Body size predicts degree in ant–plant mutualistic networks

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Summary

1. The complexity of ecological communities can often hinder understanding their structural features. With the recent application of network theory, the structure of previously neglected mutualistic communities has begun to be elucidated.

2. Mutualistic communities have now been shown to follow particular power distributions in their degree, that is, the number of species interactions per species. However, predictive variables of degree and other structures of mutualistic networks remain largely unexplored.

3. Here, we show that body size of ants is positively correlated with their degree in mutualistic networks comprised of ant interactions with extrafloral nectar (EFN) bearing plants in the Sonoran Desert. This pattern in body size and the number of plant species with which ants interact occurred among all eight sampled communities, a relationship which was not contingent upon phylogenetic history among ant species.

4. These results indicate that further study of body size in ant–plant and other mutualistic networks may yield promising insights into the processes influencing their structure. Moreover, the degree–body size relationship for ant–plant mutualistic communities is consistent with that of predator–prey food webs, possibly suggesting similar underlying processes at work.

Key-words: ant, allometry, body size, community structure, degree, extrafloral nectar, mutualism, network

Introduction

Understanding patterns in, and mechanisms for, the structure of ecological communities remains a central endeavour in ecology (Williams & Martinez 2008). With the application of network theory in recent years, ever greater recognition is being made of the structures of ecological communities, including previously neglected mutualistic communities (Bascompte *et al*. 2003; Jordano, Bascompte & Olesen 2003; Olesen *et al*. 2007; Vázquez *et al*. 2007). For example, mutualistic networks are now recognized to display non-random structural properties involving degree (number of links per species), nestedness (specialist species interacting with a subset of generalist species) and interaction strengths (Bascompte *et al*. 2003; Jordano *et al*. 2003; Vázquez 2005; Lewinsohn *et al*. 2006; Vázquez *et al*. 2007). Despite recognition of potential dynamic consequences of these and other structures for ecological networks (Dunne, Williams & Martinez 2002b; Okuyama & Holland 2008), studies are just beginning to examine some of the biological factors that contribute to the structural properties of mutualistic communities. Here, we examine whether

body size, a predictive variable of predator–prey food web structures (Brose *et al*. 2004; Woodward *et al*. 2005; Otto, Rall & Brose 2007; Petchey *et al*. 2008), contributes to the number of species interactions (i.e. links) per species in mutualistic communities.

Body size relationships among predators and prey vary systematically among habitats, scale positively with interaction strength and have been shown to contribute to community structures that may enhance stability of food webs (Brose, Williams & Martinez 2006; Otto *et al*. 2007). For example, predator–prey body size ratios of five real food webs fall within a predicted domain for community persistence (Otto *et al*. 2007). In food webs in which predators consume entire prey, body size has clear implications, as large prey are not readily consumed by smaller predators. The role of body size in mutualistic systems is less clear, as their consumer–resource interactions do not entail consumption of entire individuals, but rather resources produced by a mutualist to attract and reward its mutualistic partners (Holland *et al*. 2005). A key structural property of mutualistic networks is degree distribution, non-random patterns in the number of species with which any given species interacts. At the community level, degree distribution often follows a power or truncated-power

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distribution for mutualistic and predator–prey networks, indicating that many species interact with only a few species, and few species tend to interact with many species (Dunne, Williams & Martinez 2002a; Jordano *et al.* 2003; Montoya & Solé 2003; Proulx, Promislow & Phillips 2005; but see Okuyama 2008). While food web analyses have shown that the degree of predators and prey can vary with their respective body sizes (Otto *et al.* 2007), little or no research has explicitly examined such degree–body size relationships for mutualistic communities. Nevertheless, other studies have shown that morphological matching between species in terms of body size variables (e.g. proboscis/flower matching) can be important to the structure of mutualistic plant–pollinator and plant–seed disperser networks (Jordano *et al.* 2003; Stang, Klinkhamer & van der Meijden 2006, 2007; Dalsgaard *et al.* 2008). In turn, this supports the suggestion that degree–body size relationships may be of use in understanding the structure of mutualistic networks.

We quantified ant–plant mutualistic networks of eight communities in the Sonoran Desert to examine the extent to which the body sizes of ants correlates with their degree in mutualistic communities. Ant–plant mutualistic communities entail consumer–resource interactions between ants and plants in which ants consume extrafloral nectar (EFN) resources produced by plants and in turn protect and defend the plants from herbivores and other natural enemies (Holland *et al.* 2005; Bronstein, Alarcon & Geber 2006). We show that the number of plant species with which ants interact (i.e. ant species degree) increases with ant body size, and importantly, this relationship is not contingent upon phylogenetic relationships among ant species.

Methods

We quantified community interactions among ants and EFN bearing plants at eight sites in the Sonoran Desert of Arizona (USA) and Sonora (Mexico) during spring and summer months of 2007 (Table 1). Contrary to many tropical ant–plant systems, those in the Sonoran Desert do not include plant production of food (lipid) bodies or domatia (ant housing; Heil & McKey 2003). Most ant species were ground nesters, but some species (*Pseudomyrmex*, *Zacryptocerus*) were observed to nest within woody EFN-bearing plants (e.g. *Prosopis*). Due to high ambient temperatures of the

desert, most ant species were active only at night, except *Forelius mccooki* and *F. pruinosis*, which were active almost exclusively by day. These ant–plant communities add to the very few of such mutualistic networks thus far reported (Fonseca & Ganade 1996; Guimarães *et al.* 2006; Blüthgen *et al.* 2007).

To document species interactions comprising these ant–plant networks, we established 3·6 ha plots (120 × 300 m) randomly positioned at each of the eight sites. We censused diurnal (*c.* 16.00–18.30 h) and nocturnal (*c.* 20.00–22.00 h) ant visitation to all EFN bearing plant species in each plot of each site. Each site was censused once to avoid inclusion of species with non-overlapping phenologies (Basilio *et al.* 2006; Medan *et al.* 2006). We censused an equal number of individuals (*c.* 25) per plant species per plot to minimize biases associated with sample accumulation curves (e.g., see Gotelli & Colwell 2001). We censused each plant for 1 min each by day and by night, for a total of 2 min per individual plant. We recorded the abundance of each species of ant on all censused plants. Because the same individual plants censused by day were also censused at night, we combined both diurnal and nocturnal censuses for analyses. We calculated degree for each ant species at each site by counting the number of plant species with which ant species interacted. Although particular pairwise interactions between ant and plant species may vary in space and time, recent evidence from plant–pollinator communities suggests that structural properties such as degree are relatively invariant in time despite often large variation in the identity of particular species interactions (Petanidou *et al.* 2008).

Body size for each ant species was estimated from 1 to 23 workers per ant species. Only minor workers were measured for dimorphic species (e.g. *Camponotus*). Head capsule length of each worker was measured with a dissecting microscope (to 0·01 mm) equipped with an ocular micrometer, which was calibrated with a stage micrometer. Body mass was then estimated using allometric equations derived by Kaspari & Weiser (1999). The equation $M = aL^b$, where L is the head capsule length, was used to convert head capsule length to body mass for each species, with subfamily specific constants for Dolichoderinae ($a = 3·870 \times 10^{-4}$, $b = 2·621$), Formicinae ($a = 6·319 \times 10^{-4}$, $b = 3·493$), Myrmicinae ($a = 5·1475 \times 10^{-4}$, $b = 3·361$) and Pseudomyrmicinae ($a = 3·7024 \times 10^{-4}$, $b = 3·342$) (Kaspari & Weiser 1999). A mean measure of ant body size was calculated for each species.

We examined ant degree distributions, and their best model fits, for each of the eight sites. Due to difficulties in estimating the fit of models to degree distributions for small (e.g. Semilla Flats, where $n = 12$ species in the community) networks (Albert & Barabási 2002; Guimarães *et al.* 2007), we show degree distributions for all eight sites, but only test model fits to six of the eight sites. Using the R package BIPARTITE, we examined the fit of exponential ($P(k) \sim \exp(-\gamma k)$),

Table 1. Eight study sites sampled for ant–plant interactions and their respective latitude, longitude, altitude (meters above sea level), and geographic location in the Sonoran Desert

Site name	Latitude	Longitude	Altitude	Location
Seri flats (SF)	28°52′35·6″ N	111°57′17·8″ W	2	Sonora, MX
Atta flats (AF)	28°52′54·6″ N	111°57′47·8″ W	7	Sonora, MX
Teddy peak (TP)	28°57′23·7″ N	111°58′24·5″ W	63	Sonora, MX
Staghorn saddle (SS)	28°58′28·1″ N	112°02′59·1″ W	182	Sonora, MX
Alamo canyon (AC)	32°04′16·6″ N	112°43′41·4″ W	700	Arizona, USA
Arches (AR)	32°02′18·2″ N	112°42′56·6″ W	790	Arizona, USA
Semilla flats (SM)	32°11′31·6″ N	112°48′59·0″ W	498	Arizona, USA
Cholla garden (CG)	32°10′54·6″ N	112°46′24·4″ W	542	Arizona, USA

Plant species	Ant species	Ant species abbr.
Acacia constricta	*Brachymyrmex depilis*	Bd
Acacia greggii	*Camponotus atriceps/sayi*	Ca
Acacia willardiana	*Camponotus fragilis/festinatus*	Cf
Carnegiea gigantea	*Camponotus ocreatus*	Co
Cassia sp.	*Camponotus ulcerosus*	Cu
Cylindropuntia acanthocarpa	*Cephalotes rowheri*	Cr
Cylindropuntia arbuscula	*Crematogaster depilis/opuntiae*	Cd
Cylindropuntia bigelovii	*Crematogaster larreae*	Cl
Cylindropuntia fulgida	*Dorymyrmex bicolor*	Db
Cylindropuntia leptocaulis	*Dorymyrmex insanus/sp.1/sp.2*	Di
Ferocactus emoryi	*Forelius mccooki*	Fm
Ferocactus sp.	*Forelius pruinosis*	Fp
Ferocactus wislizeni	*Monomorium n.sp.desert*	Md
Fouquieria splendens	*Myrmecocystus mimicus*	Mm
Opuntia engelmannii	*Paratrechina terricola*	Pt
Pachycereus pringlei	*Pheidole obtusospinosa*	Po
Pachycereus schottii	*Pheidole vistana*	Pv
Prosopis velutina	*Pseudomyrmex apache*	Pa
Stenocereus thurberi	*Pseudomyrmex gracilis*	Pg
	Pseudomyrmex pallidus	Pp
	Solenopsis xyloni	Sx
	Tetramorium hispidum	Th

Table 2. Extrafloral nectar bearing plant species and ant species in the mutualistic networks of sampled communities in the Sonoran Desert. Ant species abbreviations are used in Figs 2,3

power-law ($P(k) \sim k^{-\gamma}$) and truncated power-law ($P(k) \sim k^{-\gamma} \exp(-k/k_x)$) models to cumulative distributions $P(k)$ for each site (where γ is the fitted constant, and k_x is the truncation value). We assessed model fit using r^2 values.

For each of the eight communities ($n = 8$–13 species per site), we examined the relationship between degree and ant species body size using Pearson correlation coefficients (r). We then re-calculated r using standardized contrasts (see below). Ant body size was ln-transformed prior to calculating r. Although we present best-fit lines in the main text, actual data points are presented in the appendices (see Appendices S1 and S2 in Supplementary material). To synthesize r among all eight sites, we used meta-analysis techniques. All correlation coefficients were summarized by calculating effect sizes using Fisher's z-transformation in METAWIN 2.2 (Rosenberg, Adams & Gurevitch 2000)

$$z = \frac{1}{2} \ln\left(\frac{1+r}{1-r}\right), \qquad \text{eqn 1}$$

where r is the Pearson correlation coefficient. Asymptotic variance was calculated as $v_z = 1/n - 3$, where n is the sample size (number of ant species). Fisher's z ranges from $-\infty$ to $+\infty$, representing negative and positive relationships between ant body size and degree. We then calculated the weighted mean effect size (Zr). We also calculated a bias-corrected 95% bootstrap confidence interval around this weighted mean effect size using resampling with 999 iterations. Weighted mean effect sizes whose confidence intervals do not overlap with zero differ significantly from zero.

We also conducted phylogenetically independent contrasts (PICs) of the correlations between degree and ant body size (Felsenstein 1985). Using PICs allowed us to examine patterns between the two variables while controlling for the evolutionary relatedness of ants. Using MESQUITE software (Maddison & Maddison 2007), we constructed ancestral relationships of ants for each site in our study based on published phylogenies (Chiotis, Jermiin & Crozier 2000; Ward & Downie 2005; Moreau *et al.* 2006). We calculated standardized

contrasts for an ant species body size and its degree using the PDAP:PDTREE module within MESQUITE (Midford, Garland & Maddison 2002). Branch lengths in each phylogeny were set to unity, an accepted approach when true branch lengths are not known, which is in turn robust to underlying assumptions (Garland, Midford & Ives 1999).

Results

In total, we observed 19 EFN bearing plant species and 22 ant species among the eight sampled communities throughout the Sonoran Desert (Table 2). The number of plant and ant species per community ranged from 4 to 12 and 8 to 13, respectively, with total community size ranging from 12 to 25 species. Degree (number of plant species with which an ant species interacted) distributions among the eight sites were qualitatively similar (Fig. 1), but varied in the model that best fit their distributions. Although two of the sites had communities that were problematic for model fitting due to small size (SF, SM), the remaining six sites had a mean ($\pm$ SE) degree exponent γ for the exponential model fit of $0 \cdot 13 \pm 0 \cdot 02$. The best model fit in five out of seven sites to ant degree distributions was the exponential model (mean $r^2 = 0 \cdot 94$). The next best model overall was power-law, with mean $r^2 = 0 \cdot 88$. Although mean r^2 ($0 \cdot 95$) was high from truncated power-law fits to degree distributions, degree exponents γ were not significantly different from zero (all $P > 0 \cdot 10$). When ant species visitation to plants throughout the range of the eight sites was taken as a whole, ant species were found to visit an average of $1 \cdot 8$ plant species (range $0 \cdot 1$–$6 \cdot 3$, $n = 22$ ant species; Fig. 2). Thus, there is variation in the number of plant species (degree) that ant species visit among different sites, and some species are more variable than others in their degree among sites (Fig. 2).
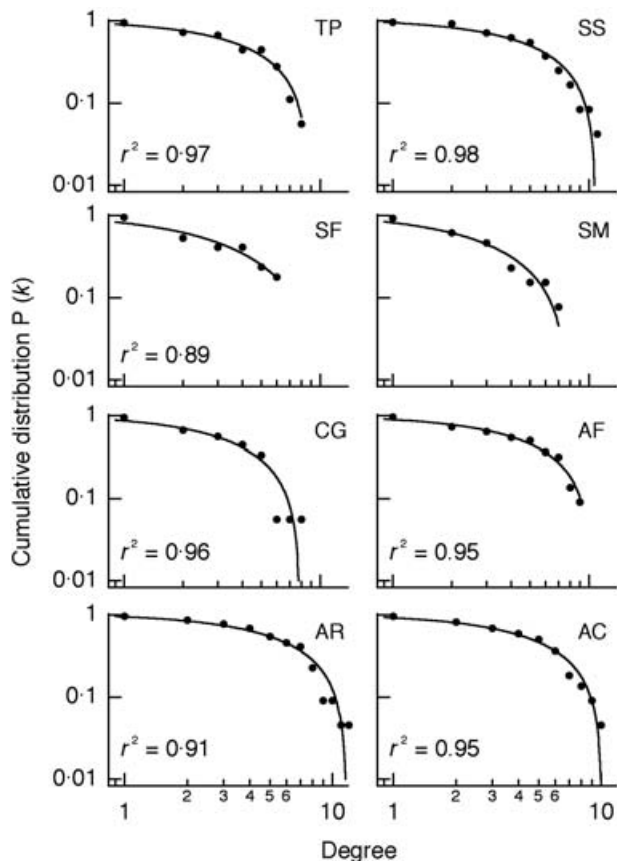
Fig. 1. Cumulative degree distribution for each of eight ant–plant mutualistic networks sampled in the Sonoran Desert. Dots represent frequencies of ant species with *k* or more links. Lines are exponential model fits to the data. The fit of exponential models is represented by r^2 values in the lower left corner. See Table 1 for site abbreviations (upper right hand corner of each panel).

Fig. 2. Mean (± 1 SE) degree for ant species in the study. The mean degree is calculated for each ant species across only those sites where the ant species was present; species lacking SE around the mean were only present at one site. Species on the abscissa are sorted in ascending mean degree. See Table 2 for ant species abbreviations.

Discussion

Though well recognized, non-random structures of mutualistic networks (Bascompte *et al.* 2003; Jordano *et al.* 2003; Olesen *et al.* 2007) are currently not easily predicted. Body size is important to many ecological processes (Brown *et al.* 2004), and has been shown to predict degree (number of species interactions) and other structural properties in predator–prey networks (Otto *et al.* 2007; Petchey *et al.* 2008). Here, we have shown that ant body size may predict the number of EFN bearing plant species with which ant species interact. Phylogenetic history among the ant species did not confound these positive relationships between degree and ant body size (Fig. 3c,d), suggesting that, in addition to their evolutionary histories (Rezende, Jordano & Bascompte 2007a; Rezende *et al.* 2007b), ecological aspects of mutualistic communities can contribute to degree–body size relationships. These positive degree–body size relationships were not statistically significant for any of the eight individual communities analyzed alone. Two factors may have contributed to this statistical insignificance. First, body size of the 22 ant species varied by only 2·7 orders of magnitude, and less within individual communities (Fig. 3a). With such low variation, body size may not necessarily be expected to predict patterns within a community (Tilman *et al.* 2004). Second, insignificant effects likely occurred due to low statistical power associated with the small number of ant species per community (i.e. small sample size; *n* = 8–13 species per site). Nevertheless, employing a meta-analytic approach to examine results among all eight communities did show a significant positive relationship between degree and ant body size (Fig. 3d). These results suggest that degree–body size relationships warrant further study as a means with which to examine the structures of mutualistic networks.

Ant species degree distributions in our study depart from the typical degree distribution in mutualistic networks. Although Jordano *et al.* (2003) showed that truncated

The body sizes of the ant species varied by 2·7 orders of magnitude, ranging from 0·04 mg for *Brachymyrmex depilis* to 18·5 mg for *Camponotus ocreatus* (Fig. 3a). Despite no correlation among degree and ant body size averaged over all eight communities (Pearson correlation coefficient *r* = 0·12, *P* = 0·61, *n* = 22 ant species), positive correlations were consistently observed among the eight individual communities between degree and ant body size (Fig. 3b,d; see Appendix S1). These degree–body size correlations remained positive after incorporating phylogenetic history among the ant species through PICs (Fig. 3c,d; see Appendix S2). Although each community alone did not show a statistically significant positive correlation (*r*), either with or without PICs, a meta-analysis test incorporating results among all eight communities did show a significant positive relationship between degree and body size. Specifically, the standardized effect size (Zr, with bias-corrected 95% CI) of correlations between degree and ant species body mass did not overlap with zero either with or without PICs (Fig. 3d, inset). In addition, standardized effect sizes with and without PICs (Fig. 3d, inset) did not differ significantly from one another.
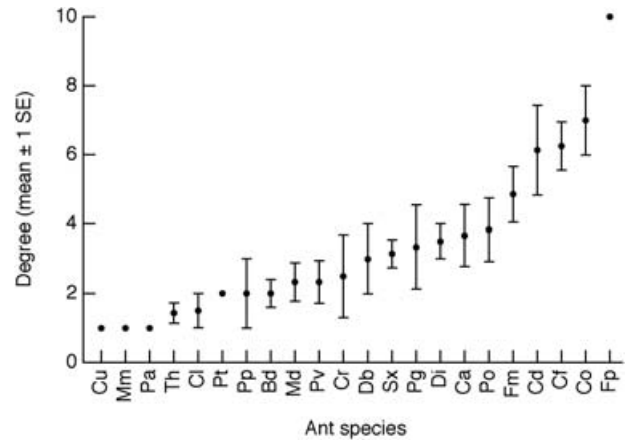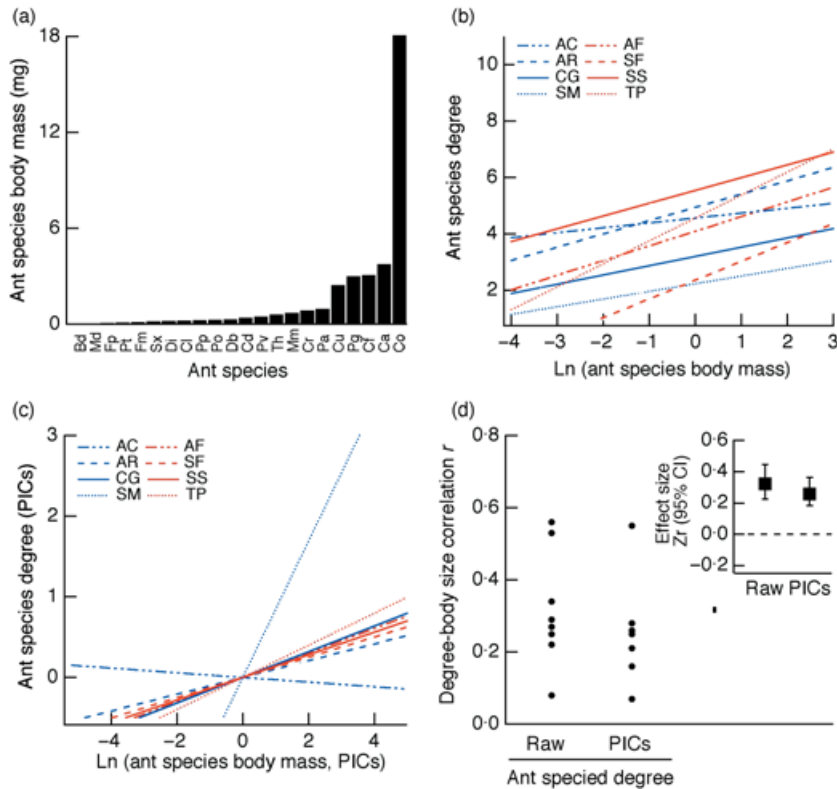
Fig. 3. Relationships between ant body size and degree, the number of plant species with which an ant species interacts. (a) Variation in ant species body size (mg) of the 22 species occurring among the eight sampled ant–plant communities. (b) Correlations ($r = 0.08$–0.56, $P = 0.1$–0.8) between degree and ant body size for each of the eight communities alone. (c) Phylogenetically independent contrasts (PICs) of such correlations ($r = 0.07$–0.55, $P = 0.1$–0.8) between degree and ant species body size for each of the eight communities alone, with best fit lines constrained through the origin (see Methods). Lines in (b) and (c) are colour coded by geographic region (blue for Arizona, USA; red for Sonora, Mexico). (d) Degree–body size correlations (r) incorporating all eight communities. Inset: standardized effect size (Zr, with bias-corrected 95% CI) of correlations between degree and ant species body mass are presented for analyses with and without phylogenetically independent contrasts (PICs). See Tables 1 and 2 for site and ant species abbreviations, respectively.

power-law best fit degree distributions for mutualistic networks, in networks in which exponential model fit best the mean degree exponents γ for exponential model fit to animal species degree distributions in mutualisms is 0·97, far higher than the mean degree exponent γ found in this study for ants. The discrepancy may simply be a factor of the relatively small size of the ant communities in our studies ($n = 8$–13 ant species) compared to those in Jordano *et al.* (2003; 17–952 animal species), which inherently limits the ability to fit models to their degree distributions. The notion that exponential models adequately represent degree distribution's of relatively small networks was recognized previously (Albert & Barabási 2002; Camacho, Guimer & Amaral 2002a,b). For example, Medan *et al.* (2007) found that in five plant–pollinator mutualistic networks, the two smallest (range $n = 38$ and 101 animal species) of five empirical networks analyzed in the study had degree distributions that were best approximated by an exponential model, while the larger networks (range $n = 275$–1428 animal species) were best approximated by a truncated power-law. These results for degree distributions suggest that ant communities in our studies lack super-generalists to a greater extent (the tail of the degree distribution decays faster than power or truncated-power) than larger mutualistic networks.

Although our study is of only one type of mutualism (ant–plant protection), other types of mutualisms are likely to share a positive degree–body size relationship. In plant–pollinator networks, because tongue length scales with body size of pollinators, the plants that pollinators visit, and subsequent degree patterns, are strongly correlated with body size (Stang

et al. 2006; Santamaría & Rodriguez-Gironés 2007). In plant–bird dispersal networks, body size and the correlated sizes of bird beaks explains 24% of possible, but unrealized interactions with plants in one community (Jordano *et al.* 2003). In a study of bird–plant interactions, hummingbird body size across five species was correlated with their functional specialization (approximate degree) on plants (Dalsgaard *et al.* 2008). Though limited to one type of mutualism, our results and those of others for pollinator and bird dispersal networks, suggest that degree–body size relationships may be general for mutualism.

Degree–body size relationships could be a result of larger species foraging over a greater area than small species, as associated with home ranges of individuals being correlated positively with body size (Woodward *et al.* 2005; Ottaviani *et al.* 2006; Greenleaf *et al.* 2007) or through larger species being more widely distributed (Leather 1991; Gaston & Blackburn 1996; Pyron 1999). In addition, some research has shown that abundance (and presumed mutualistic partner interaction frequency) can predict mutualistic degree distri-bution (Vázquez 2005; Vázquez *et al.* 2005), specifically that more abundant species interact with more species. Thus, degree should positively correlate with both abundance and body size. However, there is a consistent negative correlation among body size and abundance across most organisms (Brown *et al.* 2004). Thus, degree positively correlates with body size, and negatively correlates with abundance, a result which may be inconsistent with Vázquez (2005). Competition among ant species for EFN resources of plants may vary with ant body size, thereby contributing to the degree of ant species. For example, LeBrun (2005) showed that recruitment of

foraging ants to a resource is strongly and negatively correlated with ant body size. As ant body size increases, the number of recruiting foragers decreases, which can lead to a body size-driven competition hierarchy in which larger ant species visit more plant species. Home range, abundance and body size scaling may be general to species interactions, whereas size structured competition may be more influential in ant–plant than in pollinator or disperser mutualisms.

Consistent with recent work showing that predator and prey degree increase and decrease, respectively, with body size (Otto *et al.* 2007), results of our analyses also support degree relationships being driven by consumer body size in ant–plant mutualistic networks. While many different mechanisms could lead to degree–body size relationships in mutualistic and predator–prey networks, it may also be that such relationships arise from some common biological processes associated with consumer foraging biology and consumer–resource dynamics (Otto *et al.* 2007; Petchey *et al.* 2008). Although predator–prey and mutualistic interactions are most often dichotomized by differences in their interaction outcomes, body size relationships in both cases emerge from consumer–resource dynamics (Murdoch, Briggs & Nisbet 2003; Holland *et al.* 2005). Alternatively, degree–body size correlations in pollinator and seed disperser mutualisms, like predator–prey food webs, may arise from constraints (e.g. predator gape size; pollinator proboscis/flower matching) imposed by body size (Stang *et al.* 2006; Dalsgaard *et al.* 2008). To this end, scaling relationships between structural properties of networks and body size may transcend predator–prey and mutualistic communities. Though our results are limited in scope, we hope they stimulate further studies of body size relationships in mutualistic communities, and their similarities and differences with predator–prey food webs.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Ant species degree–body size correlations using raw, non-phylogenetically corrected data, for eight ant–plant mutualistic networks in the Sonoran Desert. Ordinate and abscissa scales were chosen to match that of Fig. 3b in the main text.

Appendix S2. Ant species degree–body size correlations using phylogenetically corrected (PICs) data for eight ant–plant mutualistic networks in the Sonoran Desert. Best fit lines are constrained through the origin (0,0). Ordinate and abscissa scales were chosen to match that of Fig. 3 c in the main text.

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