

Self-regulation and the stability of large ecological networks

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Abstract

Stability of complex ecological networks depends both on the interactions between species and the direct effects of the species on themselves. These self-effects are known as “self-regulation” when an increase in a species’ abundance decreases its per capita growth rate. Sources of self-regulation include intraspecific interference, cannibalism, time scale separation between consumers and their resources, spatial heterogeneity, and nonlinear functional responses coupling predators with their prey. The influence of self-regulation on network stability is understudied; worse, the empirical estimation of self-effects poses a formidable challenge. Here we show that empirical food web structures cannot be stabilized unless the majority of species exhibit substantially strong self-regulation. We also derive an analytic formula predicting the effect of self-regulation on network stability with high accuracy, and show that even for random networks, as well as networks with cascade structure, stability requires negative self-effects for a large proportion of species. These results suggest that the aforementioned potential mechanisms of self-regulation are likely more important in contributing to the stability of observed ecological networks than previously thought.

What keeps the exponential growth capacity of natural populations in check? Some regulatory mechanism is required, a feedback decreasing growth rates when abundance is high and increasing them when abundance is low. Common regulating factors include resource shortage, predation pressure, pathogen load, refuge availability, etc. Sometimes, however, the per capita growth rate of a species has a direct negative dependence on its own abundance—this is called “self-regulation”^{1,2}. Self-regulation may be caused by direct mechanisms such as intraspecific interference or certain forms of cannibalism. Also, it is sometimes possible to eliminate from consumer-resource relationships the explicit dependence of the consumer on the resource (or vice versa) via a separation of time scales, leading to “effective” self-regulation, as was done by MacArthur in deriving the Lotka–Volterra equations from an underlying consumer-resource system³. Finally, immigration from outside sources and nonlinear functional responses coupling predators and prey can give rise to self-regulatory effects. The important commonality across all of these mechanisms is that they can cause per capita growth rates to directly depend on the abundance of the species in question.

How important is self-regulation in natural systems? To further specify what we mean by “important”, in this work we will focus on the property of local asymptotic stability, i.e., whether

small perturbations of species' abundances away from an equilibrium point tend to be dampened, with the system returning to the equilibrium. Local asymptotic stability is assessed using the community matrix (Jacobian evaluated at the equilibrium point)⁴. This matrix having its rightmost eigenvalue in the left half of the complex plane signals the stability of the system; otherwise the system is unstable. Self-regulatory effects appear in the community matrix as negative entries along its diagonal (Supplementary Information [SI], Section 1).

We ask what fraction of species in large ecological networks must exhibit self-regulation for the system to be (locally asymptotically) stable, and how strong this self-regulation must be. In two simple reference cases, the answer is known: first, a system completely devoid of any self-regulation cannot be stable; second, sufficiently strong simultaneous self-regulation of all species always leads to stability (SI, Section 1.2). The difficult question is whether stability can be achieved by something between these extremes. It is known that some ecological networks can be stabilized by just a single well-chosen self-regulating species⁵. However, such systems have especially simple topologies, and it is unclear whether empirical networks with more complex structure could be stabilized in the same way.

Views on this question differ strongly between ecologists: some believe most species must experience at least weak self-regulation at least some of the time^{2,6,7}, while others maintain that only primary producers and maybe top predators self-regulate to an appreciable degree^{8–11}. To some extent, this disagreement is undoubtedly fueled by the unfortunate fact that the empirical study of self-regulation is a formidable challenge. While it is true that measuring a population's growth rate as a function of its abundance typically yields a negative relationship between the two¹², this will in general not be due to direct self-effects but rather to depletion of consumables, greater parasitic load at high abundance, or increased predation pressure¹⁰. Though disentangling causes is not impossible^{13–16}, it is still a difficult task from an empirical point of view.

For this reason, here instead we look at the importance of self-regulation by assessing its theoretical consequences, and seeing if they are consistent with certain broad empirical patterns. Since one such pattern is the relative stability of ecological communities at certain spatiotemporal scales, one can inquire what levels of self-regulation would be required to confer stability to large ecological communities.

Results

Self-regulation in empirical food webs

To answer the question of how common and how strong self-regulation must be to achieve stability, we analyzed empirical food webs. First, we used published parameterizations obtained by Jacquet et al.¹⁷ using the Ecopath modeling framework¹⁸ (Table 1). Since these have already been parameterized, they can be used out of the box. Their disadvantage is that they are highly aggregated networks, containing between 39 and 51 species. To see also what results one might obtain from more species-rich communities, we also parameterized 12 well-resolved food webs (see Methods) containing between 170 and 484 species (Table 2). The two approaches also make it possible to compare their results for consistency.

Initially, none of the webs and parameterizations included self-effects. For each web, we gradually increased the fraction of self-regulating species P from 0 to 1. For each P , the identities of the self-regulating species were randomly assigned 1000 times, and the fraction of cases which ended up stable was tallied. This procedure was then repeated for different strengths of self-regulation.

Name	Species	Links
Chesapeake Present ⁵¹	41	167
Mid Atlantic Bight ⁵⁰	51	515
Moorea Barrier Reef ⁵²	39	267
Newfoundland Grand Banks (1900) ⁵³	48	519
Newfoundland Grand Banks (mid-1980s) ⁵³	48	519
Newfoundland Grand Banks (mid-1990s) ⁵³	48	525
Tampa Bay ⁵⁴	48	340

Table 1: Information on the seven largest Ecopath networks parameterized by Jacquet et al.¹⁷, with each row corresponding to a different web. Columns indicate, respectively, the name of the web (with a reference for the source of the original data), its number of species and the number of links.

Name	Species	Links	Structural rank
Carpinteria Salt Marsh ⁵⁵	272	3878	197
Flensburg Fjord ⁴⁶	180	1567	128
Kongs Fjorden ⁵⁶	268	1632	164
Little Rock Lake ⁴⁷	181	2316	150
Lough Hyne ⁵⁷	349	5088	287
Otago Harbour ⁴⁸	180	1856	158
Punta Banda ⁵⁵	355	5291	234
Caribbean Reef ⁵⁸	249	3293	204
San Quintin ⁵⁵	289	3934	179
Serengeti ⁴⁹	170	585	54
Sylt Tidal Basin ⁵⁹	230	3298	215
Weddell Sea ⁶⁰	484	15435	448

Table 2: As Table 1, but for the twelve highly resolved empirical food webs. An additional column shows the structural rank⁴⁵ of each web (maximum possible rank the matrix of the web can attain assuming its nonzero entries are arbitrary).

For the Ecopath webs, at least 50% of species must exhibit substantially strong self-regulation if the community is to have a realistic chance of being stable (Figure 1a). Instead of just primary producers and top predators, it is in fact a majority of species that must self-regulate. This result is even stronger in the well-resolved food webs (Figure 1b). The qualitative pattern is the same as before, but there is a large quantitative difference: instead of over half, now over 90% of species must exhibit self-regulation for the network to be stable. This was true regardless of which particular well-resolved network we analyzed, or which particular parameterization we applied to them (SI, Section 7).

Although we have performed the analysis for several different values of the strength of self-regulation, one might wonder whether imposing extremely strong self-effects on just a few species could stabilize the networks. Our results yield a counterintuitive answer to this question: given a set of self-regulating species, the most stabilized configurations are not those with the strongest self-interactions, but those with intermediate ones (Figure 1). Beyond a point, increasing the strength of self-regulation actually destabilizes the system. Though this may seem strange at first, it can be

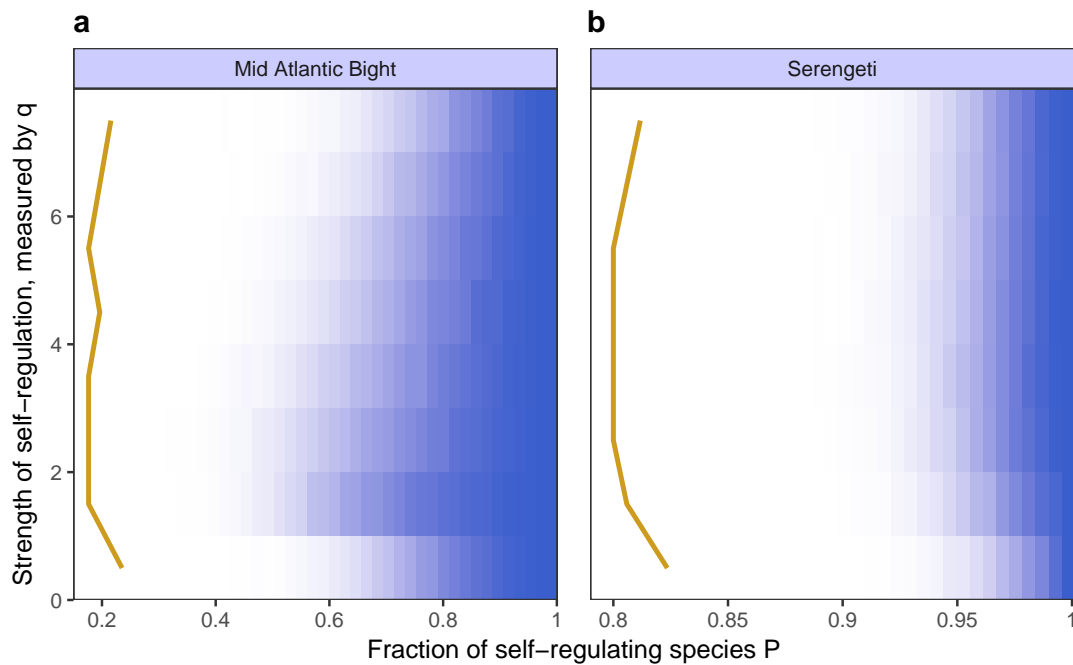


Figure 1: The fraction of self-regulating species required for stability, in (a) the Ecopath-modeled Mid-Atlantic Bight⁵⁰ web, and (b) the Serengeti⁴⁹ food web parameterized with $g = -0.95$ and no indirect effects (see Methods). Each grid of the heat-map represents the probability of stability given q and the fraction of self-regulating species P , ranging from white (0% chance of stability) to blue (100% chance). The yellow line is the lowest fraction of self-regulating species compatible with stability for the given strength of self-regulation, found using a stochastic search algorithm. Notice that the highest overall probability of stability is always obtained for an intermediate value of self-regulation strength.

understood by considering an example where all but one single species are self-regulating. Very weak self-effects will not be able to stabilize any system in the first place. On the other hand, for prohibitively strong self-regulation, the one single species without the burden of a negative self-effect has such an overwhelming advantage over all the others that it will drive them extinct. If the system is to be stable for at least some self-regulation strengths, it then must happen at intermediate ones (SI, Sections 2.4 and 5).

One could also ask whether, by choosing very carefully which particular species self-regulate, their fraction could be considerably lowered while still achieving stability. To test this, we searched for the minimal value of P compatible with local stability (Figure 1, yellow lines). This was done by choosing the identities of the self-regulating species to be the most conducive to stability via a stochastic search algorithm (SI, Section 7.4). As seen, P is indeed reduced this way, especially in the case of the Ecopath webs, where it drops to about 20–30% of the species. In the case of the well-resolved webs, P reduces only to about 80% of all species, which is still a large majority. That is, there is no way of targeting particular species with self-regulation which would alleviate the need for the majority of species to be self-regulated.

Moreover, contrary to ecological intuition, there is no obvious trophic pattern to the minimal set of self-regulating species: it is not true that primary producers or top predators are more likely to be included than species from other trophic levels. Instead, the self-regulating species are more or

less uniformly distributed across trophic levels. Additionally, it is impossible to stabilize any of the large networks by having only basal and top species self-regulate: by assigning self-regulation to all species within these two trophic groups only, the webs turned out unstable in all cases (SI, Section 7.7).

Theoretical analysis

Despite all the different empirical food webs and parameterizations considered above leading to the conclusion that the majority of species must be self-regulating, food web data is always incomplete no matter how well-resolved, and any finite set of parameterizations will fall short of the infinitely many possible ones. Furthermore, it is unclear whether food webs possess some peculiar structure which has lead us to find this result, or if they pertain to a much wider class of networks. To answer these questions, we conducted a theoretical analysis in two steps.

First, we considered random network ensembles such that the pairwise effects of species i on species j and that of j on i are drawn from a bivariate distribution with given marginal means, marginal variances V , and correlation ρ ^{19–23}. Using a new result in the mathematical theory of such systems²⁴, we show that even a handful of species lacking self-regulation are sufficient to destabilize them (SI, Section 2). Moreover, we obtained an analytical formula for the distance of such networks from stability using the recently proposed quaternionic resolvent method²⁵ (SI, Sections 3–5). From this it turns out that just two relevant quantities determine the minimum fraction of self-regulating species P required for network stability: the correlation ρ , and the scaled strength of self-regulation d/\sqrt{SV} where d is the self-regulation strength and S the number of species (Figure 2). The results show that local stability is unattainable without either the majority of species strongly self-regulating, or ρ being close to -1 .

Second, real food webs have markedly nonrandom structure, and one may wonder if the above random network results are sensitive to incorporating realistic network topology. One well-known structural feature of real food webs is that they are close to a cascade pattern^{26,27}: species may be ordered such that those lower in the hierarchy may be eaten by species higher up, but not vice versa (“big fish eat small fish”). Performing the analysis on such webs (SI, Sections 2.5 and 6), we find the following result: Figure 2 is still valid as long as one replaces the original ρ with a new effective correlation ρ_{eff} , and the original V with an effective variance V_{eff} . Both ρ_{eff} and V_{eff} can be straightforwardly calculated using the original data. Since our results are derived in the limit of a very large number of species, they are not well suited to analyzing the Ecopath webs, which had only between 39 and 51 species. However, our analytical formula does predict the stability of the well-resolved empirical networks with high accuracy (SI, Section 7.5). The accuracy is sufficiently high not to leave much room for improvement by including further structural properties of real food webs in the theoretical analysis. For instance, real food webs, apart from possessing an approximate cascade structure, are also close to being interval, and have broader degree distributions than expected by chance. Incorporating these other properties into a model is an unsolved theoretical problem—but, since the approximation is accurate even in their absence, doing so is not expected to yield any substantial improvement.

One question is where empirical systems tend to be located in the parameter space of Figure 2. Previous studies¹⁷ suggest a slight but positive correlation between ρ and \sqrt{SV} , imposing a negative correlation between the two axes of the plot. It is not yet known whether a significant relationship is retained between ρ_{eff} and $\sqrt{SV_{\text{eff}}}$ though; furthermore, the empirical difficulty in determining d means we do not know where real-world communities lie exactly. However, we calculated the

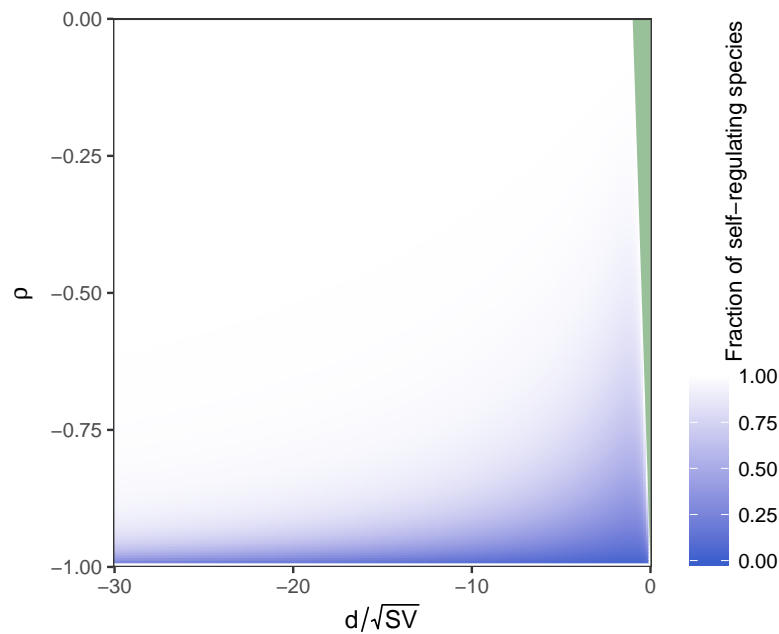


Figure 2: The minimum fraction of self-regulating species required for stability, as a function of the average pairwise correlation ρ and normalized self-regulation strength d/\sqrt{SV} (where d is the raw strength of self-regulation, S is the number of species, and V is the variance of all interaction strengths excluding self-effects). In the green shaded region the system is unstable regardless of the value of P . This theoretical map may correspond either to elliptic random networks or networks with cascade structure (in which case the effective parameters ρ_{eff} and V_{eff} must be used instead of ρ and V ; see SI, Section 6). Self-effects are sampled from a distribution equal to d with probability P and to zero with probability $1 - P$. Stability can only ever be achieved for $P \approx 1$, except for correlation values close to -1 . Note that only negative values of ρ are shown, even though $-1 \leq \rho \leq 1$ in principle—this is because stability cannot ever be achieved for $\rho > 0$, except when P is strictly equal to 1.

effective correlation ρ_{eff} for all our food webs and parameterizations. Having done so, this quantity was never found to be lower than about -0.35 . Then one can say, based on Figure 2, that a large fraction of species must self-regulate for stability, regardless of the particular value of $d/\sqrt{SV_{\text{eff}}}$. This is consistent with our results from analyzing the empirical webs.

Discussion

Our two main results are an analytical method for predicting the stability properties of large ecological networks with high accuracy, and the conclusion that local asymptotic stability cannot be achieved without the majority of the diagonal entries in the community matrix being strongly negative.

In light of this, it would seem that even the most ardent proponents of the “self-regulationist” view^{2,6,7} have been overly cautious in assessing the prevalence of negative self-effects. Yodzis² concluded, based on an analysis of relatively low-resolution food webs, that “it appears that at least one-tenth and perhaps as much as one-half of the consumer species [in these communities] need to exhibit some degree of intraspecific interference if the equilibrium viewpoint is to apply”.

Sterner et al.⁶, after finding it difficult to stabilize small ecological networks without widespread self-regulation, state that “in the absence of sufficient data on the prevalence of self-damping in different trophic levels, it seems best to allow for self-damping in all trophic levels in community models”—with the fraction of species having to self-regulate at each level being left as an open question. The closest it comes to the results expounded here can be found in an almost off-hand remark by Moore and de Ruiter⁷, who state that “arguably, most, if not all, populations are subject to intraspecific competition and self-regulation to some degree” (p. 36). Based on the results presented here, at least half and possibly more than 90% of species must be subject to self-regulation to a substantial degree.

It is important to emphasize what our results do *not* say. First, they do not imply that a large P means all species have an equally high probability of self-regulation. For instance, if all basal species self-regulate, then reaching the required fraction of self-regulating species is in principle possible with species at higher trophic levels having a lower frequency of self-regulation: if a fraction $P = 0.7$ of 100 species need to be self-regulating but half of the species are basal, then only 40% of consumers may need self-regulation. Second, they do not imply that intraspecific aggression, cannibalism, or other forms of direct interference are overwhelmingly important in stabilizing communities. As pointed out earlier, self-regulatory terms may appear in the community matrix via indirect mechanisms such as time scale separation between consumers and their resources, nonlinear functional responses, or spatial dynamics. Since our treatment of self-regulation was phenomenological, one cannot say what mechanism brought about the self-regulatory terms. All we can say is that *something* must be providing them if the system is to be stable. In fact, this is in line with several recent empirical studies of coexistence which have found not only that intraspecific effects are ubiquitous, but also that their magnitude is overwhelmingly larger than those of the interspecific ones^{28–32}. As these studies are phenomenological, they say nothing about the mechanisms behind this pattern. Let us therefore reflect on some of the possibilities for where self-effects may originate from.

Direct self-regulation via predator interference or cannibalism are, in a sense, the simplest candidate mechanisms from a conceptual point of view. The only problem is that we do not know how important they are—though it has been argued that predator interference is quite common in nature^{14,16}. Cannibalism is often important in marine systems, and cannibalism may act in a self-regulatory way under many circumstances (exceptions include the case when the fraction of individuals consumed is proportional to the total population size, or when only postreproductive individuals are eaten).

Nonlinear functional responses can also generate self-regulatory terms; moreover, though functional responses in nature may be more complicated than we tend to think³³, one may be quite sure that they will by and large be nonlinear. To explore their effect, we studied two different dynamical food web models (SI, Section 8). In the first model, based on equilibrium biomass distributions obtained from Damuth’s Law³⁴, nonlinear functional responses were unable to stabilize dynamics, and they did not even reduce the required fraction of *directly* self-regulating species if stability was to be achieved. The allometric model of Schneider et al.³⁵, on the other hand, was occasionally able to produce stable, species-rich networks without any other self-regulation mechanism. Overall, while stabilization via nonlinear functional responses is definitely a possibility, our preliminary exploration suggests that it is not the most typical outcome.

Time scale separation between consumers and resources also results in self-regulation³, though its importance in stabilizing community dynamics is understudied. However, it may in fact be more important than we think. Marine plankton use resources such as light (with instantaneous

dynamics in comparison to the planktonic life cycle), introducing self-regulatory terms in the plankton. Planktonic dynamics is notoriously complex³⁶, but probably none of that complexity matters from the point of view of a whale population consuming the plankton, since whales averages over those complexities in time and space due to their incomparably slower life cycle. Thus, planktonic dynamics may be effectively instantaneous from the whales' point of view, introducing effective self-regulation in whale dynamics. In the absence of further information, however, one cannot say how much this mechanism tends to contribute to network stability.

Finally, the fact that communities are distributed in space and are limited in their dispersal ability can impose self-regulation on all species simultaneously, and may have a large role in stabilizing real-world communities. This view is supported by recent theoretical findings³⁷ based on a random matrix perspective on multipatch dispersal. Spatial structure can stabilize dynamics via 1) the "eigenvalue pushback effect" (the bulk of the eigenvalue distribution moves in the negative direction, very much in analogy with what we see on Supplementary Figures 18 and 32); 2) the "Jacobian averaging effect" (heterogeneous interaction strengths in various patches averaged over the whole metacommunity act to reduce overall variance and thus \sqrt{SV} , leading to more stabilized communities), and 3) the "negative feedback effect" (migration can introduce effective self-regulation). We think it is very possible that the large and widespread negative diagonal entries in community matrices, necessary for their stability, are provided by communities' spatial structure. Putting it differently: were it possible to homogenize a community and thus eliminate its spatial aspect, one would predict a severe loss of species diversity due to the disappearance of self-regulation terms alone. Such a prediction is in line with classic experiments³⁸ demonstrating the stabilizing powers of spatial heterogeneity.

Apart from all the above mechanisms, there is of course an alternative interpretation of our results: that self-regulation is not actually common and therefore real-world ecosystems are inherently locally unstable. The question then becomes whether natural systems tend to reside at fixed point equilibria, or perhaps Mother Nature is indeed a strange attractor³⁹. There is some evidence that fixed point behavior is twice as common as having limit cycles⁴⁰, with examples of truly chaotic dynamics being extremely rare³⁶. However, future research in time series modeling may easily change these figures—therefore, ruling out the option of local instability on the basis of this evidence may be premature. Abandoning the idea of local asymptotic stability would of course also mean losing the mathematical and conceptual advantages it offers, since fixed point analysis is incomparably simpler than the study of nonequilibrium attractors.

We have analyzed two different types of empirical food webs: those based on the Ecopath modeling framework^{17,18} which were already parameterized but relatively small in size, and large food webs containing hundreds of species but which were not yet parameterized. The data required to parameterize these webs using Ecopath is not available; we therefore resorted to parameterization based on allometric relationships (see Methods). An advantage of these parameterizations is that they ensure the feasibility^{41–43} of the system (all species having positive equilibrium abundances). Regardless of parameterization, the qualitative pattern emerging was the same (Figure 1): a large fraction of species must self-regulate for stability, and the greatest likelihood of stability occurs at intermediate self-regulation strengths. But quantitatively, there was a significant difference between the Ecopath webs and the well-resolved ones: while in the former case, "only" half the species must self-regulate for stability, in the latter, this was closer to 90%. It is not clear at this point whether the difference is due to the different structural properties of the Ecopath and the allometric models, or rather simply due to the considerably lower species richness of Ecopath webs, or to a combination of both. However, even the more conservative Ecopath prediction requires substantially strong and widespread self-regulation for stability.

These results are in line with our theoretical analysis. Since the analysis is quite general, we expect the same conclusions on self-regulation to hold in any network of sufficient size and complexity, not just ecological ones: local stability requires widespread negative self-effects. Despite its generality, the theoretical results are of little relevance to networks where self-regulation appears naturally for every interacting component, such as biochemical or neural networks¹. Where the source of such “natural” mechanisms is not immediately obvious (as in ecology), the results still compel us to believe either that the overwhelming majority of all populations on this planet experience substantial self-regulation, or else that ecosystems are in fact locally unstable. It may yet be premature to say which is the case—but either way, we are forced to reconsider how we think about the dynamics of large ecological communities.

Methods

For the Ecopath matrices, we used the seven largest ones parameterized by Jacquet et al.¹⁷ (Table 1).

For the well-resolved networks, we took the adjacency matrices of 12 published empirical food webs (Table 2). We first removed all cannibalistic self-loops, and in the few cases two species mutually preyed upon each other, we dropped one of the two feeding links at random. Parameterization then proceeded by assuming appropriate body mass scaling allometries and type I functional responses^{27,44} (see also SI, Section 7.1). Three independent parameterizations of each web were created, with the parameter controlling the scaling between body masses and equilibrium abundances, g , being set to either -0.55 , -0.75 , or -0.95 .

Diagonal entries of the parameterized matrices \mathbf{A} were set to d with probability P and to zero with probability $1 - P$. The value of P was varied from 0 to 1 in steps of $1/S$; i.e., the number (as opposed to fraction) of self-regulating species always increased by one at every step. The strength of self-regulation d was -2^q times the leading eigenvalue of the matrix without any self-effects, where $q = 0.5, 1.5, 2.5, \dots, 7.5$ (i.e., eight different strengths of self-regulation were implemented for each web, measured in units of the leading eigenvalue).

For every combination of P , d , g , and food web identity, the diagonal entries were sampled independently 1000 times. We recorded the number of cases out of these which ended up stable; this number divided by 1000 was interpreted as the probability of achieving stability with the given P , d , g , and food web (Figure 1).

Due to the low structural rank⁴⁵ (maximum possible rank a matrix can attain assuming its nonzero entries are arbitrary) of many of the highly resolved empirical food webs, all the above was repeated for four different parameterizations of the webs in Table 2: 1) the original parameterized food webs; 2) the original web plus indirect negative interactions; 3) the original web plus indirect positive interactions; and 4) the original web plus both indirect negative and positive interactions. The indirect interactions modify the offdiagonal entries of the community matrix, contributing to them via apparent competition and indirect mutualisms. Indirect positive interactions were assigned to species sharing a common consumer, while indirect negative interactions were assigned to those sharing a common resource. Their strengths were drawn uniformly between zero and the mean positive (negative) direct interaction strength, divided by a factor f . This factor in turn assumed the values 2, 5, and 10; all simulations were repeated for all three values of f . Results proved insensitive both to the value of f and to whether indirect effects were present at all (SI, Section 7.3).

To find the minimal P compatible with stability (Figure 1b, yellow line), we took our parameterized food webs, and starting with $P \approx 1$ tried to find an arrangement of the diagonal entries such that the network was stable. We did this by minimizing the leading eigenvalue via a stochastic

search algorithm (SI, Section 7.4) and stopping the moment a stable solution was found. At that point, P was reduced and the above repeated. We did this until at least one hundred independent runs of the hill climbing and five independent runs of the genetic search algorithm failed to find a stable configuration. The smallest P where a stable configuration was found was then taken to be the minimum fraction of self-regulating species necessary for stability. We have performed this on each Ecopath web in Table 1, and all parameterizations of the Flensburg Fjord⁴⁶, Little Rock Lake⁴⁷, Otago Harbour⁴⁸, and Serengeti⁴⁹ food webs in Table 2 (see Supplementary Figures 21, 23, 25, and 29 for the results).

The analytical calculation used to obtain Figure 2 is described in detail in the SI (Sections 3-6). The dynamical models studying self-regulation generated by nonlinear functional responses are described in the SI, Section 8.

Data and code availability

All code and data used in this study are available at <https://github.com/dysordys/diagonal>.

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Author contributions

GB wrote the manuscript and supplement, performed the analytical calculations, and made figures; MJM performed simulations and made figures; SA performed simulations. All authors contributed to devising the study and editing the manuscript.

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