



HAL
open science

Unveiling dimensions of stability in complex ecological networks

Virginia Domínguez-García, Vasilis Dakos, Sonia Kéfi

► **To cite this version:**

Virginia Domínguez-García, Vasilis Dakos, Sonia Kéfi. Unveiling dimensions of stability in complex ecological networks. Proceedings of the National Academy of Sciences of the United States of America, 2019, pp.201904470. 10.1073/pnas.1904470116 . hal-02405950

HAL Id: hal-02405950

<https://hal.umontpellier.fr/hal-02405950>

Submitted on 17 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Unveiling dimensions of stability in complex ecological networks

Virginia Dominguez-Garcia^{a,1}, Vasilis Dakos^a, and Sonia Kéfi^a

^aISEM, CNRS, Univ. Montpellier, IRD, EPHE, Montpellier, France.

This manuscript was compiled on November 28, 2019

Understanding the stability of ecological communities is a matter of increasing importance in the context of global environmental change. Yet, it has proved to be a challenging task. Different metrics are used to assess the stability of ecological systems, and the choice of one metric over another may result in conflicting conclusions. Although each of the multitude of metrics is useful for answering a specific question about stability, the relationship among metrics is poorly understood. Such lack of understanding prevents scientists from developing a unified concept of stability. Instead, by investigating these relationships we can unveil how many ‘dimensions’ of stability there are (i.e. in how many independent components stability metrics can be grouped), which should help building a more comprehensive concept of stability. Here, we simultaneously measured 27 stability metrics frequently used in ecological studies. Our approach is based on dynamical simulations of multispecies trophic communities under different perturbation scenarios. Mapping the relationships between the metrics revealed that they can be lumped into three main groups of relatively independent stability components: ‘early response to pulse’, ‘sensitivities to press’ and ‘distance to threshold’. Selecting metrics from each of these groups allows a more accurate and comprehensive quantification of the overall stability of ecological communities. These results contribute to improving our understanding and assessment of stability in ecological communities.

stability | food webs | networks | ecological community

Stability has been a core topic of research in complex systems across disciplines. From socioeconomic models of political regimes (1, 2), to financial systems (3–5), social organizations (6, 7) or biological systems of genetic regulatory circuits (8, 9), the study of dynamical stability keeps drawing the attention of the scientific community. This interest has been particularly prominent in ecology, where it has fuelled decades of research (10–15). Yet, progress in understanding what determines the stability of complex systems such as ecological communities has been hampered by unclear, and sometimes, conflicting results. One of the main reasons has proved to be the broad definition of the concept of stability itself (12), which has led to confusion and a lack of clear guidelines about the practical quantification of stability in empirical studies (14, 16). Probably one of the best examples of this confusion is the long standing controversy of how stability varies with species diversity (17). While some studies have shown that biodiversity can enhance stability (18–20), others have found the opposite result (21–23), both effects (24), or even non-monotonous relationships (25). The explanation behind this apparent contradiction is that stability is a multidimensional concept: it has several ‘facets’ and can be described by different metrics, which do not all vary positively with biodiversity (13, 24, 26). While the multidimensional nature of the stability concept has been well recognized in

the literature (10–12), our understanding of it has remained limited (14). The vast majority of studies typically include only one metric of stability at a time, and the few studies that have simultaneously measured multiple metrics of stability have considered them as independent when, in fact, it has been acknowledged that they could be interdependent (27). This possible interdependence implies that measuring multiple metrics may more broadly estimate stability to the extent that these metrics quantify relatively independent components of stability. Therefore, to advance towards a thorough and more systematic assessment of ecological stability, we need to understand how stability can be decomposed into different components – also referred to as ‘dimensions’ in the literature (27) – and if so, how many there are and how they can be best measured.

We tackle this challenge from a theoretical perspective by investigating the interdependence of stability metrics in trophic ecological networks. Combining structural food-web models (28) with bioenergetic consumer-resource models (29, 30), we simulate the dynamics of multispecies trophic communities under different perturbation scenarios. Perturbations are changes in the biotic or abiotic environment that alter the structure and dynamics of communities (14, 31). We consider three main types of perturbations: *pulse* (32), i.e. instantaneous disturbances, after which community recovery can be measured (e.g. forest fires or floods), *press* (32), i.e. lasting disturbances after which post-perturbed communities can be compared to pre-perturbed ones (e.g. climatic changes or extinction of a species), and *environmental stochasticity* (33–35), where communities are constantly affected by small external changes. We quantify the stability of our simulated communities to these perturbations with 27 metrics frequently used in the ecological literature (see Table 1). We then explore how these

Significance Statement

While the need to consider the multidimensionality of stability has been clearly stated in the ecological literature for decades, little is known about how different metrics of stability relate to each other in ecological communities. By simulating multispecies trophic networks, we measure how frequently-used stability metrics relate to each other, and we identify the independent components they form based on their correlations. Our results open a way to a simplification and better understanding of the overall stability of ecological systems.

S.K., V.D.-G. and V.D. designed the study. V.D.-G. performed the simulations and their analysis. S.K., V.D.-G. and V.D. discussed the results. All authors contributed to the writing of the manuscript.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: virginia.dominguez-garcia@umontpellier.fr

metrics correlate with each other. If metrics are found to be uncorrelated, that would mean that they all inform very different aspects of stability of an ecological community and that a more coherent concept of stability currently lacks empirical support. In the opposite case, if all metrics are found to be perfectly correlated with each other, considering only a single metric would be enough to assess the overall stability of an ecological community. Therefore, by studying the correlations between stability metrics, we can evaluate whether the different metrics considered provide similar information about the stability of an ecological community or whether they form distinct groups that reflect partly independent ‘dimensions’ of community stability.

Results and Discussion

73 Community size and stability metrics’ correlations. Community size (i.e. the number of species) has been shown to play a fundamental role in the stability of ecological networks, although it is not entirely clear if it promotes their stability, hinders it, (13) or both (24, 25). For example, a food web simulation study showed that persistence (i.e. the fraction of surviving species) and population variability were either negatively or positively correlated depending on the species richness of the community (25). We therefore start by investigating if the pairwise correlations between the stability metrics are affected by community size in our simulated trophic communities. Overall, many pairwise correlations (~44% out of the 351 correlation pairs) are not highly affected by community size (Fig 1A). Some pairwise correlations (~32%) become weaker as community size grows (Fig. 1B), while others (~20%) become stronger (Fig. 1C). In a few cases (~3%), the correlation between two metrics can switch sign as community size changes (Fig. 1D). The dependence of pairwise correlations on community size is especially present in communities with less than 50 species. In contrast, most correlations (~94%) remain largely constant in species-rich communities (> 50 species; SI Appendix Fig. S1). Given the dependence of pairwise correlations on community size, we next study stability metric correlations across three levels of species richness: small (5 to 15 species), medium-sized (45 to 55 species), and large communities (85 to 95 species). In what follows, we present the results for medium-sized communities, while the results for small and large communities can be found in the SI Appendix.

101 Three groups of stability metrics. To explore if there is any structure in the way metrics are correlated with each other, we build a network of stability metrics in which nodes represent the metrics and links their weighted (unsigned) pairwise correlations (see Materials and Methods). Using a community detection algorithm based on maximizing modularity (see Materials and Methods), we find that metrics form three distinct groups such that metrics that belong to the same group are more strongly correlated with each other than with metrics outside of their group (Fig. 2A and SI Appendix Fig. S3).

The ‘early response to pulse’ group (light green in Fig. 2A) contains measures of the initial and short-term deviations of a community from its reference state after a pulse perturbation. The ‘sensitivities to press’ group (green in Fig. 2A) includes metrics that quantify changes in total and individual species’ biomass between post- and pre-perturbed communities after a press perturbation. The ‘distance to threshold’ group (blue in

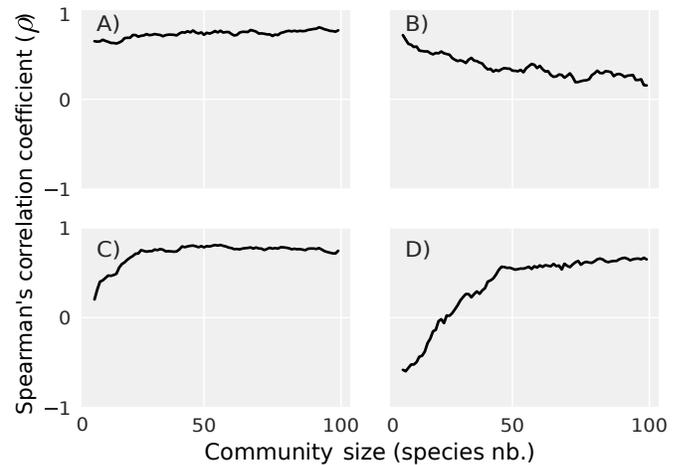


Fig. 1. <https://www.overleaf.com/project/5c361f3e4b0f20641e21ee84> Spearman's ρ pairwise correlation coefficient between stability metrics as a function of community size (i.e. number of species at steady state). A) Some pairwise correlations are not affected by community size, e.g. correlation between two metrics of tolerance to increased mortality at a global (i.e. community) and local (i.e. species) scale (resp. TM^G and $\langle TM^L \rangle$). B) Some metrics are only strongly correlated in small communities, e.g. correlation between ‘stochastic invariability’ (I_s) and ‘time to maximum amplification’ (t_{max}). C) Other metrics are only strongly correlated in large communities, e.g. correlation between resilience’ (R_{inf}) and the average strength of the sensitivity matrix ($\langle s_{ij} \rangle$). D) Some pairwise correlations change sign with community size, e.g. correlation between the resistance of total biomass (RM^G) and the sensitivity of species biomass to a global increase in mortality (SM^G). See Table 1 and Materials and Methods for metrics definitions.

Fig. 2A) consists of metrics that measure how easily a system crosses thresholds to new dynamical states, for example the amount of external pressure before a community experiences an abrupt change, the closeness of the rarest species to extinction, the population variability, and secondary extinctions caused by random extinctions.

Three metrics (in gray in Fig. 2A) were not clearly assigned to any of the three groups (see SI, section 2). These metrics include measures of the initial and transient responses of the most abundant species to pulse perturbations. Because of their idiosyncratic correlations with the rest of the metrics, we kept them apart from the other metrics.

Interestingly, the three emergent groups split metrics in terms of both the temporal scale of the response and the type of perturbation. Indeed, the ‘early response to pulse’ group only contains metrics describing transient behavior, while the ‘sensitivities to press’ and ‘distance to threshold’ groups contain metrics describing long-term (asymptotic) dynamics. Furthermore, the ‘early response to pulse’ and ‘sensitivities to press’ form two contrasting groups containing metrics that respectively refer to pulse and press perturbations, while metrics in the ‘distance to threshold’ group refer to both types of perturbations. The weak correlations between the three groups of metrics (with an average correlation of ~ 0.13 ; SI Appendix Fig. S2 and section 3) suggests that the metrics within a group can be considered as relatively independent from metrics in other groups. Therefore, these three groups reflect major components that constitute different dimensions of the stability of trophic communities (27) that should be measured in an ecological community to comprehensively assess its overall stability.

Further studying the degree of (dis)similarity between the

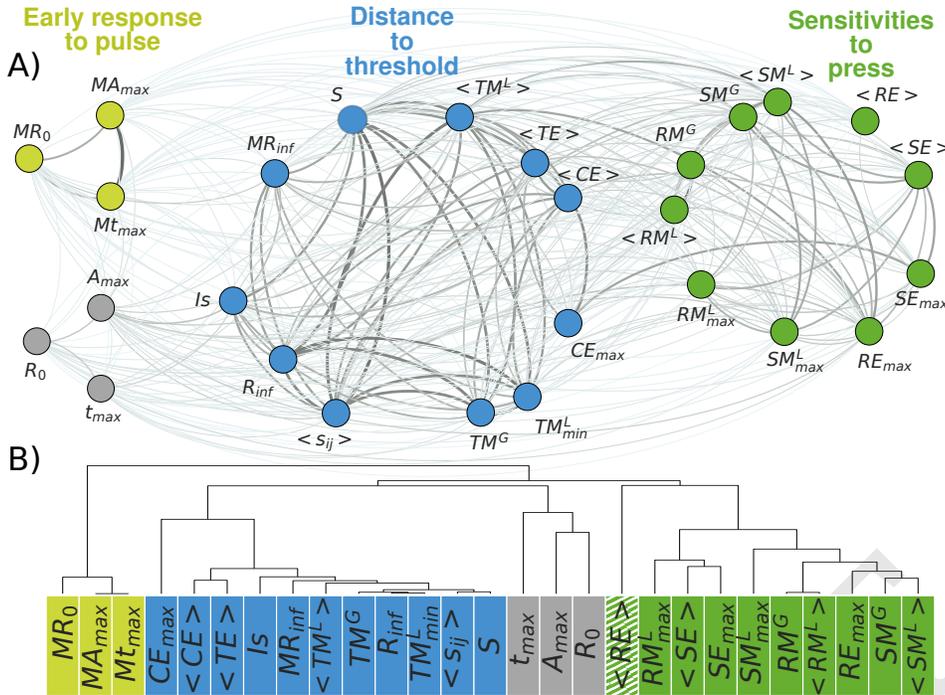


Fig. 2. A) Network of stability metrics for medium-sized communities (45 to 55 species). Nodes represent stability metrics and the thickness of links their unsigned pairwise Spearman's ρ correlation coefficients. Node colors distinguish the three groups identified by the modularity algorithm, with a modularity of $Q=0.177$: 'early response to pulse' group in light green, 'distance to threshold' group in blue, and 'sensitivities to press' group in darker green. In grey are metrics that the modularity algorithm was not able to unambiguously place in any group. B) Hierarchical clustering to the network of stability metrics. Correlations are used to compute a distance between all pairs of metrics, which are represented here by a dendrogram. The key to interpreting such a dendrogram is to focus on the first 'branch' at which any two metrics are joined together; the further away two metrics are from this 'common ancestor', the less similar they are. The goodness-of-fit of distances based on the dendrogram to the distances in the original data (pairwise correlations) is quantified by the *Cophenetic Coefficient* ($c = 0.85$). Metrics are clustered similarly as by the modularity partitioning, except for the 'resistance to extinction' metric, ($\langle RE \rangle$) represented with a striped pattern, which is therefore considered to not clearly belong to one of the groups in upcoming analyses. See Table 1 for metrics' definitions.

different stability metrics with a hierarchical clustering analysis (36, 37) (see Materials and Methods) confirms the partitioning found by the modularity algorithm, except for one outlier metric (striped in Fig. 2B), which was not attributed to the same group by both analyses (see SI, section 4) and is therefore not considered to clearly belong to one of the three groups for subsequent analyses. The generated dendrogram allows to visualize a more detailed structure, with subgroups of highly similar metrics within the three groups identified by the modularity algorithm (See SI, section 4). Practically, this implies that for these sets of highly similar metrics, only one of the metrics could be selected interchangeably. Moreover, some of these close similarities could also be of theoretical interest. For example, in the 'Distance to threshold' group, we find five strongly connected metrics of very different nature: resilience (a metric of dynamical stability, R_{inf}), tolerance metrics (which assess structural stability; TM^G , TM^L_{min}), and sensitivity metrics (which are based on the inverse Jacobian; S , $\langle s_{ij} \rangle$). Some of these connections have been previously reported (38, 39), but we still lack a complete theoretical map of most metrics' relationships.

171 The sign of the correlations between stability metrics. The

sign of the correlations between metrics is important because negative correlations between metrics would suggest trade-offs: promoting stability according to one of the metric would happen at the expense of stability according to another metric. In our simulated trophic communities, however, we only find a few negative correlations (see SI Appendix section 5 and Fig. S4). Most of the negative correlations are identified in small communities (below 20 species) between metrics of 'resistance' (i.e. total change in aggregated community biomass before and after a press perturbation) and 'sensitivity' (total change in species' populations after a press perturbation; Table 1). In fact, in communities of more than 20 species, there is only

one relatively strong negative correlation ($\rho \sim -0.4$) between 'reactivity' (R_0) and 'time to maximum amplification' (t_{max}). The relationship between these two metrics has been previously studied and found to be complex (40). Our results here suggest that communities whose abundant species initially deviate fast from their original state (i.e. high R_0), are also those that tend to start recovering early (i.e. low t_{max}); conversely, communities with abundant species that are less reactive tend to take longer before they start their recovery.

The vast majority of positive correlations (from $\sim 86\%$ of all 351 pairs in small communities to $\sim 93\%$ in large communities) found here is in line with recent experimental findings, where multiple positive correlations between stability metrics were found in communities of similar size as our simulated communities (24, 27). For example, we find a positive correlation ($\rho = 0.54$) between invariability (I_s) and resistance to small press perturbations (S) in agreement with (24). We also find a positive correlation ($\rho = 0.57$) between invariability (I_s) and the number of secondary extinctions ($\langle CE \rangle$), in communities of similar sizes as those studied by (27). In light of this, stability trade-offs seem to be a rare exception in complex trophic communities.

Mapping the stability metrics. Past reviews of stability in ecology have highlighted the multidimensional nature of stability and have attempted at grouping metrics in a few stability 'facets' based on the similarity in their definition (10–13). Here, three relatively independent groups of metrics emerged from the analysis of the correlations between metrics, and we argue that these groups can be interpreted as different 'dimensions' of stability. In what follows, we map all metrics according to their stability group (or 'dimension'), perturbation type, and stability facet in an attempt to better understand the relationships between these different categories (Fig. 3).

This mapping reveals that the stability facets and the

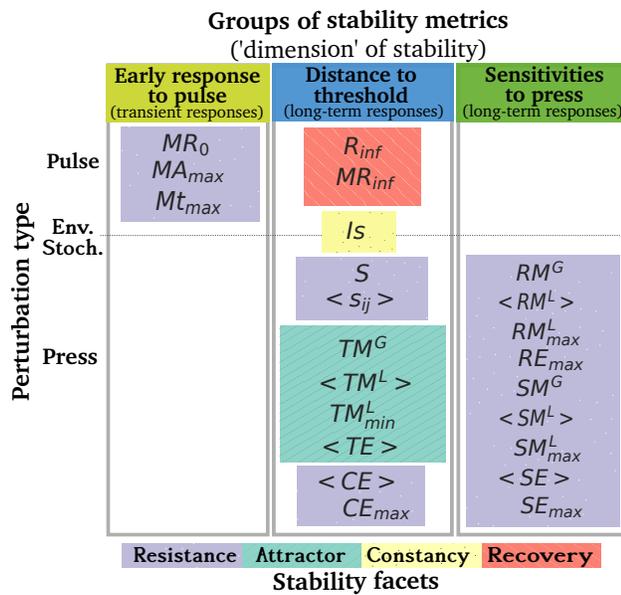


Fig. 3. Classification of the stability metrics according to three axes: the perturbation type (pulse, press or environmental stochasticity), the stability group (‘early response to pulse’, ‘distance to threshold’, and ‘sensitivities to press’) and the stability facets typically describing stability properties in the literature. There is currently no consensus on the names of these facets; we here refer to them as ‘resistance’ in purple (how much the system changes under a press perturbation), ‘attractor’ in green (the type and number of attractors of the system), ‘constancy’ in yellow (how variable the system is), and ‘recovery’ in red (if and how the system recovers from a pulse perturbation) (15). Colors of the groups of stability metrics are the same as in Fig. 2. Metrics not clearly associated to one of the three groups in Fig. 2 (i.e. the metrics in grey and $\langle RE \rangle$) were not included here. See Table 1 for metrics’ definitions.

stability groups don’t map one-to-one. For example, resistance metrics can belong to all three stability groups, while metrics from the four stability facets can be highly correlated with each other and belong to the same stability group (e.g. the ‘distance to threshold’ group). More strikingly, our mapping shows that it is not possible to simultaneously capture the three stability ‘dimensions’ with an experiment that would involve only one type of perturbation. Early response to pulse, i.e. transient responses (Fig. 3 left), can only be studied in communities that experience a pulse perturbation, while all ‘resistance’ and ‘sensitivity’ of biomass metrics are, by definition, the results of a press perturbation. The fact that knowledge about stability to a given type of perturbation does not extend to another type of perturbation confirms that we cannot get away from specifying the stability ‘of what’ and ‘to what’ (14, 16).

234 **Conclusion.** Perhaps the most important finding of our analysis is that the multiplicity of stability metrics can essentially be mapped into three relatively independent groups that reflect three different components, or ‘dimensions’, of stability. This suggests that the dimensionality of the stability of trophic ecological communities is much lower than the number of metrics used to quantify it, and that stability could therefore be assessed using a small number of metrics.

Each of the many stability metrics allows addressing specific questions by quantifying a given aspect of stability. At the same time, however, the grouping of many metrics in just a few components raises the question of which specific metrics

to choose if one wants to assess the overall stability of an ecological system. An intuitive guess is that combining metrics from each of the three groups could be a way of decreasing the amount of metrics used, while still accurately estimating the multiple ‘dimensions’ of the stability of an ecological community. Preliminary analyses suggest that using only three metrics – those with the highest explained variance in each of the groups – explains respectively 54%, 52% and 59% of the original variance in small, medium and large communities (see SI, section 6 for more details). Moreover, analyses of the volume of the covariance ellipsoid confirm that selecting metrics from the three different groups, rather than the same number of metrics from the same group, best describes the different stability ‘dimensions’ (see SI, section 7 and Fig. S7). However, due to the high correlations between metrics within a group, it is difficult to propose a single best way of selecting metric(s) in each of the groups. Although the choice of the metrics will always depend on the system studied and on practical constraints, hierarchical analyses (Fig. 2B and SI Appendix Fig. S3) and explained variance analyses (SI Appendix section 6) can help making informed choices.

Interestingly, our analysis confirms previously known relationships between metrics, but it also reveals unexpected dependencies, which could either be due to mathematical relationships yet to be investigated or because the metrics actually expose latent dimensions of stability. Although, our approach does not elucidate the causes for the metrics’ correlations, it does point towards future areas of research. In that sense, our results are of interest to both theoreticians – because they hint towards yet unknown mechanisms underlying correlations between stability metrics –, as well as to experimentalists, who can use the patterns of correlations to choose which metrics to evaluate in their experiments.

Finally, although our study focuses on the stability of food webs, the relationships found here could be of interest to understand the stability of other types of networks, in ecology as well as in other disciplines. In fact, even if the exact number of identified groups of metrics could be altered in other systems or by the incorporation of additional stability metrics, the framework we propose is flexible enough to accommodate to different conditions and opens a way towards simplifying the study of overall stability in different types of complex dynamical system. After all, directed networks of many kinds describe transport of matter, information, or capital in a similar way as food webs describe fluxes of biomass from primary producers to apex predators.

Materials and Methods

Stability metrics. We review the ecological literature to identify the most frequently used metrics for assessing community stability. Specifically, we consider metrics that quantify stability in communities that yield stable (fixed equilibrium) dynamics. We do not consider measures of community invasibility. For metrics that can be quantified in multiple ways, we only retain a single way of measuring that metric. With these criteria, we obtain 27 metrics that are described in Table 1, specifying their temporal scale (below the name) and the type of perturbation they are associated to (in bold letters in the description). Metrics include analytical responses to small pulse perturbations - i.e. instantaneous disturbances causing a sudden change in species abundances - obtained from the community matrix (or Jacobian) covering initial (*reactivity*), transient

Table 1. Stability metrics' names, characteristic time scales, definitions, and, when relevant, reference to the equation in the SI Appendix, section 10 (See Material and Methods for a guide to the metrics acronyms)

Name (time scale)	Acronym [equation in SI Appendix section 10]	Description
Reactivity (initial)	R_0 [6]	Max. instantaneous rate at which perturbations can be amplified. Measures the velocity of the system when initially going away from the equilibrium after a pulse perturbation . Driven by the most abundant species. Median Reactivity over all species (MR_0) represents the whole community.
	MR_0 [11]	
Max. amplification (transient)	A_{max} [9]	Factor by which the perturbation that grows the largest is amplified after a pulse perturbation . The factor by which the median displacement over all species deviates (MA_{max}) represents the whole community.
	MA_{max} [12]	
Time to max. amplification (transient)	t_{max}	Time to achieve the max. amplification, and time to achieve the maximum amplification of the median displacement after a pulse perturbation (Mt_{max}).
	Mt_{max}	
Resilience (long-term)	R_{inf} [10]	Asymptotic (i.e. long-term) return rate to the reference state after a pulse perturbation . Metric driven by the least abundant species. The median resilience over all species (MR_{inf}) represents the whole community.
	MR_{inf} [13]	
Stochastic invariability (long-term)	I_s [14]	Measures if the environmental noise (assumed to be white noise) is amplified i.e. if the fluctuations in species' biomass are larger than the environmental noise.
Sensitivity matrix (long-term)	$\langle sij \rangle$ [16]	Average change in the biomass of species i after a press perturbation is applied to species j (assuming that post- and pre-perturbed systems are at nearby fixed-point steady state and that perturbations are sufficiently small). The accumulated change over all species (S) represents the whole community.
	S [15]	
Tolerance (long-term)		
to mortality	TM^G [17]	Min. GLOBAL increase in mortality (press perturbation applied on all species) that leads to at least one extinction.
	$\langle TM^L \rangle$	Min. LOCAL increase in mortality (press perturbation applied on one species) that leads to at least one extinction. Each species is attacked in turn. The average (over all species) and the min. increases that caused an extinction are measured.
	TM^L_{min}	
to extinctions	$\langle TE \rangle$	Measured as 'robustness', i.e. the number of actively performed (random) extinctions (press perturbation) required to reduce the number of surviving species to 50% of the original number.
	RE_{max}	
Resistance of total biomass (long-term)		
to mortality	RM^G [18]	Relative change in total biomass before and after a GLOBAL increment of 10% mortality (press perturbation applied on all species).
	$\langle RM^L \rangle$	Relative change in total biomass before and after a LOCAL increment of 10% mortality (press perturbation applied to one species). Each species is attacked in turn. The average and max. changes in total biomass are measured.
	RM^L_{max}	
to extinctions	$\langle RE \rangle$ [20]	Relative change in total biomass before and after each of the species goes extinct (and subsequent secondary extinctions have taken place) (press perturbation). The average and max. changes in total biomass (over all extinction events) are measured.
	RE_{max}	
Cascading extinctions (long-term)		
Cascading extinctions (long-term)	$\langle CE \rangle$	Average number of secondary extinctions following one extinction (press perturbation). Each species is removed in turn. The average and max. number of secondary extinctions over all extinction events are measured.
	CE_{max}	
Sensitivity of species' biomass (long-term)		
to mortality	SM^G [19]	Total accumulated change in species' biomass before and after a GLOBAL increment of 10% mortality (press perturbation applied to all species).
	$\langle SM^L \rangle$	Total accumulated change in specie' biomass before and after a LOCAL increment of 10% mortality (press perturbation applied to one species). Each species is attacked in turn. The average and max. accumulated changes (over all events) are measured.
	SM^L_{max}	
to extinctions	$\langle SE \rangle$ [21]	Total accumulated change in individual biomass before and after each of the species goes extinct (and subsequent secondary extinctions take place) (press perturbation). Each species is attacked in turn. The average and max. accumulated changes (over all extinction events) are measured.
	SE_{max}	

(*maximum amplification* and *time to maximum amplification*), and asymptotic (*resilience*) temporal regimes, both quantified at the individual species level and at the community level (21, 40, 41). Responses to environmental noise is assessed with the *stochastic invariability* metric (34). Analytical responses to small press perturbations - i.e. lasting disturbances causing the abundance of species to be permanently changed - are measured by means of the *sensitivity matrix* (inverse of the Jacobian matrix) (32, 38, 42). We also apply two different types of more intense press perturbations empirically: an increase in mortality both at the local (i.e. only on one individual species at a time) and at the global (i.e. on all species of the community simultaneously) scales, and random extinctions of species. Structural stability (43, 44) to these two types of press perturbations is assessed with the *tolerance* metrics (Table 1). *Tolerance to mortality* is measured as in previous studies (45, 46), and *tolerance to extinctions* is measured with robustness (47). We also include metrics of community resistance to random extinctions (48) as *cascading extinctions*. Empirical measures of resistance to both types of press perturbations, named *resistance of total biomass* and *sensitivity of species' biomass*, are also quantified in a similar fashion as in previous studies (49). All the metrics are defined in such a way that an increase in their value means an increase in community stability. Definitions of metrics can be found in SI, section 10, and the dataset of stability metrics in SI Dataset S1.

The acronyms of the metrics that quantify responses to empirical press perturbations are encoded as follows: the first letter represents if they are a measure of tolerance (T) resistance (R), or sensitivity (S), followed by the initial letter of the perturbation, which is either mortality (M) or random extinctions (E). The superscript differentiates, when needed, if the perturbation is global (G) (i.e applied on all species of the communities as the same time) or local (L) (i.e. applied on one species at a time). When nothing is indicated, the perturbation is assumed to be local. In the case of local perturbations, the subscripts *min* and *max* indicate whether the metric is the extreme (resp. minimum or maximum) value observed, while the brackets $\langle \rangle$ indicate that the metric is the average of all observed values.

Generating communities and model simulations. We use the niche model (28) to construct food-web communities. We then use the produced community structure to simulate the biomass of each species using a bioenergetic consumer-resource model with allometric constraints (30):

$$\frac{dB_i}{dt} = r_i G_i B_i + B_i \sum_{j \in \text{prey}} e_{0j} F_{ij} - \sum_{k \in \text{pred}} B_k F_{ki} - x_i B_i - d_i B_i \quad [1]$$

where the interaction term F_{ij} is defined as:

$$F_{ij} = \frac{w_i a_{ij} B_j^{1+q}}{m_i (1 + w_i \sum_{k \in \text{prey}} a_{ik} h_{ik} B_k^{1+q})} \quad [2]$$

During the simulations, species biomass adjust dynamically and some extinctions may occur before a steady state is achieved. Thus, the species that comprise the final dynamical trophic networks are selected by structural constraints and energetic processes among the species. We fix the parameter of the functional response to $q = 0.3$ and the predator/prey body-mass ratio to $Z = 1.5$. Values for all the other scaling parameters are averages of values presented in (50). We generate networks with an initial species richness ranging from 5 to 115 species and a fixed connectance of $c = 0.15$. During the simulations, if species biomass crossed the extinction threshold ($1E^{-6} m_i$), we consider that species extinct. If more than 10% of the initial number of species goes extinct, we discard this community. Following this procedure, we simulate more than 10000 different dynamical trophic communities with species richness ranging from 5 to 105 species. For more details, see SI, sections 8 and 9.

Pairwise correlations and networks of stability metrics. For each community size, ranging from 5 to 100 species (with a step of 1), we sample 100 trophic communities of each size (SI Dataset S2) and compute the pairwise correlations among all stability metrics using Spearman's correlation rank, ρ . We consider that pairwise correlations remain unchanged throughout a gradient of species richness if

the variation in the correlation between the initial and final community sizes ($\Delta\rho$) is below 0.1. We use the pairwise correlations to build a network of stability metrics. In this network, each node is a metric and the links are the pairwise correlations between the metrics. The links are weighted (i.e. the stronger the correlation the thicker the link) and unsigned (i.e. we consider absolute correlations and ignore if two metrics are negatively or positively correlated). We assemble in this way networks of stability metrics for different classes of community sizes: small (5-15 species), medium (45-55 species), and large (85-95 species) communities by considering the average value of correlations (i.e. average ρ) within these size ranges.

Grouping stability metrics. We search for groups of metrics in the stability network such that pairs of metrics are more strongly correlated to other metrics of the same group than to metrics in other groups. Modularity quantifies the quality of a particular partition of a network into such ‘clusters’ (i.e. groups of nodes) (51). The **modularity algorithm** detects clusters by searching over many possible partitions of a network and finding the one that maximizes modularity (52). We apply such a community detection algorithm on our pairwise-correlation weighted networks using Gephi (53). We repeat the computations 10 times for each network, and we select the partition in clusters that renders the highest value of modularity (i.e. $Q=0.177$).

Stability metric (dis)similarity. We use **hierarchical clustering** (36) to aggregate stability metrics according to their similarity (based on correlation). Starting with the closest pair of metrics, subsequent metrics are joined together in a hierarchical fashion from the closest (i.e. most similar) to the furthest apart (most different) until all metrics are included. The distance between a pair of metrics is defined as $d = (1 - \rho)$ where ρ is the Spearman’s rank correlation. We constructed the dendrogram with the hierarchical agglomerative clustering (HAC) algorithm in Python (54). We selected the linkage method (‘average’) that rendered distances in the dendrogram closest to the original pairwise correlation (goodness-of-fit based on the cophenetic correlation coefficient $c=0.85$). The closer c is to 1, the better the correspondence.

ACKNOWLEDGMENTS. The initial idea for this project emerged from discussions with Colin Fontaine. The authors are very grateful for stimulating discussions with him. We would also like to thank Stéphane Robin for advice on the statistical analyses. We thank the two anonymous reviewers and the editor for their very constructive comments, which have considerably improved the manuscript. This work was funded by the ANR project ARSENIC (ANR-14-CE02-0012).

1. Gross T, Rudolf L, Levin S, Dieckmann U (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325:747–50.
2. Wiesner K, et al. (2018) Stability of democracies: a complex systems perspective. *European Journal of Physics* 40(1):014002.
3. da Cruz JP, Lind PG (2012) The dynamics of financial stability in complex networks. *The European Physical Journal B* 85(8).
4. Arinaminpathy N, Kapadia S, May RM (2012) Size and complexity in model financial systems. *Proceedings of the National Academy of Sciences* 109(45):18338–18343.
5. Bardoscia M, Battiston S, Caccioli F, Caldarelli G (2017) Pathways towards instability in financial networks. *Nature Communications* 8(1).
6. Hickey J, Davidsen J (2019) Self-organization and time-stability of social hierarchies. *PLOS ONE* 14(1):e0211403.
7. Prayag G, Chowdhury M, Spector S, Orcheston C (2018) Organizational resilience and financial performance. *Annals of Tourism Research* 73:193–196.
8. Becskei A, Serrano L (2000) Engineering stability in gene networks by autoregulation. *Nature* 405(6786):590–593.
9. Reznick E, Segre D (year?) On the stability of metabolic cycles. *Journal of Theoretical Biology* 266(4):536–549.
10. Orians GH (1975) Diversity, stability and maturity in natural ecosystems, eds. van Dobben WH, Lowe-McConnell RH. (Springer Netherlands, Dordrecht), pp. 139–150.
11. Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307:321–326.
12. 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(3):323–334.
13. Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. *Science* 317:58–62.
14. Donohue I, et al. (2016) Navigating the complexity of ecological stability. *Ecology Letters* 19(9):1172–1185.

15. Kéfi S, et al. (2019) Advancing our understanding of ecological stability. *Ecology Letters* 22(9):1349–1356.
16. Grimm V, Schmidt E, Wissel C (1992) On the application of stability concepts in ecology. *Ecological Modelling* 63(1):143–161.
17. McCann KS (2000) The diversity–stability debate. *Nature* 405(6783):228–233.
18. Tilman D (1994) Biodiversity and stability in grasslands. *Nature* 367:363–365.
19. Cardinale BJ, et al. (2013) Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94(8):1697–1707.
20. Johnson S, Domínguez-García V, Donetti L, Muñoz MA (2014) Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences* 111(50):17923–17928.
21. Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. *Nature* 275(5680):542–544.
22. Yodzis P (1981) The stability of real ecosystems. *Nature* 289:674–676.
23. Valdivia N, Moles M (2009) Observational evidence of a negative biodiversity–stability relationship in intertidal epibenthic communities. *Aquatic Biology* 4:263–271.
24. Pennekamp F, et al. (2018) Biodiversity increases and decreases ecosystem stability. *Nature* 563:109–112.
25. Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9(11):1228–1236.
26. Hillebrand H, et al. (2017) Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters* 21(1):21–30.
27. Donohue I, et al. (2013) On the dimensionality of ecological stability. *Ecology Letters* 16(4):421–429.
28. Williams RJ, Martinez ND (2000) Simple rules yield complex food webs. *Nature* 404(6774):180–183.
29. Yodzis P, Innes S (1992) Body Size and Consumer-Resource Dynamics. *The American Naturalist* 139(6):1151–1175.
30. Brose U, et al. (2008) Foraging theory predicts predator-prey energy fluxes. *Journal of Animal Ecology* 77(5):1072–1078.
31. RYKIEL EJ (1985) Towards a definition of ecological disturbance. *Austral Ecology* 10(3):361–365.
32. Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: Theory and practice. *Ecology* 65(1):1–13.
33. Ives AR (1995) Measuring resilience in stochastic systems. *Ecological Monographs* 65(2):217–233.
34. Arnoldi JF, Loreau M, Haegeman B (2016) Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. *Journal of Theoretical Biology* 389:47–59.
35. Yang Q, Fowler MS, Jackson AL, Donohue I (2019) The predictability of ecological stability in a noisy world. *Nature Ecology & Evolution* 3(2):251–259.
36. Fortunato S (2010) Community detection in graphs. *Physics Reports* 486(3-5):75–174.
37. Štefan RM (2014) Cluster type methodologies for grouping data. *Procedia Economics and Finance* 15:357–362.
38. Nakajima H (1992) Sensitivity and stability of flow networks. *Ecological Modelling* 62(1-3):123–133.
39. Arnoldi JF, Haegeman B (2016) Unifying dynamical and structural stability of equilibria. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Science* 472(2193):20150874.
40. Neubert MG, Caswell H (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* 78(3):653–665.
41. Arnoldi JF, Bideault A, Loreau M, Haegeman B (2018) How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. *Journal of Theoretical Biology* 436:79–92.
42. Carpenter SR, et al. (1992) Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *The American Naturalist* 140(5):781–798.
43. Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems. *Science* 345(6195):1253497–1253497.
44. Grilli J, et al. (2017) Feasibility and coexistence of large ecological communities. *Nature Communications* 8.
45. Wootton KL, Stouffer DB (2016) Species’ traits and food-web complexity interactively affect a food web’s response to press disturbance. *Ecosphere* 7(11):e01518.
46. Säterberg T, Sellman S, Ebenman B (2013) High frequency of functional extinctions in ecological networks. *Nature* 499(7459):468–470.
47. Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5(4):558–567.
48. Thébaud E, Huber V, Loreau M (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163–173.
49. Ives AR, Cardinale BJ (2004) Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429:174–177.
50. Rall BC, et al. (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1605):2923–2934.
51. Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. *Physical Review E* 69(2).
52. Blondel VD, Guillaume JL, Lambiotte R, Lefebvre E (2008) Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment* 2008(10):P10008.
53. Bastian M, Heymann S, Jacomy M (2009) Gephi: An open source software for exploring and manipulating networks. *International AAAI Conference on Weblogs and Social Media*.
54. Jones E, Oliphant T, Peterson P, et al. (2001–) SciPy: Open source scientific tools for Python. [Online; accessed <today>].