult to detect in some cases; however, this decision is unlikely to affect our results, as pollen tubes at the base and the tip of the stigma were highly correlated (Spearman's for all species pooled: $r = 0.78$, $P < 0.0001$, $n = 208$). To conduct pollination studies, we bagged branches with flower buds, and once flowers were open we removed the bags to expose flowers to one pollinator visit, recorded the identity of the visitor, and covered the branch again. When the visitor could not be identified in the field, we collected it for identification in the laboratory with the aid of experts (see *Acknowledgments*). For *C. atamisquea*, we counted the number of fruits once they were ripe. For the remaining species, two to three days after pollination we cut the pistil at the base of the ovary and stored it in 70% alcohol. Once in the lab, we prepared pistils for quantification of pollen grains and pollen tubes. To this end, we washed the pistil in tap water, softened the pistil's tissues in sodium hydroxide (1 mol/L NaOH) for 2–24 hours at room temperature, depending on its size, washed it with tap water, and stained it with aniline blue dissolved in monoacid potassium phosphate (K_2HPO_4) for two hours. We counted conspecific pollen grains and pollen tubes under the microscope.

Interaction frequency I_{ij} was calculated as the number of visits of pollinator species j to plant species i, relative to all visitor species recorded for plant species j. Interaction strength p_{ij} and species impact t_{ij} were calculated with P_{ij} and I_{ij} as explained above (see *Defining interaction strength and species impact*).

Quantification of interaction strength, interaction frequency, and species impact of plants on pollinators.— This work was conducted in 2006 in the same two sites studied between 2006 and 2009 for the visitation network, in one additional site in 2007, and in 12 additional sites in 2008. We placed trap nests at 30 points separated 20 m from each other (2006 and 2007) or at six points separated 100 m from each other (2008). Each trap nest was a wood piece with a longitudinal hole. Three hole sizes were used: 140 mm depth by 5 mm diameter, 140 mm depth by 8 mm diameter, and 280 mm depth by 11 mm diameter. Bees nesting in our trap nests included in this study belonged to four genera and seven species (Appendix A): *Anthidium decaspilum* (34 nests), *A. rubripes* (31 nests) and *A. vigintipunctatum* (54 nests) (Megachilidae, Anthidinae), *Megachile* sp. A (an unidentified taxon that was undoubtedly a single species,

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according to specialists; 181 nests) and *M. ctenophora* (66 nests) (Megachilidae, Megachilinae), *Trichothurgus laticeps* (Megachilidae, Lithurginae; 37 nests), and *Xylocopa ordinaria* (Apidae, Xylocopinae; 38 nests). Although this is a small proportion of the flower visitors in the network, it is a representative subset of one taxonomic group (bees) responsible for 46% of all visits in the network. The focal species are also representative in terms of degree of specialization and time of activity. First, the group includes generalist species with a relatively high number of plants used for pollen (*M. ctenophora*, with 22 species), several species with an intermediate number of pollen sources (*A. rubripes* and *X. ordinaria* with 15, *A. vigintipunctatum* and *M.* sp. A with 13, and *A. decaspilum* with 11), and a more specialized species with a relatively low number of pollen sources (*T. laticeps*, with 8, of which >90% were from *O. sulphurea*). Second, species in this group are active at different moments in the flowering season, with the two *Megachile* species starting their activities relatively early in the flowering season, the three *Anthidium* species starting later, *T. laticeps* starting toward the end of the flowering season, and *X. ordinaria* being active throughout the entire season.

Trap nests were checked weekly. Occupied traps were taken to the laboratory and replaced by empty ones. Once in the laboratory, nests were opened to record the number of cells. One cell per nest was extracted for pollen identification; the extracted cell was located at the central position of the nest to ensure that pollen content was representative of that in the whole nest. The percentage of pollen of each species present in the nest was obtained from the pollen present in this cell and used to calculate z, our measure of the contribution of each pollen grain to bee fitness (see next paragraph). Pollen identification was done by comparison with a reference collection, prepared including all plant species that flowered at each study plot. The rest of the cells in each nest were kept in the laboratory at ambient conditions until adult emergence. After emergence, the number of adults and the species identity were recorded. Voucher specimens are stored at the Entomology Collection of the Instituto Argentino de Investigaciones de las Zonas Áridas, CONICET, Mendoza, Argentina. Further details on trap nest methods are given in Dorado et al. (2011).

We used a generalized linear model (GLM) approach to calculate the interaction strength for the effect of plants on pollinators. Predictor variables in the GLM were the proportion of pollen of each plant species out of the total pollen grains in a nest. We used only pollen, not nectar, for our predictor variables because only the former could be identified taxonomically from trap nest samples. Although the lack of consideration of nectar may bias our estimates of interaction strength, we believe this is a minor problem, as comparison of visitation and trap nest data suggests that these bee species use the same plant species as pollen and nectar sources (Dorado et al. 2011). Furthermore, larvae of the study bee species feed mostly from pollen, and nectar is used only in small quantities. The response variable was the number of brood cells in each nest, which is assumed to represent the fitness of the mother bee. In so doing we are assuming that each mother builds only one nest or, if she builds more than one nest, that the number of cells in the studied nest is representative of the average number of cells built by that female in all nests. We are also assuming that females feed on the same pollen used to feed larvae, and that such pollen affects the ability of females to lay eggs; we believe this is a reasonable assumption, as pollen is critical to develop ovaries in young females, thus affecting directly their ability to lay eggs (Michener 2000). To circumvent problems related to the use of proportions in linear models, each predictor variable x was transformed as $\log(x + 2)/2$, so as to break the linear dependence among predictors. The glm function of R reports a z value, which is the Wald statistic used to test the hypothesis that the corresponding parameter (regression coefficient) is zero, under the null hypothesis that z has an approximately normal distribution with a mean of zero and a variance of one. We used this statistic as a measure of the effect size (Bring 1994) of plants on the reproductive success of bees, P_{ji}.

Interaction frequency I_{ji} was calculated as the use of pollen from each plant species relative to all plant species found in the bee nests. This estimate came from trap nests and not from flower visitation observations because in our study system the latter tend to detect only a subset of plant species used by the bees in the nests (Dorado et al. 2011). Interaction strength p_{ji} and species impact t_{ji} were calculated with P_{ji} and I_{ji} as explained above (see *Defining interaction strength and species impact*).

Calculation of asymmetry in species impacts.—We calculated interaction asymmetry with an index (Bascompte et al. 2006) that depicts the relative dissimilarity in species impacts of interacting species, $A_{ij} = |t_{ij}t_{ji}|/\max(t_{ij}, t_{ji})$. The index ranges from 0 (maximum symmetry) to 1 (maximum asymmetry). We calculated A_{ij} using both species impacts computed with our measure of interaction strength and with interaction frequency as a surrogate.

Results

Interaction frequency was highly, positively correlated with the impact of both plant and pollinator species on their interaction partners (Fig. 1a, b). Thus, the most frequent flower visitors have the greatest reproductive impact on the plants they visit, and, likewise, the plant species most frequently used as pollen sources make the greatest contribution to the reproduction of the pollinators that use them. However, interaction strength does play the fundamental role of determining the direction (sign) of the interaction (cf. Fig. 1b and Appendix B).

The distribution of asymmetry values calculated with species impacts was very similar to the distribution of
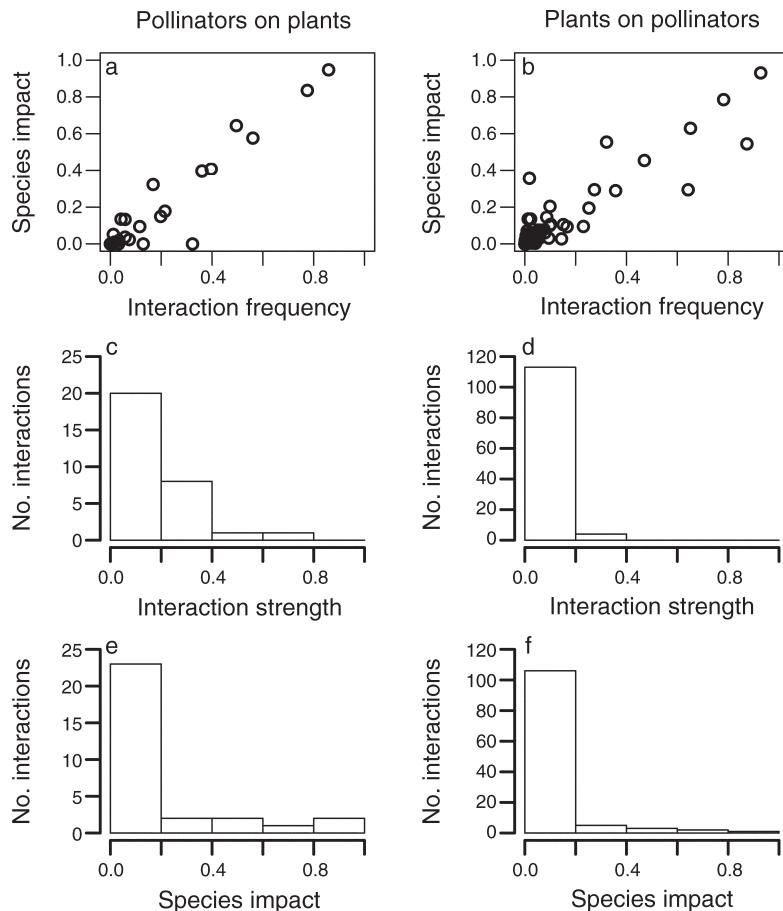
FIG. 1. Interaction strengths and species impacts in the Villavicencio network. (a, b) Interaction frequency as a surrogate for species impacts. Scatterplots show the relationship between species interaction frequencies and impacts in the plant–pollinator network of Villavicencio Nature Reserve, for (a) the effect of pollinators on plants (Spearman rank correlation: $r = 0.8$, $n = 30$, $P \ll 0.0001$), and (b) the effect of plants on pollinators (Spearman rank correlation: $r = 0.92$, $n = 117$, $P \ll 0.0001$). In panel (b), absolute values are shown (see Appendix B for untransformed values). (c–f) Histograms of interaction strengths and species impacts in the Villavicencio network of (c, e) pollinators on plants and (d, f) plants on pollinators. In panels (d) and (f) the absolute values of strengths and impacts are shown (see Appendix C for untransformed values). See *Defining interaction strength and species impact* for an explanation of the calculation of species impact and interaction strength.

asymmetry values calculated with interaction frequencies (Fig. 2). In fact, both estimates were highly correlated (Spearman's $r = 0.98$, $n = 9$, $P < 0.0001$). In addition, the distribution of asymmetries for the subset of interactions for which we measured interaction strength did not differ significantly from the distribution observed for the whole network (Fig. 2).

The distribution of interaction strengths and impacts in our study system was skewed toward few strong and many weak interactions (Fig. 1c–f and Appendix C). The distribution of interaction frequencies was also skewed, with many infrequent and few frequent interactions (Appendix D), matching the pattern found for interaction strength and species impact.

DISCUSSION

We have shown that the frequency of interaction between plants and pollinators is a good predictor of the

magnitude of species impacts of plants on pollinators, the reciprocal species impacts of pollinators on plants, and their asymmetry. These results have profound conceptual implications: interaction strength, which measures the quality of the interaction, seems virtually irrelevant to determine the magnitude of the impact of species on their interaction partners. Instead, an estimate of the number of encounters between each pair of interacting species in a community (measured here as the frequency of visitation of pollinator species to plants and the frequency of use of plant species for pollen in pollinator nests) is enough to estimate the magnitudes of species impacts, in agreement with the conclusions of previous studies (Vázquez et al. 2005, Sahli and Conner 2006). For this reason, even though our measures of interaction strength of plants on animals and animals on plants may have limitations, those limitations become unimportant when estimating species impacts from
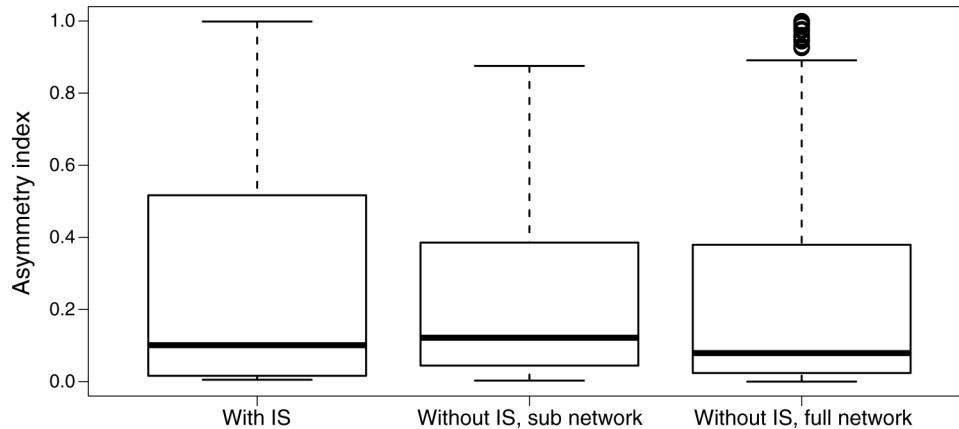
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FIG. 2. The distribution of asymmetry in species impacts in the Villavicencio network. The left-most box plot shows the asymmetry index using species impact as a function of both interaction frequency and interaction strength (IS) for the 17 plant–pollinator pairs studied. The center box plot shows the asymmetry index using only interaction frequency as a surrogate of species impact for the same 17 plant–pollinator pairs. The right-most box plot shows the asymmetry index using only interaction frequency as a surrogate of species impact for all 727 plant–pollinator pairs in the network. In each box plot, the middle line indicates median, box limits are the first and third quartiles, whiskers indicate most extreme points ≤1.5 times the interquartile range, and circles indicate outliers.

interaction frequencies. However, the fact that interaction strength determines the sign of the interaction underscores its importance: although interaction frequency can tell us whether an interaction is important or not, only interaction strength can tell us whether the interaction is importantly good or importantly bad, which of course makes a huge difference for the interacting species. Thus, the whole picture of interaction patterns in a community cannot be captured by solely studying interaction frequencies and ignoring interaction strengths.

It is noteworthy that interactions in our study system are skewed toward symmetry in species impacts (see Fig. 2), with few asymmetric and many symmetric interactions, which contrasts with findings for other systems showing that interactions tend to be asymmetric (Bascompte et al. 2006). This striking result may be a consequence of the type of ecosystem considered in our study, as arid ecosystems are greatly underrepresented in studies of plant–pollinator networks (Chacoff et al. 2012). Once our catalog of networks becomes more complete, it will be important to evaluate formally how aridity influences structural features of plant–pollinator networks.

We have also shown that, in our study system, few plant–pollinator interactions are strong and most are weak, both at the level of single interactions (interaction strength) and whole populations (species impact). This result agrees with the pattern observed in food webs (Wootton and Emmerson 2005) and supports previous findings for mutualistic networks using interaction frequency to estimate species impact (Bascompte et al. 2006), thus suggesting that the community-wide organization of species interactions is fundamentally similar between mutualistic and antagonistic interactions. Our finding should illuminate future theoretical research in

community ecology, given the key role of these attributes of species interactions for community dynamics and stability (Yodzis 1981, McCann et al. 1998, Wootton and Emmerson 2005, Bascompte et al. 2006, Okuyama and Holland 2008). Furthermore, the fact that only a few interactions in a community are strong may help focus management and conservation efforts, as it is strong mutualistic interactions that contribute the most to community stability (Okuyama and Holland 2008).

Our study represents an important step toward understanding and predicting the relative importance of interactions in a community. We have provided, for the first time, field estimates of the bidirectional interaction strengths and species impacts in a community context for any type of plant–animal mutualism. We have shown that these estimates of the magnitudes of species impacts do not seem to depend on the quality of the mutualist and, instead, can be well approximated with interaction frequencies in the two directions of interactions (plants on animals and animals on plants). The implications of this finding are far-reaching, as it reinforces the notion that interaction frequencies can be used to estimate the magnitudes of scores of pairwise species impacts in the context of mutualistic networks. At the same time, our study should sound a note of caution for future network studies, as interaction strengths do play the key role of determining the sign of the interaction. Furthermore, the skewed statistical distribution of these estimates indicates that mutualistic and antagonistic interactions in a community are organized in a similar fashion, which highlights the relevance of incorporating mutualism to the core of ecological theory. Future studies should evaluate the generality of our findings by studying the distribution of strengths and impacts in other types of mutualistic interactions and biomes.

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Supplemental Material

Appendix A

Photographs of nests of bee species included in the study (*Ecological Archives* E093-062-A1).

Appendix B

Untransformed species impacts of plants on pollinators vs. interaction frequency in the Villavicencio network (*Ecological Archives* E093-062-A2).

Appendix C

Untransformed values of interaction strengths and impacts of plants on pollinators (*Ecological Archives* E093-062-A3).
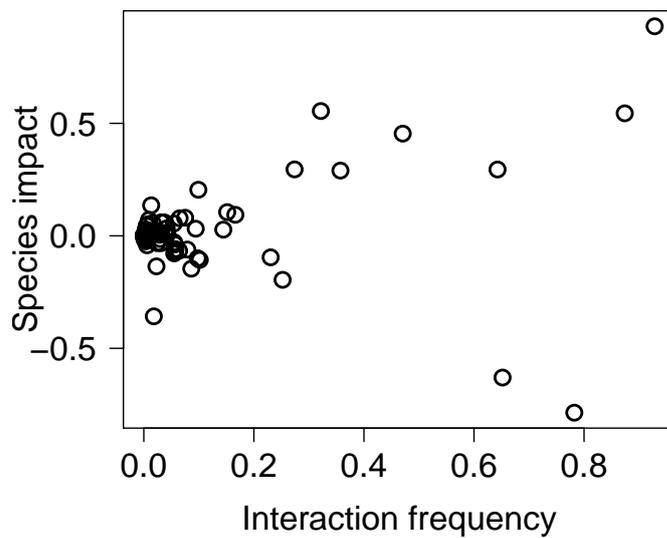
Appendix D

The distribution of interaction frequencies in the Villavicencio plant–pollinator network (*Ecological Archives* E093-062-A4).

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Electronic Appendices

Appendix A. Photographs of nests of bee species included in the study. Bees studied to quantify interaction strength. **a,** *Megachile* sp. A visiting a flower of *Larrea divaricata*. **b,** Detail of brood cells of *Megachile* sp. A with petals of *Larrea* sp. **c,** Nest of *Megachile* sp. A with brood cells built with petals of *Larrea* sp. **d,** Nest of *Anthidium* sp. built with hairs of fruits of unidentified plant species. **e,** Nest of *Trichothurgus laticeps*, with pollen mostly of *Opuntia sulphurea*. **f,** Nest of *Xylocopa ordinaria*, with seven brood cells at different stages of development, from larva (left) to pupa (center) to adult (right).

Appendix B. Untransformed species impacts of plants on pollinators vs. interaction frequency in the Villavicencio network. Spearman rank correlation: $r = -0.10$, $n = 117$, $P << 0.2722$.
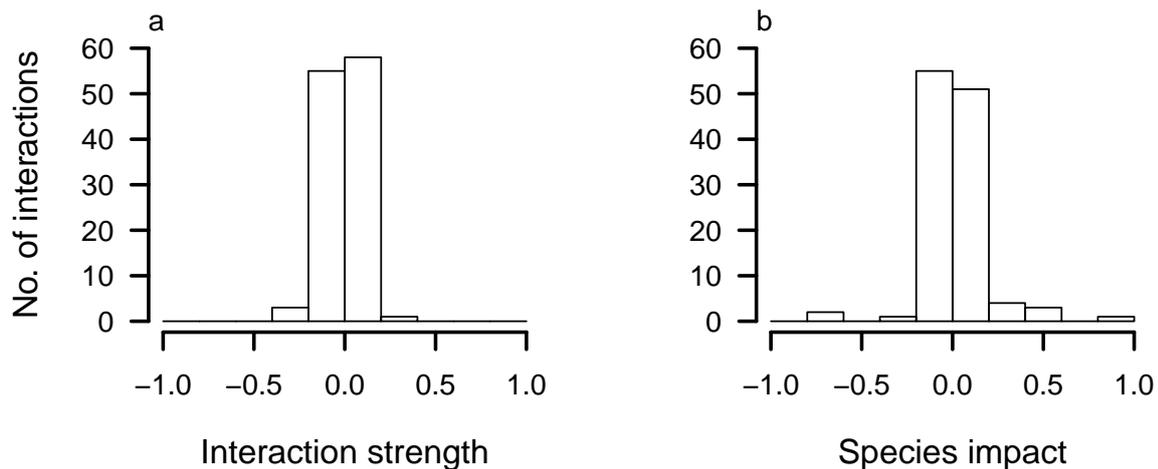
Appendix C. Untransformed values of interaction strengths and impacts of plants on pollinators. Histograms show the frequency distribution of interaction strengths and species impacts in the plant–pollinator network of Villavicencio Nature Reserve. **a,** Interaction strength of plants on pollinators. **b,** Species impact of plants on pollinators.
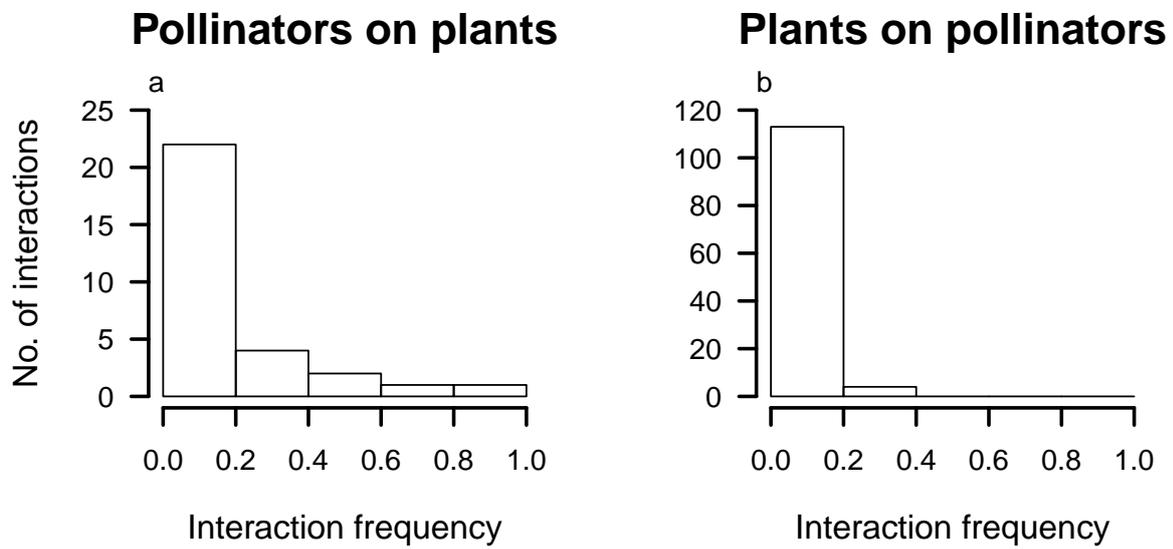
Pollinators on plants

Plants on pollinators

a

b

No. of interactions

Interaction frequency

Interaction frequency

Appendix D. The distribution of interaction frequencies in the Villavicencio plant–pollinator network. Histograms show the frequency distribution of interaction frequencies in the plant–pollinator network of Villavicencio Nature Reserve. **a,** Interaction frequency for plants, calculated from data on pollinator visits to flowers. **b,** Interaction frequency for pollinators, calculated as the relative use of pollen from each plant species in trap nests.