Trophic coherence determines food-web stability

Samuel Johnson[a,1,2], Virginia Domínguez-García[b,1], Luca Donetti[c], and Miguel A. Muñoz[b]

[a]Warwick Mathematics Institute, and Centre for Complexity Science, University of Warwick, Coventry CV4 7AL, United Kingdom; [b]Departamento de Electromagnetismo y Física de la Materia, and Instituto Carlos I de Física Teórica y Computacional, Universidad de Granada, 18071 Granada, Spain; and [c]Departamento de Electrónica y Tecnología de Computadores and Centro de Investigación en Tecnologías de la Información y de las Comunicaciones, Universidad de Granada, 18071 Granada, Spain

Edited* by Robert M. May, University of Oxford, Oxford, United Kingdom, and approved November 3, 2014 (received for review May 16, 2014)

Why are large, complex ecosystems stable? Both theory and simulations of current models predict the onset of instability with growing size and complexity, so for decades it has been conjectured that ecosystems must have some unidentified structural property exempting them from this outcome. We show that trophic coherence—a hitherto ignored feature of food webs that current structural models fail to reproduce—is a better statistical predictor of linear stability than size or complexity. Furthermore, we prove that a maximally coherent network with constant interaction strengths will always be linearly stable. We also propose a simple model that, by correctly capturing the trophic coherence of food webs, accurately reproduces their stability and other basic structural features. Most remarkably, our model shows that stability can increase with size and complexity. This suggests a key to May's paradox, and a range of opportunities and concerns for biodiversity conservation.

food webs | May's paradox | diversity–stability debate | dynamical stability | complex networks

In the early seventies, Robert May addressed the question of whether a generic system of coupled dynamical elements randomly connected to each other would be stable. He found that the larger and more interconnected the system, the more difficult it would be to stabilize (1, 2). His deduction followed from the behavior of the leading eigenvalue of the interaction matrix, which, in a randomly wired system, grows with the square root of the mean number of links per element. This result clashed with the received wisdom in ecology—that large, complex ecosystems were particularly stable—and initiated the "diversity–stability debate" (3–6). Indeed, Charles Elton had expressed the prevailing view in 1958: "the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, especially of animals, and more vulnerable to invasions" (7). Even if this description were not accurate, the mere existence of rainforests and coral reefs seems incongruous with a general mathematical principle that "complexity begets instability," and has become known as May's paradox.

One solution might be that the linear stability analysis used by May and many subsequent studies does not capture essential characteristics of ecosystem dynamics, and much work has gone into exploring how more accurate dynamical descriptions might enhance stability (5, 8, 9). However, as ever-better ecological data are gathered, it is becoming apparent that the leading eigenvalues of matrices related to food webs (networks in which the species are nodes and the links represent predation) do not exhibit the expected dependence on size or link density (10). Food webs must, therefore, have some unknown structural feature that accounts for this deviation from randomness—irrespectively of other stabilizing factors.

We show here that a network feature we call trophic coherence accounts for much of the variance in linear stability observed in a dataset of 46 food webs, and we prove that a perfectly coherent network with constant link strengths will always be stable. Furthermore, a simple model that we propose to capture this property suggests that networks can become more stable with size and complexity if they are sufficiently coherent.

Results

Trophic Coherence and Stability. Each species in an ecosystem is generally influenced by others, via processes such as predation, parasitism, mutualism, or competition for various resources (11–14). A food web is a network of species that represents the first kind of influence with directed links (arrows) from each prey node to its predators (15–18). Such representations can therefore be seen as transport networks, where biomass originates in the basal species (the sources) and flows through the ecosystem, some of it reaching the apex predators (the sinks).

The trophic level of a species can be defined as the average trophic level of its prey, plus 1 (19, 20). Thus, plants and other basal species are assigned level 1, pure herbivores have level 2, but many species will have fractional values. A species' trophic level provides a useful measure of how far it is from the sources of biomass in its ecosystem. We can characterize each link in a network with a trophic distance, defined as the difference between the trophic levels of the predator and prey species involved (it is not a true "distance" in the mathematical sense, because it can be negative). We then look at the distribution of trophic distances over all links in a given network. The mean of this distribution will always be equal to 1, and we refer to its degree of homogeneity as the network's trophic coherence. We shall measure this degree of order with the SD of the distribution of trophic distances, q (we avoid using the symbol σ because it is often assigned to the SD in link strengths). A perfectly coherent network, in which all distances are equal to 1 (implying that each species occupies an integer trophic level), has $q=0$, and less coherent networks have $q>0$. We therefore refer to this q as an incoherence parameter. (For a technical description of these measures, see *Methods*.)

Significance

The fact that large, complex ecosystems are particularly robust is mysterious in the light of mathematical arguments that suggest they should be unstable; i.e., susceptible to runaway fluctuations in species' abundances. Here we show that food webs (networks describing who eats whom in an ecosystem) exhibit a property we call trophic coherence, a measure of how neatly the species fall into distinct levels. We find that this property makes networks far more linearly stable than if the links (predator–prey interactions) were placed randomly between species, or according to existing structural models. A simple model we propose to capture this feature shows that networks can, in fact, become more stable with size and complexity, suggesting a possible solution to the paradox.

Author contributions: S.J., V.D.-G., and M.A.M. designed research; S.J., V.D.-G., L.D., and M.A.M. performed research; S.J., V.D.-G., and M.A.M. analyzed data; L.D. devised the proof for maximally coherent networks; and S.J., V.D.-G., and M.A.M. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

[1]S.J. and V.D.-G. contributed equally to this work.

[2]To whom correspondence should be addressed. Email: S.Johnson.2@warwick.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1409077111/-/DCSupplemental.

A fundamental property of ecosystems is their ability to endure over time (13, 18). "Stability" is often used as a generic term for any measure of this characteristic, including for concepts such as robustness and resilience (21). When the analysis regards the possibility that a small perturbation in population densities could amplify into runaway fluctuations, stability is usually understood in the sense of Lyapunov stability, which in practice tends to mean linear stability (22). This is the sense we shall be interested in here, and henceforth stability will mean linear stability. Given the equations for the dynamics of the system, a fixed (or equilibrium) point will be linearly stable if all of the eigenvalues of the Jacobian matrix evaluated at this point have negative real part. Even without precise knowledge of the dynamics, one can still apply this reasoning to learn about the stability of a system just from the network structure of interactions between elements (in this case, species whose trophic interactions are described by a food web) (2, 23–25). In *Methods* (and, more extensively, in *SI Appendix*), we describe how an interaction matrix W can be derived from the adjacency (or predation) matrix A representing a food web, such that the real part of W's leading eigenvalue, $R = Re(\lambda_1)$, is a measure of the degree of self-regulation each species would require in order for the system to be linearly stable. In other words, the larger R, the more unstable the food web. For the simple yet ecologically unrealistic case in which the extent to which a predator consumes a prey species is proportional to the sum of their (biomass) densities, the Jacobian coincides with W, and R describes the stability for any configuration of densities (global stability). For more realistic dynamics—such as Lotka–Volterra, type II or type III—the Jacobian must be evaluated at a given point, but we show that the general form can still be related to W (*Methods*). Furthermore, by making assumptions about the biomass distribution, it is possible to check our results for such dynamics (*SI Appendix*). In the main text, however, we shall focus simply on the matrix W without making any further assumptions about dynamics or biomass distributions.

May considered a generic Jacobian in which link strengths were drawn from a random distribution, representing all kinds of ecological interactions (1, 2). Because, in this setting, the expected value of the real part of the leading eigenvalue (R) should grow with $\sqrt{SC}$, where S is the number of species and C the probability that a pair of them be connected, larger and more interconnected ecosystems should be less stable than small, sparse ones (26). (Allesina and Tang have recently obtained stability criteria for random networks with specific kinds of interactions: although predator–prey relationships are more conducive to stability than competition or mutualism, even a network consisting only of predator–prey interactions should become more unstable with increasing size and link density; ref. 27.)

We analyze the stability for each of a set of 46 empirical food webs from several kinds of ecosystem (the details and references for these can be found in *SI Appendix*). In Fig. 1*A* we plot the R of each web against $\sqrt{S}$, observing no significant correlation. Fig. 1*B* shows R against $\sqrt{K}$, where $K = SC$ is a network's mean degree (often referred to as "complexity"). In contrast to a recent study by Jacquet et al. (10), who in their set of food webs found no significant complexity–stability relationship, we observe a positive correlation between R and $\sqrt{K}$. However, less than half the variance in stability can be accounted for in this way. In *SI Appendix* we also compare the empirical R values to the estimate derived by Allesina and Tang for random networks in which all links are predator–prey. Surprisingly, the correlation is lower than for $\sqrt{K}$ ($r^2 = 0.230$). The conclusion of Jacquet et al.—namely, that food webs must have some nontrivial structural feature that explains their departure from predictions for random graphs—therefore seems robust.

Might this feature be trophic coherence? In Fig. 1*C* we plot R for the same food webs against the incoherence parameter q. The correlation is significantly stronger than with complexity – stability increases with coherence. However, there are still outliers, such as the food web of Coachella Valley. We note that although most forms of intraspecies competition are not

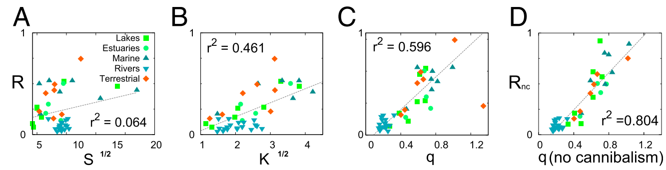

Fig. 1. Scatter plots of stability (as measured by R, the real part of the leading eigenvalue of the interaction matrix) against several network properties in a dataset of 46 food webs; Pearson's correlation coefficient is shown in each case. (*A*) Stability against $\sqrt{S}$, where S is the number of species ($r^2 = 0.064$). (*B*) Stability against $\sqrt{K}$, where K is the mean degree ($r^2 = 0.461$). (*C*) Stability against incoherence parameter q ($r^2 = 0.596$). (*D*) Stability after all self-links (representing cannibalism) have been removed (R_{nc}) against incoherence parameter q ($r^2 = 0.804$).

described by the interaction matrix, there is one form which is: cannibalism. This fairly common practice is a well-known kind of self-regulation that contributes to the stability of a food web (mathematically, negative elements in the diagonal of the interaction matrix shift its eigenvalues leftwards along the real axis). In Fig. 1*D* we therefore plot the R and q we obtain after removing all self-links. Now Pearson's correlation coefficient is $r^2 = 0.804$. In other words, cannibalism and trophic coherence together account for over 80% of the variation in stability observed in this dataset. In contrast, when we compare stability without self-links to the other measures, we find that for $\sqrt{S}$ the correlation becomes negative (although insignificant), for $\sqrt{K}$ it rises very slightly to $r^2 = 0.508$, and for Allesina and Tang's estimate it drops below significance (*SI Appendix*). In *SI Appendix*, we measure stability according to Lotka–Volterra, type II and type III dynamics, and show that in every case trophic coherence is the best predictor of stability.

Modeling Food-Web Structure. Many mathematical models have been put forward to simulate various aspects of food webs (18, 26, 28, 29–34). We shall focus here on so-called structural, or static, models: those which attempt to reproduce properties of food-web structure with a few simple rules. The best known is Williams and Martinez's niche model (35, 36). This is an elegant way of generating nontrivial networks by randomly assigning each species to a position on a "niche axis," together with a range of axis centered at some lower niche value. Each species then consumes all other species lying within its range of axis, and none without. The idea is that the axis represents some intrinsic hierarchy among species that determines who can prey on whom. The niche model is itself based on Cohen and Newman's cascade model, which also has an axis, but species are randomly assigned prey from among all those with lower niche values than themselves (37). Stouffer et al. proposed the generalized niche model, in which some of a species' prey are set according to the niche model and the rest ensue from a slightly refined version of the cascade model, the proportion of each being determined by a contiguity parameter (38). [The generalized cascade model is like the original cascade model except that the numbers of prey species are drawn from the beta distribution used in the niche model and subsequent niche-based models (39). This is the version of the model used throughout this paper, as explained in *SI Appendix*.] The minimum potential niche model of Allesina et al. is similar, but includes (random) forbidden links within species' ranges, instead of extra ones, as a way of emulating the effects of more than one axis—with the advantage that all of the links of real food webs have a nonzero probability of being generated by this model (40). Meanwhile, the nested hierarchy model of Cattin et al. takes into account that phylogenetically close species are more likely to share prey than unrelated ones (41). (For details of the models, see *SI Appendix*.)

These models produce networks with many of the statistical properties of food webs (36, 39, 40). However, as we go on to show below, they tend to predict significantly less trophic

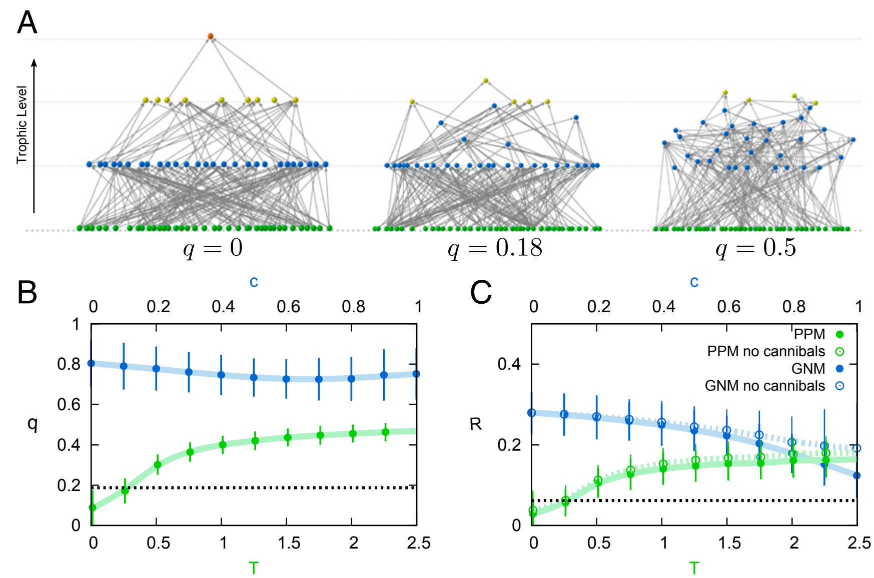

Fig. 2. (*A*) Three networks with differing trophic coherence, the height of each node representing its trophic level. The networks on the left and right were generated with the PPM, with $T = 0.01$ and $T = 10$ yielding a maximally coherent structure ($q = 0$) and a highly incoherent one ($q = 0.5$), respectively. The network in the middle is the food web of a stream in Troy, Maine, which has $q = 0.18$ (43). All three have the same numbers of species, basal species, and links. (*B*) Incoherence parameter, q, against T for PPM networks with the parameters of the Troy food web (green); and against c for generalized niche model networks with the same parameters (blue). The dashed line indicates the empirical value of q. (*C*) Stability (as given by R, the real part of the leading eigenvalue of the interaction matrix) for the networks of *B*. Also shown is the stability of networks generated with the same models and parameters, but after removing self-links (empty circles). In *B* and *C*, the dashed line represents the empirical value of R, and bars on the symbols are for 1 SD.

coherence (larger q) than we observe in our dataset. We therefore propose the preferential preying model (PPM) as a way of capturing this feature. We begin with B nodes (basal species) and no links. We then add new nodes (consumer species) sequentially to the system until we have a total of S species, assigning each their prey from among available nodes in the following way. The first prey species is chosen randomly, and the rest are chosen with a probability that decays exponentially with their absolute trophic distance to that initial prey species (i.e., with the absolute difference of trophic levels). This probability is set by a parameter T that determines the degree of trophic specialization of consumers. The number of prey is drawn from a beta distribution with a mean value proportional to the number of available species, just as the other structural models described use a mean value proportional to the niche value. (For a more detailed description, see *Methods*.)

The PPM is reminiscent of Barabási and Albert's model of evolving networks (42), but it is also akin to a highly simplified version of an "assembly model" in which species enter via immigration (29, 32). It assumes that if a given species has adapted to prey off species A, it is more likely to be able to consume species B as well if A and B have similar trophic levels than if not. It may seem that this scheme is similar in essence to the niche model, with the role of niche axis being played by the trophic levels. However, whereas the niche values given to species in niche-based models are hidden variables, meant to represent some kind of biological magnitude, the trophic level of a node is defined by the emerging network architecture itself. We shall see that this difference has a crucial effect on the networks generated by each model.

The Origins of Stability. Fig. 2*A* shows three networks with varying degrees of trophic coherence. The one on the left was generated with the PPM and $T = 0.01$, and because it falls into perfectly ordered, integer trophic levels, it is maximally coherent, with $q = 0$. For the one on the right we have used $T = 10$, yielding a highly incoherent structure, with $q = 0.5$. Between these two extremes we show the empirical food web of a stream in Troy, Maine (43), which has the same number of basal species, consumers, and links as the two artificial networks, and an intermediate trophic coherence of $q = 0.18$. Fig. 2*B* shows how trophic coherence varies with T in PPM networks. At about $T = 0.25$ we obtain the empirical trophic coherence of the Troy food web (indicated with a dashed line). We also plot q for networks generated with the generalized niche model against "diet contiguity," c, its only free parameter (38). At $c = 0$ and $c = 1$ we recover the cascade and niche models, respectively (*SI Appendix*). However, diet contiguity has little effect on trophic coherence.

Fig. 2*C* shows the stability—as measured by R, the leading eigenvalue of the interaction matrix—for the networks of Fig. 2*B*. For the PPM networks, stability closely mirrors trophic coherence: as T decreases, the networks become more stable (smaller R) as well as more coherent (smaller q). The empirical value of R is obtained at about the same T that best approximates the empirical q. The generalized niche model also generates more stable networks as diet contiguity is increased, but this effect cannot be due to trophic coherence, which remains nearly constant. The origin of increasing stability in this model is revealed when we measure R_{nc} (R after removing all self-links from the networks): the generalized niche model now displays only a very small dependence of stability on diet contiguity. In contrast, the behavior of R_{nc} with T in the PPM networks remains qualitatively the same as in the previous case, and the empirical stability continues to be obtained at $T \simeq 0.25$ (in this case, the empirical stabilities R and R_{nc} coincide, because the Troy food web has no cannibals).

We perform this analysis for each of the 46 food webs in our dataset, obtaining the value of T that best captures the empirical trophic coherence according to the PPM. We then compute the ensemble averages of R and R_{nc} generated at this T, for comparison with the empirical values. Similarly, we compute the average values of these measures predicted by each of the niche-based models described above: the cascade, niche, nested hierarchy, generalized niche, and minimum potential niche models. The last two models have free parameters, but as these do not have a significant effect on trophic coherence, we use the values published as optimal in refs. 39 and 40, respectively (or the mean optimal values for those food webs that were not analyzed in these papers). Fig. 3 *A–C* shows the average absolute deviations from the empirical values for trophic coherence and stability, before and after removing self-links, for each model. In Fig. 3*A* we observe that, as mentioned above, the niche-based models fail to capture the trophic coherence of these food webs. Stability, with or without considering self-links, is predicted by the PPM significantly better than by any of the other models, as shown in Fig. 3 *B* and *C*. This is in keeping with Allesina and Tang's observation that current structural models cannot account for food-web stability (27). In *SI Appendix* we show the results of similar model comparisons for several other network measures: modularity, mean chain length, mean trophic level, and numbers of cannibals and of apex predators. The PPM does as well as any of the other models in regards to the numbers of cannibals and apex predators, and is significantly better at predicting the other measures. Allesina et al. have developed a likelihood-based approach for comparing food-web models (40). We have not yet been able to obtain the corresponding likelihoods for the PPM, but if this is done in the future it would provide a firmer basis from which to gauge the models' relative merits, and perhaps to build a more realistic model drawing on each one's strengths.

Why does the trophic coherence of networks determine their stability? The case of a maximally coherent structure, with $q = 0$ (such as the one on the left in Fig. 2*A*), is amenable to mathematical analysis. In *SI Appendix* we consider the undirected network that results from replacing each directed link of the predation matrix with a symmetric link, the nonzero eigenvalues of which always come in pairs of real numbers $\pm\mu_j$. We use this to prove that the eigenvalues of the interaction matrix we are actually interested in, if $q = 0$, will in turn come in pairs $\lambda_j = \pm\sqrt{-\eta}\mu_j$, where η is a parameter related to the efficiency of predation (considered, for the proof, constant for all pairs of species). All of the eigenvalues will therefore be real if $\eta < 0$, zero if $\eta = 0$, and imaginary if $\eta > 0$. A positive η is the situation that corresponds to a food web—or any system in which the gain in a "predator" is accompanied by some degree of loss in its "prey." Therefore, a perfectly coherent network is a limiting case that can be stabilized by an infinitesimal degree of self-regulation (such as cannibalism or other intraspecies competition). Any realistic situation would involve some degree of self-regulation, so we can conclude that a maximally coherent food web with constant link strengths would be stable.

Although a general, analytical relationship between trophic coherence and stability remains elusive, it is intuitive to expect that a deviation from maximal coherence will drive the real part of the leading eigenvalue toward the positive values established for random structures, as is indeed observed in our simulations.

May's Paradox. As we have seen, the PPM can predict the stability of a food web quite accurately just with information regarding numbers of species, basal species and links, and trophic coherence. But what does this tell us about May's paradox—the fact that large, complex ecosystems seem to be particularly stable despite theoretical predictions to the contrary? To ascertain how stability scales with size, *S*, and complexity, *K*, in networks generated by different models, we must first determine how *K* scales with *S*; i.e., if $K \sim S^{\alpha}$, what value should we use for α? Data in the real world are noisy in this regard, and both the link-species law ($\alpha = 0$) and the constant connectance hypothesis ($\alpha = 1$) have been defended in the past, although the most common view seems to be that α lies somewhere between 0 and 1/2 (12, 26, 44). The most recent empirical estimate we are aware of is close to $\alpha \simeq 0.5$, depending slightly on whether predation weights are considered (45). In our dataset, the best fit is achieved with a slightly lower exponent, $\alpha = 0.41$.

In Fig. 3*D* we show how stability scales with *S* in each of the niche-based models when complexity increases with size according to $\alpha = 0.5$. The dashed line shows the slope that May predicted for random networks ($R \sim \sqrt{K} = S^{0.25}$) (1). We also plot the curve recently shown by Allesina and Tang to correspond to random networks in which all interactions are predator–prey (27), which has a similar slope to May's at large *S*. This scaling is indeed closely matched by the cascade model. The behavior of the other models is similar (except for the nested hierarchy model, in which *R* increases more rapidly at high *S*), and, as expected, networks always become less stable with increasing size and complexity. In Fig. 3*E* we show how the stability of PPM networks scales in the same scenario. For high *T*, their behavior is similar to that of the cascade model: $R \sim S^{\gamma}$, with $\gamma \simeq 0.25$. However, the exponent γ decreases as *T* is lowered, until, for sufficiently large and coherent networks, it becomes negative; in other words, stability increases with size and complexity. Fig. 3*E*, *Inset*, shows the exponent γ obtained against *T*, for different values of α. The smaller α, the larger the range of *T* that yields a positive complexity–stability relationship. [Plitzko et al. recently showed that there exists a range of parameters (in a generalized modeling framework; ref. 46) for which niche model networks can increase in stability with complexity (47). However, for this study networks were rejected unless they were stable and had exactly four

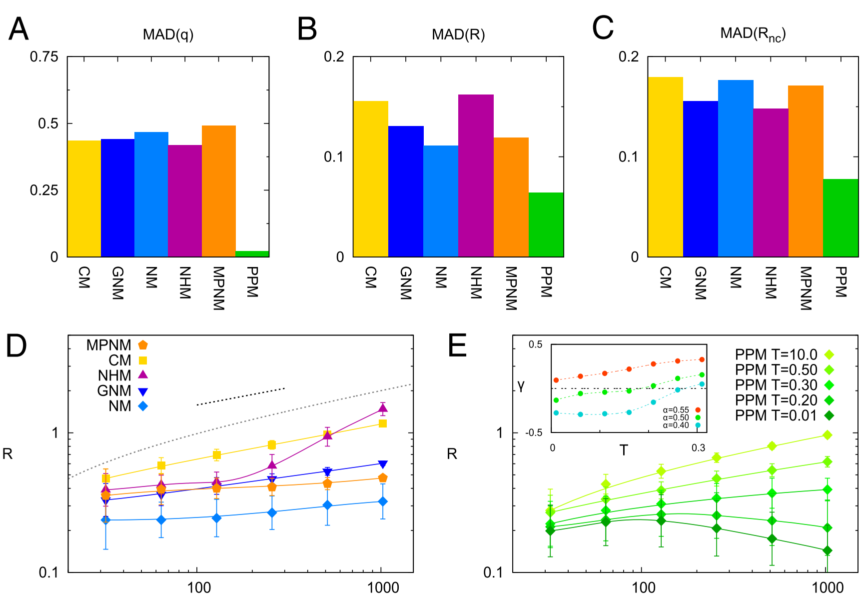

Fig. 3. (*A*) Mean absolute deviations (MAD) from empirical values of the incoherence parameter, *q*, for each food-web model—cascade (CM), generalized niche (GNM), niche (NM), nested hierarchy (NHM), minimum potential niche (MPNM), and PPM—compared with a dataset of 46 food webs. (*B*) MAD from empirical values of stability, *R*, for the same models and food webs as in *A*. (*C*) MAD from empirical values of stability, *R*, after removing self-links, for the same models and food webs as in *A* and *B*. (*D*) Scaling of stability, *R*, with size, *S*, in networks generated with each of the models of previous panels except for the PPM. Mean degree is $K = \sqrt{S}$. The dashed line indicates the slope predicted for random matrices by May (1), and the dotted curve is from Allesina and Tang (27). (*E*) Scaling of stability, *R*, with size, *S*, in PPM networks generated with different values of *T*. In descending order, $T = 10$, 0.5, 0.3, 0.2 and 0.01. $B = 0.25S$. (*Inset*) Slope, γ, of the stability-size line against *T* for $\alpha = 0.55$, 0.5, and 0.4, where the mean degree is $K = S^{\alpha}$. In *D* and *E*, bars on the symbols are for 1 SD.

trophic levels. This selection may have screened for trophic coherence, cannibalism, or other structural features.]

In *SI Appendix* we extend this analysis to specific dynamics—Lotka–Volterra, type II and type III—by assuming an exponential relationship between biomass and trophic level, which can be described as a pyramid. The positive complexity–stability relationship does not appear to depend on the details of dynamics. However, the slope of the $R-S$ curve varies with both the squatness of the biomass pyramid and the extent to which the pyramid is corrupted by noise. A squat pyramid (more biomass at low trophic levels than at high ones) has the strongest relationship, but for an inverted pyramid (more biomass at high trophic levels than at low ones) the slope can flatten out or change sign. Noise in the biomass pyramid tends always to weaken the positive complexity–stability relationship, and can also change its sign.

Discussion

The predation matrices corresponding to real ecosystems are clearly peculiar in some way, because their largest eigenvalues do not depend solely on their size or complexity, as we would expect both from random graph theory and structural food-web models. This is in keeping with the empirical observation that large, complex ecosystems are particularly stable, but challenges current thinking on food-web architecture. We have shown that the structural property we call trophic coherence is significantly correlated with food-web stability, despite other differences between the ecosystems and the variety of empirical methods used in gathering the data. In fact, cannibalism and trophic coherence together account for most of the variance in stability observed in our dataset. Furthermore, we have proved that a maximally coherent food web with constant interaction strengths will always be stable.

We have suggested the preferential preying model as a simple algorithm for generating networks with tunable trophic coherence. Although this model does not attempt to replicate other characteristic features of food webs, such as a phylogenetic signal or body-size effects, it reproduces the empirical stability of the 46 webs analyzed quite accurately once its only free parameter has been adjusted to the empirical degree of trophic coherence. Most remarkably, the model predicts that networks should become more stable with increasing size and complexity, as long as they are sufficiently coherent and the number of links does not grow too fast with size. Although this result should be followed up with further analytical and empirical research, it suggests that we need no longer be surprised at the high stability of large, complex ecosystems.

We must caution that these findings do not imply that trophic coherence was somehow selected for by the forces of nature to improve food-web function. It seems unlikely that there should be any selective pressure on the individuals making up a species to do what is best for their ecosystem. Rather, many biological features of a species are associated with its trophic level. Therefore, adaptations which allow a given predator to prey on species A are likely to be useful also in preying on species B if A and B have similar trophic levels. This leads to trophic coherence, which results in high stability.

If stability decreased with size and complexity, as previous theoretical studies have assumed, ecosystems could not grow indefinitely, for they would face a cutoff point beyond which they would become unstable (26). On the other hand, if real ecosystems are coherent enough that they become more stable with size and complexity, as our model predicts, then the reverse might be true. We must also bear in mind, however, that our results are only for linear stability, whereas structural stability, for instance, may depend differently on size and coherence, and could become the limiting factor (18). In any case, ascertaining whether the loss of a few species would stabilize or destabilize a given community could be important for conservation efforts, particularly for averting tipping points (14).

The findings we report here came about by studying food webs. However, directed networks of many kinds transport energy, matter, information, capital, or other entities in a similar way to how food webs carry biomass from producers to apex predators. It seems likely that the relation between a network's trophic coherence and its leading eigenvalue will be of consequence to other disciplines, and perhaps the preferential preying model, although overly simplistic for many scenarios, may serve as a first approximation for looking into these effects in a variety of systems.

Methods

Measuring Stability. Let us assume that the populations of species making up an ecosystem (each characterized by its total biomass) change through time according to some set of nonlinear differential equations, the interactions determined by the predation matrix, A (whose elements a_{ij} take the value 1 if species i preys on species j, and 0 otherwise). If the system persists without suffering large changes it must, one assumes, find itself in the neighborhood of a fixed point of the dynamics. We can study how the system would react to a small perturbation by expanding the equations of motion around this fixed point and keeping only linear terms. The subsequent effect of the perturbation is then determined by the corresponding Jacobian matrix, and the system will tend to return to the fixed point only if the real parts of all its eigenvalues are negative (22).

Even without knowledge of the details of the dynamics, it is possible to draw some conclusions about the stability of a food web solely from its predation matrix (23). Independently of the exact interaction strengths, we know that not all of the biomass lost by a prey species when consumed goes to form part of the predator; in fact, this efficiency is relatively low (48). It is therefore natural to assume that the effect of species j on species i will be mediated by $w_{ij}=\eta a_{ij}-a_{ji}$, where η is an efficiency parameter that, without further information, we can consider equal for all pairs of species. We can thus treat the interaction matrix $W=\eta A-A^T$ as the Jacobian of some unspecified dynamics. However, we have ignored the stabilizing effect of intraspecies competition—the fact that individuals within a species compete with each other in ways which are not specified by the predation matrix. This would correspond to real values to be subtracted from the diagonal elements of W, thereby shifting its set of eigenvalues (or spectrum) leftward along the real axis. Therefore, the eigenvalue with largest real part of W, as defined above, can be seen as a measure of the minimum intraspecies competition required for the system to be stable. Thus, the lower this value, $R=Re(\lambda_1)$, the higher the stability.

In *SI Appendix*, we describe this analysis in more detail. Beginning with a general consumer–resource differential equation for the biomass of each species, we obtain the Jacobian in terms of the function $F(x_i, x_j)$, which describes the extent to which species i consumes species j. For the simple (and unrealistic) case $F=x_i+x_j$, the Jacobian reduces to the matrix W as given above, independently of the fixed point. For more realistic dynamics, the Jacobian depends on the fixed point. For instance, for the Lotka–Volterra function $F=x_ix_j$, the off-diagonal elements of the Jacobian are $J_{ij}=w_{ij}x_i$. If we set $F=x_iH(x_j)$ (with $H(x)=x^h/(x^h+x_0^h)$, x_0 the half-saturation density and h the Hill coefficient), we have either type II ($h=1$) or type III ($h=2$) dynamics (49). Then the off-diagonal elements are $J_{ij}=[\tilde{\eta}(x_i,x_j)a_{ij}-a_{ji}]H(x_i)$, where the effective efficiency is $\tilde{\eta}(x_i,x_j)=\eta h x_0^h x_i x_j^{-(h+1)}H(x_j)^2/H(x_i)$.

The Jacobians for Lotka–Volterra, type II and type III dynamics are all similar in form to the matrix W, although for an exact solution we require the fixed point. In the main text we therefore use the leading eigenvalue of W as a generic measure of stability. However, in *SI Appendix* we consider the effects that different kinds of biomass distribution have on each of these more realistic dynamics. The results are qualitatively the same as those for the matrix W, although we find that both the squatness of a biomass pyramid and the level of noise in this structure affect the strength of the diversity–stability relationship described in the main text.

This measure of stability depends on the parameter η. In *SI Appendix* we show that the results reported here remain qualitatively unchanged for any $\eta\in(0,1)$, and discuss how stability is affected when we consider $\eta>1$ or $\eta<0$. We also look into the effects of including a noise term so that η does not have the same value for each pair of species, and find that our results are robust to this change too. For the results in the main text, however, we use the fixed value $\eta=0.2$.

Trophic Levels and Coherence. The trophic level s_i of species i is defined as the average trophic level of its prey, plus 1 (19). That is,

$$s_i=1+\frac{1}{k_i^{in}}\sum_j a_{ij}s_j, \qquad [1]$$

where $k_i^{in}=\sum_j a_{ij}$ is the number of prey of species i (or i's in degree), and a_{ij} are elements of the predation matrix A. Basal species (those with $k^{in}=0$) are assigned $s=1$. The trophic level of each species is therefore a purely structural (i.e., topological) property that can be determined by solving a system of linear equations. Because we only consider unweighted networks here (the elements of A are ones and zeros), we omit the link strength term usually included in Eq. **1** (19).

We can write Eq. **1** in terms of a modified graph Laplacian matrix, $\Lambda\mathbf{s}=\mathbf{v}$, where $\mathbf{s}$ is the vector of trophic levels, $\mathbf{v}$ is the vector with elements $v_i=\max(k_i^{in},1)$, and $\Lambda=\mathrm{diag}(\mathbf{v})-A$. Thus, every species can be assigned a trophic level if and only if Λ is invertible. This requires at least one basal species (else zero would be an eigenvalue of Λ). However, note that cycles are not, in general, a problem, despite the apparent recursivity of Eq. **1**.

We define the trophic distance spanned by each link $(a_{ij}=1)$ as $x_{ij}=s_i-s_j$ (which is not a distance in the mathematical sense because it can take negative values). The distribution of trophic distances over the network is $p(x)$, which will have mean $\langle x\rangle=1$ (because for any node i the average over its incoming links is $\sum_j a_{ij}(s_i-s_j)/k_i^{in}=1$ by definition). We define the trophic coherence of the network as the homogeneity of $p(x)$: the more similar the trophic distances of all of the links, the more coherent. As a measure of coherence, we therefore use the SD of the distribution, which we refer to as an incoherence parameter: $q=\sqrt{\langle x^2\rangle-1}$, where $\langle\cdot\rangle=L^{-1}\sum_{ij}(\cdot)a_{ij}$, and L is the total number of links, $L=\sum_{ij}a_{ij}$.

Trophic coherence bears a close resemblance to Levine's measures of trophic specialization (19). However, our average is computed over links instead of species, with the consequence that we need not consider the distinction between resource and consumer specializations. It is also related to measures of omnivory: in general, the more omnivores one finds in a community, the less coherent the food web.

The Preferential Preying Model. We begin with B nodes (basal species) and no links. We then add, sequentially, $S-B$ new nodes (consumer species) to the system according to the following rule. A new node i is first awarded a random node j from among all those available when it arrives. Then another κ_i nodes l are chosen with a probability P_{il} that decays with the trophic distance between j and l. Specifically, we use the exponential form

$$P_{il}\propto\exp\left(-\frac{|s_j-s_l|}{T}\right),$$

where j is the first node chosen by i, and T is a parameter that sets the degree of trophic specialization of consumers.

The number of extra prey, κ_i, is obtained in a similar manner to the niche model prescription, because this has been shown to provide the best approximation to the in-degree distributions of food webs (39). We set $\kappa_i=x_i n_i$, where n_i is the number of nodes already in the network when i arrives, and x_i is a random variable drawn from a beta distribution with parameters

$$\beta=\frac{S^2-B^2}{2L}-1,$$

where L is the expected number of links. In this work, we only consider networks with a number of links within an error margin of 5% of the desired L; thus, for all of the results reported, we have imposed this filter on the PPM networks and those generated with the other models.

To allow for cannibalism, the new node i is initially considered to have a trophic level $s_i=s_j+1$ according to which it might then choose itself as prey. Once i has been assigned all its prey, s_i is updated to its correct value.

ACKNOWLEDGMENTS. We are grateful to J. Dunne and U. Jacob for providing food-web data and to J. Hidalgo for technical help. Many thanks also to N. S. Jones, D. C. Reuman, D. B. Stouffer, J. Bascompte, I. Mendoza, J. A. Bonachela, S. A. Levin, O. Al Hammal, A. Thierry, A. Maritan, N. Guisoni, G. Baglietto, E. Albano, B. Moglia, J. J. Torres, and J. A. Johnson for conversations and comments on versions of the manuscript. We acknowledge financial support from the Spanish Ministerio de Ciencia e Innovación, and the European Regional Development Fund, under Project FIS2009-08451 and from Junta de Andalucía Proyecto de Excelencia P09FQM-4682. S.J. is grateful for support from the Oxford Centre for Integrative Systems Biology, University of Oxford, and from the European Commission under the Marie Curie Intra-European Fellowship Programme PIEF-GA-2010-276454.

1. May RM (1972) Will a large complex system be stable? *Nature* 238(5364):413–414.
2. May RM (1973) *Stability and Complexity in Model Ecosystems* (Princeton Univ Press, Princeton, NJ).
3. MacArthur R (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–535.
4. Paine R (1966) Food web complexity and species diversity. *Am Nat* 100:65–75.
5. McCann KS (2000) The diversity-stability debate. *Nature* 405(6783):228–233.
6. Dunne JA, Brose U, Williams RJ, Martinez ND (2005) Modeling food-web dynamics: complexity-stability implications. *Aquatic Food Webs: An Ecosystem Approach* (Oxford Univ Press, Oxford), pp 117–129.
7. Elton CS (1958) *Ecology of Invasions by Animals and Plants* (Chapman and Hall, London).
8. DeAngelis DL, Waterhouse JC (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecol Monogr* 57:1–21.
9. Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. *Ecol Lett* 9(11):1228–1236.
10. Jacquet C, et al. (2013) No complexity-stability relationship in natural communities. *arXiv:1307.5364*.
11. Elton CS (1927) *Animal Ecology* (Sidgwick and Jackson, London).
12. Pimm SL (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities* (The Univ of Chicago Press, Chicago).
13. Solé RV, Bascompte J (2006) *Self-Organization in Complex Ecosystems* (Princeton Univ Press, Princeton, NJ).
14. Sutherland WJ, et al. (2013) Identification of 100 fundamental ecological questions. *J Ecol* 101:58–67.
15. Pimm SL (1982) *Food Webs* (Chapman and Hall, London).
16. Dunne JA, Williams RJ, Martinez ND (2004) Network structure and robustness of marine food webs. *Mar Ecol Prog Ser* 273:291–302.
17. Drossel B, McKane AJ (2003) Modelling Food Webs. *A Handbook of Graphs and Networks: From the Genome to the Internet* (Wiley-VCH, Berlin).
18. Rossberg AG (2013) *Food Webs and Biodiversity: Foundations, Models, Data* (Wiley, New York).
19. Levine S (1980) Several measures of trophic structure applicable to complex food webs. *J Theor Biol* 83:195–207.
20. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F, Jr (1998) Fishing down marine food webs. *Science* 279(5352):860–863.
21. Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334.
22. Holmes P, Shea-Brown ET (2006) Stability. *Scholarpedia* 1:1838.
23. May RM (1973) Qualitative stability in model ecosystems. *Ecology* 54:638–641.
24. Logofet DO (2005) Stronger-than-Lyapunov notions of matrix stability, or how "flowers" help solve problems in mathematical ecology. *Linear Algebra Appl* 398:75–100.
25. Logofet DO (1993) *Matrices and Graphs: Stability Problems in Mathematical Ecology* (CRC Press, Boca Raton, FL).
26. Solé R, Alonso D, McKane A (2000) Scaling in a network model of a multispecies ecosystem. *Physica A* 286:337–344.
27. Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483(7388): 205–208.
28. Caldarelli G, Higgs PG, McKane AJ (1998) Modelling coevolution in multispecies communities. *J Theor Biol* 193(2):345–358.
29. Bastolla U, Lässig M, Manrubia SC, Valleriani A (2001) Diversity patterns from ecological models at dynamical equilibrium. *J Theor Biol* 212(1):11–34.
30. Loeuille N, Loreau M (2005) Evolutionary emergence of size-structured food webs. *Proc Natl Acad Sci USA* 102(16):5761–5766.
31. Rossberg AG, Matsuda H, Amemiya T, Itoh K (2006) Food webs: Experts consuming families of experts. *J Theor Biol* 241(3):552–563.
32. McKane AJ, Drossel B (2006) Models of food web evolution. *Ecological Networks: Linking Structure to Dynamics in Food Webs*, eds Pascual M, Dunne JA (Oxford Univ Press, Oxford).
33. Allesina S, Pascual M (2009) Food web models: A plea for groups. *Ecol Lett* 12(7): 652–662.
34. Rossberg AG, Brännström A, Dieckmann U (2010) Food-web structure in low- and high-dimensional trophic niche spaces. *J R Soc Interface* 7(53):1735–1743.
35. Williams RJ, Martinez ND (2000) Simple rules yield complex food webs. *Nature* 404(6774):180–183.
36. Williams RJ, Martinez ND (2008) Success and its limits among structural models of complex food webs. *J Anim Ecol* 77(3):512–519.
37. Cohen JE, Newman CM (1985) A stochastic theory of community food webs I. Models and aggregated data. *Proc R Soc Lond B Biol Sci* 224:421–448.
38. Stouffer DB, Camacho J, Amaral LAN (2006) A robust measure of food web intervality. *Proc Natl Acad Sci USA* 103(50):19015–19020.
39. Stouffer DB, Camacho J, Guimerà R, Ng CA, Amaral LAN (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology* 86:1301–1311.
40. Allesina S, Alonso D, Pascual M (2008) A general model for food web structure. *Science* 320(5876):658–661.
41. Cattin MF, Bersier LF, Banasek-Richter C, Baltensperger R, Gabriel JP (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature* 427(6977):835–839.
42. Barabási AL, Albert R (1999) Emergence of scaling in random networks. *Science* 286(5439):509–512.
43. Thompson R, Townsend C (2003) Impacts on stream food webs of native and exotic forest: an intercontinental comparison. *Ecology* 84:145–161.
44. Rossberg AG, Farnsworth KD, Satoh K, Pinnegar JK (2011) Universal power-law diet partitioning by marine fish and squid with surprising stability-diversity implications. *Proc Biol Sci* 278(1712):1617–1625.
45. Banasek-Richter C, et al. (2009) Complexity in quantitative food webs. *Ecology* 90(6): 1470–1477.
46. Gross T, Rudolf L, Levin SA, Dieckmann U (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325(5941):747–750.
47. Plitzko SJ, Drossel B, Guill C (2012) Complexity-stability relations in generalized food-web models with realistic parameters. *J Theor Biol* 306:7–14.
48. Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399–418.
49. Real L (1977) Kinetics of functional response. *Am Nat* 111:289–300.