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RESEARCH

Many weak and few strong links: the importance of link strength distributions for stabilising patterns in competition networks

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Abstract

Ecological networks tend to contain many weak and only a few strong links. Furthermore, link strengths are often patterned within a network in ways that enhance system stability considerably, increasing the ability of the system to return to equilibrium after a perturbation. However, little attention has been given to the relation between the skewed "many weak and few strong links" distribution and the stabilising effect of patterning. Here, we focus on the stabilising effect of a hierarchical patterning in bryozoan competition networks and demonstrate that this stabilising effect critically depends on a skewed distribution of link strengths. We first show that, in line with many other ecological networks, the empirically derived link strengths in these competition networks were characterised by a high level of skewness, with many weak and few strong links. Then, we analysed the relationship between the link strength distributions, hierarchy and stability by comparing theoretical competition matrices with different distributions of link strengths. We found that the full stabilising effect of hierarchy only appeared when we used skewed link strengths produced by a gamma distribution, but not in matrices built with uniform or half-normal distributions. This has important methodological implications, since theoretical studies often assume normal or uniform distributions to investigate ecological stability, and therefore might overlook stabilising mechanisms. These implications are relevant for theory on the relation between structure and stability of ecological networks in general, since skewed link strengths are also a common feature of food webs and mutualistic systems.

Keywords Ecological networks · Competition · Stability · Hierarchy · Interaction strengths

Introduction

In diverse communities, direct and indirect interactions between species form complex ecological networks. This complexity makes it challenging to predict how assemblages, communities and whole ecosystems will react to environmental changes and disturbances (Montoya et al. 2006; Woodward et al. 2010; Strona and Lafferty 2016; Barnes et al. 2021). Understanding how the strengths of interactions in ecological networks relate to system stability, a system's ability to return to equilibrium after a perturbation (May 1972; Landi et al. 2018), has therefore been a long-standing focus in the field of community and ecosystem ecology (Yodzis 1981; Ruiter et al. 1995; McCann et al. 1998; Emmerson and Yearsley 2004; Jacquet et al. 2016; Landi et al. 2018).

There is ample evidence of a characteristic distribution of many weak and few strong links in empirical studies on ecological networks, in particular in food webs (Paine 1992; Neutel et al. 2002; Berlow 1999; O'Gorman et al. 2010; Jacquet et al. 2016) but also in mutualistic systems (Jordano 1987; Bascompte et al. 2006). Theoretical studies (McCann et al. 1998; Emmerson and Yearsley 2004; James et al. 2015; Van Altena et al. 2016; Gellner and McCann 2016; Jacquet et al. 2016) as well as some experimental evidence (O'Gorman and Emmerson 2009) suggest that these weak links have a stabilising effect, meaning they increase a system's ability to return to equilibrium after being disturbed. Weak links contribute to stability by lowering the

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overall mean link strength (May 1972), as well as through a dampening effect on oscillations, which has been well studied in small network modules (McCann et al. 1998; Emmerson and Yearsley 2004). However, studies based on observed networks have demonstrated that patterning, that is, how exactly weak and strong links are arranged within a network, also has an important stabilising effect (Yodzis and Innes 1992; Ruiter et al. 1995; James et al. 2015). Examples of stabilising patterns include the presence of weak links in omnivorous loops in food webs (Neutel et al. 2002; Emmerson and Yearsley 2004; Bascompte et al. 2005; Wootton and Stouffer 2016) as well as hierarchical patterns in competitive systems (Koch et al. 2023).

Thus, it is known that both the distribution of many weak and few strong links and the patterning of link strengths are important for stability. This is in apparent contradiction to analytical results derived from random matrix theory. It has been shown that the exact shape of the distribution of link strengths does not influence the stability of large networks with randomly arranged links (Tao et al. 2010). For simplicity, many theoretical studies consequently use standard uniform or normal distributions (Allesina and Tang 2012, 2015), instead of more realistic, skewed distributions. However, for networks where link strengths are derived from observations and are thus not arranged randomly, it remains unclear whether, and if so, how the distribution of link strengths influences the stabilising effect of patterning.

Here, we explore the relationship between the distribution of link strengths, their patterning and system stability in realistic, multi-species competitive communities. While it is obvious that some level of variation in strengths is needed to enable patterning, we do not know whether greater variation in link strengths will lead to stronger stabilising effects or how exactly the "many weak and few strong" links distribution influences stability in patterned systems. In this study, we address these open questions by analysing the stabilising effect of a hierarchical pattern of link strengths, which was recently identified in assemblages of encrusting, marine bryozoan colonies (Koch et al. 2023, see Box 1 for details). Koch et al. (2023) find a competitive hierarchy in these assemblages, a clear ranking from strongest to weakest competitor. They show that this strict ranking causes asymmetric patterns in community matrices, both within pairs of competitive interactions and at the whole assemblage level. Koch et al. (2023) explain the stabilising effect of hierarchy based on the strength of feedback loops, closed chains of interactions that either amplify or dampen disturbances (see Fig. 1 for details).

In a first step, we show that the "many weak and few strong" link distribution that has been found in other network types also appears in competitive systems. Then, we ask if and to what extent the stabilising effect of hierarchy depends on this underlying distribution of link strengths. To address this question, we generated theoretical matrices in which we varied the proportion of strong and weak links by using random link strengths drawn from distributions with different shapes. For each type of distribution, we quantified the stabilising effect of hierarchy by comparing the stability of asymmetric matrices to randomly patterned ones (see Fig. 2 for a visual overview of our approach). We find that the stabilising effect of hierarchy critically depends on the skewness of link strengths. This suggests that the "many weak and few strong" link distribution plays a critical role in the stability of these competitive systems.

Box 1: explaining the stabilising effect of asymmetry in bryozoan assemblages (Koch et al. 2023)

Bryozoans are small, aquatic animals that grow in colonies on the seabed, where they form diverse assemblages. The dynamics of these assemblages are almost entirely driven by interference competition as individual colonies compete for space by overgrowing each other. The outcomes (win/loss/draw) of these ongoing competitive interactions can be assessed visually (Barnes and Rothery 1996; Barnes and Dick 2000). Based on data sets that contained records of overgrowth interactions in 30 bryozoan assemblages, Koch et al. (2023) analyse the stability of these systems by deriving inter- and intraspecific link strengths (see Methods).

Interference competition networks derived from bryozoan data sets have a hierarchical structure, meaning that all species can be ranked from weakest to strongest competitor. This hierarchy results in asymmetric patterns of link strengths within the competition networks. Asymmetry can be found both within pairwise interactions, where a strong link is coupled with a weak link (Fig. 1a), and at the community level, where strong links are concentrated on one side of the community matrix diagonal (Fig. 1b). While the observed competition networks are found to be unstable, their instability is reduced compared to randomised systems. This stabilising effect of asymmetric patterns of link strengths can be explained based on the concept of feedback loops, that is, closed chains of interactions that connect one network element back to itself (Levins 1974). They determine how perturbations propagate through the nodes and links of a network, through both direct and indirect effects (Zelnik et al. 2024). A loop is quantified as the product of all link strengths within the loop. Positive feedback loops (those with a positive product, for example 2-link loops in competitive systems) amplify disturbances that are introduced into the system, while negative feedback loops (those with a negative prod-

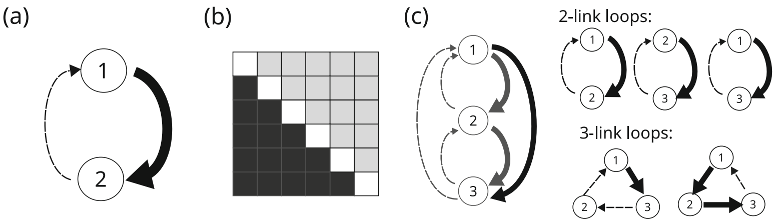

Fig. 1 Asymmetric patterns in link strengths caused by hierarchical competition. **a** Pairwise asymmetry means that the loop formed by each pair of competing species consists of a strong link, coupled to a much weaker link. **b** Community asymmetry means that when we order the community matrix according to the hierarchical ranking, from strongest to weakest competitor, all strong links appear below the diagonal while all weak links appear above the diagonal. **c** A hierarchical ranking reduces the strength of all feedback loops in a competitive network. Due to the asymmetric arrangement of weak links (dashed arrows) and strong links (thick arrows), each loop contains at least one weak link

uct, for example 3-link loops in competitive systems) counteract them (Levins 1974).

Using an approach that was developed for trophic networks (Neutel et al. 2002, 2007; Neutel and Thorne 2014) and extending it for competition networks, Koch et al. (2023) show that the asymmetric patterns of link strengths reduce network instability by keeping short and long feedback loops weak. Pairwise asymmetry reduces the instability of empirical competition networks by weakening the effect of positive 2-link feedback loops. As the effect of a loop depends on the product of link strengths, pairwise asymmetry means that a strong link is multiplied with a weak link (Fig. 1c), so that the overall product remains low. The stabilising effect of community asymmetry, on the other hand, is related to longer, negative loops, which can cause unstable oscillations (Levins 1974). Community asymmetry avoids the formation of such long negative loops, as all longer loops also contain at least a single weak link, which keeps the overall effect of the loops low (Fig. 1).

Methods

Empirical link strength distributions

We obtained empirical distributions of link strengths (which can also be called interaction strengths) from Koch et al. (2023). For background on the methodology used by Koch et al. (2023), we describe the procedure of deriving empirical link strengths here. Following May (1972), link strengths are defined as the elements of the Jacobian or “community matrix”, which contains the partial derivatives of an underlying system of differential equations, evaluated at equilibrium. The elements describe the per-capita effect (dimension $1/t$) of a change in the biomass of species j on the biomass of species i. Koch et al. (2023)’s calculation assumes Lotka-Volterra equations at equilibrium, with the observed abundances corresponding to equilibrium densities. This equilibrium assumption is used as a methodological step to be able to test whether the empirical systems can be considered stable (see Koch et al. 2023 for more details).

First, the amount of biomass loss due to competition between two species is estimated from observed outcomes of spatial contests between bryozoan colonies. In bryozoan assemblages, individual colonies compete for space by overgrowing each other, and these ongoing competitive interactions can be visually assessed (Barnes and Rothery 1996; Barnes and Dick 2000). The data sets used by Koch et al. (2023) consist of records of such overgrowth interactions, where the outcome of each observed interaction between two colonies was classified as either a win/loss or a draw (following the methodology described in Barnes et al. 2014). If one colony of species A overgrew at least 5% of another colony of species B, this was scored as a win for A and a loss for B. Draws were scored when the colonies ceased growth along their boundaries or were mutually overgrowing each other. The data sets also contain records of intraspecific interactions, where two colonies of the same species interacted.

In a second step, these biomass loss rates are combined with the observed abundances to translate them to link strengths (see Supplementary Note 1 for a more detailed description). Finally, link strengths are normalised by dividing all off-diagonal matrix elements by their corresponding diagonal matrix elements (following Neutel and Thorne 2014). This scaling procedure preserves the essential stability characteristics (see Thorne et al. 2021 for a detailed explanation) and makes the matrices dimensionless, which simplifies the comparison of stability (see Section “Calculation of network stability via the critical amount of self-regulation).

As a starting point of our analysis, we describe the shapes of the empirically based normalised distributions of link strengths observed by Koch et al. (2023) by calculating mean, variance, minimum, maximum and skewness and kurtosis (using the R-package *“moments”*) of the non-zero interspecific link strengths in each of the 30 empirical matrices.

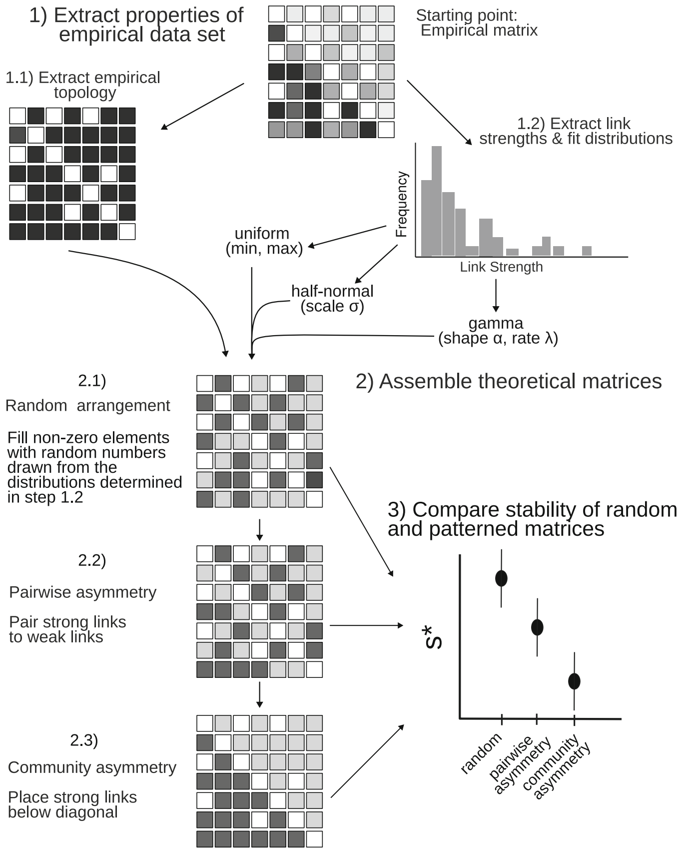

Fig. 2 Assessing the relation between link strength distribution and the stabilising effect of hierarchy using theoretical matrices. We started with a community matrix derived from empirical data, which contained normalised interspecific links of varying strengths (indicated by different shades of grey). Due to the normalisation, diagonal matrix elements, which represent intraspecific links, are equal to -1 (shown here in white for simplicity). As a first step (1.1), we extracted the empirical topology, the location of missing links (white off-diagonal cells), and we fitted uniform, half-normal and gamma distributions to the empirical link strengths (1.2). In a second step, the theoretical matrices were assembled using random link strengths generated with the fitted distributions. We then imposed three types of patterns on the theoretical matrices by arranging the theoretical link strengths in random (2.1), pairwise asymmetric (2.2) and community asymmetric (2.3) patterns. We preserved the locations of non-zero links extracted from the empirical matrix in this step. In a third step, we compared the stability of random, pairwise asymmetric and community asymmetric matrices. We measured stability as the critical amount of self-regulation s^*. Lower values of s^* indicate more stable systems

Using theoretical matrices to quantify the stabilising effect of asymmetry under different distributions of link strengths

We used theoretical competition matrices with random link strengths to explore the stabilising effect of pairwise and community asymmetry under varying distributions of link strengths (see Fig. 2 for a visual overview of our approach). Our goal was to create theoretical matrices that closely resembled the empirical systems, but differed in their proportion of weak and strong links. For each empirical data set, we extracted the empirical topology, that is the network size, connectance and the location of non-zero links (Fig. 2, step 1.1). Then, we fitted distributions with different shapes to the empirical link strengths (Fig. 2, step 1.2). These were then used to generate artificial link strengths (Fig. 2, step 2; see section *"Theoretical link strength distributions"* for details). We arranged the artificial link strengths within the theoretical matrix to form random, pairwise asymmetric and community asymmetric pattern (Fig. 2, steps 2.1–2.3; see section *"Patterning of link strengths in theoretical matrices"* for details). We quantified the stabilising effect of the asymmetric pattern by comparing the stability of a set of random matrices to a set of patterned matrices (Fig. 2, step 3).

As a frame of reference that allowed us to compare the behaviour of the theoretical matrices to the empirical systems, our analysis also included an additional set of matrices using the observed, empirical link strength distributions but arranged in the same way as the theoretical link strengths.

Theoretical link strength distributions

The off-diagonal matrix elements, representing interspecific link strengths, were randomly drawn from probability distributions. Our goal was to obtain distributions with comparable ranges, but with different proportions of weak and strong values across this range. To achieve this, we first fitted half-normal, uniform and gamma distributions to each empirical data set using the *fitdistrplus* R-package (Delignette-Muller and Dutang 2015). We chose the gamma distribution as it allowed us to generate random link strengths that closely resembled the empirical data. In contrast to that, half-normal and uniform distributions were chosen as they have often been used to generate random link strengths in previous studies (see, e.g. Allesina and Tang 2012). Then, we used the parameters of these fitted distributions (uniform: min and max; half-normal: scale σ ; gamma: shape α and rate λ, all fitted parameter values can be found in Supplementary Table 2) to generate random links strengths. As the gamma and half-normal distributions are defined for positive values, we fitted to the absolute values of the link strengths. As our goal was to preserve the range of values, we could not preserve the mean link strengths in the half-normal and uniform distributions. For uniform distributions, the means were on average 3.6 times higher than the empirical mean. The means of the half-normal distributions were on average 1.5 times higher than the empirical means, while there was no difference between the means of the gamma distributions and the means of the empirical distributions.

The diagonal elements of each matrix, which represent intraspecific link strengths, were set to -1. We did this to make them comparable to the normalised, empirical matrices. It is also consistent with previous theoretical work using random matrices (May 1972; Allesina and Tang 2012), which thus implicitly uses the assumption that the matrix elements represent normalised link strengths.

Patterning of link strengths in theoretical matrices

We then imposed three types of patterns on the theoretical matrices: random, pairwise asymmetric and community asymmetric (following Koch et al. 2023). To preserve empirical topology, we placed random link strengths only in locations that also had non-zero link strengths in the original empirical matrix. We also created matrices with random topologies, to test the generality of our results (Supplementary Fig. 1).

In the randomly arranged matrices used for the main analysis (Fig. 2, step 2.1), each link strength was independently placed in a random position within the matrix. These matrices served as null models, which allowed us to quantify the stabilising effect of asymmetry. To impose pairwise asymmetry (Fig. 2, step 2.2), we made sure that within each pair, a strong link was paired with a weak link. This was achieved by sorting the set of random link strengths from weakest to strongest. The weakest link was then paired with the strongest link, the second strongest with the second weakest, etc. The location within the matrix was assigned randomly. To impose community asymmetry (Fig. 2, step 2.3), we additionally controlled the positions above or below the matrix diagonal, so that all strong links were located below the matrix diagonal.

Calculation of network stability via the critical amount of self-regulation

The theoretical competition matrices were assumed to represent Jacobian matrices of some underlying (potentially non-linear) system of differential equations, which has been linearised around an equilibrium point (May 1972). System stability here is the local asymptotic stability of this equilibrium point, which describes whether a system has the ability to return to its steady state after an infinitesimally small disturbance. Stability is measured using the real part of the dominant eigenvalue, $Re(\lambda_d)$, of the Jacobian matrix, which in the case of a stable system ($Re(\lambda_d) < 0$) is also called resilience (the speed of return to equilibrium). If $Re(\lambda_d) > 0$, the system is unstable and will hence not return to equilibrium, but the level of instability can still be compared in terms of the magnitude of $Re(\lambda_d)$, which describes how fast the system moves away from its equilibrium point.

In general, any unstable system can be made stable by artificially increasing the absolute value of the diagonal matrix elements (the intraspecific link strengths), making these negative elements stronger, while any stable system can be made unstable by decreasing the absolute value of the diagonal matrix elements. The critical amount of self-regulation uses this mechanism to measure stability. It is defined as the factor by which the observed intraspecific link strengths have to be multiplied to bring the matrix to the threshold between stability and instability (Neutel et al. 2002). In the case of an unstable system, s^* is larger than 1, and its value describes how much more self-regulation needs to be added to make the system stable. In the case of a stable system, $s^* < 1$, it describes the “buffering capacity” of a system.

As all matrices used in this study have uniform diagonals (all $a_{11} = -1$, see section 2.2.1), the critical amount of self-regulation (s^*) is equivalent to $Re(\lambda_d)$ of the same matrix but with the diagonal set to 0 (for details, see Supplementary Material of Neutel and Thorne 2014). Hence, we could have used $Re(\lambda_d)$ as a stability metric here. However, $Re(\lambda_d)$ of the Jacobian matrix is time-dependent, while s^* offers a dimensionless measure of stability that works for matrices with varying diagonal terms, representing different time scales (Neutel et al. 2002). This is usually the case when deriving link strengths from empirical data, where intraspecific competition can differ a lot between species in a given community or assemblage. In order to emphasise our focus on stabilising patterns in realistic systems and to enable comparison to the results of Koch et al. (2023), we therefore use the critical amount of self-regulation instead of $Re(\lambda_d)$.

Results

Empirical link strengths can be closely approximated by a gamma distribution

We analysed the shapes of the distributions of link strengths from 30 empirical competition networks published in Koch et al. (2023). Link strengths were the normalised elements of the Jacobian matrix (see Methods and Supplementary Note 1). For each of the 30 data sets, we calculated not only the mean and variance but also the skewness ($\hat{S}$) and kurtosis ($\hat{K}$) (Supplementary Table 1). Skewness describes a distribution's asymmetry, while kurtosis describes how peaked a distribution is (Cristelli et al. 2012; Gross et al. 2021). We found that overall, the empirical link strengths showed distributions that were very asymmetric (mean $\hat{S} = -2.4$) and peaked (mean $\hat{K} = 9.9$), with a large variability in their skewness and kurtosis values (Fig. 3a).

The shapes of these empirical distributions thus differ clearly from half-normal and uniform distributions, which are more symmetric ($\hat{S} = 0.96$ and $\hat{S} = 0$, respectively) and have low kurtosis ($\hat{K} = 3.9$ and $\hat{K} = 1.8$). A gamma distribution (shown as the dashed line in Fig. 3a) allows for varying skewness and kurtosis values and is able to capture the shape of empirical distributions much better. Fitting a gamma distribution to empirical link strengths allowed us to generate random link strengths with a more realistic pattern of many weak and few strong values (shown in Fig. 3b for one example data set). In contrast to that, a half-normal distribution produced too many intermediate values, while strong values were too rare. A uniform distribution, where all values are equally likely, generated too many strong values and too few weak ones (Fig. 3c).

The stabilising effect of community asymmetry depends on the distribution of link strengths

We tested whether and how the distribution of link strengths affected the stabilising effect of asymmetries by comparing asymmetric to randomised theoretical competition matrices with uniform, half-normal and gamma-shaped distributions of link strengths. For each type of distribution, we compared the stability (measured as critical self-regulation s^*) of randomly patterned matrices to asymmetric ones, where strong links were paired to weak links as well as to community asymmetric ones, where strong links were also paired to weak links and all strong links additionally appear on one side of the diagonal (see Methods and Fig. 2).

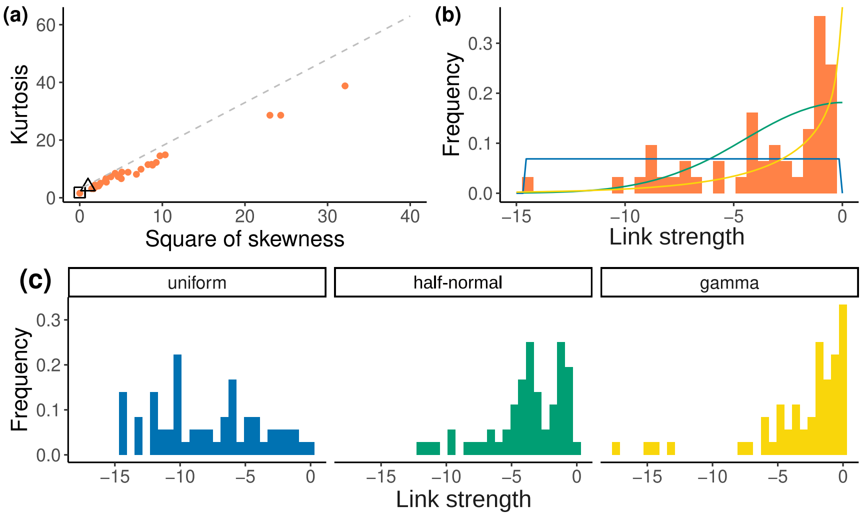

Fig. 3 Skewed empirical link strengths are best represented by a gamma distribution **a** Skewness-kurtosis relationship of the empirical distributions of link strengths on a Cullen and Frey graph, which can be used to differentiate between different types of distributions (Delignette-Muller and Dutang 2015). Each orange dot represents one empirical data set. Normal and uniform distributions both only have one possible skewness $\hat{S}$ and kurtosis $\hat{K}$ value (half-normal: $\hat{S} = 0.9$, $\hat{K} = 3.9$, shown as a black triangle; uniform: $\hat{S} = 0$, $\hat{K} = 1.8$ shown as a black square). The gamma distribution allows for varying $\hat{S}$ and $\hat{K}$ values and is represented as a dashed line, that represents how $\hat{S}$ and $\hat{K}$ depend on the shape parameter. **b** Histograms showing the empirical distribution of link strength for one example matrix (Rothera 3) as well as a uniform (blue), half-normal (green) and gamma (yellow) distribution fitted to these empirical values. **c** Example sets of random link strengths drawn from these fitted theoretical distributions

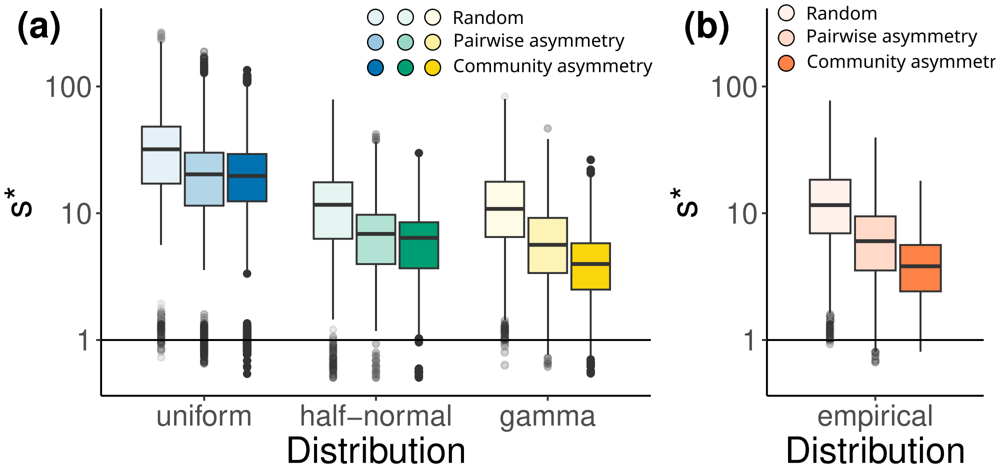

Fig. 4 The stabilising effect of asymmetries in theoretical matrices with varying distributions of link strengths. We quantify this effect by comparing the stability of randomly patterned and asymmetric matrices for theoretical distributions (a). For comparison, we also quantify the effect in theoretical matrices with the observed, empirical distribution of link strengths (b). The level of (in)stability was compared using the critical amount of self-regulation, s^*. As most matrices were unstable, this described how much self-regulation would have to be added to reach stability. Size, connectance and topology of each theoretical matrix were chosen based on one of the 30 empirical systems. They contained link strengths drawn from a uniform, normal or gamma distribution fitted to the same empirical counterparts' link strengths (a) or the observed link strengths (b). This was repeated 100 times per empirical data set, resulting in $30 \times 100 = 3000$ data points per boxplot

Almost all theoretical matrices had critical amounts of self-regulation (s^*) larger than 1 (Fig. 4a), indicating that the networks were unstable, and that additional self-regulation would be required to reach stability (where $s^* = 1$, or equivalently, $Re(\lambda_d) = 0$). This was no surprise, as the random link strengths were fitted to link strengths from empirical community matrices that were also unstable (Koch et al. 2023). Throughout this analysis, we were thus comparing different levels of instability. Similarly, also, the differences in instability between randomly patterned matrices of different distributions were expected (Fig. 4a, light boxes). They arise from differences in mean link strengths (May 1972): As the uniform distributions contained a higher proportion of strong values, these matrices were more unstable.

In theoretical matrices with empirical distributions of link strengths, which we use as a reference, pairwise asymmetric patterns reduced instability and community asymmetry reduced instability even further (Fig. 4b, in line with the findings of Koch et al. 2023). Correspondingly, for all theoretical distributions, a pairwise asymmetric pattern resulted in a reduction of instability as well. However, adding community asymmetry only had an additional stabilising effect in systems with a gamma distribution. In matrices with half-normal or uniform distributions, there was no additional effect of community asymmetry (Fig. 4a). This implies that a certain level of skewness is required to enable an additional stabilising effect of community asymmetry. This result was independent of the specific architectures or sizes of the networks and also held for random topologies (Supplementary Fig. 1) and for larger networks involving hundreds of species (Supplementary Fig. 2).

Skewness enables the stabilising effect of community asymmetry

In a final step, we wanted to obtain a better understanding of how skewness affected the stabilising effect of pairwise and community asymmetry. We created additional sets of matrices using gamma distributions in which we systematically varied the level of skewness, while keeping matrix size S, connectance C and the mean link strength constant. For each level of skewness, we quantified the stabilising effect of asymmetry by calculating stability gain, the ratio of mean s^* of randomly patterned to asymmetric matrices (Fig. 5a). We found that for low skewness values between $\hat{S} = 0$ and $\hat{S} = 2$, stability gain due to pairwise asymmetry and stability gain due to community asymmetry increased equally. An additional stabilising effect of community asymmetry only appeared for higher levels of skewness. For skewness values above $\hat{S} = 2$, the stability gain due to pairwise asymmetry remained constant at about 2, while the effect of community asymmetry kept increasing strongly.

In gamma distributions, increasing skewness also increases variance, so that these two properties cannot be separated. We therefore conducted a similar experiment with half-normal distributions, where variance can be increased but skewness is constant (Fig. 5b). In this case, we found no relationship between stability gain and the level of variance. Thus, we can

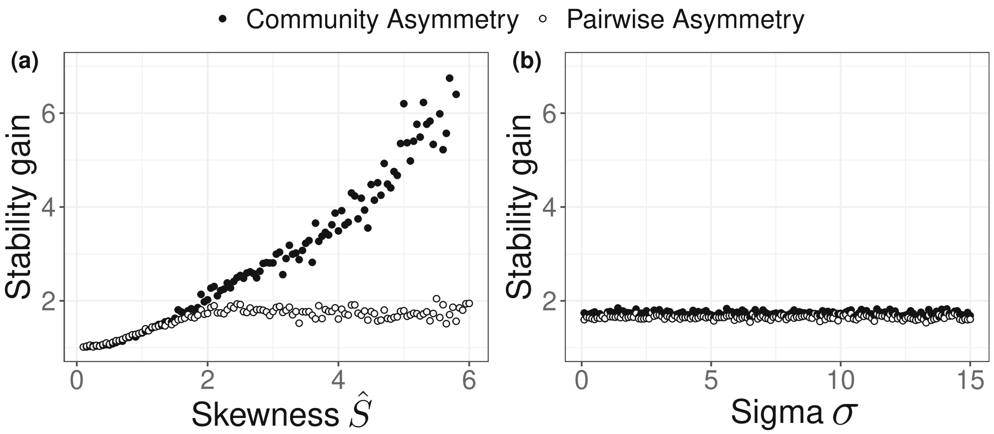

Fig. 5 Relation between the shape of link strength distribution and the effect of patterning on system stability. Comparison between gamma distributions (**a**) and half-normal distributions (**b**). Levels of skewness (in **a**) and variance (in **b**) were related to the gain in stability obtained by introducing pairwise and community asymmetric patterning. We calculated stability gain as the mean s^* of 100 randomly arranged matrices divided by the mean s^* of 100 asymmetric matrices. Matrix size and connectance were kept constant at $S = 10$ and $C = 0.8$, and the location of non-zero links was chosen randomly. **a** Stability gain in matrices constructed with gamma distributions of varying skewness values. To isolate the effect of skewness, we kept the mean link strength constant at -3. To vary the skewness $\hat{S}$ of a gamma distribution while keeping the mean m constant, we calculated the shape α and rate λ paramters as: $\alpha = 4/(\hat{S}^2)$ and $\lambda = \alpha/m$. **b** Stability gain in matrices constructed with half-normal distributions with increasing scale parameters σ and thus increasing variance

conclude that the stabilising effect of community asymmetry indeed depended on skewness, which describes the specific proportion of strong and weak links, and not on variance alone.

Discussion

Our results show the importance of having many weak and few strong links for enabling stabilising patterns of link strengths in competition networks. First, we showed that link strengths derived from empirical competition assemblages have very skewed distributions. Then, we demonstrated that this skewness is necessary to reproduce a stabilising effect of community asymmetry, and hence of hierarchy, which has been found in empirical competition networks (Koch et al. 2023). We did this using theoretical matrices in which asymmetric patterns were generated using random link strengths drawn from distributions with varying shapes. We compared uniform, half-normal and gamma distributions and found that a stabilising effect of community asymmetry could only be observed with skewed gamma distributions. By systematically varying the skewness level of gamma distributions, we could confirm that the stabilising effect of community asymmetry indeed depended on skewness.

Competition for space or other resources is often fundamental to realised richness and persistence of biodiversity (Paine 1966). Yet, our understanding of patterns, mechanisms, drivers and stability underpinning this at the assemblages or community level still has significant gaps. One of these gaps is that studies of empirical distributions of competitive link strengths are scarce. While there are many studies that quantify the intensity of competition in some way, they tend to focus on individual effects that cannot be easily transferred to the population level link strengths used in ecological network models (Goldberg et al. 1999; Wootton and Emmerson 2005; Hart et al. 2018). Studies on competitive networks, often in the context of intransitive competition, have therefore been using binary who-beats-whom networks (Laird and Schamp 2006; Allesina and Levine 2011; Gallien et al. 2018).

To the best of our knowledge, the only other empirically quantified competitive community matrix, apart from the ones published by Koch et al. (2023), is the one presented by Roxburgh and Wilson (2000). In contrast to our results, they identified an approximately uniform distribution of link strength in a single matrix based on a (terrestrial) lawn community. However, their parametrisation was based on experiments with isolated pairs of species rather than on multi-species systems where biomass distributions have naturally formed. In the 30 empirical networks we used for the present study, which were based on observations of whole assemblages (Koch et al. 2023), the skewness we saw in the link strengths was largely the result of assemblage dynamics, which generated very skewed distributions of observed species abundances and biomass loss rates (see Supplementary Note 2).

In trophic networks, where there is a long tradition of determining link strengths from observations (Paine 1992; Polis 1994; Ruiter et al. 1995; Wootton 1997; Berlow 1999;

Emmerson and Yearsley 2004; Neutel et al. 2007; Neutel and Thorne 2014), there is ample evidence of skewed link strengths across various types of environments (Ruiter et al. 1995; Berlow et al. 2004; Wootton and Emmerson 2005; Jacquet et al. 2016). The "few strong and many weak" link distribution has also been observed in mutualistic systems (Jordano 1987; Bascompte et al. 2006). Even though the exact methods and definitions for quantifying link strengths often differ, skewed link strengths are a consistent observation and thus appear to be a common property of natural ecological networks.

In this study, we quantified stability as the amount of self-regulation needed for system stability, i.e. for all eigenvalues of the matrix to have negative real parts. Using this stability measure, we analysed the stabilising effect of hierarchy by comparing the stability of theoretical matrices with a hierarchical pattern of link strengths to that of matrices with randomly arranged links. Our analysis was focussed on matrices with different levels of instability, as we chose theoretical link strengths with similar ranges as the empirical link strengths derived by Koch et al. (2023). In this derivation, Koch et al. (2023) assumed equilibrium conditions, in order to test the hypothesis that the observed systems represent stable equilibria, where growth and loss rates are in balance. They find that for all empirical systems, the observed intraspecific competition is not strong enough to make the system stable and conclude that their systems are unstable. Using a community matrix approach, which is based on linearisation around a hypothesised equilibrium point, to analyse systems that are changing over time (see also Gaedke et al. 2025) opens up important questions about the ecological meaning of these stability measures for assessing a system's ability to respond to perturbations. However, our study was focussed on the mathematical properties of community matrices, and in this context, it does not matter whether we quantify a stabilising effect by comparing different levels of stability or instability.

Our result that the effect of hierarchy on stability only appeared with skewed distributions of link strengths was found to hold for random topologies and for larger theoretical matrices with several hundred species (Supplementary Figs. 1 and 2). This is interesting, as previous results based on very large matrices with randomly arranged links indicate that the exact shape of the distribution of link strengths does not influence stability (Allesina and Tang 2012, 2015). For these matrices, only the mean and the variance of matrix elements affect stability, while higher moments of the distribution, like skewness, are not relevant (Tao et al. 2010). Our findings indicate that the proportion of strong and weak links can have an important effect on stability when we look at matrices with non-random patterns.

Our results can be understood by looking at the feedback structure of the systems. In general, pairwise asymmetry is stabilising, as it reduces the amplifying effect of positive 2-link loops. In contrast to this, community asymmetry is stabilising as it reduces the strength of long, negative feedback loops (Koch et al. 2023). If these long, negative feedback loops are too strong compared to shorter loops, the excessive negative feedback can cause oscillatory instability (Levins 1974). Community asymmetry avoids this destabilising imbalance, which explains its additional stabilising effect compared to pairwise asymmetry. As we found that the stabilising effect of community asymmetry only appeared when link strengths were skewed, our results indicate that this imbalance can only form when there is a sufficient level of skewness. Further analysis of feedback loop strengths would be necessary to confirm this and to uncover the exact conditions that lead to the emergence of oscillatory instability.

The contrasting mechanisms that explain the stabilising effects of pairwise and community asymmetry mean that we have to consider two "regimes" of instability, one governed by positive feedback, the other governed by excessive negative feedback (Levins 1974). These two regimes are not only relevant to competitive systems, but may also play a role in food webs. In fact, the idea that instability is caused by overshoots leading to unstable oscillations is common in food web literature (McCann et al. 1998; Emmerson and Yearsley 2004; Gellner and McCann 2016), although it is usually not linked to the concept of feedback loops.

In conclusion, we showed that similar to what has been found in food webs and mutualistic systems, competition networks contain many weak and few strong links. We furthermore demonstrated that this type of distribution enables stabilising patterns in competition webs. These insights have important implications for theoreticians exploring structure in random matrices, which often use normal or uniform distributions of matrix elements (Emmerson and Yearsley 2004; Allesina and Tang 2012). Our study shows that when specific patterns of link strengths are introduced, the shape of distributions can have an effect on stability. This needs to be considered when we want to explore and understand stabilising mechanisms in real systems, which typically have very skewed link strengths.

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Author contribution FK conceived the study and carried out the initial analysis. DKAB provided empirical datasets. FK, AMN and KTA designed further analysis steps and discussed the results. FK wrote the first manuscript draft, with input from KTA and AMN. All authors contributed critically to revisions.

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Data availability Code to generate all results and figures can be downloaded from zenodo (DOI: 10.5281/zenodo.17199201). The empirical data sets used in this study have been published in Koch, F. et al. 'Data and code for "Competitive hierarchies in bryozoan assemblages mitigate network instabillity by keeping short fand long feedback loops weak" ' (DOI:10.5281/zenodo.8010450).

Declarations

Conflict of interest The authors declare no competing interests.

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