

## LETTER

## Network structural properties mediate the stability of mutualistic communities

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### Abstract

Key advances are being made on the structures of predator–prey food webs and competitive communities that enhance their stability, but little attention has been given to such complexity–stability relationships for mutualistic communities. We show, by way of theoretical analyses with empirically informed parameters, that structural properties can alter the stability of mutualistic communities characterized by nonlinear functional responses among the interacting species. Specifically, community resilience is enhanced by increasing community size (species diversity) and the number of species interactions (connectivity), and through strong, symmetric interaction strengths of highly nested networks. As a result, mutualistic communities show largely positive complexity–stability relationships, in opposition to the standard paradox. Thus, contrary to the commonly-held belief that mutualism’s positive feedback destabilizes food webs, our results suggest that interplay between the structure and function of ecological networks in general, and consideration of mutualistic interactions in particular, may be key to understanding complexity–stability relationships of biological communities as a whole.

### Keywords

Asymmetry, community structure, complexity, connectivity, degree, food web, interaction strength, mutualistic network, nestedness, species diversity, stability.

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### INTRODUCTION

One of the most enduring problems in ecology is understanding how the stability of a community is influenced by the structural properties that arise from interactions among species comprising the community. Through the later portion of the last century, the commonly-held belief was that complexity, as often inferred by species diversity, begets stability (McCann 2000; Ives & Carpenter 2007). May’s (1974) results called into question such positive complexity–stability relationships, as increasing species diversity and the number and strength of species interactions of randomly structured communities tended to diminish stability. Since then, much consideration has been given to complexity–stability relationships of predator–prey food webs and competitive communities (McCann 2000; Ives & Carpenter 2007). Insights are being made into the community structures and features of species interactions that confer stability in food webs and competitive systems, including, for example, community size, compartments, structural asymmetries, connectivity, interaction strengths, foraging biology and body size (McCann *et al.* 1998; Berlow

1999; Ives *et al.* 1999; Lehman & Tilman 2000; Ives & Hughes 2002; Neutel *et al.* 2002; Kondoh 2003; Krause *et al.* 2003; Woodward *et al.* 2005; Rooney *et al.* 2006).

On the other hand, little attention has been given to complexity–stability relationships of mutualistic communities involving beneficial (rather than antagonistic) interactions among species. Lotka–Volterra models with linear functional responses suggest that mutualistic interactions are either unstable, leading to unbounded population growth due to never-ending positive feedback, or stable only when their interaction strengths are weak and/or asymmetric (Gause & Witt 1935; Bascompte *et al.* 2006a). In this regard, May’s (1974) linear models suggest that mutualism destabilizes predator–prey food webs. We now recognize, however, that when nonlinear functional responses are incorporated into models, mutualistic systems are not inherently unstable (May 1981; Holland *et al.* 2002, 2006; Thompson *et al.* 2006). Although studies have begun to examine coexistence and diversity–stability relationships of mutualistic communities (Dodds & Henebry 1996; Pachepsky *et al.* 2002; Hoeksema & Kummel 2003; Zhang 2003), few have explicitly examined how particular structures affect the

stability of mutualistic communities involving appropriate nonlinear functional responses.

We have been limited in our ability to investigate how structural properties influence the dynamics and stability of mutualistic communities, largely due to the lack of a general means with which to characterize their community structures, like that of a food web for predator–prey interactions. Recently, however, the extension of network theory to mutualistic communities [and food webs (Dunne *et al.* 2002; Williams *et al.* 2002; Garlaschelli *et al.* 2003; Pascual & Dunne 2006)] has provided such a means with which to describe their structural properties arising from interactions (edges) among species (nodes) comprising a community (network). Bipartite networks have been employed to depict mutualistic communities composed of plant–pollinator, plant–seed disperser, plant–ant, cleaner–client fishes and anemonefish–sea anemone interactions (Bascompte *et al.* 2003, 2006a; Jordano *et al.* 2003; Vázquez 2005; Guimarães *et al.* 2006, 2007; Lewinsohn *et al.* 2006; Ollerton *et al.* 2007; Vázquez *et al.* 2007). In ecological terms, depicting such mutualistic communities as bipartite networks is simply a way of describing their two trophic-level food webs, as nearly all mutualisms are mediated by their consumer–resource interactions (Holland *et al.* 2005).

Through the aid of network theory, mutualistic communities are now recognized to entail structural properties of community size, nestedness, degree and the strength and (a)symmetry of species interactions (Bascompte *et al.* 2003, 2006a; Jordano *et al.* 2003; Vázquez 2005; Guimarães *et al.* 2006, 2007; Lewinsohn *et al.* 2006; Ollerton *et al.* 2007; Vázquez *et al.* 2007). Community size is the number of species comprising a community (species diversity). Nestedness is the topology of an ordered bipartite network describing non-random interactions among species. Mutualistic networks are often nested, entailing a core of species with many interactions among themselves, species with few interactions interacting with proper subsets of species with many interactions and few if any interactions among species with few interactions (Bascompte *et al.* 2003; Guimarães *et al.* 2006, 2007; Lewinsohn *et al.* 2006; Ollerton *et al.* 2007). Degree is the number of links a species has with other species. For mutualistic networks (and food webs), degree often follows a power distribution,  $P(k) \propto k^{-\gamma}$ , where  $k$  is degree and  $\gamma$  is the degree exponent characterized by negative values ( $\gamma < -1$ ; Dunne *et al.* 2002; Jordano *et al.* 2003; Vázquez 2005). As  $\gamma$  increases (i.e. less negative values), the number of links per species and community connectivity increase. Finally, the symmetry of interaction strengths describes the congruence between the pairwise per capita benefits of interacting species. Using frequency (or relative frequency) of interaction as an estimate of interaction strength, mutualistic communities have been suggested to be characterized by many weak, few strong and

asymmetric interaction strengths (Memmott 1999; Bascompte *et al.* 2006a; Vázquez *et al.* 2007).

Although progress is being made in elucidating the structural properties of ecological networks, we are just beginning to grasp their functional consequences for the stability of dynamically nonlinear systems (Proulx *et al.* 2005). With the recent identification of some general structural properties, studies can begin to more thoroughly examine complexity–stability relationships of mutualistic communities involving appropriate nonlinear functional responses, which in turn may provide a foundation upon which to develop general theory and guide empiricism. Here, we take a step towards understanding complexity–stability relationships of mutualistic communities by examining how their stability varies with the structural properties of community size, nestedness, degree and the strength and symmetry of species interactions.

## DYNAMIC MODEL OF MUTUALISTIC COMMUNITIES

To examine relationships between the structural properties and stability of mutualistic communities, we developed a dynamic model that moves beyond Lotka–Volterra models with linear functional responses to one that incorporates the biological feature of mutualism’s benefits on a species saturating with the population densities of others (May 1981; Holland *et al.* 2002, 2006; Thompson *et al.* 2006). As they are often bipartite in nature, we describe mutualistic communities as being composed of two separate groups of species (partite M, partite A, e.g. plants, pollinators), for which  $N_M$  and  $N_A$  are the numbers of mutualistic species in partites M and A, respectively, and  $M_i$  and  $A_j$  represent the densities of species  $i$  and  $j$  of each partite:

$$\frac{dM_i}{dt} = r_i M_i - S_i M_i^2 + \sum_{j=1}^{N_A} \frac{c_{ij} A_j M_i}{\alpha_{ij}^{-1} + \sum_k I_{[\alpha_{ik}>0]} A_k} \quad (1)$$

$$\frac{dA_j}{dt} = q_j A_j - T_j A_j^2 + \sum_{i=1}^{N_M} \frac{w_{ji} M_i A_j}{\beta_{ji}^{-1} + \sum_k I_{[\beta_{jk}>0]} M_k} \quad (2)$$

The first of the three terms on the right-hand side of the equations represent population growth, for which  $r_i$  and  $q_j$  are intrinsic growth rates. The second term modifies population growth by density-dependent self-limitation, strengths of which are described by  $S_i$  and  $T_j$ . The third term represents the beneficial effects of mutualism on population growth. We simply employed a hyperbolic functional response to represent that the benefits to mutualists saturate with the densities of mutualistic species with which they interact. Interaction strengths are described by the half-saturation constants ( $\alpha_{ij}$  and  $\beta_{ji}$ ) of the functional

responses, and symmetry of interaction strengths is described by the similarity in the magnitudes of such pairwise interaction strengths. Parameters  $c$  and  $w$  are the maximum benefits of mutualistic interactions. The summation factor in the denominator of the third term incorporates the total density of species that interact with a mutualist. The indicator function,  $I$ , is used to express the presence of a species interaction, such that  $\sum_k I_{[z_{ik}>0]} A_k$  for example, is the total density of mutualistic species that interact with the  $i$ th species of partite  $M$ . A summary of the model's parameters and variables is shown in Table S1.

## MODEL ANALYSES

We conducted numerical analyses of the model to examine how community stability varies with the structural properties of community size, nestedness, degree and the strength and symmetry of mutualistic interactions. We varied each structural property systematically, with the range of their parameter values informed by empirical estimates (Table S2) from real mutualistic communities (Bascompte *et al.* 2006a). The empirical data show realistic ranges for parameter values of each structural property, but the parameter values may be confounded by one another, as any biological mechanism responsible for one structure (e.g. nestedness, degree distribution) may contribute to and vary with another structure (e.g. community size). Simulations allowed us to evaluate the effect of each structural property (holding others constant) and to evaluate interactions among them, thereby minimizing any confounding effects of the structural properties. The range of parameter values for each structure, and default values for other model parameters, are shown in Table S1.

The model was simulated with initial values randomly generated from a uniform distribution [domain (1, 2) and (0.5, 1.5) for  $M_i$  and  $A_j$ , respectively]. We performed > 100 simulations of the model for each set of analyses of the structural properties. A number of different metrics may be employed to measure community stability (McCann 2000; Ives & Carpenter 2007). Because our model exhibited a stable equilibrium regardless of parameter values, we examined stability using community resilience, that is increases in return rates to the equilibrium following a perturbation (May 1974; McCann 2000; Ives & Carpenter 2007), as evaluated by the absolute value of the dominant eigenvalue of the Jacobian matrix at equilibrium (Appendix S1). In this way, our results are consistent with the framework of May (1974), and are directly comparable with his and more recent results on food webs.

## Community size

Community size is the total number of species making up a network, i.e. the sum of mutualistic species  $N_M$  and  $N_A$  in

the community. Community size of the empirical database exhibited great variation, ranging from 13 to 951 species (Table S2). Because most of the empirical networks clustered towards the lower end of this range, we limited our analyses of community size to 100 species ( $N_M = 30$ ,  $N_A = 70$ ), unless otherwise stated.

## Degree distribution

Degree,  $k$ , is the number of links (interactions) species have with other species, which for a community of interacting species often follows a power distribution,  $P(k) \propto k^{-\gamma}$ , where  $\gamma$  is the degree exponent and is typically a negative value. We assumed that degree distribution follows a modified power distribution  $P(k) = Ck^\gamma$ , where  $k = 1 \dots N_M$ ,  $\gamma < 0$ , and  $C = (\sum_{i=1}^{N_M} k^{-\gamma})^{-1}$  is a normalization factor. Thus, the domain of the degree distribution is constrained by  $N_M$ . Increasing  $\gamma$  (i.e. less negative values) leads to an increase in the average number of species interactions per species and a decrease in variation among species in their degree. The  $\gamma$  parameter of the empirical database was estimated using a maximum likelihood approach. To simulate degree, we assigned the number of species interactions for each species in partite A by generating random deviates from the modified power distribution, which were then assigned to each species in partite A (see *Nestedness* below).

## Nestedness

To simulate nestedness, we ranked species based on their degree, after degree was first simulated for each species of partite A. The actual species associations were determined by a modified multinomial distribution of size  $N_A$ ,  $\text{Multi}(U, \mathbf{p})$ . Each element of a random vector was constrained to either 0 for no interaction or 1 for an interaction. For the  $j$ th species of partite A, we set  $U = Z_j$ , where  $Z_j$  (the simulated degree distribution) is the number of species of partite M with which the  $j$ th species of partite A interacts. The probability vector  $\mathbf{p}$  is:

$$\mathbf{p} = \frac{[(n_1 + 1)^v, (n_2 + 1)^v, (n_3 + 1)^v, \dots, (n_{N_A} + 1)^v]}{\sum_j (n_j + 1)^v}, \quad (4)$$

where  $n_i$  is the number of species of partite A with which the  $i$ th species of partite M has already formed an association. Because this procedure was performed sequentially from the most to least connected species, we were able to manipulate nestedness by varying  $v$ . When  $v = 0$ , each mutualistic species forms interactions independent of other species. Thus, in this algorithm  $v$  and nestedness are positively correlated. For consistency with prior studies (Bascompte *et al.* 2003), we report nestedness as  $(100 - T)/100$ , where  $T$  is matrix temperature (Atmar

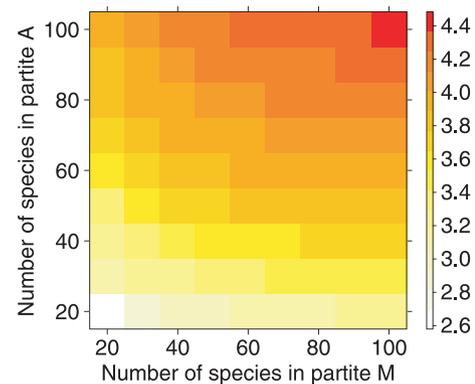
and Patterson 1993), such that large values represent highly nested networks. We also calculated nestedness for the empirical networks to guide parameter values of the simulations (Table S2).

### Strength and symmetry of mutualistic interactions

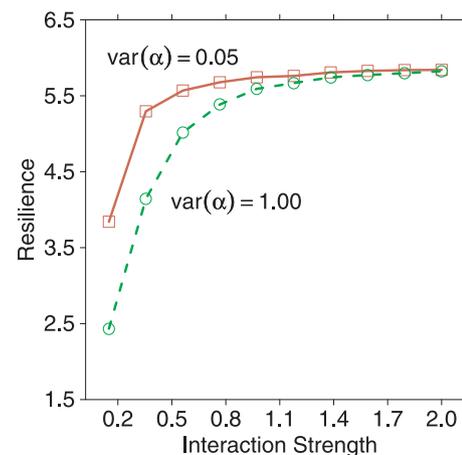
Mean, variance and correlation of pairwise interaction strengths were simulated through  $\alpha_{ij}$  and  $\beta_{ji}$ , for which larger values mean stronger interaction strengths. Symmetric interaction strengths are described by positive correlations between  $\alpha_{ij}$  and  $\beta_{ji}$ , whereas asymmetric interaction strengths are described by negative correlations. Pairwise interaction strengths were generated from a bivariate lognormal distribution, with a specified symmetry between  $\alpha$  and  $\beta$ , and mean values and variances of  $\mu = \ln(\mu_{LN}) - \frac{1}{2} \ln\left(1 + \frac{\sigma_{LN}^2}{\mu_{LN}^2}\right)$  and  $\sigma^2 = \ln\left(1 + \frac{\sigma_{LN}^2}{\mu_{LN}^2}\right)$ . The normal variates were exponentiated to convert them to lognormal random variables. This creates lognormal samples with an expected mean and variance of  $\mu_{LN}$  [e.g.  $E(\alpha)$ ] and  $\sigma_{LN}^2$  [e.g.  $\text{var}(\alpha)$ ]. In examining the strengths of interactions, for simplicity we assumed that the mean and variance of  $\alpha$  and  $\beta$  were the same [ $E(\alpha) = E(\beta)$ ,  $\text{var}(\alpha) = \text{var}(\beta)$ ]. In examining the symmetry of interaction strengths, the correlation between  $\alpha_{ij}$  and  $\beta_{ji}$  were varied through the correlation parameter,  $\rho$ . For consistency with Bascompte *et al.* (2006a), we express asymmetry of interaction strengths using the equation  $A_{\alpha,\beta} = |\alpha - \beta|/\max(\alpha,\beta)$ , ranging from 0 for perfectly symmetric (i.e.  $\alpha = \beta$ ) to 1.0 for highly asymmetric interactions (i.e. great disparity between values of  $\alpha$  and  $\beta$ ).

## RESULTS

Regardless of the particular parameter values of the model, mutualistic communities always exhibited a stable equilibrium and each of the five structural properties contributed to their resilience, as measured by their transient dynamics in return rates to the equilibrium after a perturbation. Resilience increased with community size, whether through increases in the number of mutualistic species of partite M, A or both (Fig. 1), thereby indicating that species diversity does indeed beget the stability of mutualistic communities. This positive diversity–stability relationship did not depend on or vary with other community structures. Resilience also showed a positive relationship with interaction strengths ( $\alpha$  and  $\beta$ ), such that strong rather than weak interactions facilitated stability (Fig. 2). Like species diversity, the positive relationship between interaction strengths and resilience did not depend on other community structures. Although this positive relationship between interaction strength and resilience remained for both low and high variance in interaction strengths, high variance [ $\text{var}(\alpha) = 1.0$ ,



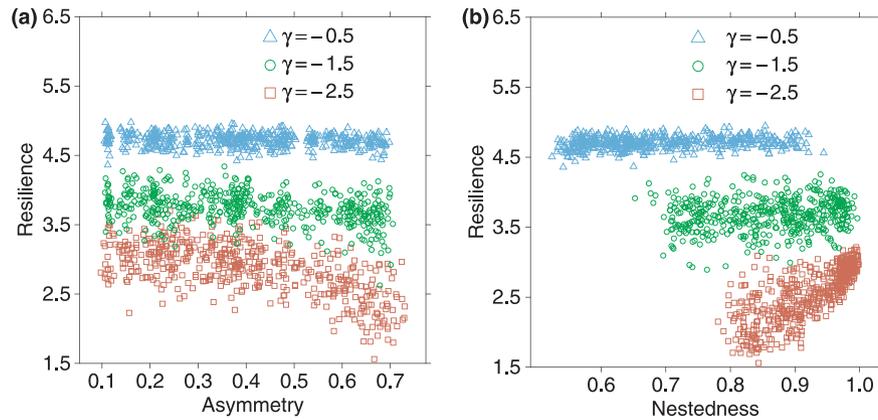
**Figure 1** Resilience of mutualistic communities and their structural property of community size. Community size is the sum of the total number of species comprising the mutualistic community. Resilience, as depicted by the colour code scale, increases with the absolute value of eigenvalues and colour shading from white to red. Results are reported for simulation averages.



**Figure 2** Community resilience and the strength of mutualistic interactions. The relationship between resilience and mean interaction strength is reported for both low and high variance in interaction strengths. Results are reported for simulation averages. Note that, for simplicity, we set  $E(\alpha) = E(\beta)$  and  $\text{var}(\alpha) = \text{var}(\beta)$  (see *Model analyses*).

Fig. 2] in interaction strengths had a small, negative effect on resilience compared with low variance [ $\text{var}(\alpha) = 0.05$ , Fig. 2].

Like community size and interaction strength, the effects of (a)symmetric interaction strengths and nestedness on resilience were qualitatively robust, but their quantitative effects on resilience did depend on and vary with another structural property, namely degree (number of species interactions). Asymmetric interaction strengths showed no prominent effect on resilience except when the degree exponent  $\gamma$  was small (more negative values), in which case



**Figure 3** Community resilience and structural properties of asymmetry of interactions strengths and community nestedness. (a) Asymmetry of interaction strengths between  $\alpha$  and  $\beta$  is measured by  $|\alpha - \beta|/\max(\alpha, \beta)$ , where a large value indicates asymmetry, and 0 indicates perfect symmetry. (b) Nestedness is reported as  $(100 - T)/100$ , where  $T$  is matrix temperature; 1.0 is a completely nested community. Potential interactions with degree distribution ( $\gamma$ , the exponent for a modified degree distribution) are shown for both symmetry of interaction strength (a) and nestedness (b).

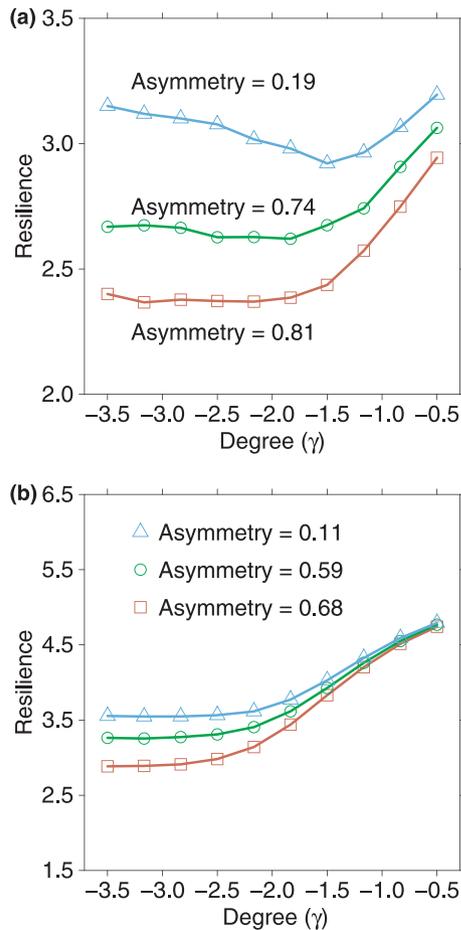
there was a negative relationship with resilience (Fig. 3a). In other words, for communities with small degree exponents, that is lower connectivity, increasing asymmetry of interaction strengths reduced resilience. Similarly, resilience was largely independent of nestedness except when degree ( $\gamma$ ) values were small; in this case, there was a positive relationship between resilience and highly nested communities of low connectivity (Fig. 3b). Indeed, nestedness of empirical communities is high (0.86 on average, Table S2) and interaction strengths appear to be highly asymmetric (minimum estimate = 0.55, Table S2; but see Discussion), implying that the stability of mutualistic communities in nature may be sensitive to nestedness and asymmetric interaction strengths. However, stability may not be strongly influenced by either nestedness or asymmetric interaction strengths, as empirical estimates of degree ( $\gamma$ ) indicate intermediate to less negative values (mean  $\gamma \pm \text{SE}$ :  $-1.46 \pm 0.15$ ; Table S2), rather than small (more negative) values ( $\gamma = -2.5$ ) required of our analyses for such negative and positive relationships to arise.

Community resilience showed a positive relationship with degree, but its quantitative effects diminished with increases in asymmetry of interaction strengths (Fig. 4). Increasing the degree exponent  $\gamma$  (less negative values; Figs 3 and 4), corresponding with an increase in the mean number of species interactions and a decrease in the disparity (variance) among species in their degree, enhanced resilience, implying that the stability of mutualistic communities increases with community connectivity. This positive relationship between resilience and degree was further enhanced by symmetric (small asymmetry values) rather than asymmetric interaction strengths, whether variance in interaction strength was low or high (Fig. 4). Yet, when interaction strengths were

relatively symmetric (asymmetry = 0.19) and their variance high, a parabolic relationship occurred between resilience and degree (Fig. 4a). Because values of  $\gamma$  affect both the mean and variance of a community's degree distribution, we were unable to distinguish their relative effect on resilience. Nonetheless, interplay between degree and other structural properties (symmetry of interaction strengths, nestedness; Figs 3 and 4) suggests that degree and community connectivity do play key roles in both the structure and dynamics of mutualistic communities.

## DISCUSSION

Central to the complexity–stability debate is reconciling the standard paradox of negative relationships between community stability and species diversity, connectivity and interaction strengths (May 1974). With the recent identification of some of their general topological and structural properties (Bascompte *et al.* 2003, 2006a; Jordano *et al.* 2003; Vázquez 2005; Guimarães *et al.* 2006, 2007; Ollerton *et al.* 2007; Vázquez *et al.* 2007), we have been able to conduct some of the first analyses of how particular structures of mutualistic communities affect their stability. Our results indicate that mutualistic communities, like predator–prey and competitive communities, may too entail intricate relationships between structure and stability. Yet, contrary to the negative complexity–stability relationships of food webs that sparked the debate (May 1974), our initial analyses show largely positive complexity–stability relationships for mutualistic communities. In particular, stability was enhanced by increasing species diversity (Fig. 1); by increasing community connectivity through a greater number of species interactions (larger degree exponents; Figs 3 and 4); and by



**Figure 4** Community resilience and structural properties of degree distribution and interaction strengths. Degree is measured by  $\gamma$ , the exponent for a domain constrained degree distribution. Results are reported for (a) high variance [i.e.  $\text{var}(\alpha) = 1.0$ ] and (b) low variance [i.e.  $\text{var}(\alpha) = 0.05$ ] in interaction strengths. For each plot, high, intermediate and low asymmetry values are based on the simulation averages with  $\rho = -0.99, 0$  and  $0.99$ , respectively.

increasing the strength and symmetry of pairwise mutualistic interactions (Figs 2–4). Collectively, our theoretical analyses, guided by empirically described mutualistic communities, indicate that stability is enhanced by large nested communities with many species interactions and strong, symmetric interaction strengths. Mutualistic networks show great variation in their structures, suggesting the importance of such studies that delineate relationships between their structural properties and community dynamics.

A key feature of mutualistic interactions that distinguishes them from other interspecific interactions is their positive feedback on population growth rates. Our treatment of this positive feedback through nonlinear functional responses differs fundamentally from historic (Gause & Witt 1935) and more recent analyses (Bascompte *et al.* 2006a) with linear functional responses. Our mutualistic communities with

satürating functional responses always had a stable equilibrium, while mutualistic communities with linear functional responses have a locally stable equilibrium, only if interaction strengths are weak and/or asymmetric (Bascompte *et al.* 2006a; see Discussion in Holland *et al.* 2006). As different forms of functional responses may influence complexity–stability relationships (Nunney 1980; but see Abrams & Allison 1982), it is critical to use biologically appropriate forms, otherwise misleading results may ensue. In spite of recent claims to the contrary (Bascompte *et al.* 2006b), linear functional responses are unlikely to occur for mutualistic interactions (Holland *et al.* 2002; Thompson *et al.* 2006) and consumer–resource interactions more generally, as they apply only to a specific group (filter feeders) of organisms (Jeschke *et al.* 2004). Moreover, animals foraging on resources supplied by their mutualistic partners (e.g. plant–pollinator interactions) are likely to entail handling times (Ivey *et al.* 2003; Goyret & Raguso 2006), which is well recognized to lead to saturating functional responses.

Because of such differences in equilibrium stability arising from different forms of functional responses, we measured stability through resilience, that is transient dynamics (return rates) of mutualistic communities to their stable equilibrium, whereas analyses of mutualistic communities with linear functional responses have measured the qualitative stability (stable or unstable) of equilibrium. Our results indicate that strong, symmetric interaction strengths enhance resilience (Figs 2–4), while weak and/or asymmetric interaction strengths have been suggested to facilitate local equilibrium stability of mutualistic communities with linear functional responses (Bascompte *et al.* 2006a). Although these results appear contradictory, different definitions of stability can change conclusions drawn about the effects of an ecological factor on stability (Chen & Cohen 2001). For the case at hand, local equilibrium stability is lost for mutualistic communities with linear functional responses when interaction strengths are not weak and/or asymmetric. Yet, communities with linear functional responses exhibit the same positive effect of strong, symmetric interaction strengths on resilience, when they are examined within the parameter range of the locally stable equilibrium.

Our theoretical result that strong, symmetric interaction strengths enhance stability appears to be at odds with the purported empirical finding that mutualistic communities are often characterized by weak, asymmetric interaction strengths (Bascompte *et al.* 2006a). Although precise definitions of interaction strength vary among empirical and theoretical studies (Berlow *et al.* 2004; Wootton & Emmerson 2005), per capita measures of them have been advocated, as they incorporate variation in species densities and ultimately per capita measures underlie most other concepts of interaction strength, including parameters of theoretical models that they can be used to evaluate (Paine

1992; Laska & Wootton 1998). Without some measure of species densities (Wootton 1997; Holland *et al.* 2006), empirical measures of the relative frequency of species interactions (Bascompte *et al.* 2006a) do not correspond with and are inadequate to estimate and evaluate predictions of per capita interaction strengths of theoretical models of mutualistic communities (Bascompte *et al.* 2006a; Holland *et al.* 2006; this study). Although recent asymmetry indices do effectively compare the congruence between interaction strengths (Bascompte *et al.* 2006a; Vázquez *et al.* 2007), the relative frequency metric within them assumes that the sum of per capita interaction strengths is the same among species (i.e. the summation constraint of the denominator of a relative measure). Consider one species that interacts 100 times with each of two species and another species that interacts 100 times with each of four species. While frequency of interaction (100) is the same for both species, relative frequencies of interaction differ, 0.5 (100/200) and 0.25 (100/400). In this way, the relative frequency of interaction for any given species likely decreases with increases in community size and its degree. For these reasons, relative frequency of interaction is not an effective measure of the asymmetry between species interaction strengths or frequency distributions of interaction strengths of mutualistic communities (i.e. 'dependencies'; Bascompte *et al.* 2006a). Similar relative measures have been found to be inadequate to describe interaction strength in other consumer–resource systems (e.g. Paine 1980). Interaction strength is an important concept in understanding species interactions, but empirical descriptions of them are currently lacking for mutualistic systems, thereby representing an important area of future study (Wootton & Emmerson 2005).

Before discussing the implications of our results for complexity–stability relationships of ecological systems as a whole, we first address two potential caveats for the study of complexity–stability relationships of mutualistic communities. First, the effects of structural properties on stability may not necessarily be independent of one another, as the same underlying biological processes responsible for one structure (e.g. nestedness) may influence or vary with another structure (e.g. community size and degree). For example, even though we used the same algorithm in our analyses, the range of observed nestedness among communities depended on their degree exponents,  $\gamma$  (Fig. 3b). If particular structures of ecological communities are studied in isolation of others, empirical or theoretical analyses may produce misleading conclusions about their effects on community dynamics or the underlying biological mechanisms responsible for those structures (Santamaría & Rodríguez-Gironés 2006).

Second, because we analysed resilience of Jacobian matrices at equilibrium, relationships between structure

and community density at equilibrium may contribute to increased resilience because of the increased negative effects of diagonal elements (intraspecific interactions) of matrices. With this reasoning, community structures may have the same correlation sign (positive or negative) with both resilience and community density. For example, increasing species diversity, the number of species interactions (degree), and the strength and symmetry of interactions did lead to monotonic increases in community density and resilience, as each enhanced population growth due to mutualism and return rates to the community equilibrium following a perturbation. Yet, not all structural properties had a strong effect on community density, nor did they affect community density and resilience in a similar manner. For example, while community density always increased with degree  $\gamma$ , the generally positive relationship between resilience and degree shifted to a parabolic relationship when interaction strengths were more symmetric and their variance high (Fig. 4a). Thus, the resilience of mutualistic communities does result to some degree from the positive density-dependent feedback of mutualism on community density, but the effects of each structural property on resilience were not mediated solely through community density, nor were they a mere artefact of model structure. Rather, it is the biology of nonlinear functional responses of mutualistic communities, i.e. their saturating positive feedback on population growth, which contributes to their positive complexity–stability relationships.

We have shown that positive relationships occur between the stability and structural properties of mutualistic communities, including community size, nestedness, degree (number of species interactions) and the strength and symmetry of interspecific interactions. Yet, our studies considered mutualistic communities in isolation of other interspecific interactions. Although this simplifying assumption is a reasonable starting point, the more realistic inclusion of other species interactions such as predation and competition may be crucial to understanding the influences of their structural properties. Moreover, when mutualistic communities are stable and do not grow unbounded, as suggested by this study, their role in predator–prey food webs may be through the transient dynamics. To this end, complexity–stability relationships of food webs may too hinge on the inclusion of mutualistic interactions. Contrary to the often-held belief that the positive feedback of mutualism destabilizes food webs, resolving the ongoing complexity–stability debate may be aided by the recognition of the complementary effects of mutualistic and predator–prey interactions on the stability of ecological communities as a whole. For instance, the stable equilibrium of mutualistic communities involving saturating functional responses (May 1981; Holland *et al.* 2002, 2006; Thompson *et al.* 2006) may balance

predator–prey food webs that tend to oscillate and often have non-equilibrium solutions (McCann *et al.* 1998; McCann 2000; Rooney *et al.* 2006). Similarly, the positive feedback of strong, symmetric mutualistic interactions that enhances stability may complement the ‘many weak, few strong’ interactions and structural asymmetries that dampen negative feedbacks and oscillations of predator–prey food webs (McCann *et al.* 1998; Berlow 1999; McCann 2000; Neutel *et al.* 2002; Rooney *et al.* 2006). Additionally, nested mutualistic communities (Bascompte *et al.* 2003; Guimarães *et al.* 2006, 2007; Lewinsohn *et al.* 2006; Ollerton *et al.* 2007) may complement compartmentalized structures of antagonistic food webs (Krause *et al.* 2003; Lewinsohn *et al.* 2006; Rooney *et al.* 2006). Given the ubiquity of mutualisms in real food webs, it may well be that these and other synergistic features of mutualistic and predator–prey interactions collectively contribute to the stability of ecological communities as a whole.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Jacobian matrix of the model of mutualistic communities.

**Table S1** Symbols, definitions, and the range and default values of model parameters.

**Table S2** Empirical estimates of structural properties of mutualistic networks.

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### Appendix S1: Jacobian Matrix of the model of mutualistic communities.

The Jacobian matrix ( $\mathbf{J}$ ) of the model (eqs 1, 2) is described as:

$$\mathbf{J} = \begin{bmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{bmatrix},$$

where  $\mathbf{M}_{11}$  is an  $N_M$  by  $N_M$  diagonal matrix whose  $ii^{th}$  element is  $r - 2M_i S + \sum_j \frac{c_{ij} A_j}{\alpha_{ij}^{-1} + \sum_k I_{[\alpha_{ik} > 0]} A_k}$ .

$\mathbf{M}_{12}$  is an  $N_M$  by  $N_A$  matrix whose  $ij^{th}$  element is  $\frac{c_{ij} M_i}{\alpha_{ij}^{-1} + \sum_k I_{[\alpha_{ik} > 0]} A_k} - \frac{c_{ij} A_j M_i}{(\alpha_{ij}^{-1} + \sum_k I_{[\alpha_{ik} > 0]} A_k)^2}$ .  $\mathbf{M}_{21}$  is

an  $N_A$  by  $N_M$  matrix whose  $ji^{th}$  element is  $\frac{w_{ji} A_j}{\beta_{ji}^{-1} + \sum_k I_{[\beta_{jk} > 0]} M_k} - \frac{w_{ji} M_i A_j}{(\beta_{ji}^{-1} + \sum_k I_{[\beta_{jk} > 0]} M_k)^2}$ . Lastly,  $\mathbf{M}_{22}$

is an  $N_A$  by  $N_A$  diagonal matrix whose  $jj^{th}$  element is  $q - 2A_j T + \sum_i \frac{w_{ji} M_i}{\beta_{ji}^{-1} + \sum_k I_{[\beta_{jk} > 0]} M_k}$ .

Equilibrium densities were used to evaluate the eigenvalues of the Jacobian matrix.

**Table S1.** Symbols, definitions, and the range and default (in parentheses) values of model parameters. Values for parameters of the structural properties were guided by estimates from an empirical database (Bascompte *et al.* 2006a) of mutualistic communities (Table S2). Unless otherwise stated, results of the numerical solutions are based on default values.

Symbol	Definition	Default Values
$r$	Intrinsic rate of population growth of species of partite M	(0.50)
$q$	Intrinsic rate of population growth of species of partite A	(0.325)
$S$	Density-dependent self-limitation of species of partite M	(1.00)
$T$	Density-dependent self-limitation of species of partite A	(2.00)
$c$	Maximum mutualism benefit for species of partite M	(3.00)
$w$	Maximum mutualism benefit for species of partite A	(3.00)
$N_M$	Number of species in partite $M$	20 to 100 (30)
$N_A$	Number of species in partite $A$	20 to 100 (70)
$\alpha$	Half saturation of mutualism benefit for species of partite M	$\mu_{LN}, \sigma_{LN}^2$
$\beta$	Half saturation of mutualism benefit for species of partite A	$\mu_{LN}, \sigma_{LN}^2$
$\mu_{LN}$	Mutualism strengths, $E(\alpha)$ and $E(\beta)$	0.15 to 2.0 (0.15)
$\sigma_{LN}^2$	Mutualism variation, $\text{Var}(\alpha)$ and $\text{Var}(\beta)$	0.05 to 1.0 (0.05)
$\rho$	Asymmetry in mutualism strengths Asymmetric ( $\rho = -1$ ) to symmetric ( $\rho = 1$ )	-0.99 to 0.99 (-0.99)
$\nu$	Nestedness Random ( $\nu = 0$ ) to highly nested (large number)	0 to 4 (4)
$\gamma$	Degree distribution parameter	-0.5 to -2.5 (-1.5)

**Table S2.** Empirical estimates of structural properties of mutualistic communities. Data set is the code from the empirical data base (Bascompte *et al.* 2006a), where P and SD are plant-pollinator and plant-seed disperser systems, respectively.  $N_M$  and  $N_A$  are the numbers of species comprising each partite of the bipartite mutualistic communities, such that community size is equal to their sum.  $\gamma$  is the maximum likelihood estimate of the parameter of the modified power distribution for degree. Nestedness is  $(100-T)/100$ , where  $T$  is matrix temperature. Mean(DN) and Var(DN) are the mean and variance of dependency (relative frequency of visits or interactions) of a plant species on an animal species from the database (surrogate for  $\alpha$ ). Asymmetry is the mean asymmetry index of the community, as calculated by Bascompte *et al.* (2006a).

Data Set	$N_M$	$N_A$	$\gamma$	Nestedness	Asymmetry	Mean(DN)	Var(DN)
P01	31	75	-1.04	0.75	0.61	0.068	0.007
P02	24	118	-2.08	0.87	0.73	0.099	0.013
P03	29	81	-1.83	0.94	0.77	0.162	0.065
P04	112	839	-2.19	0.99	0.83	0.060	0.018
P05	36	81	-1.69	0.91	0.72	0.147	0.049
P06	112	314	-2.06	0.98	0.74	0.146	0.049
P07	64	187	-1.98	0.96	0.71	0.149	0.050
P08	91	677	-2.47	0.99	0.85	0.076	0.029
P09	90	354	-2.07	0.98	0.74	0.104	0.026
P10	11	18	-1.74	0.80	0.70	0.290	0.074
P11	10	40	-1.99	0.63	0.83	0.139	0.052
P12	8	42	-1.69	0.62	0.75	0.101	0.020
P13	28	82	-1.60	0.86	0.76	0.112	0.030
P14	10	12	-1.34	0.67	0.60	0.333	0.076
P15	18	60	-1.94	0.74	0.66	0.150	0.024
P16	41	139	-1.78	0.92	0.70	0.110	0.026
P17	49	118	-1.85	0.94	0.68	0.142	0.027
P18	7	33	-1.59	0.87	0.79	0.108	0.038
P19	99	294	-2.26	0.98	0.72	0.168	0.055
SD1	31	9	-0.08	0.82	0.71	0.260	0.079
SD2	7	6	0.00	0.83	0.79	0.318	0.132
SD3	16	10	0.00	0.85	0.55	0.145	0.028
SD4	12	7	0.00	0.68	0.70	0.300	0.074
SD5	35	29	-1.21	0.88	0.60	0.240	0.066
SD6	25	33	-1.19	0.94	0.81	0.167	0.056
SD7	16	17	-0.23	0.86	0.78	0.132	0.033