

Many weak interactions and few strong; food-web feasibility depends on the combination of the strength of species' interactions and their correct arrangement

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Abstract Ecological communities consist of generalists who interact with proportionally many species, and specialists who interact with proportionally few. The strength of these interactions also varies, with communities typically exhibiting a few strong links embedded within many weak links. Historically, it has been argued that generalists should interact more weakly with their partners than specialists and, since weak interactions are thought to increase community stability, that this pattern increases the stability of diverse communities. Here, we studied model-generated predator-prey communities to explicitly investigate the validity of this argument. In feasible communities—those which were both locally stable and all species had positive biomass—we indeed found that species with many predators or prey are affected by them more weakly than species with few. This relationship, however, is only part of the story. While species with many predators (or prey) tend to be only weakly affected by each of them, these many weak interactions are balanced by a few strong interactions with prey (or predators). These few strong interactions are large enough that, when the effect of predator and prey interactions are combined, it seems that species with many interactions actually interact more strongly than species with few interactions. Though past research has tended to focus on either the arrangement of species interactions or the strength of those interactions, we show here that the two

are in fact inextricably linked. This observation has implications for both the realistic design of theoretical models, and the conservation of ecological communities, especially those in which the strength and arrangement of species' interactions are impacted by biodiversity-loss disturbances such as habitat alteration.

Keywords Interaction strength · Stability · Food-web structure · Predator-prey · Community matrix

Introduction

In the face of increasing global biodiversity loss, understanding the effect of biodiversity on the stability of ecological communities and their constituent populations of species is a pressing issue (Tilman and Downing 1994; McCann 2000; Loreau et al. 2003; Pereira et al. 2010; Cardinale et al. 2012). While early theoretical research suggested that diversity had a negative effect on stability (Gardner and Ashby 1970; May 1972; Pimm and Lawton 1977, 1978), decades of successive research have shown that many features of natural communities increase stability to the point that highly diverse communities can in fact be stable (McCann and Hastings 1997; McCann 2000; Dunne et al. 2002; Allesina and Pascual 2008). The investigation of potentially important stabilizing mechanisms thus remains an active area of research (Tilman and Downing 1994; McCann et al. 1998; Worm and Duffy 2003; Ives and Cardinale 2004; Stouffer and Bascompte 2010; Gravel et al. 2011; Stouffer and Bascompte 2011; Rooney and McCann 2012).

Adding to the discussion surrounding the relationship between diversity and stability are the many types of stability (Ives and Carpenter 2007; Donohue et al. 2013). Some, such as ecosystem-level functioning, tend to increase with

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diversity—more species leads to more redundancy and thus greater stability of the functioning of the ecosystem as a whole (Tilman and Downing 1994; Tilman 1996; Haddad et al. 2011; de Mazancourt et al. 2013). Others, such as the stability of population dynamics, tend to decrease with diversity—more interacting populations makes it more difficult for each population to persist at a stable level (May 1972; Tilman 1996; McCann and Hastings 1997; Allesina and Pascual 2008). Here, we focus on the stability of population dynamics and what mechanisms increase this aspect of stability as diversity increases.

Food webs—the network of trophic interactions underlying an ecological community—are a useful tool frequently employed when studying the stability of population dynamics as they allow us to track the changes in each population and to see how that affects other populations. In their simplest form, studies of this network of interactions within a community have focused primarily on the number of species and the number of interactions between those species as measures of network complexity (May 1972). Subsequently, both theoretical and empirical studies have shown that higher order properties such as compartments or the distribution of species' degree—the number of interactions a species has—can also play a key role in enhancing stability (Dunne et al. 2002; Arii and Parrott 2004; Stouffer et al. 2005; Stouffer and Bascompte 2010; Thébault and Fontaine 2010; James et al. 2012). Other studies have also shown that the strength of interactions is important, and weak interactions in particular have been found to be very stabilizing (Paine 1992; Fagan and Hurd 1994; de Ruiter et al. 1995; Wootton 1997; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002; Otto et al. 2007).

Combining the distribution of species' degree and the importance of weak interactions, it has long been speculated that species with many interactions should interact weakly while species with few interactions should interact strongly (MacArthur 1955; May 1972; Montoya and Solé 2003; Montoya et al. 2005; Wootton and Emmerson 2005). Such speculation makes intuitive sense since highly connected species should not need to interact as strongly with any one species of prey or be able to withstand high predation pressure from many predators (Montoya et al. 2005; O'Gorman et al. 2010). There is some evidence for this in empirical studies (O'Gorman et al. 2010), and theoretical studies have incorporated this assumption when showing a positive relationship between biodiversity and stability (MacArthur 1955; Mougi and Kondoh 2012). This assumption that species with many interactions should have weaker interactions arises predominantly from behavioral or physiological constraints: interaction frequency is limited by the time the consumer can spend searching for or handling a prey species (Holling 1959). As a predator exploits more prey species, the interaction frequency with any one prey species

should necessarily decrease. It is likely, however, that there is also an underlying “dynamical” constraint on the relationship between the number of interactions a species has and the strength of those interactions based on the notion that communities which are less stable are less likely to be observed in nature (Borrelli and Ginzburg 2014; Borrelli 2015; Borrelli et al. 2015). A species with many strong interactions with prey will likely have an excessively high biomass while a species with many strong interactions with predators will likely be unable to sustain a positive biomass. Neither case is conducive to the stability and feasibility of the community as a whole.

These two types of constraints—behavioral and dynamical—are different. Nevertheless, that does not mean that both cannot play a role in determining the relationship between the number and strength of a species' interactions. Here, we use simulated networks to explore this relationship. Furthermore, we consider both resilience and feasibility, instead of focusing exclusively on local stability. A more resilient community is one which returns to its original state more quickly after a disturbance (Pimm and Lawton 1977) while a feasible community is one which is both locally stable and all species have a positive biomass (Emmerson and Yearsley 2004). Finally, rather than concentrating on how an individual species affects those species it interacts with, we consider how an individual species is *affected by* the species it interacts with. Thus, we explore the hypotheses that, in feasible and/or more resilient food webs, species who have many prey are less reliant on each prey than those species with few prey and that species with many predators are impacted less by each of their predators than those species with few predators.

Methods

Simulating model communities

We studied the properties of simulated communities across a range of species richness $S \in [4, 6, \dots, 48, 50]$ and a range of connectance $C \in [0.05, 0.10, \dots, 0.35, 0.4]$, where connectance represents the probability that any two species have a direct effect on each other. We chose these values of connectance to span the range commonly seen in natural food webs (Williams and Martinez 2000; Dunne et al. 2002; Stouffer and Bascompte 2011), whereas the sizes were constrained by the computational effort required for the subsequent calculations.

To introduce greater heterogeneity in the number of links per species (also known as degree) than would be observed in networks generated completely at random (Barabási and Albert 1999; Dunne et al. 2002; Stouffer et al. 2005), we randomly assigned each species i a probability p_i of

interacting with other species, such that species with higher values of p_i will tend to have a higher degree. Studies of empirical networks indicate that an approximately-exponentially-decaying degree distribution, where a few species have many interactions and many species have few interactions, gives a strong fit to that observed empirically (Dunne et al. 2002; Camacho et al. 2002; Stouffer et al. 2005; Williams and Martinez 2008). We therefore drew the species-specific values p_i at random from a beta distribution $\beta\left(1, \frac{1-C}{C}\right)$ (Williams and Martinez 2000; Camacho et al. 2002; Stouffer et al. 2005). The probability that any off-diagonal value in the community matrix is non-zero was then given by $p_{ij} = \frac{p_i+p_j}{2}$ (Bascompte et al. 2003).

To characterize species dynamics within our simulated communities, we studied a system of generalized Lotka-Volterra equations (Law and Morton 1993; Emmerson and Yearsley 2004; Williams 2008)

$$f_i = \frac{dX_i}{dt} = r_i X_i (1 - X_i) + \sum_{j \neq i} \alpha_{ij} X_i X_j, \tag{1}$$

where X_i represents the total biomass of species i , r_i is the per capita growth rate of species i , and α_{ij} quantifies the per capita effect of species j on species i . Given an equilibrium solution \vec{X}^* , the behavior of this community at or very near to equilibrium is provided by its community matrix \mathbf{M} (Levins 1968; May 1972; Yodzis 1988; Laska and Wootton 1998), whose elements $m_{ij} = \left. \frac{\partial f_i}{\partial X_j} \right|_{X^*}$. Substituting in Eq. 1 here gives

$$m_{ii} = r_i(1 - 2X_i^*) + \sum_{j \neq i} \alpha_{ij} X_j^* \tag{2}$$

and

$$m_{ij} = \alpha_{ij} X_i^*. \tag{3}$$

We parametrized the community matrices \mathbf{M} studied here as follows. First, we drew the non-zero off-diagonal elements m_{ij} from a normal distribution $N(0, 1)$. To ensure that our community only featured predator-prey interactions, we imposed that all interacting pairs m_{ij} and m_{ji} always had opposite sign structure (i.e., $m_{ij} > 0$ if $m_{ji} \neq 0$ and $m_{ji} < 0$) (Yodzis 1988). After setting m_{ij} and m_{ji} , we set all diagonal elements $m_{ii} = -1$ (May 1972; Allesina and Pascual 2008). While the relationship of diagonal values to each other and to off-diagonal values is important for the stability of the food web and adds extra biological detail and structure (Haydon 1994, 2000), incorporating this additional complexity is beyond the scope of the present study; therefore, we instead follow the assumption of a common value for all diagonal values.

Note that, other than ensuring interacting pairs had opposite sign, we did not impose any further correlation

between interaction strengths. Many studies impose correlation between per capita interaction strengths (α_{ij} and α_{ji}) as an attempt to better reflect natural systems (e.g., Neutel et al. 2002; Montoya et al. 2009; Mougi and Kondoh 2012). Because we set *per population* interaction strengths (m_{ij}) and then used these to calculate per capita interaction strengths, there was no effective way of setting a meaningful correlation between the per population interaction strengths (m_{ij} and m_{ji}) which would result in a meaningful correlation between per capita interaction strengths (α_{ij} and α_{ji}) without knowing the population sizes of each species (which were not determined until after m_{ij} and m_{ji} were set). However, it was possible that those networks which were stable may be more or less likely to show a correlation between m_{ij} and m_{ji} and/or between α_{ij} and α_{ji} , and our analyses later therefore accounted for this possibility.

With our generalized Lotka-Volterra model parametrized in this way, it was possible to directly solve for all r_i and X_i^* using Eqs. 1, 2, and 3 when given the matrix \mathbf{M} (Allesina and Tang 2012) as follows. For each species, substituting Eq. 3 into Eq. 1 gives:

$$\frac{dX_i^*}{dt} = r_i X_i^* (1 - X_i^*) + \sum_{j \neq i} m_{ij} X_j^* = 0. \tag{4}$$

Recalling that we set all $m_{ii} = -1$ and multiplying both sides of Eq. 2 by X_i^* gives:

$$r_i X_i^* (1 - 2X_i^*) + \sum_{j \neq i} \alpha_{ij} X_i^* X_j^* = -X_i^*. \tag{5}$$

Substituting Eq. 3 into Eq. 5 then gives:

$$r_i X_i^* (1 - 2X_i^*) + \sum_{j \neq i} m_{ij} X_j^* = -X_i^*. \tag{6}$$

Subtracting Eq. 6 from Eq. 4 gives:

$$r_i X_i^{*2} = X_i^*, \tag{7}$$

which implies that $r_i = \frac{1}{X_i^*}$. Substituting this relationship into Eq. 4 gives:

$$(1 - X_i^*) + \sum_{j \neq i} m_{ij} X_j^* = 0 \tag{8}$$

Which can be rearranged as:

$$-X_i^* + \sum_{j \neq i} m_{ij} X_j^* = -1. \tag{9}$$

Once an equation for each species in the form of Eq. 9 is obtained, these equations can then be rewritten in matrix form:

$$\mathbf{M} \times \vec{X}^* = \vec{-1}, \tag{10}$$

from which the unknown \vec{X}^* can be solved for with linear algebra:

$$\vec{X}^* = \mathbf{M}^{-1} \times \vec{-1}. \tag{11}$$

Having solved for X_i^* , all the per capita effects α_{ij} can be directly calculated as

$$\alpha_{ij} = \frac{m_{ij}}{X_i^*}. \quad (12)$$

From the equilibrium densities X_i^* solved in this manner, we were able to determine whether the community matrix had a non-trivial, *feasible* equilibrium point. A feasible equilibrium point is one where all $X_i > 0$ (May 1972; Roberts 1974; Gilpin 1975; Kokkoris and Jansen 2002; Jansen and Kokkoris 2003). We also calculated the resilience of the community matrix—and hence this equilibrium point X^* —by quantifying its dominant eigenvalue (Pimm and Lawton 1977). Some studies include the restriction that intrinsic growth rates are positive for basal species and negative for non-basal species (Emmerson and Yearsley 2004). We have not included this restriction as, due to the way we calculate growth rates, all species end with a positive growth rate in the absence of interactions. Calculating the growth rate in this way does imply that a species' biomass is inversely proportional to their growth rate. It is entirely possible that real-world systems behave differently, so future tests of this assumption may provide valuable new insights.

Following the above methodology, we attempted to generate 100 feasible community matrices and 100 unfeasible community matrices for each combination of S and C , discarding any that contained species which did not interact with any other species. If we failed to reach these targets after generating 100,000 candidate matrices, we kept the reduced number and moved onto the next combination. In total, this gave us a total of 26,786 matrices that we studied in greater detail as described below.

Statistical analysis

We first aimed to determine whether, in feasible and/or more resilient communities, species with many links are impacted less by the species they interact with than those with few links. To do so, we considered two values of interaction strength: per capita (α_{ij}) and per population (m_{ij}). The first, α_{ij} , therefore describes the effect of an individual of species j on an *individual* of species i while m_{ij} describes the effect of an individual of species j on the *population* of species i . For each species i , we calculated these as the mean of the absolute value of all interaction strengths for an individual of species j on an individual ($|\alpha_{ij}|$) or population ($|m_{ij}|$) of species i . To control for differences in size and connectance across networks, we used species' "relative degree" as a measure of whether or not they had few

or many interactions, where relative degree was calculated as a species' degree divided by the average degree for the network (k_i/z), and average degree (z) is given by the total number of interactions in the network divided by number of species $z = L/2S$. Note that the 2 in the denominator of this expression arises because each interaction contributes two "units" of degree, one to the predator and one to the prey.

Lastly, we focused on two measures of stability: resilience and feasibility. Resilience was quantified as the dominant eigenvalue, with a larger value indicating a less resilient network. Since a feasible network is one which was stable and where all species could co-exist with a positive biomass at equilibrium, feasibility is a binary variable that indicates a network is either feasible or unfeasible.

Note that, by design, there should be no relationship between the number of interactions a species has and the strength of the effect of those interactions in our synthesized community since we assigned all interactions and interaction strengths at random. However, the stability of a network is an emergent property that can only be determined after all parameters are set. This means that any stabilizing relationship between the number of interactions a species has and the strength of those interactions could manifest itself more frequently in feasible or resilient networks than it does in unfeasible or less resilient networks. With this in mind, we used a linear mixed model to determine whether the data indicated a significant relationship with stability. Given our initial hypothesis, we were particularly interested in whether or not we would observe a negative relationship between relative degree and mean interaction strength which also depended on our measures of stability.

Original networks

To compare across our original 26,786 food webs, we used either mean $|\alpha_{ij}|$ or mean $|m_{ij}|$ as the dependent variable in the mixed model, relative total degree of species i ($k_i/2z$), a measure of stability (either resilience or feasibility), and their statistical interaction as independent variables, and we also included a random effect term for the network. Here, the random effect accounts for the fact that we have included multiple species from each network in the model, but those species are not independent since the stability of the network is an emergent property of all species and all interactions therein. To investigate whether interactions with predators or prey contributed more to any eventual pattern we might find, we repeated the above analyses separately for each interaction type. To do so, we substituted in the mean negative ($|\alpha_{ij}^-|$ or $|m_{ij}^-|$) or positive ($|\alpha_{ij}^+|$ or $|m_{ij}^+|$) interaction strength as the dependent variable. In place of relative total

degree, we likewise used k_i^-/z , the relative number of negative interactions (i.e., interactions with predators) or k_i^+/z , the relative number of positive interactions (i.e., interactions with prey). Note that we use $2z$ when considering interactions with both predators and prey combined, but only z when considering them separately.

Controlling for topology

When comparing across networks, there can be structural variations, in terms of who interacts with whom, which can also affect stability. This “structure” is often referred to as network topology, and examples of topological patterns thought to influence stability include the degree distribution of the network (Dunne et al. 2002; Arie and Parrott 2004; Stouffer et al. 2005; Otto et al. 2007; Estrada 2007), compartmentalization (Thébault and Fontaine 2010; Stouffer and Bascompte 2011), and the level of omnivory (McCann and Hastings 1997; Holyoak and Sachdev 1998; Tanabe and Namba 2005; Gellner and McCann 2012). It is possible that such patterns can have a stabilizing effect on networks which can outweigh the effect of the strength of interactions between species. Since we are most interested in the relationship between a species’ degree and how strongly it is affected by its interactions, we aimed to also control for potentially stabilizing or destabilizing effects of different topological structures. To do so, we took each of our 26,786 networks and shuffled all m_{ij} values within the network while maintaining who was predator and prey in each interaction. Doing so consisted of randomly reassigning the positive and negative off-diagonal elements of the network separately in order to keep the sign structure of all predator-prey interactions identical. We repeated this process 100 times for each network to generate 26,786 ensembles of 101 topologically identical networks.

We then compared each of these sets to each other to determine whether, when controlling for the effect of topology, a significant relationship between relative degree and mean interaction strength still impacted stability. Here, we again used a linear mixed model; however, we fit it separately to each of the 26,786 sets of m_{ij} -shuffled networks. Again, either mean $|\alpha_{ij}|$ or $|m_{ij}|$ was the dependent variable, relative degree, a measure of stability (either resilience or feasibility), and their statistical interaction were the independent variables. This time, we also included a random effect for species to account for pseudoreplication caused by the fact that the replicates of each species across the shuffled networks are not independent, as they will always have the same degree and interact with the same species. We then compared the results of these 26,786 models by using a Chi

square test to determine whether we observed a significant interaction between relative degree and stability more than we would expect at random at $\alpha = 0.05$.

Results

Original networks

Per capita interaction strength, $|\alpha_{ij}|$

Contrary to our initial hypothesis, we observed that species’ relative degree was not related to its mean $|\alpha_{ij}|$ as a function of the resilience of the community matrix ($p = 0.950$). When interactions were broken down into positive (prey) and negative (predator) interactions, we again found no relationship between the number of interactions and per capita interaction strength as a function of resilience (positive interactions, $p = 0.962$; negative interactions, $p = 0.971$). The above also held when testing for a relationship between mean $|\alpha_{ij}|$ and relative degree in either feasible or unfeasible simulated networks (all interactions, $p = 0.894$; positive interactions, $p = 0.494$; negative interactions $p = 0.719$).

Per population interaction strength, $|m_{ij}|$

We similarly observed no relationship between mean $|m_{ij}|$ and relative degree when considering resilience as a measure of stability (total interactions, $p = 0.789$; positive interactions, $p = 0.454$; negative interactions, $p = 0.148$). In contrast, we observed a significant relationship between number of interactions and mean $|m_{ij}|$ when feasibility was our stability measure ($p < 0.001$). Intriguingly, it is in the opposite direction to what we hypothesized (Fig. 1a). Here, the more interactions a population has, the *stronger* those interactions are. On the other hand, we found entirely contradictory patterns upon breaking this down into predator and prey interactions. When considering only predator or only prey interactions, the more interactions a species has, the *weaker* those interactions are in feasible networks (positive interactions, $p < 0.001$; negative interactions, $p < 0.001$; Fig. 1b, c). This occurs because species in feasible networks tend to have many predators and few prey or many prey and few predators ($p < 0.001$; Fig. 2). In both cases, the many predators (or prey) impact the focal species weakly, giving rise to a negative interaction strength-degree relationship overall. The few prey (or predators), however, impact the focal species sufficiently strongly that, when the effect of all interactions on the focal species’ population

are lumped together, species with many interactions are impacted *more strongly* by each species they interact with than species with few interactions. While the strength of the positive and negative relationships described above appear to be weak (Fig. 1a–c), they are far stronger than we would expect to observe at random (Fig. 1d–f).

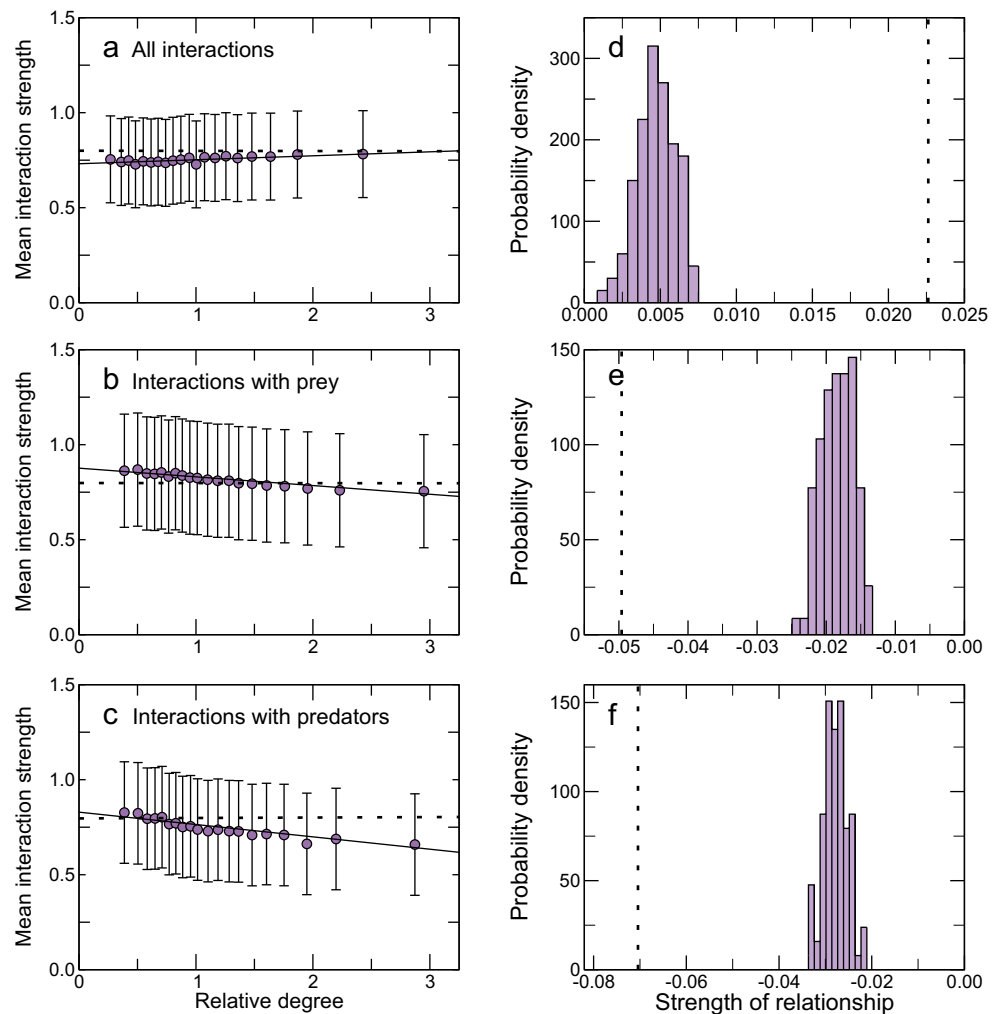
The relationship that we observe between interaction strength and degree shows that species with many predators or prey tend to have *weaker* than expected per population (m_{ij}) interaction strengths. This only occurs, however, when interaction strength is measured as per population (m_{ij}), but not per capita (α_{ij}). The reason we see this discrepancy between the different measures of interaction strength may be explained by the relationship between biomass (X_i^*) and degree. We found that species with a low biomass tend to have more interactions than species with a high biomass in stable webs ($p < 0.001$). Thus,

as $\alpha_{ij} = m_{ij}/X_i^*$, a species with a low biomass is likely to have many interactions and higher than expected per capita (α_{ij}) interaction strengths. This effect of biomass on per capita interaction strength offsets the negative relationship between per population (m_{ij}) interaction strength and degree, such that we do not find a significant relationship between per capita (α_{ij}) interaction strengths and degree.

Correlation between interaction pairs

Although per population interaction strengths were set at random and thus should not be correlated on average, it was possible that stable networks could exhibit higher correlation between m_{ij} and m_{ji} or α_{ij} and α_{ji} than unstable networks. Indeed, we found that there was higher correlation between interaction strength pairs than in unstable

Fig. 1 In feasible food webs (a–c, points and solid lines), species' mean population interaction strength shows significant relationships with their relative number of interactions. **a** The mean strength of all interactions ($|m_{ij}|$) increases with relative total degree ($k_i/2z$), whereas **b** the mean of interaction strength with prey ($|m_{ij}^+|$) and **c** the mean of interaction strength with predators ($|m_{ij}^-|$) show a negative relationship with relative degree (k_i^+/z and k_i^-/z respectively). Dashed lines show the equivalent relationship for unfeasible networks. **d–f** Although these relationships appear relatively weak, they are far stronger than what would be expected at random given the variation of interaction strengths imposed on the data. Here, we show the null distribution of these three relationships but measured across 100 randomizations of the data. In each case, the dashed vertical line indicates the strength of the relationship observed in the corresponding panel on the left



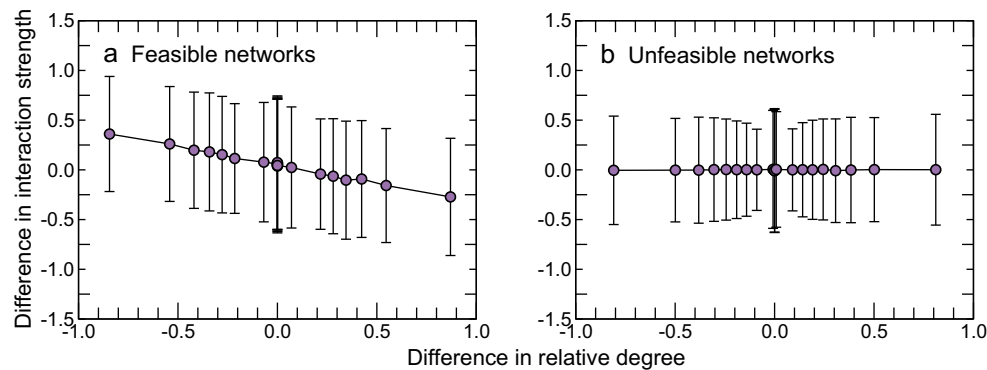


Fig. 2 Feasibility depends on the strength and correct arrangement of a species' interactions. **a** When a species in a feasible web has more prey than predators, the effect of those prey on the population of species i is weaker than the equivalent effect of those predators on species i , and vice versa. **b** The same is not true in unfeasible food webs where no such relationship is observed. In both panels, the x -axis shows species' relative number of prey interactions minus

the relative number of predator interactions ($(k_i^+ - k_i^-)/z$): species with positive values have more interactions with prey while species with negative values have more interactions with predators. The y -axis shows species' mean prey interaction strength minus the mean of predator interaction strength ($|m_{ij}^+| - |m_{ij}^-|$): species with values above zero have stronger prey than predator interactions while species with values below zero have stronger predator than prey interactions

networks for both m ($p < 0.001$) and α ($p < 0.001$). We therefore added a term for correlation in the above models to determine whether this affected the strength of the relationship between interaction strength and degree. In stable networks, we found that the level of correlation between m_{ij} and m_{ji} significantly affected the relationship between total mean $|m_{ij}|$ and relative degree, such that the relationship was more positive at higher levels of correlation ($p = 0.007$); correlation therefore strengthened the relationship we previously observed. There was no significant effect of the level of correlation in unstable networks ($p = 0.510$) whether considering per capita interaction strength ($p = 0.432$) or when interactions were separated into positive ($|m_{ij}|$, $p = 0.178$; $|\alpha_{ij}|$, $p = 0.661$) and negative ($|m_{ij}|$, $p = 0.883$; $|\alpha_{ij}|$, $p = 0.779$) interactions.

Controlling for topology

Of the 26,786 m_{ij} -shuffled sets of networks, very few exhibited a relationship between total degree and mean $|\alpha_{ij}|$ that was a function of feasibility (907; 3.4 %) or resilience (1060; 4.0 %) (Fig. 3). For predator and prey interactions, we found only 2.4 and 2.9 % of networks, respectively, showed a significant interaction when feasibility was the measure of stability and 3.5 and 3.9 % when resilience was the stability measure. In all cases, the proportion was significantly lower than would be expected at random in terms of false positives ($p > 0.05$). This would appear to imply that, even when controlling for network topology, a negative

relationship between degree and mean per capita interaction strength does not contribute to increase resilience or feasibility of the community.

When considering m_{ij} as our dependent variable, we saw a higher number of shuffle sets (1270; 4.7 % for feasibility, 2066; 7.7 % for resilience) with a significant effect of stability on the m_{ij} -degree relationship than we observed when mean $|\alpha_{ij}|$ was the dependent variable. When considering positive and negative interactions separately, we also see a higher number of significant interactions. Of course, these proportions still do not provide clear support for the stabilizing impact of a negative degree - m_{ij} relationship since they are again roughly consistent with what would be expected purely at random.

Nevertheless, we did find some evidence that the topology of the network alone can be important in determining stability: networks which are originally feasible are more likely to be feasible after shuffling than those which are not ($p < 0.001$). Importantly, it appears that the interplay between topology and the distribution of interaction strengths is most important for stability. We separated the m_{ij} -shuffled sets of networks into two categories: (i) those in which the original network was feasible and (ii) those in which it was not. The percentage of m_{ij} -shuffled sets which showed a significant effect of the interaction strength-degree relationship on stability was much higher in the originally feasible category than the originally unfeasible category (Fig. 3). This observation is most evident when studying mean $|m_{ij}|$ and feasibility. In this case, when positive and negative links are combined, we see only

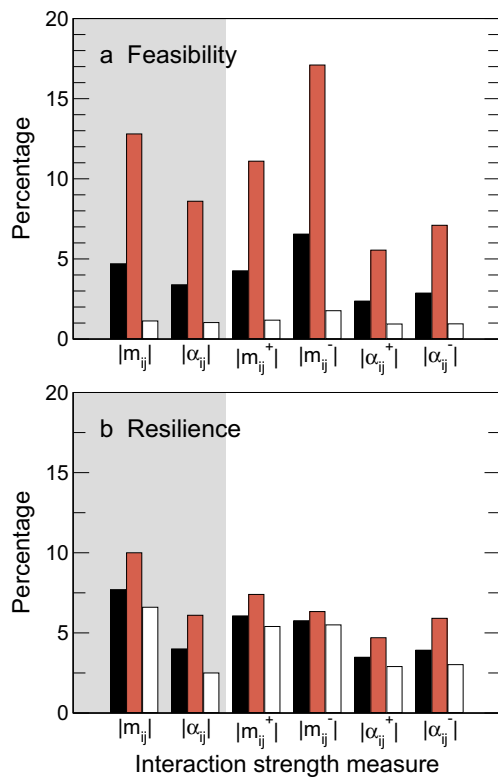


Fig. 3 Bars show the percentage of m_{ij} -shuffled network sets which showed a relationship between degree and mean interaction strength that was a function of stability. A greater percentage of shuffle sets where the original network was feasible (orange bars) showed a significant relationship than those where the original network was unfeasible (white bars) or all networks together (black bars). This was true for both **a** feasibility and **b** resilience and both population (m_{ij}) and per capita (α_{ij}) interaction strength. The first two values in each graph—those shaded by the gray background—show the results for all interactions considered together, while the remainder show the results when interactions with predators ($|m_{ij}^-|$ and $|\alpha_{ij}^-|$) and prey ($|m_{ij}^+|$ and $|\alpha_{ij}^+|$) are considered separately

4.7 % of networks which exhibit a significant interaction. Conversely, when separated, we see that only 1.1 % of the 18,457 originally unfeasible networks exhibit this interaction, while 12.8 % of those which were originally feasible have a significant interaction. Notably, this result holds whether mean $|\alpha_{ij}|$ or $|m_{ij}|$ is used as the dependent variable and whether stability is measured as resilience or feasibility (Fig. 3).

Discussion

With the increasing support for the importance of weak interactions in stabilizing food web dynamics (de Ruiter et al. 1995; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002), and intuitive arguments that generalists should interact more weakly than specialists, it has

long been assumed that a species with many interactions in a community should interact more weakly, on average, than a species with few interactions (MacArthur 1955; May 1972; Montoya and Solé 2003; Wootton and Emmerson 2005). While we found that this is indeed the case, the relationship between species' degree and mean interaction strength observed here is not as simple as we initially hypothesized. When considering both positive and negative links together, we find the feasibility of a network depends on the relationship between the number of interactions a species has and the strength of those interactions. However, in contrast to the negative relationship we expected, and which has been assumed in many previous studies, we found a *positive* relationship overall, namely, the more interactions a species has, the stronger those interactions are. Yet when we delved deeper and separated positive (interactions with prey) and negative (interactions with predators) interactions, we found the opposite relationship between mean population interaction strength and degree. For both positive and negative interactions, we specifically observed that specialists have stronger interactions than generalists. This result makes greater intuitive sense—generalists may be less efficient than specialists (Yamada and Boulding 1998; Bernays et al. 2004; Terraube et al. 2011), species cannot withstand heavy predation from many predators (Gunzburger and Travis 2004; Paterson et al. 2009; Rodriguez-Girones 2012), etc.—and is the relationship we originally expected to see. Nevertheless, it presents a paradox when compared with what we saw when positive and negative interactions are lumped together.

The solution to this conundrum lies in the interplay between network topology and interaction strength distribution. We found that species which have many interactions tend to have many positive or many negative interactions, but not both, and these tend to be weak but are balanced by a few strong interactions of the opposite type. What's more, these few strong interactions are sufficiently strong such that, when we lump all interactions together, it appears that species with many interactions have stronger interactions. Due to the trophic structure of natural food webs, it is likely that this is a pattern which is commonly found in nature; species near the bottom of the food web have many predators but few prey, while those near the top have many prey and few predators (Williams and Martinez 2000; Camacho et al. 2002). What is intriguing is that this pattern emerged in our feasible networks even when our networks were assembled in a random fashion with no predefined trophic structure. While many recent studies emphasize the importance of weak interactions, some have also found that weak interactions can be destabilizing, particularly in predator-prey systems (Allesina and Pascual 2008; Allesina and Tang 2012). They suggest that the reason we find many weak interactions in nature is that the correct combination

of network structure and interaction strength is required for weak interactions to be stabilizing (Allesina and Tang 2012). Here, we have shown that this is indeed the case while also demonstrating precisely how these interactions need to be arranged.

We have focused on *feasible* food webs, where the biomass of all species must be positive as well as the network being stable, rather than focusing only on stability. Also, rather than examining how a focal species impacts other species, we have turned the tables and looked at how other species affect the focal species. In this way, the distribution of interaction strengths with the topological pattern described above may have an intuitive and logical explanation; a species with many prey but few predators must be preyed on more heavily by those few predators or its population would increase to an extent that the network would no longer be feasible, while a species with few prey and many predators must prey heavily on those few prey to prevent being driven to extinction by its many predators. The stabilizing effect of weak interactions is well supported (de Ruiter et al. 1995; Wootton 1997; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002), and the reason for this is that weak interactions dampen the potentially chaotic effect of strong interactions (McCann and Hastings 1997). Thus, it may be that the pattern we observe here, with species having many weak positive or negative interactions countered by a few strong interactions of the opposite type, is an efficient way of ensuring that most strong interactions are sufficiently dampened by weak interactions.

Ultimately, it appears that the combination of an asymmetric arrangement of a species' interactions and the strength of those interactions is most important for feasibility. This conclusion is most strongly supported by the results we obtained upon shuffling interaction strengths. For very few networks which were originally unfeasible—and therefore were unlikely to show this asymmetric interaction pattern—was feasibility affected by the relationship between species' degree and mean interaction strength. In contrast, in networks which *were* originally feasible—and therefore likely *did* show this asymmetric interaction pattern—feasibility was far more likely to be dependent on the relationship between species' degree and mean interaction strength. Clearly, it is important to have a food-web structure which is conducive to feasibility before the stabilizing effect of a relationship between number and strength of interactions can be observed.

In conclusion, it seems that studies which have assumed that species with many prey (or predators) interact more weakly than those with few prey (or predators) have done so correctly. Nevertheless, this is only the tip of the iceberg. While the literature has tended to focus on either the topology of interactions or the strength of those interactions when studying food webs, our results indicate that these are

two sides of the same coin and are too tightly interwoven to be treated independently. Thinking more broadly, this observation has clear impacts for the conservation and management of ecological communities (Brose 2010; Tylianakis et al. 2010); while it is important to focus on conserving species and thus their interactions, it may also be important to focus on conserving the strength of those interactions. In particular, for a species with many prey, it may be more important to maintain the few predators which have a strong impact than the many prey it relies on weakly, and vice versa.

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