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Generalized models reveal stabilizing factors in food webs

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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, undermining their relevance, or only examine few replicates of small food webs, hampering the robustness of findings. Here we use generalized modeling to study several billion replicates of food webs with nonlinear interactions and up to 50 species. In this way, we show, first, 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 high trophic level feed on multiple prey species and (ii) species at 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. While it has often been pointed out that food webs can persist in non-stationary states, there is growing evidence that May's stability-complexity relationship also holds for non-stationary dynamics (*18*). Moreover, population cycles or external forcing averages out if food webs are considered on longer timescales, 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 (e.g., *12*). Here, we avoid these constraints through the use of generalized modeling (*19,20*).

For a given class of mathematical models, generalized modeling (GM) identifies para-

meters that together capture the local stability properties of all stationary states. Some of these parameters (scale parameters) quantify the scaling of biomass fluxes, while 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 $i = 1, \ldots, N$ follows a differential equation of the form

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

where S_i, F_i, M_i, 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. Importantly, 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, while the predation gain vanishes for producers. Similarly, the predation loss is zero for top-predators, while 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 Tab. S1.

To assess the dependence of food-web stability on the exponent parameters, we generate a sample of 10^8 food webs with a fixed number of species. In this sample, the exponent parameters are drawn independently and randomly from suitable uniform distributions, while the topological parameters are computed from randomly generated niche-model topologies (20, 21). We estimate 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 Figure 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, e.g., quadratic, mortality promote stability (12). By 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 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 cor-

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relate 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 (Tab. S1) and focus on the effects of food-web topology on stability. We start 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 generate samples with random niche-model topologies, with N and C changing on a logarithmic grid. At every vertex of this grid, we compute 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. Fig. 2B shows that the dependence of $\log(\text{PSW})$ on $\log(CN)$ closely follows a power law.

We now turn 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 must 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 measure link-strength variability in a predator-centric way, by determining the coefficient of variation (CV) of all biomass fluxes normalized individually 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 normalized individually by the total biomass outflow of the flux's source.

To explore the impact of link-strength variability, we generate a large ensemble of food webs (approx. 10^7) in which link strengths are 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 (e.g., $N = 5$), large jumps occur in the PSW as a function of the CV (not shown). 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 about $N = 10$. We find that in small and intermediate food webs ($N < 30$), the PSW increases with increasing CV (Fig. 3A), confirming the stabilizing effect of link-strength variability previously reported in the literature (*4*). However, in larger foods web, this relationship is reversed, so that increasing the CV decreases the PSW.

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 oc-

curs at low CVs. Therefore increasing the CV has a stabilizing effect if the CV is low (not shown). 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 Figure 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 determine the correlations between the PSW and (a) the number of predator species exploiting the focal species and (b) 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, while 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 (not shown) 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 by 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. By contrast, larger food webs are destabilized by increasing 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 (e.g., *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. Perhaps most importantly, the approach of generalized modeling, used here, has much potential for addressing a large class of related questions.

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Supporting online material

Figure captions

Figure 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 grey), 20 (medium grey), and 30 species (dark grey). 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.

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

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

Figure 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 measured by its trophic-rank index z. Stability is enhanced if most species prey upon intermediate species, 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, while intermediate predators are specialists.
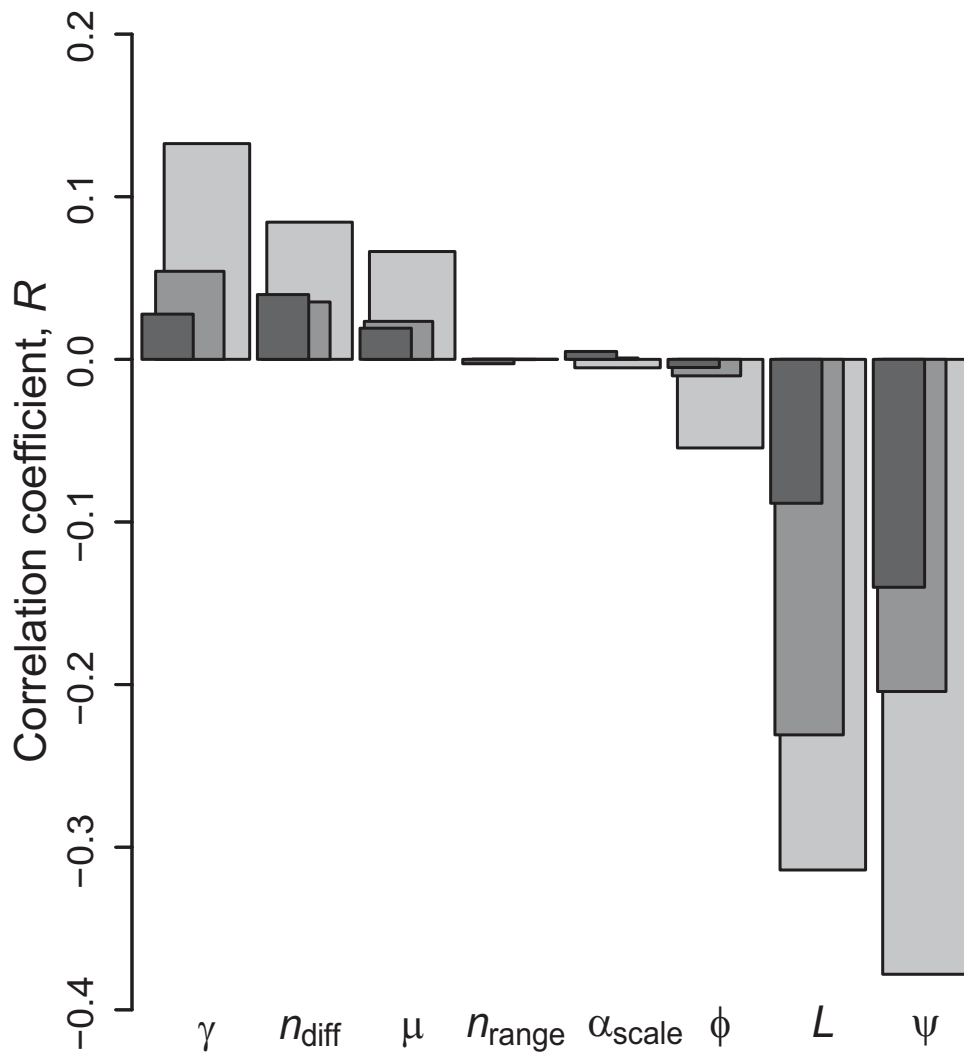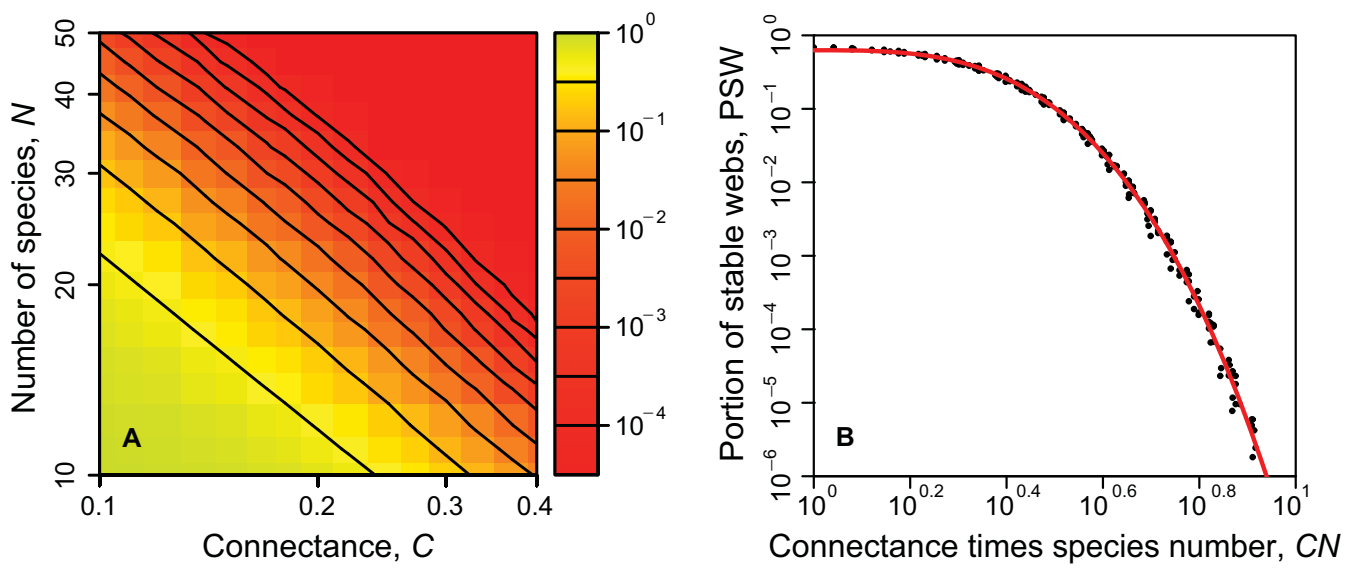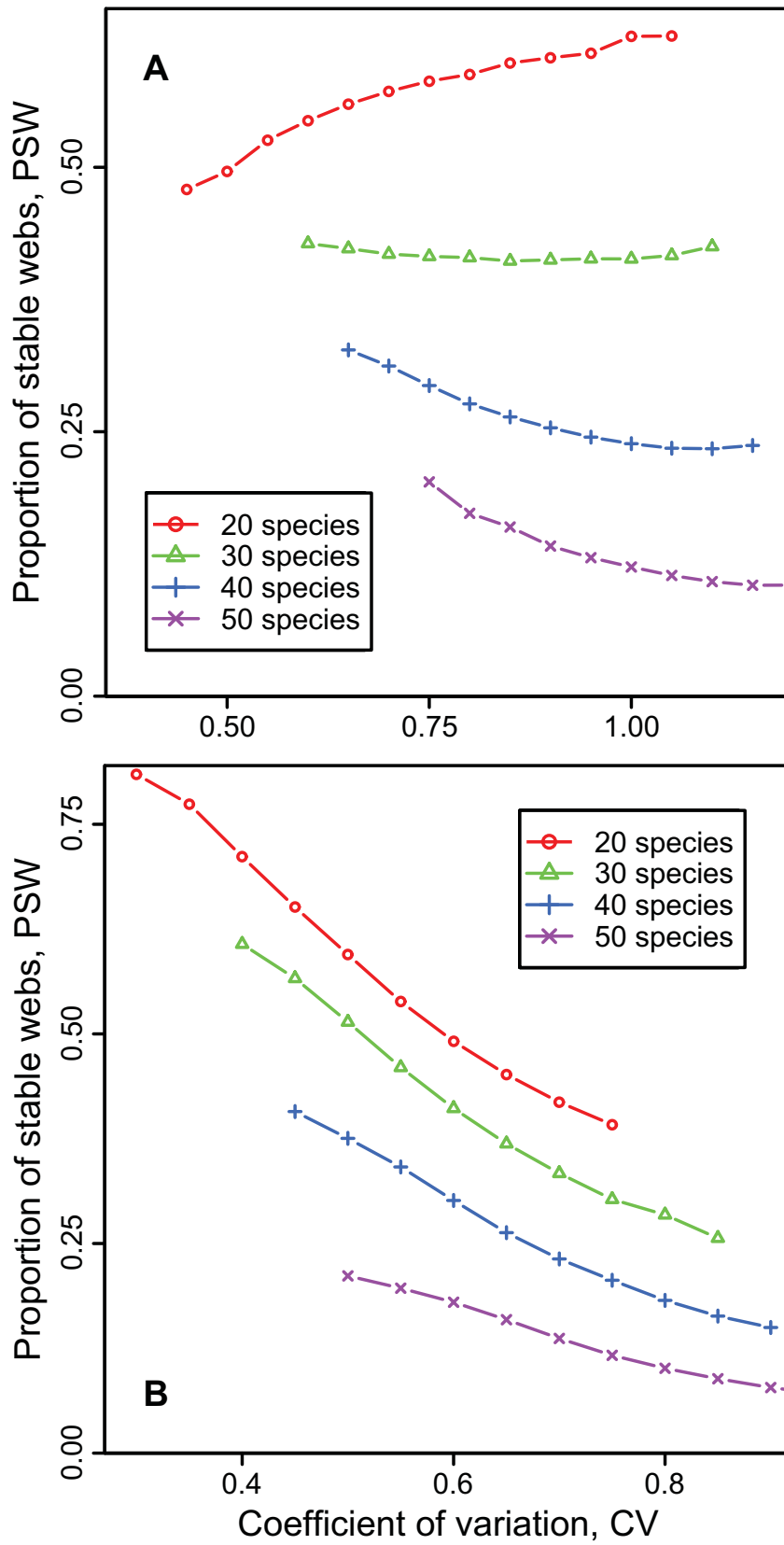
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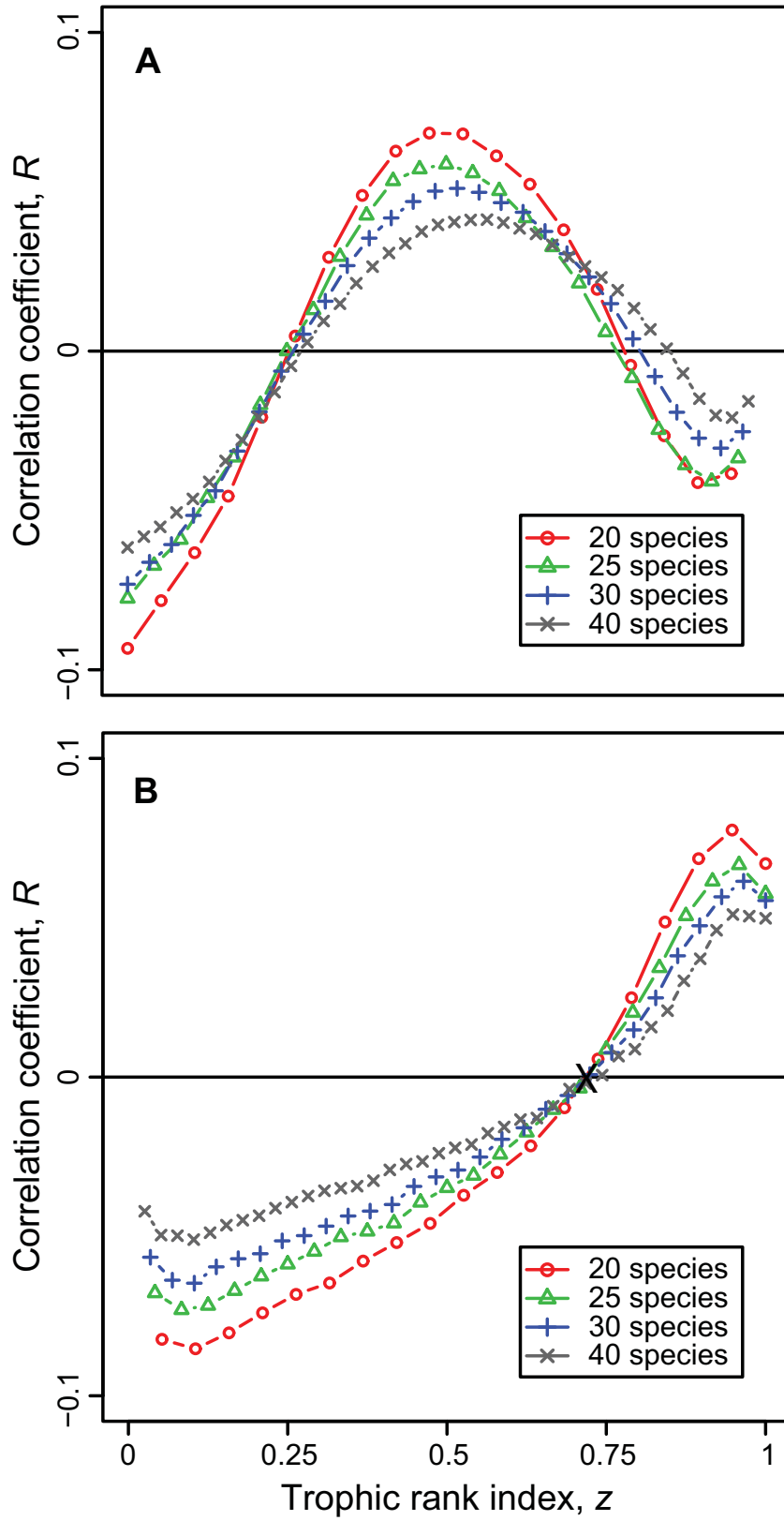
Figure 2

Figure 3

Figure 4

Supporting Online Material for
Generalized Models Reveal Stabilizing Factors in Food Webs

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Methods

Generalized modeling. GM is based on the insight that, in general, the computation of steady states is much more difficult and computationally expensive than the investigation of the local dynamics around them. Once a steady state is given, its stability is determined by the corresponding Jacobian matrix, which can be analyzed at low computational cost.

In the GM of food webs, computation of steady states can be avoided as follows: for every arbitrary steady state, we formally map the species densities X_i and the functions describing production, predation, and mortality to 1 by a suitable normalization. The Jacobian of the normalized system contains a number of unknown terms, which can be identified as free parameters with clear biological interpretations. These GM parameters can be treated just like parameters in conventional modeling.

GM parameters fall into two classes: (a) scale parameters, which determine the topology and magnitude of biomass fluxes, and (b) exponent parameters, which measure the local nonlinearity of the considered functions. For mononomial functions, the corresponding exponent parameter simply is the monomial's exponent. For instance, a linear function corresponds to a parameter value of 1, a quadratic function to a value of 2, and a square-root function to a value of 0.5. However, we do not restrict the functional forms in our model to monomials. For general functions, the exponent parameter measures the sensitivity of a process, say predation, to a variable, e.g., prey density (for details, see S1). Exponent parameters are called elasticities in the context of metabolic control theory.

It is always possible to step back and forth between a conventional model and the corresponding generalized model. For a given steady state in the conventional model, the corresponding GM parameters are unique and can be computed straightforwardly. Conversely, for a

given generalized model, one can always construct a class of conventional models that generate the given GM parameters. For instance, an exponent parameter $\gamma = 1$, indicating a locally linear functional response, corresponds to a Lotka-Volterra functional response for all prey densities, to a Holling type-II functional response for low prey densities, and to a Holling type-III functional response for intermediate prey densities. Utilizing these commonalities, analyzing a single set of GM parameters reveals information on a large class of different conventional models.

Example: Single species. To illustrate the GM approach, we consider a single population with density X. We assume that this population grows due to reproduction at rate $S(X)$, while also suffering from predation at rate $G(X)$, and from natural mortality at rate $M(X)$. In this simple example, we do not model the population of predators explicitly. The population dynamics is therefore given by a single differential equation,

$$\dot{X} = S(X) - G(X) - M(X). \tag{S1}$$

In conventional modeling, one would now parameterize the functions S, G, and M, and thereby restrict them to specific functional forms.

Using GM, we instead parameterize the Jacobian matrix that governs the stability of all steady states in the whole class of models conforming to Eq. S1. For this purpose, we denote a steady state by X^*. Using the notation $S^* := S(X^*)$, $G^* := G(X^*)$, and $M^* := M(X^*)$, we define a normalized density $x := X / X^*$ and normalized functions $s(x) := S(X)/S^*$, $g(x) := G(X)/G^*$, and $m(x) := M(X)/M^*$. It is always possible to normalize in this way as long as X^*, S^*, G^*, and M^* are positive. Substituting the scaled quantities into Eq. S1, we obtain

$$\dot{x} = \frac{S^*}{X^*} s(x) - \frac{G^*}{X^*} g(x) - \frac{M^*}{X^*} m(x).$$

For this equation, the considered steady state is $x^* = 1$, with $s(x^*) = g(x^*) = m(x^*) = 1$. The price we pay for normalizing the unknown steady state to $x^* = 1$ is the introduction of the unknown factors in front of the functions. These factors, however, are constants and can be treated just as unknown parameters in conventional modeling. We define $\alpha := S^* / X^*$ and $\sigma := G^* /(G^* + M^*)$, which, using $S^* = M^* + G^*$, allow us to rewrite the differential equation above as

$$\dot{x} = \alpha[s(x) - \sigma g(x) - (1 - \sigma)m(x)].$$

The parameter $\alpha > 0$ denotes the per-capita birth rate in the steady state (i.e., the turnover rate), while $\sigma \geq 0$ denotes the stationary fraction of losses resulting from predation. Together, α and σ are the system's GM scale parameters. Although the scale parameters could have been defined differently, the present definition is particularly advantageous, as separating the turnover rate from the parameters weighting contributions to this rate facilitates interpretation.

We can now compute the Jacobian in the considered steady state as

$$J = \frac{\partial}{\partial x} \dot{x}\bigg|_{x=1} = \alpha[\phi - \sigma\gamma - (1-\sigma)\mu],$$

where $\phi := s'(1)$, $\gamma := g'(1)$, and $\mu := m'(1)$ are the GM exponent parameters, denoting the sensitivities of the corresponding functions around $x^* = 1$.

The considered steady state is stable if all eigenvalues of the Jacobian have negative real parts. In our one-dimensional example, there is only one eigenvalue, which is directly given by J. The steady state is therefore stable if

$$\phi - \sigma\gamma - (1-\sigma)\mu < 0.$$

We can summarize this result by stating that in all models conforming to Eq. S1 every possible steady state is stable in which the sensitivity of the source term S is smaller than the sensitivity of the loss terms F and M, weighted according to their relative contributions to the total loss rate. This allows us to infer, for example, that a system with linear reproduction, $\phi = 1$, constant predation (e.g., through harvesting), $\gamma = 0$, and quadratic natural mortality, $\mu = 2$, can only be stable if less than half of the losses result from predation, $\sigma \le 0.5$.

When extending this simple example to multiple species with arbitrary trophic interactions, only two additional difficulties arise. First, as the number of species grows, the eigenvalues of the Jacobian have to be computed numerically. Computing the eigenvalue spectrum of a real matrix is a standard numerical task that can be accomplished very efficiently by existing tools. Second, trophic interactions link the gain of a predator species to the loss of its prey. We therefore include algebraic equations that capture the resultant dependencies. These equations can be normalized just as the differential equations and therefore pose no additional difficulties. For further details see Ref. S1.

Food-web generation. Following Ref. S2, each species i is assigned a niche value n_i, randomly drawn from a uniform distribution over the interval $[0,1]$. This niche value is often interpreted as an indicator of body size. Consequently, a species' rate of biomass turnover, α_i, is chosen according to the allometric scaling relation $\alpha_i = \alpha_{\text{scale}}^{n_i}$, with $0 < \alpha_{\text{scale}} < 1$ and a default value of $\alpha_{\text{scale}} = 0.008$. Species i exploits other species j that posses a niche value $n_j \in [c_i - \frac{1}{2}r_i, c_i + \frac{1}{2}r_i)$, where the width of the feeding range, r_i, is drawn randomly from a beta distribution over the interval $[0, n_i]$, while the center of the feeding range, c_i, is drawn randomly from a uniform distribution over the interval $[\frac{1}{2}r_i, n_i - \frac{1}{2}r_i]$. Species that do not feed on any other species are assumed to be primary producers. The total range of niche values is $n_{\text{range}} = \max_i n_i - \min_i n_i$, and the average difference in niche value between predators and their prey is obtained as $n_{\text{diff}} = \frac{1}{L}\sum_{ij \text{ with } l_{ij}>0} |n_i - n_j|$.

To avoid degenerate food webs, we draw link strengths l_{ij} from a narrow Gaussian distribution with a 10% coefficient of variation. In the investigation of link-strength variability (Fig. 3), the link strength is instead drawn from a uniform distribution over the interval

$[1-\tau, 1+\tau]$, where τ is, in turn, drawn for every food web from a uniform distribution over the interval $[0,1]$. Further results, shown in Figures S1 and S2, are based on link strengths being drawn from a lognormal distribution.

For Figures 1 to 4, we only consider food-web topologies that consist of a single connected component and for which double links, self links (through cannibalism), and trophic loops (e.g., through parasitism) are avoided. We have checked that the omission of trophic loops does not qualitatively change our results. For this purpose, we have repeated the analysis shown in Figure S1 while including a realistic number of trophic loops as generated by the niche model. Figure S2 shows that, while trophic loops slightly diminish the overall stability of food webs, results are qualitatively equivalent to those found for loop-free webs.

Stability analysis. We consider a food web as being stable if the real part of all eigenvalues of the corresponding Jacobian matrix are smaller than -10^{-6}. As shown in Ref. S1, the diagonal elements of a food web's Jacobian matrix can be expressed in terms of GM parameters as

$$J_{ii} = \alpha_i \left[\tilde{\rho}_i \phi_i + \rho_i \psi_i - \tilde{\sigma}_i \mu_i - \sigma_i \left(\sum_{k=1}^{N} \beta_{ki} \lambda_{ki} [(\gamma_k - 1)\chi_{ki} + 1] \right) \right]$$

and the non-diagonal elements ($i \neq j$) as

$$J_{ij} = \alpha_i \left[\rho_i \gamma_i \chi_{ij} \lambda_{ij} - \sigma_i \left(\beta_{ji} \psi_j + \sum_{k=1}^{N} \beta_{ki} \lambda_{kj} (\gamma_k - 1)\chi_{kj} \right) \right].$$

All parameters contained in these equations are explained in Tab S1.

A notable difference between most random-matrix models and GM lies in the diagonal entries of the Jacobian, which are particularly important for stability. In many random-matrix models, these terms are assumed to equal -1 (e.g., Ref. S3). By contrast, in the class of models studied here, the diagonal entries corresponding to intermediate predators are always positive, if predation is assumed to be linear in predator density and less than linear in prey density.

Correlations with stability. The correlation of a parameter x with stability is given by

$$R = \frac{\sum_{i=1}^{\nu_s} x_{s,i} - \frac{\nu_s}{\nu} \sum_{i=1}^{\nu} x_i}{\nu \sigma_x \sigma_s},$$

where $x_{s,i}$ and x_i, respectively, are the sets of parameter values giving rise to the stable webs and in the entire ensemble, ν is the total size of the ensemble, ν_s is the number of stable webs, σ_x is the standard deviation of x, and σ_s is the standard deviation of the stability s_i, with $s_i = 1$ characterizing stable and $s_i = 0$ unstable webs.

Measures of trophic position. The trophic index z, defined in the main text, provides a basic measure of the trophic position of a species. We have confirmed that using the niche value

directly yields very similar results. Other, more advanced, measures of trophic position, proposed in the literature, have a slightly different emphasis and therefore reveal different information.

Table

Table S1. List of GM parameters for food-web dynamics

Parameter	Interpretation	Range	Value
Scale parameters			
α_i	Rate of biomass turnover in species i	n.a.	$\alpha_{\text{scale}}^{n_i}$
β_{ij}	Contribution of predation by species i to the biomass loss rate of species j	n.a.	$l_{ij}/\sum_k l_{kj}$
χ_{ij}	Contribution of species i to the prey of species j	n.a.	$l_{ij}/\sum_k l_{ik}$
ρ_i	Fraction of growth in species i resulting from predation	n.a.	0 if i is a producer, 1 if i is a consumer
$\tilde{\rho}_i$	Fraction of growth in species i resulting from production	n.a.	$1-\rho_i$
σ_i	Fraction of mortality in species i resulting from predation	n.a.	0 if i is a top-predator, 1 otherwise
$\tilde{\sigma}_i$	Fraction of mortality in species i not resulting from predation	n.a.	$1-\sigma_i$
Exponent parameters			
γ_i	Sensitivity of predation in species i to the density of prey	[0.5,1.5]	0.95
λ_{ii}	Exponent of prey switching in species i	n.a.	1 (passive switching)
μ_i	Exponent of closure in species i	[1,2]	1
ϕ_i	Sensitivity of primary production in species i to the density of primary producers	(0,1)	0.5
ψ_i	Sensitivity of predation in species i to the density of predators	[0.5,1.5]	1

Figures

Figure S1. Dependence of food-web stability on link-strength variability when link strengths are drawn from a lognormal distribution. As in Figure 3, link strength is normalized by (A) the predator's total influx or (B) the prey's total outflux.
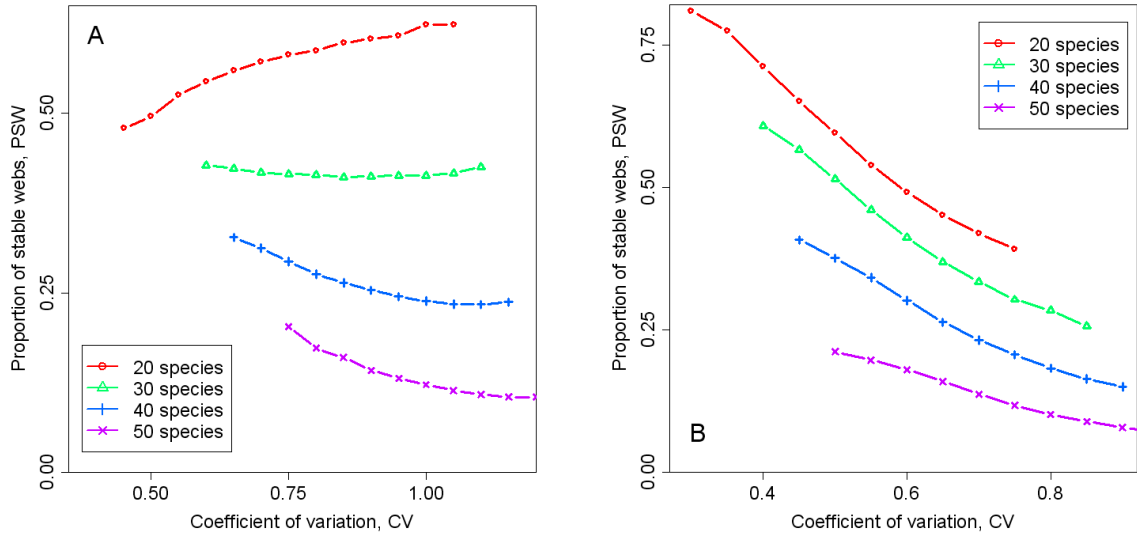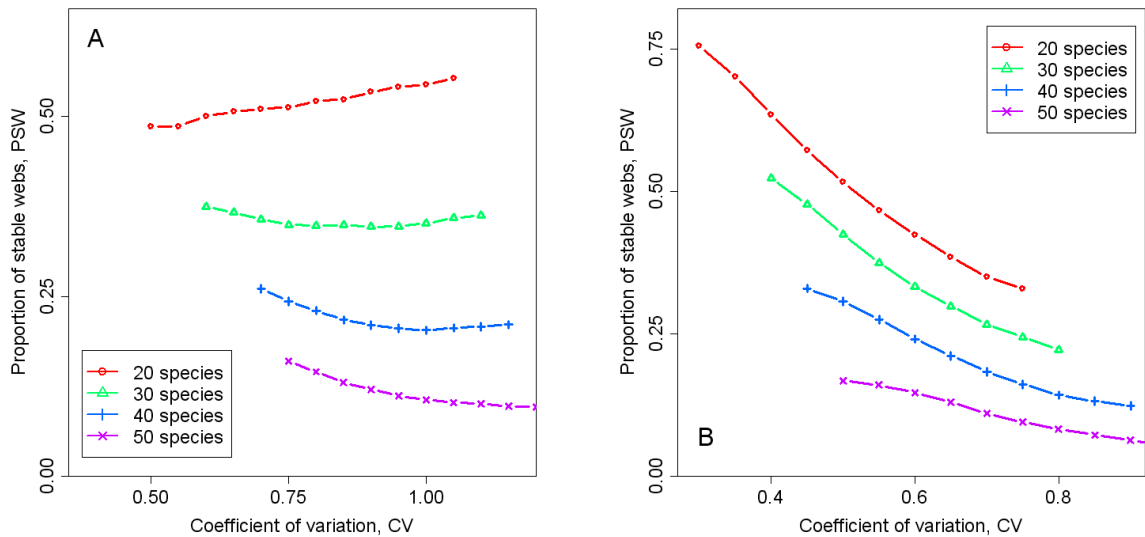

Figure S2. Dependence of food-web stability on link-strength variability when link strengths are drawn from a lognormal distribution and trophic loops are generated by the original variant of the niche model (Ref. S2). As in Figs 3 and S1, link strength is normalized by (A) the predator's total influx or (B) the prey's total outflux.

References

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S2. R. J. Williams, N. D. Martinez, *Nature* **404**, 180–183 (2000).
S3. R. M. May, *Nature* **238**, 413–414 (1972).