Skewness enables stabilising effect of hierarchy in complex competition networks

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1 Abstract

In observed ecological networks of interference-competition, hierarchy has been shown to generate asymmetric patterns of interaction strengths which enhance system stability. However, it remains unknown whether this stabilising effect of competitive hierarchies depends on the distribution of link strengths. Here, we analysed the relationship between interaction strength distributions, patterning, and system stability. We found that the interaction strengths within 30 observed encrusting, marine bryozoan networks were characterised by a high level of skewness, with many weak and few strong links. We showed that this distribution of link strengths is necessary for the stabilising effect of hierarchy, as skewness enables a patterning that strongly reduces the weight of short and long feedback loops. The stabilising effect of hierarchy did not appear in systems with uniform or normal distributions of interaction strengths. This has important ecological implications, since theoretical studies using random matrices often assume normal or uniform distributions. Since skewed interaction strengths are a common feature of ecological networks, including trophic and mutualistic systems, such theoretical approaches might overlook stabilising mechanisms present in living systems.

2 Introduction

In diverse communities, direct and indirect interactions between species form complex ecological networks. Their complexity makes it challenging to predict how assemblages, communities and whole ecosystems will react to environmental changes and disturbances [1–4]. Understanding how patterns of interaction strengths in ecological networks relate to system stability has therefore been a long-standing focus in the field of community and ecosystem ecology [5–9].

Recently, competitive hierarchy has been found to cause stabilising patterns in interference competition networks derived from observations of overgrowth between encrusting, marine bryozoan colonies [10]. Hierarchy generates asymmetric patterns of interaction strengths, both within pairs of competitors, where strong links are coupled with weak links (Fig 1 A) as well as at the whole assemblage level. Representing the assemblages as Jacobian community matrices, [10] find that this "community asymmetry" translates to strong below diagonal vs. weak above diagonal interaction strengths (Fig 1 B). [10] explain the stabilising effect of hierarchy in terms of the strength of feedback loops, closed chains of interactions [11]. Using the approach by [8, 12, 13], which was developed for trophic networks and extending it for competition networks, [10] showed that the asymmetric patterns of interaction strengths mitigate network instability by keeping short and long feedback loops weak (Fig 1 C).

In the current work, we explore the generality of the relation between hierarchy and stability and we ask to what extent the stabilising effect depends on the empirical distribution of strong and weak links.

Although interaction strengths have been little studied in competition networks, there is ample evidence of a characteristic distribution of many weak and few strong links in empirical studies on ecological networks, in particular food webs [8, 14–18] but also mutualistic systems [19, 20]. Theoretical studies [17, 21–25] as well as some experimental evidence [26] suggest that these weak links have a stabilising effect. A possible explanation is that weak links reduce the mean interaction strength [27] or, more specifically, that they have a dampening effect on oscillations [22, 23]. However, it has also been demonstrated that this stabilising effect depends on the particular arrangement (patterning) of strong and weak links [21]. This is often explained with respect to omnivorous loops [8, 23, 28, 29]. Thus, both the distribution of many weak and few strong links, and the patterning of link strengths matter.

Theoretical studies of large ecological networks often use random interaction strengths, with the aim to obtain general theorems on structure-stability relationships [27, 30]. The empirical findings on network structure and the importance of the patterning of strong and weak links have so far remained unrecognised by random matrix theory [21, 31] and obtaining analytical results for structured matrices is challenging [30]. While skewed distributions with a higher proportion of weak links have been included in unstructured random matrix models, they surprisingly do not seem to have an effect on stability. Only

the mean and the variance seem to be influential [32, 33]. For simplicity, link strengths used in theoretical studies on large interaction networks are hence usually chosen from normal or uniform distributions [23, 30], despite the consistent observations of many weak, few strong links in empirical data. The question remains whether and how the distribution of links strengths affects stabilising patterns in complex, structured ecological networks.

Here, we explore this question and extend our understanding of the relation between hierarchy and stability in competition networks. Specifically, we ask whether the distribution of link strengths constrains the stabilising effect of hierarchy. We first analysed the distribution of interaction strengths found in selected empirical data sets. Then, based on these observed distributions we generated random matrix models with various theoretical distributions and analysed how the skewness of these distributions is related to the stabilising properties of asymmetric patterns. We explain our results by quantifying the feedback loops in the networks, following [8].

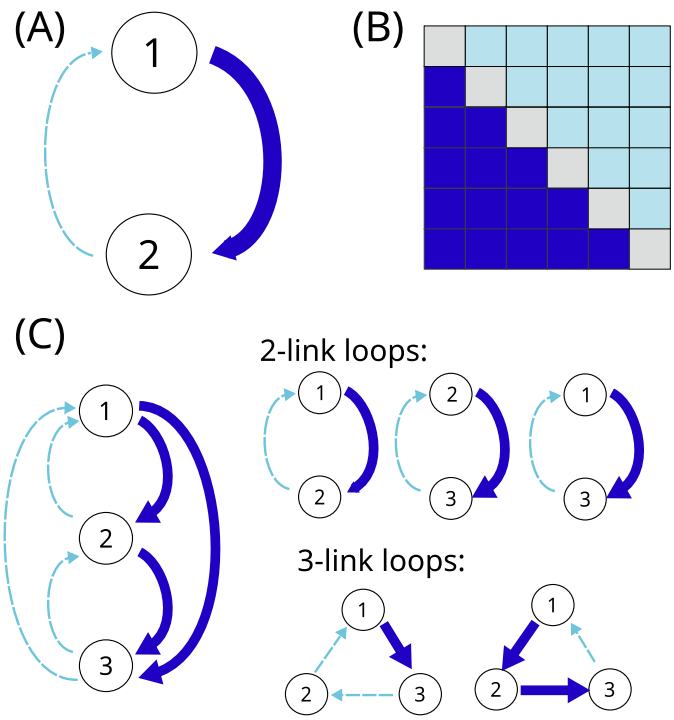

Figure 1: **Asymmetric patterns in interaction strengths caused by hierarchical competition** (A) Pairwise asymmetry means that the loop formed by each pair of competing species consists of a strong link, describing the effect of the stronger competitor on the weaker competitor, coupled to a much weaker link, describing the effect of the weaker competitor on the stronger competitor. (B) A strict hierarchical ranking additionally leads to community asymmetry. 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) Hierarchy reduces the strength of feedback loops, which is defined as the product of all links in a loop. In this small example system, hierarchy means that each 2 - or 3-link loop contains at least one weak link which keeps loops from becoming very strong.

3 Results

3.1 Empirical interaction strengths can be closely approximated by a gamma distribution

We analysed the shapes of the distributions of the interaction strengths from 30 empirical competition networks published in [10]. Interaction strengths were the normalised elements of the Jacobian matrix (see 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 [34, 35]. We found that overall, the empirical interaction strengths showed distributions that were very asymmetric and peaked, with a large variability in their skewness and kurtosis values (Fig 2 A).

The shapes of these empirical distributions thus differ clearly from normal and uniform distributions, which are both symmetric ($\hat{S} = 0$) and have a low kurtosis ($\hat{K} = 3$ and 1.8, respectively). A gamma distribution (shown as the dotted line in Fig. 2 A) 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 interaction strengths allowed us to generate random interaction strengths with a realistic pattern of many weak and few strong values (Fig.2 B). In contrast to that, fitting an (absolute negative) 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. 2 C).

3.2 The stabilising effect of community asymmetry depends on skewness

We tested whether and how the distribution of link strengths affected the stabilising effect of asymmetries by creating artificial competition networks with varying distributions of random interaction strengths. We chose matrix size, connectivity and topology based on the empirical data sets, so that for each of the 30 empirical networks we created a set of random matrices with the same properties. However, the matrices differed in their distribution of interaction strengths: We fitted normal, uniform and gamma distributions to the empirical interaction strengths and used them to parameterise the non-zero off-diagonal matrix elements (see Table *S2* for the fitted parameters for each empirical data set). Then, we compared the stability of randomly patterned, pairwise asymmetric and community asymmetric matrices. Matrix stability was measured as the critical amount of self-regulation s^* [8], following [10]. In addition, for comparison to the three types of theoretical distributions (Fig 3 A), we also built random matrices using the empirical distributions (Fig 3 B).

Almost all model networks had critical amounts of self-regulation (s^*) larger than 1, indicating that the networks were unstable and that additional self-regulation would be

required to reach stability. This was no surprise, as the random interaction strengths were fitted to link strengths from empirical community matrices that were also unstable [10]. We found that randomly patterned matrices with a uniform distribution led to relatively high levels of instability. In comparison, randomly patterned matrices with normally distributed interaction strengths had lower s^* values, followed by randomly patterned matrices that contained gamma-distributed interaction strengths. The latter had almost the same level of instability as those randomly patterned matrices based on empirical distributions of interaction strengths. These stability differences between random patterns (Fig 3A, light boxes) could be explained by differences in mean interaction strengths [27]: The uniform distributions contained a higher number of strong values, explaining their increased instability.

For matrices with empirical distributions, pairwise asymmetric patterns reduced instability and community asymmetry reduced instability even further (3 B, in line with the findings of [10]). Correspondingly, for all theoretical distributions, a pairwise asymmetric pattern resulted in a reduction of instability. However, adding community asymmetry only had an additional stabilising effect in systems with a gamma distribution. In matrices with normal or uniform distributions, there was no additional effect of community asymmetry (Fig 3 A). This result was independent of the specific architectures or sizes of the networks and also held for random topologies (Supplementary Fig 2) and for larger networks involving hundreds of species (Supplementary Fig 3).

We analysed this in more detail by relating the level of skewness of each individual data set to the stability gains we observed after introducing asymmetries, which was measured as the mean s^* of the set of randomly patterned matrices relative to the mean s^* of the set of asymmetric matrices (Fig 4). We found that the stability gain due to community asymmetry increased with higher skewness values, both with theoretical (A) and empirical distributions (B). The effect of pairwise asymmetry on the other hand increased only slightly with skewness in matrices with theoretical distributions and we observed no increase in matrices with empirical distributions.

To understand why the effect of community asymmetry on system stability depends on skewness but the effect of pairwise asymmetry apparently does not, we quantified the feedback loops in the system. [10] found that the stabilising effect of hierarchy could be attributed to a weakening of the feedback loops in the system, measured as the maximum loop weights of the positive 2-link loops and those of the longer, negative and positive loops. Therefore, we quantified the feedback loops and related loop weights to the skewness of the interaction strengths. When we compared maximum loop weights in randomly patterned matrices with those in asymmetric matrices, we found that pairwise asymmetry actually caused a greater reduction in maximum positive 2-link loops in networks with more skewed interactions (Fig. 5 A and B). This was surprising, given that the stabilising effect of pairwise asymmetry did not increase with skewness (Fig 4).

We also quantified the reduction in longer, negative loops in the system by measuring

the maximum 3-link loop weight. Again, we found that the reduction in loop weight increased with skewness (Fig 5 C and D). This indicated that only when 2-and 3-link were decreased in tandem, a further stability gain was obtained. It is known that where 3-link loop weights are very high relative to the shorter 2-link loops weights high-level feedback can become a limiting factor for stability [11]. Our results suggest that this imbalance only appears when interaction strengths show a sufficient level of skewness. In matrices with a low skewness of interaction strength, we saw a smaller reduction in 2-link loop weight due to pairwise asymmetry (Fig 5 A). As the 2-link loops in asymmetric systems remained relatively strong, no imbalance was created, which explains why we did not observe an additional stabilising effect of community asymmetry in these systems (Fig 4 A).

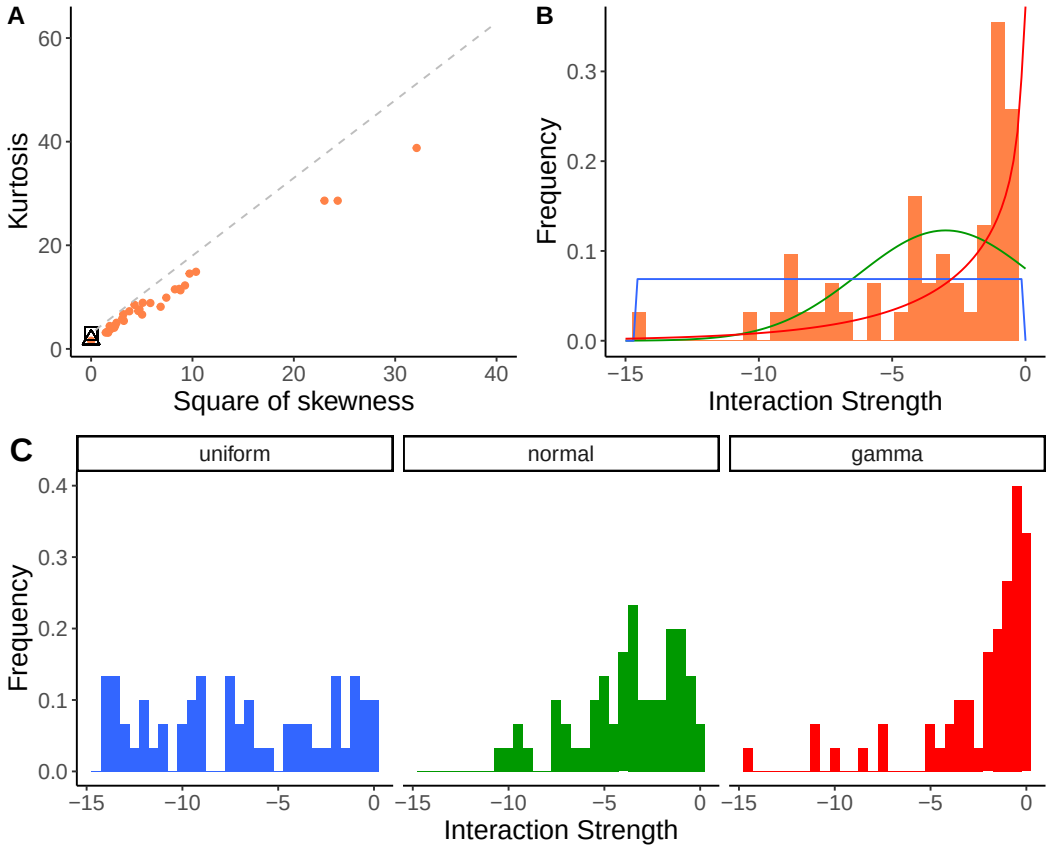

Figure 2: **Skewed empirical interaction strengths are best represented by a gamma distribution** A) Skewness-kurtosis relationship of the empirical distributions of interaction strengths on a Cullen and Frey graph, which can be used to differentiate between different types of distributions [36]. Normal and uniform distributions both only have one possible skewness and kurtosis value (normal: $\hat{S} = 0$, $\hat{K} = 3$ shown as a black square; uniform: $\hat{S} = 0$, $\hat{K} = 1.8$ shown as a black triangle). The gamma distribution is represented as a dashed line, as it allows for varying $\hat{S}$ and $\hat{K}$ values. B) Histograms showing the empirical distribution of interaction strength for one example matrix (Rothera 3) as well as a uniform (blue), normal (green) and gamma (red) distribution fitted to these empirical values. (C) Example sets of random interaction strengths drawn from these fitted theoretical distributions.

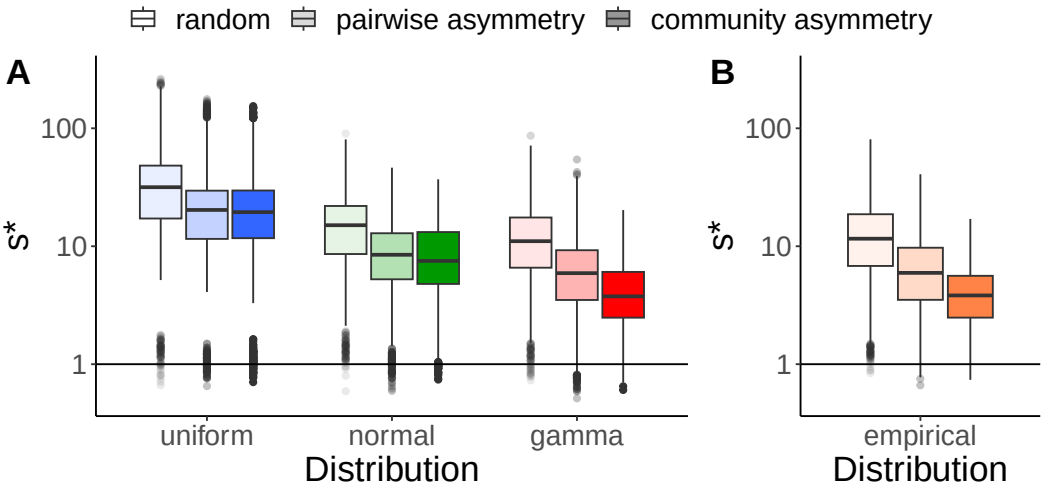

Figure 3: **The stabilising effect of asymmetries in matrices with varying distributions of interaction strengths.** A comparison of stability of randomly patterned and asymmetric matrices based on three types of theoretical distributions (A) as well as the empirical distributions (B). Stability was measured as the critical amount of self-regulation, s^*, with values > 1 indicating instability. Matrix models were based on the 30 empirical systems, meaning that each of the models had exactly the same size S, connectance C and topology as their empirical counterpart. They contained random interaction strengths drawn from a uniform, (absolute negative) normal or gamma distribution fitted to same empirical counterparts' interaction strengths. This was repeated 100 times per empirical data set, resulting in $30 \times 100 = 3000$ data points per boxplot. B) The same manipulations were applied directly to the observed distribution, again with 100 randomisations per empirical data set.

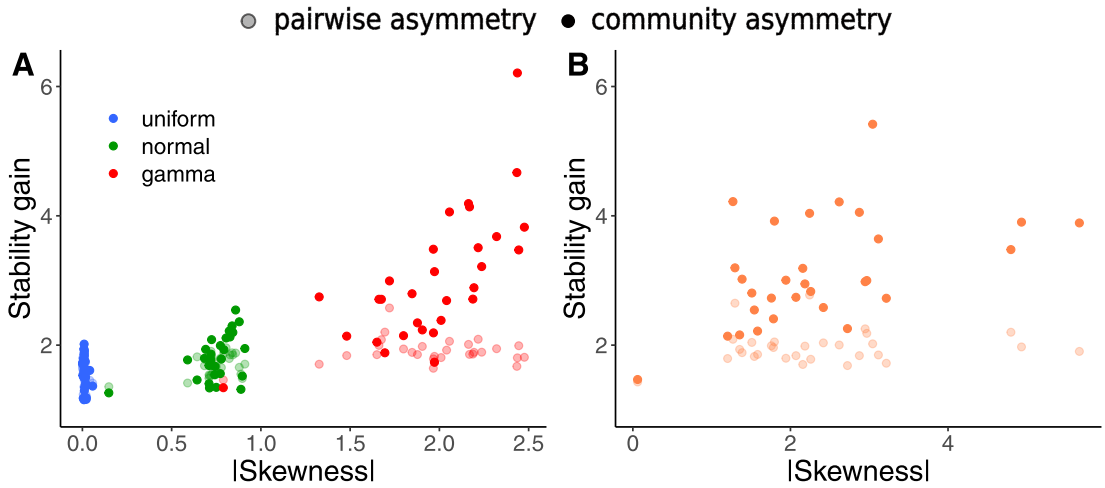

Figure 4: **Effect of skewness on stability gain due to asymmetries**. Stability gain due to the effect of pairwise (light hue) and community (dark hue) asymmetry in matrices with theoretical (A) and empirical (B) distributions. In (A) each point represents matrices with one theoretical distribution, fitted to one empirical distributions, while in (B) each point corresponds to matrices with one of the empirical distributions. The y-axis shows the absolute skewness value of each distribution. Stability gain is defined as the ratio between mean s^* in all matrices with random arrangement and the mean s^* in (pairwise or community) asymmetric arrangement.

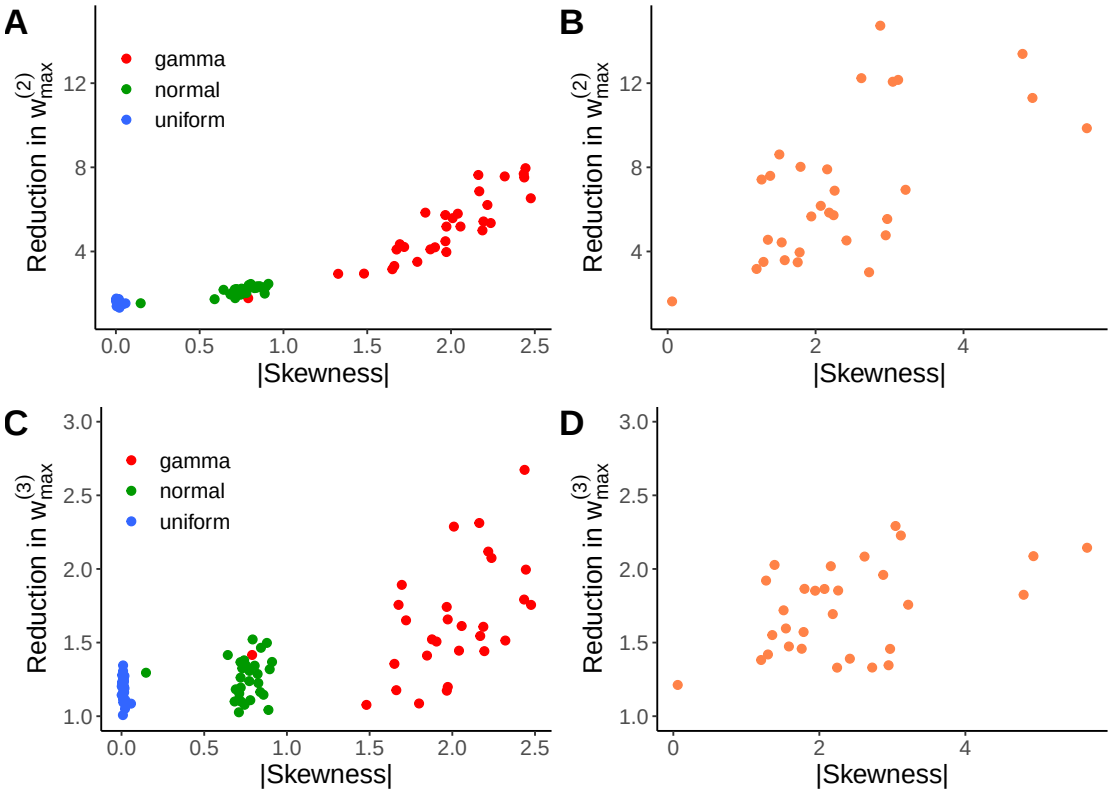

Figure 5: **Relation between skewness and reduction in loop weight due to asymmetry** Reduction in maximum 2-link loop weight due to pairwise asymmetry (A and B) and a reduction in maximum 3-link loop weight due to community asymmetry (C and D), in relation with the absolute value of skewness. Both are compared in theoretical (A and C) as well as empirical distributions (B and D). The y-axis shows the absolute skewness value of each distribution. Reduction in loop weight is calculated as a ratio, e.g. a reduction of 2 means loop weight in asymmetric matrix is half as strong as loop weight in random matrix.

4 Discussion

Our results highlight the importance of skewed interaction strengths in enabling stabilising patterns of interaction strengths in competition networks. We first showed that competitive link strengths derived from empirical data have very skewed distributions. Then, we demonstrated that such skewness is necessary to reproduce the stabilising effect of community asymmetry and hence of hierarchy, that has been found in empirical competition networks [10] in matrices parameterised with random interaction strengths. Finally, we showed that skewness increases both the capacity for reducing the feedback in the system, but also the capacity to create an imbalance in the feedback structure which offers a potential explanation for our stability results.

Competition for space or other resources is often fundamental to realised richness and persistence of biodiversity [37]. Yet understanding of patterns, mechanisms, drivers and stability underpinning this at assemblages and community level still has significant gaps. One of these gaps is that empirical measurements of competitive interaction strengths are scarce. While there are many studies that quantify intensity of competition in some way, they tend to focus on individual effects which cannot be easily transferred to the population level link strengths used in ecological network models [38–40]. To the best of our knowledge, the only other empirically quantified competitive community matrix, apart from the one published by [10] is the one presented by [41]. 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 [10], the skewness in the interaction strengths is largely the result of assemblage dynamics and a very skewed distribution of observed species abundances (see Supplementary Note 2).

In trophic networks, where there is a long tradition of determining interaction strengths from observations [7, 8, 12–15], there is ample evidence of skewed interaction strengths across various types of environments [16, 17, 39]. The "few strong, many weak links" distribution has also been observed in mutualistic systems [19, 20]. It thus appears that skewed interaction strengths might be a common property of natural ecological networks.

Our result that the effect of hierarchy on stability depends on skewness was found to hold also for random topologies and for larger random matrices, with several hundred species (Supplementary Figs. 2 and 3). This contrasts with insights from random matrix theory [30], as it has been shown mathematically that in very large matrices, the exact distribution of interaction strengths does not matter, and that only the mean and variance do [32, 33]. However, this result only holds for matrices which have randomly patterned interaction strengths. Randomisation experiments of empirical food web data on the

other hand confirm our finding that the empirical distribution of interaction strengths plays a key role for stability [17, 21].

Random matrix studies offer a potentially powerful and cost-efficient tool to gain general insights into the relation between structure and stability in complex ecological networks, even if empirical data remain scarce. However, such theoretical approaches often assume normal or uniform distributions of interaction strengths [23, 30], despite the above mentioned empirical evidence of skewed distributions. Our finding that the full stabilising effect of hierarchy only appears if interaction strengths are skewed enough, implies that some stabilising mechanisms might have been overlooked as a result of using normal or uniform distributions. It is thus necessary to include more realistic, ground-truthed distributions of interaction strengths in theoretical studies.

Our feedback analysis suggests an explanation for the effect of skewed interaction strengths on stability. It indicates that the additional stabilising effect of community asymmetry that appeared with enough skewness is caused by the fact that pairwise asymmetry creates a very strong imbalance between long and short feedback loops. This suggests that matrices can be separated into two different "regimes" of instability, one governed by positive feedback, the other governed by excessive negative feedback [11, 13]. These two regimes of instability are not only relevant to competitive systems, but 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 [22–24], although it is usually not linked to the concept of feedback loops. One important next step would be to quantify the effect of excessive negative feedback on stability, in order to develop a feedback loop metric that is able to reflect both regimes of instability and is applicable to networks with more than just one type of interaction.

In conclusion, our findings not only underpin the importance of “many weak and few strong links” in ecological systems for enabling stabilising hierarchical patterns but also send a strong message to theoreticians using random matrices. It is crucial to incorporate skewness as a variable in model systems and not only use normal or uniform distributions of link strengths, if we want to explore and understand the stabilising mechanisms present in real systems.

5 Methods

5.1 Analysing empirical distributions

We analysed empirical interaction strengths from interference competition in 30 encrusting, marine bryozoan assemblages presented in [10]. Interaction strengths are the elements of the community matrices [27] representing these assemblages. The term "assemblage" is used in the context of bryozoans, since the datasets include only competition for space and no other potential interactions involving e.g. prey and predator species. The calculation of interaction strengths is based on the estimation of energy flow rates from observed outcomes of spatial contests between bryozoan colonies. These energy flow rates were then divided by biomass to calculate the interaction strengths. Finally, the raw interaction strengths were normalised following ([13], see also [42] for an explanation of normalisation). For a more detailed description of the derivation of interaction strengths see Supplementary Note 1.

We calculated the mean, variance, minimum, maximum, as well as skewness and kurtosis (using the R-package *moments*) of the non-zero interspecific interaction strengths in each of the 30 assemblages (Supplementary Table 1). To be able to draw random interaction strengths from probability distributions with comparable ranges of values to the empirical data, we fitted normal, uniform and gamma distributions to each empirical data set using the *fitdistrplus* R-package [36]. The fitted parameter values (Supplementary Table 2) were then used for random matrix generation, as explained below.

5.2 Generating random interaction strengths

We used competition matrices with random interaction strengths as model networks to explore the stabilising effect of pairwise and community asymmetry under varying distributions of interaction strengths. Each random matrix that we created was based on one of the empirical data sets and thus had the same size, connectance and topology (location of non-zero links) as its empirical counterpart. For each random matrix, the number of non-zero interaction strengths was calculated based on the empirical matrices' number of species S and connectance C. Then, the required number of interaction strengths was drawn from a probability distribution with parameters that had been fitted to the empirical data set. For normal distributions, these parameters were the mean and the variance, for uniform distributions, the minimum and maximum and for the gamma distributions it was the rate and shape. For the normal distribution, we made sure that all values were negative by taking the absolute values and multiplying them with -1. Our approach was meant to compare the distributions with comparable ranges of values but with different proportions of weak and strong values across this range. This meant however, that the mean of those distributions was not preserved, especially for uniform distributions. Additionally, we created matrices using the empirical values themselves for comparison.

5.3 Asymmetric pattern in random matrices

To recreate asymmetric patterns in the model networks, we controlled how random links were placed within the matrices. These artificial asymmetries represented idealised versions of the asymmetric arrangements that were observed in empirical networks. The procedure was similar to the manipulations used to artificially restore asymmetries in randomised matrices presented in [10]. To preserve empirical topology, we placed random interaction strengths only in locations that also had non-zero link strengths in the empirical matrix. For comparison, we also created randomly arranged matrices, where each link strength was independently placed in a random position (Supplementary Fig. 2).

To recreate pairwise asymmetry, we made sure that within each pair, a strong link was paired with a weak links. 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 and whether the stronger link appeared below or above the diagonal was assigned randomly. To also recreate community asymmetry, we furthermore made sure that all strong links were located below the matrix diagonal.

5.4 Calculation of network stability as the critical amount of self-regulation

We calculated the local asymptotic stability, which describes whether a system has the ability to return to its steady state after an infinitesimally small disturbance. Whether a matrix is stable can be determined by calculating its dominant eigenvalue λ_d, which is the eigenvalue with the largest real part. If the real part of this dominant eigenvalue is negative, $Re(\lambda)_d < 0$, then the matrix is stable, meaning that the system will return to equilibrium after a perturbation. If it is positive, $Re(\lambda_d) > 0$, then the matrix is unstable, meaning that the system will not return to equilibrium.

However, $Re(\lambda_d)$ is not suitable to compare the level of (in)stability of different systems encompassing different time scales in a meaningful way. Therefore, following [10] and [8]'s work on food webs, we used the critical amount of self-regulation s^* to compare the levels of instability of different networks. It represents the factor by which the observed intraspecific interaction strengths have to be multiplied to obtain stability. In the case of an unstable system, $s^* > 1$ it describes how far the system is from stability. In the case of a stable system, $s^* < 1$ it describes the "buffering capacity" of a system. We calculated all s^* via the normalised Jacobian matrices, by setting the matrix diagonal to 0 and then calculating the real part of the dominant eigenvalue of this matrix [10, 13, 42].

5.5 Quantification of feedback loops

Feedback loops are closed chains of interactions, that connect one network element back to itself [11]. They determine how perturbations propagate through the nodes and links of a network. A loop is quantified as the product of all interaction strengths within the loop. Positive feedback loops (those with a positive product) amplify disturbances that are introduced into the system while negative feedback loops (those with a negative product) counteract them [11]. As an illustration of what this means for competition networks, consider two competitors A and B. Any perturbation from the steady state that causes an increase in the abundance of competitor A would lead to a higher competition pressure for competitor B (assuming that space is limiting), resulting in decreasing abundance B, which in turn releases A from competition pressure and reinforces the initial increase in abundance. Along similar lines, if a competitive 3-link loop is considered, an increase in A puts more pressure on B, which releases C, which in turn leads to an increased competition pressure on A that counteracts its initial increase.

We quantified the strengths of feedback loops as loop weights, which allowed us to compare loops of different lengths [8, 10, 12]. The loop weight of a loop with k links, $w^{(k)}$, is defined as the geometric mean of the absolute values of all k normalised interaction strengths a_{ij} in the loop. For example, for each pair of interacting species i and j we calculated the weight of the 2-link loop between them as:

$$w^{(2)} = \sqrt{|a_{ij}a_{ji}|} \tag{1}$$

For each triplet of species i, j, k, we calculated the weights of the 3-link loops between them as:

$$w_1^{(3)} = \sqrt[3]{|a_{ij}a_{jk}a_{ki}|} \tag{2}$$

and

$$w_2^{(3)} = \sqrt[3]{|a_{ji}a_{ik}a_{kj}|} \tag{3}$$

5.6 Quantifying the effect of asymmetric patterns: Stability gain and loop weight reduction

For each distribution of interaction strengths used, we quantified the effects of introducing asymmetric patterns on stability, measured as the critical amount of self-regulation s^*, as well as on feedback structure, which we characterised via the maximum 2- and 3-loop weights.

We quantified the effect on stability by calculating the "stability gain" achieved by introducing asymmetry. As higher s^* values indicate more instability, a gain in stability means a reduction in s^*. For a given distribution of interaction strengths we calculated stability gain as the mean s^* of 100 randomly arranged matrices divided by the mean s^* of 100 asymmetric matrices. Thus, a stability gain of 2 indicated that the asymmetric pattern would require half as much self-regulation as the random pattern to obtain stability.

Similarly, we quantified the effect on feedback structure by calculating the reduction in the maximum loop weight of 2- and 3-link loops. As in the calculation of stability gain, we divided the mean maximum loop weight in 100 random matrices by the mean maximum loop weight in 100 asymmetric matrices for each distribution of link strengths. A loop weight reduction of 2 indicated that the maximum loop weight in asymmetric matrices is half that of the random matrices.

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Author contributions

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.

Data availability

All 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 instability by keeping short and long feedback loops weak’. doi:10.5281/zenodo.8010451. and can be downloaded from zenodo (https://zenodo.org/record/8010451)

Code availability

Code to generate all results and figures will be made available via zenodo before publication. Competing interests The authors declare no competing interests

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