
Generalized Models Reveal Stabilizing Factors in Food Webs

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Insights into what stabilizes natural food webs have always been limited by a fundamental dilemma: Studies either need to make unwarranted simplifying assumptions, which undermines their relevance, or only examine few replicates of small food webs, which hampers the robustness of findings. We used generalized modeling to study several billion replicates of food webs with nonlinear interactions and up to 50 species. In this way, first we show that higher variability in link strengths stabilizes food webs only when webs are relatively small, whereas larger webs are instead destabilized. Second, we reveal a new power law describing how food-web stability scales with the number of species and their connectance. Third, we report two universal rules: Food-web stability is enhanced when (i) species at a high trophic level feed on multiple prey species and (ii) species at an intermediate trophic level are fed upon by multiple predator species.

Understanding the dynamic properties of food webs is a problem of both theoretical and practical importance (*1–16*), especially as concerns about the robustness of natural systems escalate. Further, the discovery of stabilizing factors in food webs can yield much-needed

design principles for institutional networks (*17*). Robert May (*1*) showed that randomly assembled webs became less robust (measured in terms of their dynamical stability) as their complexity (measured in terms of the number of interacting species and their connectivity) increased. Although it has often been

pointed out that food webs can persist in nonstationary states, there is growing evidence that May's stability-complexity relationship also holds for nonstationary dynamics (18). Moreover, population cycles or external forcing averages out if food webs are considered on longer time scales, so that time-averaged dynamics can be considered as stationary. However, detailed investigations aiming at a deeper understanding of what makes food webs robust have generally been hampered by computational constraints (12). We avoided these constraints through the use of generalized modeling (GM) (19, 20).

For a given class of mathematical models, GM identifies parameters that together capture the local stability properties of all stationary states. Some of these parameters (scale parameters) quantify the scaling of biomass fluxes, whereas others (exponent parameters) quantify the nonlinearity of model functions. For any given model, the GM parameters can be expressed as functions of conventional model parameters. More importantly, however, the GM parameters are directly interpretable in their own right. To capture the complexity of real-world problems, the number of GM parameters is often large. Yet, the numerical performance of GM is so favorable that billions of randomly chosen replicates, defined by sample sets of GM parameters, can be analyzed.

Our study focuses on realistic food-web topologies generated by the niche model (20, 21). The dynamics of the population density X_i of each species $i = 1, \dots, N$ follows a differential equation of the form

$$\dot{X}_i = S_i(X_i) + F_i(X_1, \dots, X_N) - M_i(X_i) - \sum_{j=1}^N G_{ij}(X_1, \dots, X_N)$$

where S_i , F_i , M_i , and G_{ij} are nonlinear functions describing the gain due to primary production, the gain due to predation, the loss due to natural mortality, and the loss due to predation, respectively. We do not restrict these functions to any specific functional form but rather consider the whole class of such models. The production term is assumed to vanish for all species except producers, whereas the predation gain vanishes for producers. Similarly, the predation loss is 0 for top predators, whereas natural mortality is assumed to be negligible for all species except top predators. Finally, a relationship between the gain of a predator and the loss of its prey species is assumed that is consistent with passive prey switching. GM parameters for this class of models have been derived before (19) and are listed together with their interpretations in table S1.

To assess the dependence of food-web stability on the exponent parameters, we generated a sample

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of 10^8 food webs with a fixed number of species. In this sample, we drew the exponent parameters independently and randomly from suitable uniform distributions, whereas we computed the topological parameters from randomly generated niche-model topologies (20, 21). We estimated the average impact of an exponent parameter on stability by computing the correlation between that parameter and local stability (20). Results for food webs with 10, 20, and 30 species, shown in Fig. 1, reveal the following: The sensitivity of predation to prey density (γ) and the sensitivity of top-predator mortality to top-predator density (μ) correlate positively with stability. This corresponds to the well-known fact that low saturation of predators and nonlinear (for example, quadratic) mortality promote stability (12). In contrast, the sensitivity of primary production to the number of primary producers (ϕ) and the sensitivity of predation to predator density (ψ) are negatively correlated with stability. This confirms that stability increases when primary production is strongly limited by external factors such as nutrient availability or when predation pressures are not very

Fig. 1. Dependence of food-web stability on GM parameters. Correlation coefficients R describing the correlation between food-web stability and GM parameters (20) are shown for 10^8 randomly generated food webs with 10 (light gray), 20 (medium gray), and 30 species (dark gray). Error bars are too small to be visible. High sensitivities of predation to prey density (γ), large average differences between the niche values of a predator and its prey (n_{diff}), and high exponents of closure (μ) promote stability. High sensitivity of primary production to the number of primary producers (ϕ), large number of links (L), and high sensitivity of predation to the number of predators (ψ) destabilize. The total range of niche values (n_{range}) and the total range of time scales (α_{scale}) have little effect on stability.

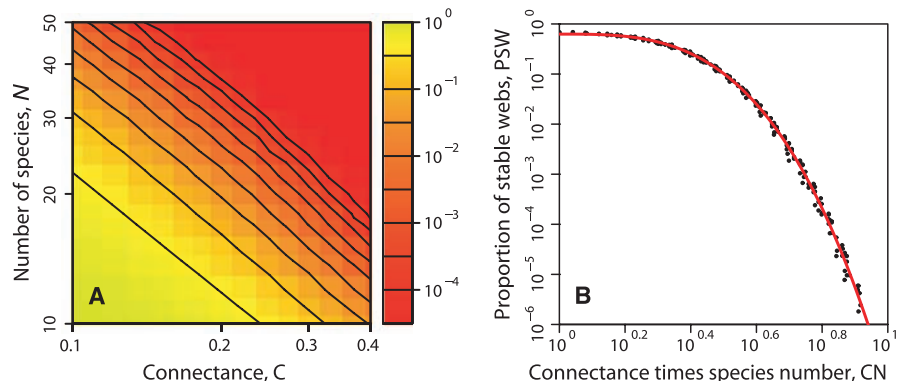


Fig. 2. Dependence of food-web stability on N and C . (A) The PSW decreases with increasing N and C , as shown by the color coding and the logarithmically spaced level lines. (B) The power law $\log_{10}(\text{PSW}) + a = b \log_{10}(CN)^c$ (red curve) with $x = \log_{10}(CN)$, $a = 0.2090$, $b = -7.025$, and $c = 3.138$ explains 99.64% of the shown variation.

sensitive to predator density (22). The range of turnover rates (α_{scale}) as well as the total range of niche values (n_{range}) do not correlate with stability. However, increasing the average difference between the niche values of a predator and its prey (n_{diff}) has a stabilizing effect (12). Our analysis also confirms that the number of links, and therefore a food web's connectivity, is negatively correlated with stability.

As a next step, we set all exponent parameters to realistic values (table S1) and focused on the effects of food-web topology on stability. We began by investigating how stability is affected by the relationship between the number of species (N) and the number of links (L). For better comparison, we express the number of links in terms of the connectance $C = \frac{L}{N(N-1)}$. We generated samples

by means of random niche-model topologies, with N and C changing on a logarithmic grid. At every vertex of this grid, we computed the proportion of stable webs (PSW), which describes the probability of randomly drawing a stable food web from our sample. Figure 2 shows PSW results computed from

35 billion food webs. As expected, the PSW decreases as N and C increase. Moreover, we find that the level lines in Fig. 2A are almost perfectly straight with a slope of 1, so that the PSW is determined almost exclusively by the product of N and C . Figure 2B shows that the dependence of $\log(\text{PSW})$ on $\log(\text{CV})$ closely follows a power law.

We next turned to the effect of link-strength variability within a food web, which has previously been proposed as a potentially important determinant of food-web stability (4, 7, 9–11, 23). In order to compare link strength, we had to take into account that, because of allometric scaling, biomass fluxes at higher trophic levels are on average much weaker than at lower trophic levels. We therefore measured link-strength variability in a predator-centric way by determining the coefficient of variation (CV) of all biomass fluxes, which were individually normalized by the total biomass inflow of the flux's recipient. An alternative prey-centric definition, providing independent information, can be devised based on the CV of

all biomass fluxes, which were individually normalized by the total biomass outflow of the flux's source.

To explore the impact of link-strength variability, we generated a large ensemble of food webs ($\sim 10^7$) in which link strengths were drawn from a uniform distribution. Figure 3A shows the PSW as a function of the observed CV of predator-centric link strengths. In very small food webs (such as $N=5$), large jumps occur in the PSW as a function of the CV. This is due to the relatively low number of feasible topologies, each giving rise to a characteristic range of CVs and PSWs. In larger food webs, the number of topologies grows combinatorially, so that the PSW becomes a smooth function of the CV above approximately $N=10$. We find that in small and intermediate food webs ($N < 30$), the PSW increases with increasing CV (Fig. 3A), which confirms the stabilizing effect of link-strength variability previously reported in the literature (4). However, in larger food webs, this relationship is reversed, so that increasing the CV decreases the PSW.

Erratum: In the original article, Fig. 3 was accidentally replaced with the similar Fig. S1, a mistake that has been corrected in this reprint.

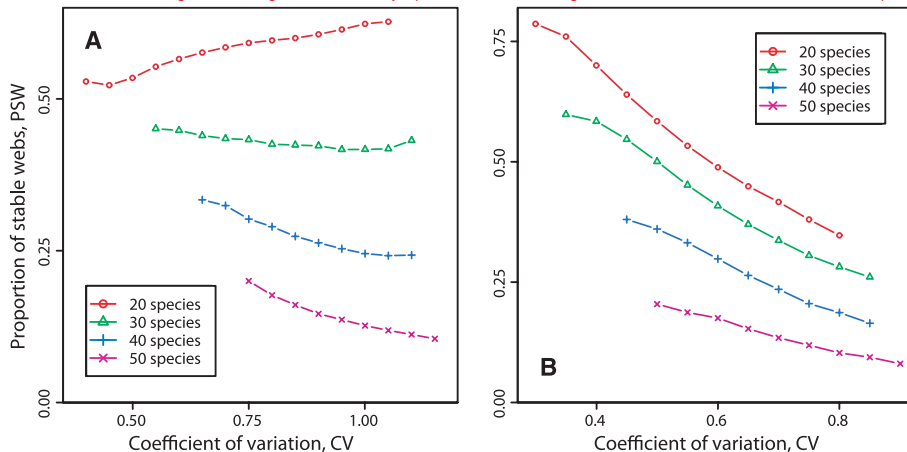


Fig. 3. Dependence of food-web stability on link-strength variability. The former is characterized by PSW and the latter by CV. Link strength is normalized by (A) the predator's total influx or (B) the prey's total outflow. Link-strength variability enhances stability in small food webs but has a destabilizing effect in larger webs.

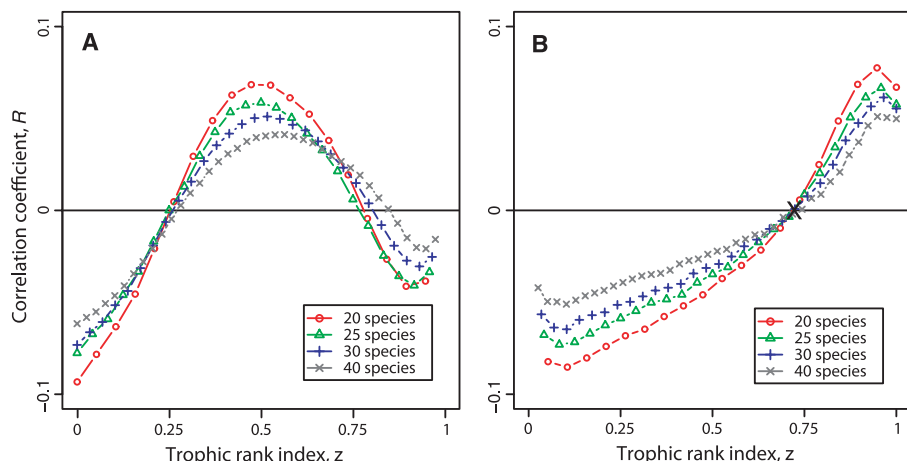


Fig. 4. Dependence of food-web stability on the distribution of links. (A) Correlation of stability with the number of predator species preying on a focal species, in dependence on the trophic position of the focal species as measured by its trophic-rank index z . Stability is enhanced if most species prey upon intermediate species, which are characterized by indices around $z = 0.5$. (B) Correlation of stability with the number of prey species predated upon by a focal species, in dependence on the trophic position of the focal species. Stability is enhanced if apical predators are generalists, whereas intermediate predators are specialists.

Repeating this investigation with the alternative, prey-centric measure of link variability yields slightly different results. For small food webs ($N < 20$), a local PSW maximum occurs at low CVs. Therefore, increasing the CV has a stabilizing effect if the CV is low. For larger food webs, this maximum becomes less pronounced and eventually disappears so that, also with this alternative measure, we find that increasing the CV destabilizes large food webs (Fig. 3B). Additional investigations (20), of lognormally distributed link strengths and of food webs with trophic loops, underscore the robustness of the patterns reported in Fig. 3.

The GM approach can be used to exhaustively search for properties that stabilize food webs. Here, we focus on the stabilizing or destabilizing effects of links depending on the trophic levels they connect. In an ensemble of food webs with fixed connectivity $K = \frac{L}{N}$, a trophic-rank index z is assigned to each species (20). This index enumerates species, from lowest to highest trophic position, according to their niche value, which in turn is often interpreted as an indicator of body size. We normalized the index to the interval $[0,1]$, so that the most basal species in a web is always characterized by $z = 0$ and the most apical species by $z = 1$, with all other species occupying an equidistant grid of index values in between. For all focal species with a given z , we then determined the correlations between the PSW and (i) the number of predator species exploiting the focal species and (ii) the number of prey species exploited by the focal species.

Figure 4A shows the correlation of food-web stability with the number of predator species as a function of z . Increasing the number of predator species preying on basal species ($z < 0.25$) has a destabilizing effect on the food web. Likewise, increasing the number of predator species preying on apical species ($z > 0.75$) has a destabilizing effect. In between, there is a large intermediate range ($0.25 < z < 0.75$) in which the correlation is positive, showing that for a given number of links the stability of food webs is enhanced if predators mainly prey upon species of intermediate trophic position.

Figure 4B shows the correlation of food-web stability with the number of prey species as a function of z . For most species ($z < 0.719$), the PSW correlates negatively with the number of prey species, whereas a positive correlation is found for species at high trophic levels ($z > 0.719$). For a given number of links, stability is therefore enhanced by generalist predators at the top of a food web and specialist predators below. The threshold $z = 0.719$ is independent of most GM parameters, including N and K . Additional investigations reveal that the nonlinearity of top-predator mortality is the only parameter in the model that has a detectable impact on this threshold.

Our study adds independent support for some previously proposed stabilizing factors. The mutual reinforcement of similar results obtained with different methods establishes a broader basis for understanding food-web stability. Our analyses show that variability in trophic link strength exerts a stabilizing influence only in relatively small food webs. In contrast, larger food webs are destabilized by in-

creasing the coefficient of variation of normalized link strength. This indicates that large food webs follow qualitatively different rules than smaller webs (16) and suggests that extreme link strengths should be rarer in larger food webs. Further, we found a power law for the scaling of food-web stability with species number and connectance and identified two topological rules governing food-web stability: For a given number of species and links, food-web stability is enhanced when (i) species at high trophic levels feed on multiple prey species and (ii) species at intermediate trophic levels are fed upon by multiple predator species. This pattern, with generalist apical predators preying upon intermediate specialist predators, is often encountered in empirical food webs (7, 11, 14, 15) and is consistent with reported effects of allometric degree distributions (15) and of top predators connecting otherwise separate energy channels (14). In comparison with previous results, our study offers more predictive specificity based on a wider ensemble of models, which enhances confidence in the universality of the reported rules. Per-

haps most importantly, the GM approach used here has much potential for addressing a large class of related questions.

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Supporting Online Material

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Materials and Methods

Figs. S1 and S2

Table S1

References

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