

# Critical slowing down as early warning for the onset of collapse in mutualistic communities

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**Significance** Little is known on whether structurally diverse ecological networks may respond abruptly to anthropogenic stress and even less on our ability to detect such responses in advance. By simulating mutualistic communities en route to a tipping point, we show how critical slowing down indicators may be used as early warnings for the collapse of ecological networks. Our findings not only confirm the existence of the generic dynamical signatures of tipping points in ecological networks, but also suggest a novel way for identifying most vulnerable components in a broad class of networks at the brink of collapse.

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1 Tipping points are crossed when small changes in external condi-  
2 tions cause abrupt unexpected responses in the current state of a  
3 system. In the case of ecological communities under stress, the risk  
4 of approaching a tipping point is unknown, but its stakes are high.  
5 Here we test recently developed critical slowing down indicators as  
6 early-warning signals for detecting the proximity to a potential tip-  
7 ping point in structurally complex ecological communities. We use  
8 the structure of 79 empirical mutualistic networks to simulate a sce-  
9 nario of gradual environmental change that leads to an abrupt first  
10 extinction event followed by a sequence of species losses until the  
11 point of complete community collapse. We find that critical slowing  
12 down indicators derived from time series of biomasses measured at  
13 the species and community level signal the proximity to the onset  
14 of community collapse. In particular, we identify specialist species  
15 as likely the best-indicator species for monitoring the proximity of  
16 a community to collapse. In addition, trends in slowing down indi-  
17 cators are strongly correlated to the timing of species extinctions.  
18 This correlation offers a novel way for mapping species resilience and  
19 ranking species risk to extinction in a given community. Our findings  
20 pave the road for combining theory on tipping points with patterns  
21 of network structure that might prove useful for the management  
22 of a broad class of ecological networks under global environmental  
23 change.

24 **Keywords:** Resilience | Critical transition | Mutualism | Ecological networks

1 Systems as complex as the climate (1), financial markets (2), or ecosystems (3) have  
2 experienced tipping points in the past and may do so in the future. Tipping points are  
3 crossed when small changes in external conditions trigger the sudden collapse of a system  
4 to an undesirable state that is usually difficult to reverse. For example, the shutdown  
5 of the thermohaline circulation in the North Atlantic (4), or the occasional switches of  
6 shallow lakes from clear to turbid waters (5) are examples of sudden transitions that might  
7 have been caused by gradual changes in external conditions. It is this “small changes can  
8 have big effects” pattern that makes tipping points important to study but notoriously  
9 difficult to detect. Nonetheless, recent work has suggested that the possibility of detecting  
10 nearby tipping points may not be that distant (6).

11 According to theory, prior to tipping points, systems tend to recover slowly back to  
12 equilibrium upon a random disturbance (7). This phenomenon of “critical slowing down”  
13 appears to be generic for a wide class of local bifurcations (8), at which the current  
14 equilibrium state of a system loses stability before being replaced by another equilibrium  
15 state. Critical slowing down may be captured by two simple statistical signals in the  
16 dynamics of complex systems (6): increasing variance and rising correlation. These signals  
17 can be used to indicate the proximity of a system to a tipping point and are suggested  
18 to serve as indicators of loss of resilience, or, more broadly, as early-warning signals for  
19 the impending transition (6). Critical slowing down indicators (CSD indicators hereafter)  
20 have been experimentally shown to detect abrupt transitions between alternative states  
21 in yeast cultures (9), plankton chemostats (10), zooplankton populations (11), or even  
22 whole lake communities (12). Yet, these indicators have been mostly studied in systems  
23 with single populations or few aggregated components that lack the complexity that  
24 characterizes structurally heterogeneous systems of interacting species, such as ecological  
25 networks.

1        Although ecological networks have been experiencing an increasing amount of anthro-  
2 pogenic pressures, it is still unclear how strongly they may respond to this stress. Re-  
3 sponses might range from local extinctions and species distribution shifts (13), to whole  
4 community reorganisation and massive biodiversity losses (14). In the best-case scenar-  
5 ios, these responses will be gradual, predictable, or even reversible. But little is known  
6 on whether ecological networks could also respond in abrupt and unexpected ways (15).  
7 Theoretical work shows that gradual environmental change in mutualistic communities  
8 may have different effects on species tolerance to stress but the path to extinction appears  
9 to be gradual (16). Only recently, it has been suggested that strongly nested mutualistic  
10 networks may run a high risk of experiencing a tipping point (17). For these latter cases,  
11 the challenge is to detect if they are approaching a tipping point in advance.

12        Here, we explore whether we can detect tipping points in structurally diverse ecologi-  
13 cal networks with CSD indicators. We used the structure of 79 mutualistic communities  
14 reconstructed from empirical plant-pollinator and plant seed-disperser networks to sim-  
15 ulate dynamical scenarios of gradual environmental change that lead to species loss and  
16 community-wide collapses. We demonstrate that CSD indicators derived from monitoring  
17 biomasses at the species and community level may signal the proximity to the onset of  
18 community collapse. We investigate how species structural traits influence the predictive  
19 performance of the indicators at the species level. Lastly, we suggest that species-level  
20 indicators may be used to rank species risk to extinction even before the onset of commu-  
21 nity collapse. Despite the challenge of identifying these patterns in empirical dynamics of  
22 observed populations, our work offers a first theoretical framework for detecting tipping  
23 points and mapping species resilience in mutualistic communities that can help to detect  
24 potential abrupt transitions in a broad class of ecological networks.

25

# 1 Results and Discussion

## 2 The abrupt onset of community collapse

3 We estimated changes in CSD indicators, variance and autocorrelation at lag 1, in sim-  
4 ulated time series of 79 empirically described bi-partite plant-pollinator and plant seed-  
5 disperser mutualistic communities before their collapse. We assumed that species compete  
6 weakly with each other but coexist due to their mutualistic benefits (i.e., obligate mutu-  
7 alism). We simulated community dynamics in the presence of environmental noise, and  
8 we exposed all communities to a scenario of gradual environmental stress. Although our  
9 simulations do not necessarily capture the complexity of observed dynamics, they serve  
10 as a good first approximation. We slowly decreased the strength of mutualistic interac-  
11 tions between plant and animal species. This led to species extinctions until the complete  
12 community collapsed. Our scenario follows the overall weakening or even disruption of  
13 mutualistic interactions (18) that has been observed in declining visitation rates (19),  
14 or phenological mismatching (20) due to habitat fragmentation or changes in seasonal  
15 temperature patterns.

16 Fig. 1 demonstrates a simulated example of a collapsing plant-pollinator community  
17 from the Chilean Andes (Fig. 1A). As benefits from species mutualistic interactions  
18 gradually declined, species were progressively decreasing in biomass. In our communities,  
19 we assumed a trade-off between the strength of mutualistic interactions and the number  
20 of species interactions. This meant that specialists benefited strongly from their partners  
21 whereas generalists did not (Materials and Methods). As a result, all species suffered  
22 proportional losses up to a point where the first extinction event suddenly occurred (Fig.  
23 1B). We defined this first extinction event as the tipping point that marked the onset  
24 of the complete collapse of the community. We observed an abrupt onset of community

1 collapse in all 79 communities.

2       What makes such tipping points important to detect is that they happen without  
3 any prior substantial loss in species biomass (Supporting Information S1). Obviously,  
4 a gradually declining trajectory towards extinction would by itself be evidence that the  
5 community is at risk. At the moment, we are largely unaware of how general an abrupt  
6 onset of community collapse is, although there is theoretical evidence that the nested  
7 pattern of mutualistic networks would favor the occurrence of abrupt transitions (17). In  
8 that case CSD indicators can prove useful for anticipating abrupt transitions. Comparing  
9 time series of species far and close to the onset of community collapse, we found that both  
10 their variability and correlation increased (Fig. 1C, D). A similar pattern was also found  
11 when looking at aggregate measures of total community biomass (Fig. 1C, D), implying  
12 that CSD indicators can indeed be used to identify the onset of collapse in structurally  
13 complex mutualistic communities.

14

## 15 **Critical slowing down indicators at species and community level**

16 We confirmed increasing patterns in critical slowing indicators in all our 79 communities  
17 prior to the onset of community collapse. We measured variance as coefficient of variation  
18 ( $CV = \frac{std\ dev}{mean}$ ), and autocorrelation at lag 1 (AR1) as the correlation of the time series to  
19 itself shifted by one time step. As CV and AR1 tend to smoothly change up to the onset  
20 of collapse (Fig. S1), we reported only their relative changes (natural log differences) at  
21 the start of the simulation and just before the onset of community collapse (Fig. S1,  
22 Materials and Methods). Indicators increased both at species and community level (Fig.  
23 2), regardless of being estimated for plant or animal species (Fig. S2). We also found  
24 similar patterns when we estimated the change in indicators 10 steps instead of just 1

1 step prior to collapse (Fig. S3). AR1 trends were stronger than CV trends (paired t-test  
2 206.45,  $P < 0.05$ ,  $df = 11194$ ). However, AR1 trends at the species level were occasionally  
3 negative, while CV always increased (Fig. 2A). Instead, AR1 and CV trends estimated  
4 at the community rather than the species level were always positive as differences across  
5 species smoothed out at the aggregate level (Fig. 2).

6

### 7 **Best-indicator species for detecting community collapse**

8 Although these results broadly support that CSD indicators could announce abrupt tran-  
9 sitions in a community, they are constrained by the need of collecting high resolution time  
10 series for all species. However, a closer look at indicator trends across species shows that  
11 some species have better reflected community proximity to the collapse than others (Fig.  
12 2). Such species could qualify as best-indicator species of community collapse (i.e. the  
13 ones with the potential to demonstrate the strongest changes in CSD indicators). We  
14 searched for the profile of these best-indicator species by estimating correlations between  
15 indicator trends and species structural traits. We selected two commonly used structural  
16 traits: degree (i.e. number of the interactions of a species), and contribution to nestedness  
17 (i.e. the level of shared interacting partners in the community). We chose these traits  
18 based not only on the fact that they have been related to the persistence of mutualistic  
19 communities (21), but also because they can be easily derived from species interaction  
20 matrices.

21 We found negative correlations between CV trends and species degree, and negative  
22 but weak correlations between AR1 trends and species degree (Fig. 3). Similar but more  
23 variable patterns were observed for correlations between indicator trends and contribution  
24 to nestedness (Fig. 3). Despite the variation in the correlations, specialists (and to a less

1 extent least contributors to nestedness) tended to be best-indicator species of community  
2 collapse. This can be best explained by the fact that specialists were generally the first  
3 to collapse (Fig. S4 A, B), and that specialists' dynamics were less muffled by noise as  
4 opposed to generalists whose dynamics were affected by the multiple noisy dynamics of  
5 their partners. These observations imply that declining community resilience might be  
6 strongly reflected in CSD indicators when measured from peripheral species in a network.  
7 Although this qualifies specialists as target species for monitoring community resilience,  
8 CSD indicators from specialist dynamics might not always reflect community-wide risk of  
9 collapse. As specialists are usually most vulnerable to disturbances, changes in their dy-  
10 namics might just imply individual rather than community-wide risk of extinction. Thus,  
11 monitoring a mix of specialists and generalists in a network may help avoid such potential  
12 false positives. Still, the challenge will be to strike the right balance between monitoring  
13 the minimum number of species in a network and the effort required for robustly estimat-  
14 ing community resilience.

15

## 16 **From detecting tipping points to mapping species resilience**

17 The fact that most species indicated the proximity to the onset of community collapse  
18 implies that differences in indicator trends across species might reflect how close a species  
19 is to its own point of extinction or more general how resilient a species is. In the ex-  
20 ample of the plant-pollinator community from Fig. 1, we ordered species according to  
21 their timing of extinction, and we colored them based on the magnitude of the change  
22 in their CVs (Fig. 4, white reflects weak, black reflects strong changes). As expected,  
23 species that went first extinct showed the strongest changes in CV. This was generally true  
24 for specialists. We confirmed such correlations between the timing of species extinctions



1 and trends in CSD indicators in all 79 communities. Correlations for CV were stronger  
2 than for AR1 (Fig. S4 C,D). This finding implies that we could rank species risk to ex-  
3 tinction before any event of collapse by just comparing species' relative changes in CV.  
4 Such across-species comparisons of CV have been proposed earlier for estimating species  
5 resilience (22), and have been used for exploring population vulnerability, for instance,  
6 to overexploitation in fish stocks (23, 24). Nonetheless, these comparisons are based on  
7 snapshot measurements that might be compromised by differences in species traits (like  
8 mortality or growth rates). Instead, comparing relative changes in CSD indicators might  
9 reduce such biases and allow direct across-species comparisons given that all species in a  
10 community are experiencing similar environmental stress.

11

## 12 **Challenges to detecting tipping points in mutualistic communities**

13 Although our results show that we could implement CSD indicators for mapping species re-  
14 siliance and detecting abrupt community transitions, we are still largely ignorant whether  
15 abrupt collapses are the rule or rather the exception in mutualistic communities. Theory  
16 suggests that the nested structure of mutualistic networks would increase the probability  
17 of abrupt transitions (17), but it is unresolved how the overall parameter space affects  
18 the probability of community collapse and the performance of the CSD indicators. For  
19 example, it has been demonstrated that species tend to reorganize their interactions in  
20 a community, especially under stress (25). Such adaptation would probably minimize  
21 the probability of an abrupt collapse. Additionally, it has been theoretically shown that  
22 species responses to environmental stress in mutualistic communities are largely depen-  
23 dent on how mutualistic strengths are assigned between species (16). For example, in  
24 our communities we assumed a trade-off between mutualistic strength and the number

1 of species interactions ( $\delta = 1$ ) (26, 27). Under such trade-off, the gradual decrease in  
2 mutualistic strength caused the abrupt onset of community collapse as all species suf-  
3 fered proportional losses (Fig. 5A, plant-pollinator community from Fig. 1). Had we,  
4 however, assumed no trade-off for the same community ( $\delta = 0$ ), generalists would enjoy  
5 mutualistic benefits proportional to the number of their mutualistic partners and suffer  
6 less losses than specialists. Consequently, we would expect specialists to first go extinct  
7 probably in a gradual rather than abrupt way (Fig. 5B). Indeed, only in 21 out of the  
8 79 communities the onset of community collapse remained abrupt when we assumed no  
9 mutualistic trade-off while keeping the rest of the parameters the same. Nonetheless, even  
10 in the case of gradual transitions, we still found positive CSD trends mostly at the species  
11 (Fig. 5D, F) rather than community level (Fig. 5C, E).

12       Regardless of the type of transition, our ability to detect CSD in a network is con-  
13 sequent with monitoring stochastic community dynamics around an underlying stable  
14 equilibrium (6). However, observed population dynamics usually follow erratic, highly  
15 variable patterns driven by a mix of nonlinear and stochastic effects (28, 29), at times  
16 interrupted by long transients far from equilibrium (30). This may question whether  
17 CSD indicators could be identified at all under such non-equilibrium conditions (31). Or  
18 it might be challenging to conclude whether CSD indicators are consequence of the pro-  
19 gressive approach to a tipping point or due to the natural patterns of variability in real  
20 populations (32). Despite the real topologies we used, our simulated communities repro-  
21 duced dynamics that are far from the variability found in empirical data (Fig. S5). Such  
22 difference challenges the capacity of interpreting natural patterns of variability from a CSD  
23 perspective. Instead, at the moment, the theory behind CSD indicators only allows us to  
24 explore how CSD indicators may be identified in structurally complex communities under  
25 stable equilibrium dynamical regimes in the presence of weak stochasticity.

1 Clearly, our work is only a first step when it comes to assessing our ability to detect  
2 community collapses. Although we confirmed our conclusions also under an alternative  
3 stress scenario (Fig. S6), there are more cases to be explored. For instance, species will  
4 most likely be differentially affected by changing conditions (18). Similarly, variation in  
5 stochastic effects across species will affect indicators' performance, as CSD indicators have  
6 been shown to be sensitive to the magnitude and color of environmental noise (33, 34).  
7 Further studies would need to test the possibility of detecting tipping points under such  
8 conditions and to expand the current findings to other types of networks like food webs,  
9 competition communities, or metapopulations.

10

## 11 **Conclusions**

12 In this study, we showed that critical slowing down indicators can be used to infer prox-  
13 imity to tipping points and to map species risk to extinction in systems as structurally  
14 diverse as mutualistic networks. No doubt we remain largely ignorant of whether such  
15 networks will respond abruptly to increasing pressure at all. However, in the case they  
16 do, the generality of the dynamical signatures of tipping points implies that critical slow-  
17 ing down indicators may be used for identifying vulnerable system components and for  
18 detecting abrupt transitions in networks ranging from ecological communities to globally-  
19 linked financial markets.

20

## 21 **Materials and Methods**

22 **Empirical networks.** Our mutualistic plant-pollinator and plant seed-dispersal net-  
23 works were accessed from the Web of Life database ([www.web-of-life.es](http://www.web-of-life.es)). We only selected

1 networks that have more than 20 species. This resulted in 79 networks covering a wide  
 2 geographic range across all continents and climatic zones and with a high variation in  
 3 their architectural properties. Table S1 summarizes the ranges of the most important  
 4 structural properties of these communities.

5  
 6 **Model.** The empirical mutualistic networks provided the skeleton that we used to sim-  
 7 ulate the dynamics of our communities. The dynamics of plants  $P$  and animals  $A$  (i.e.  
 8 pollinators, seed dispersers) were given by a model presented by Ref (35):

$$\begin{aligned} \frac{dP_i}{dt} &= P_i(\alpha_{P_i} - \sum_j \beta_{P_{ij}} P_j + \frac{\sum_j \gamma_{P_{ij}} A_j}{1+h \sum_j \gamma_{P_{ij}} A_j}) + u \\ \frac{dA_k}{dt} &= A_k(\alpha_{A_k} - \sum_j \beta_{A_{kj}} A_j + \frac{\sum_j \gamma_{A_{kj}} P_j}{1+h \sum_j \gamma_{A_{kj}} P_j}) + u \end{aligned} \quad (1)$$

$$\text{for } i = [1, n], k = [1, m],$$

9  
 10 where both plant and animal biomasses grow with rate  $\alpha$ , compete within their respective  
 11 guilds with interspecific rate  $\beta$ , and enjoy a mutualistic benefit following a saturating  
 12 function with handling time  $h$  ( $= 0.1$ ) and mutualistic strength  $\gamma$  between plants and  
 13 animals. We slightly modified the model by assuming that there is a small immigration  
 14 rate  $u$  ( $= 10^{-5}$ ) for all species. Parameter  $u$  does not affect the dynamics of the model,  
 15 but helps to avoid the occurrence of underflow errors in the presence of environmental  
 16 noise.

17 To account for asymmetries in the strength of interactions between generalist and  
 18 specialist species (36), we used a trade-off  $\gamma_{ij}$  that defines the mutualistic dependence  
 19 between species  $j$  and  $i$  and that depends on species degree (number of mutualistic links)  
 20 (16):

$$\gamma_{ij} = \frac{\gamma_o y_{ij}}{k_i^\delta}. \quad (2)$$

1  $\gamma_o$  represents the average level of mutualistic strength,  $k_i$  the degree of species  $i$ , and  
 2  $y_{ij} = 1$  if species  $i$  and  $j$  interact and zero otherwise. Parameter  $\delta$  modulates the trade-off  
 3 and determines the actual mutualistic interaction strength of plant (animal) species  $i$  and  
 4 the  $j$  animal (plant) species in the community (16). Here, we adopt a scenario of equal  
 5 total strengths for all species by assuming an inversely proportional mutualistic strength  
 6 to species degree ( $\delta = 1$ ) that can be justified by classical empirical (26) and theoretical  
 7 work (27).

8 Lastly, to ensure that our communities are feasible (all species present) before we  
 9 impose any stress, and to minimize the chance that transitions are driven by the direct  
 10 competition within plants or animals ( $\beta$ ), we did not allow interspecific competition to  
 11 exceed intraspecific competition ( $\sum_j (\beta_{ij} \leq 1 \ (i \neq j))$ ) (37). We did this by sampling com-  
 12 petition coefficients  $\beta_{ij}$  for each plant and animal guild from a uniform distribution with  
 13 minimum 0.001 and mean  $\bar{\beta} = \frac{1}{n^{(A),(P)}}$  where  $n^{(P),(A)}$  are the number of plant or animal  
 14 species respectively until the assumption  $\sum_j \beta_{ij} \leq \beta_{ii} \ (i \neq j)$  was fulfilled. Intraspecific  
 15 competition  $\beta_{ii}$  was set to 1.

16

17 **Collapsing mutualistic communities by declining mutualistic strength.** In our  
 18 numerical experiments, we slowly decreased mutualistic strength  $\gamma_o$  for all plant-animal  
 19 interactions (16). We started simulations assuming conditions of obligate mutualism (38),  
 20 which implies that species can survive only in the presence of strong mutualistic benefits.  
 21 We imposed obligate mutualism by drawing negative growth rates for plants and animals  
 22  $\alpha_{(P),(A)}$  uniformly from [-0.5, -0.1].

23 To ensure that the level of mutualistic strength that we chose was relative to the

1 actual size and structure of each community, we assigned mutualistic strengths  $\gamma_o$  to be  
 2 higher than the limit  $\tau$  ( $\gamma_o = 8\tau$ ) at which mutualistic benefits exceeded competitive  
 3 costs for all communities (16). Under these conditions we randomly initialized species  
 4 biomasses from a uniform distribution ( $[0, 10]$ ) and let communities reach equilibrium. We  
 5 only selected parameterizations that allowed all species to be present in each community  
 6 (feasible equilibrium). If that condition was not satisfied, we resampled competition and  
 7 growth rate terms and repeated the initialization. Once we attained parameters that  
 8 allowed for a feasible equilibrium, we gradually decreased  $\gamma_o$  to zero in 200 equal steps.

9 At each step, we discarded transients by simulating for 500 timesteps before recording  
 10 equilibrium species biomasses. We assumed that species went extinct when their biomass  
 11 was lower than 10 times the immigration rate  $u$  (i.e.  $< 10^{-4}$ ). The gradual decrease of  
 12 mutualistic strength led to the progressive loss of species until the collapse of the com-  
 13 plete community. At each extinction event, we recorded the level of mutualistic strength  
 14  $\gamma_o$  and the identity of species that went extinct. We categorized the first extinction event  
 15 as abrupt or gradual depending on the slope of the decline in species biomasses (where  
 16 the slope was given by  $\frac{N_{(t)} - N_{(t-1)}}{\gamma_{(t)} - \gamma_{(t-1)}}$  and  $t$  was the time index corresponding to the first  
 17 extinction event). If the slope was larger than 15, we characterised the onset of com-  
 18 munity collapse as abrupt (17). If that condition was not satisfied, we characterised the  
 19 transition as gradual. We repeated the above procedure to attain an abrupt transition in  
 20 all communities for 10 of the total 79 networks (on average 3.6 times for each).

21

22 **Critical Slowing Down Indicators as Early Warnings for the onset of com-**  
 23 **munity collapse.** We quantified CSD indicators in the mutualistic communities to test  
 24 whether they can provide early warnings for the proximity to the onset of community  
 25 collapse. We measured variance (expressed as  $CV = \frac{std}{mean}$ ) (39) and autocorrelation at

1 lag 1 (AR1, as the  $corr(x_t, x_{t+1})$ , where  $x_t$  denotes a point in the time series) (40).

2 To estimate these indicators, we simulated a stochastic version of our differential  
3 equations 1:

$$\begin{aligned} dP_i &= f(P_i, A_k)dt + \sigma P_i dW_i \\ dA_k &= f(P_i, A_k)dt + \sigma A_k dW_k \end{aligned} \quad (3)$$

4  
5 where  $f()$  is the deterministic part of eq 1 and  $dW$  is a Wiener process uncorrelated  
6 across all species with mean 0 and variance scaled by  $\sigma(= 0.025)$  and species biomasses  
7 (multiplicative noise). We used Euler integration with timestep 0.01 following Ito calculus  
8 to solve the equations and to generate the stochastic time series for all species in the  
9 community.

10 We chose CV as an unbiased measure of variability rather than the commonly used  
11 standard deviation (39) to account for the scaling effect of environmental stochasticity  
12 to species biomass (multiplicative noise). Multiplicative noise can alter patterns in vari-  
13 ance when studying critical slowing down indicators (34). We discuss this issue in the  
14 Supporting Information S3.

15 Previous studies have shown that CSD indicators change smoothly prior to bifurca-  
16 tion points (8, 41). We confirmed smooth changes in CV and AR1 in our mutualistic  
17 communities under a gradual decline of mutualistic strength (Fig. S1). Based on these  
18 observations, we only estimated CV and AR1 far (i.e.,  $\gamma_o = 8\tau$ ) and close (i.e., one step  
19 before the threshold  $\gamma_o = \gamma_{thr-1}$ ) to the onset of community collapse. We did this by  
20 simulating communities for 100 time steps far and close to the first tipping event starting  
21 from equilibrium conditions. To reduce random effects due to noise, we repeated this  
22 20 times. For each repetition, we estimated CV and AR1 and used average values to  
23 estimate indicators for each species. We also measured CV and AR1 on total community

1 biomass by aggregating plant and animal biomasses. We lastly computed a community  
2 level multivariate index of variability based on the maximum eigenvalue of the variance-  
3 covariance matrix of all species biomasses at equilibrium (42) that is commonly used in  
4 multivariate analysis of community changes (e.g. Principal Component Analysis). We  
5 quantified the strength of the change in the indicators as the natural log difference of the  
6 indicator values close and far from the onset of collapse ( $\ln(\frac{indicator_{thr-n}}{indicator_o})$ ) for each species  
7 in all communities.

8  
9 **Structural traits.** We used Spearman rank correlation to explore correlations between  
10 changes in CSD indicators and structural traits for identifying potential best-indicator  
11 species. The two structural traits were degree (number of mutualistic links) and contri-  
12 bution to nestedness. Contribution to nestedness for each species quantifies the amount  
13 to which nestedness compares with the nestedness when randomizing the interactions of  
14 that particular species (21). In calculating nestedness contributions, the interactions of  
15 a species are randomized according to the null model specified in (43); we used 1,000  
16 random replicates.

17  
18 We did all analyses in MATLAB (R2010b, The Mathworks) using Grind for MATLAB  
19 (available online at <http://www.sparcs-center.org/grind>).

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## Figure Captions

**Fig. 1.** Detection of the abrupt onset of collapse using critical slowing down indicators (CSD) in mutualistic communities. (A) A plant-pollinator community from Cordón del Cepo, Chile. Black boxes represent mutualistic links between plants and animals. We used the structure of 79 empirical mutualistic networks to simulate their dynamics and potential collapse under gradual environmental change. (B) Decreasing mutualistic strength  $\gamma$  stresses species biomasses until unexpectedly an abrupt transition is induced. This first transition marks the onset of a sequence of extinctions until the collapse of the complete community. (C, D) Identifying critical slowing down at the species and community level. Close to the onset of community collapse, variance and correlation tend to increase. This increase is evident measured both from species biomasses and from the aggregated total community biomass.

**Fig. 2.** Performance of critical slowing down (CSD) indicators measured at the species ( $N = 11,195$ ) and community ( $N = 79$ ) level in 79 mutualistic communities. Performance was estimated as the natural logarithmic ratio of autocorrelation at lag 1 ( $AR1$ ) and coefficient of variation ( $CV$ ) close and far from the onset of community collapse. The multivariate index of variability was estimated on the community biomass variance-covariance matrix. Positive values indicate an increase in the indicators before the onset collapse. Boxplots include the median, box edges represent the 5 and 95 percentiles, and box whiskers indicate the minimum and maximum values.

**Fig. 3.** Structural traits and critical slowing down (CSD) indicators. Spearman rank correlations between species traits (degree and contribution to nestedness) and

species indicators performance. Boxplots include the median, box edges represent the 25 and 75 percentiles, and box whiskers indicate the 5 and 95 percentiles.

**Fig. 4.** Mapping species resilience based on critical slowing down (CSD) indicators. Each node represents a species in the plant-pollinator community from Fig. 1. Species are ranked according to their order of extinction (from left to right), their size corresponds to the number of their interactions (degree), and are colored according to their changes in  $CV$  before the onset of community collapse. Black colors indicate strong increases in  $CV$ . We used color boxes to group species that went co-extinct. We found a positive correlation between the magnitude of the  $CV$  change and the order of species extinctions. Similar patterns were confirmed in all 79 communities (Fig. S4). This information can be used to rank species risk to extinction.

**Fig. 5.** The effect of trade-offs in mutualistic strengths on critical slowing down indicators. (A) In the presence of a trade-off, mutualistic strengths are inversely proportional to the number of species interactions ( $\delta = 1$ ). All species suffer similar losses to the decreasing mutualistic strength and the onset of community collapse usually occurs abruptly. (B) In the absence of a mutualistic trade-off ( $\delta = 0$ , all the rest of the parameters are the same as in A), mutualistic strengths are the same across all species. As a result, mutualistic benefits are proportional to the number of their interactions and the onset of community collapse is gradual. (C, E) Community level  $CV$  and  $AR1$  indicators clearly increase up to the onset of collapse in the presence of the trade-off ( $\delta = 1$ ). (D, F) Indicators at species level have mostly positive trends but perform poorer in the absence of the mutualistic trade-off ( $\delta = 0$ ).

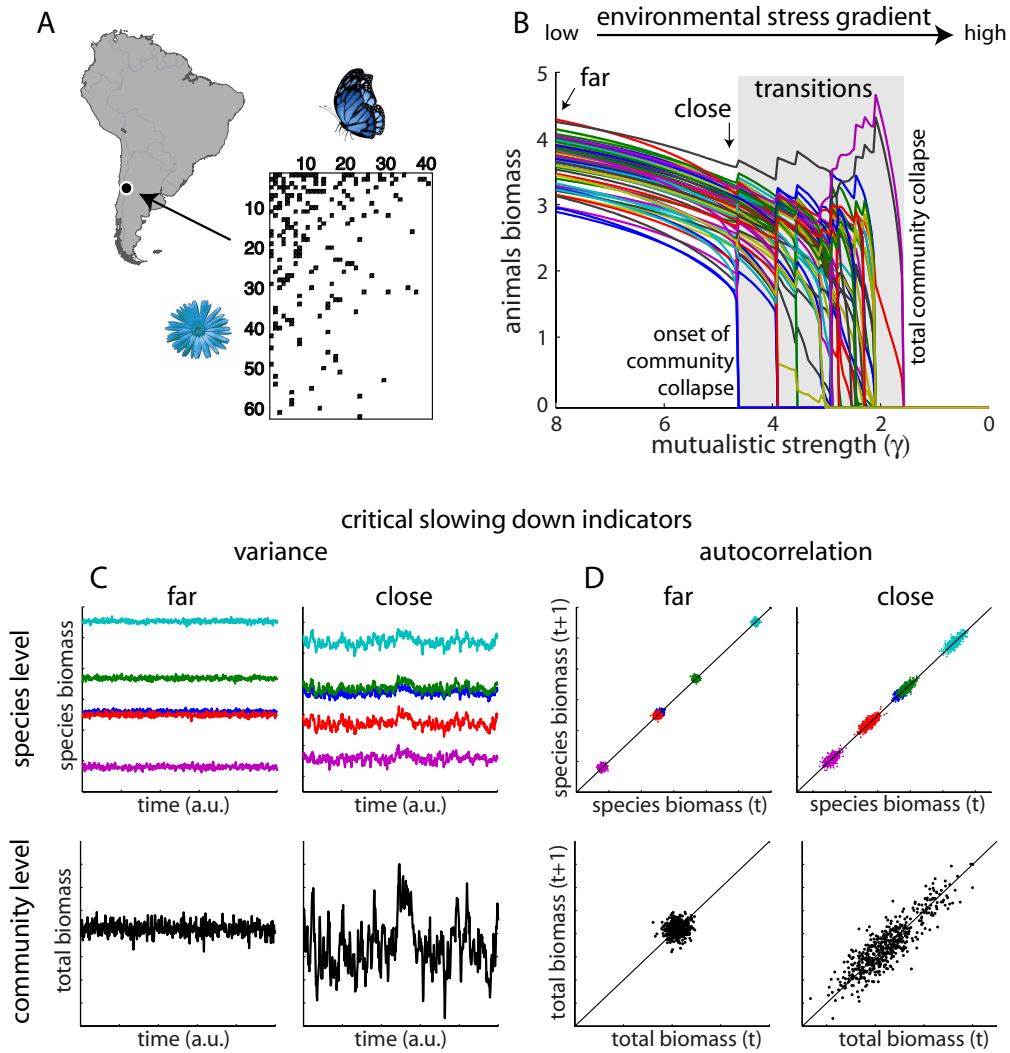


Figure 1

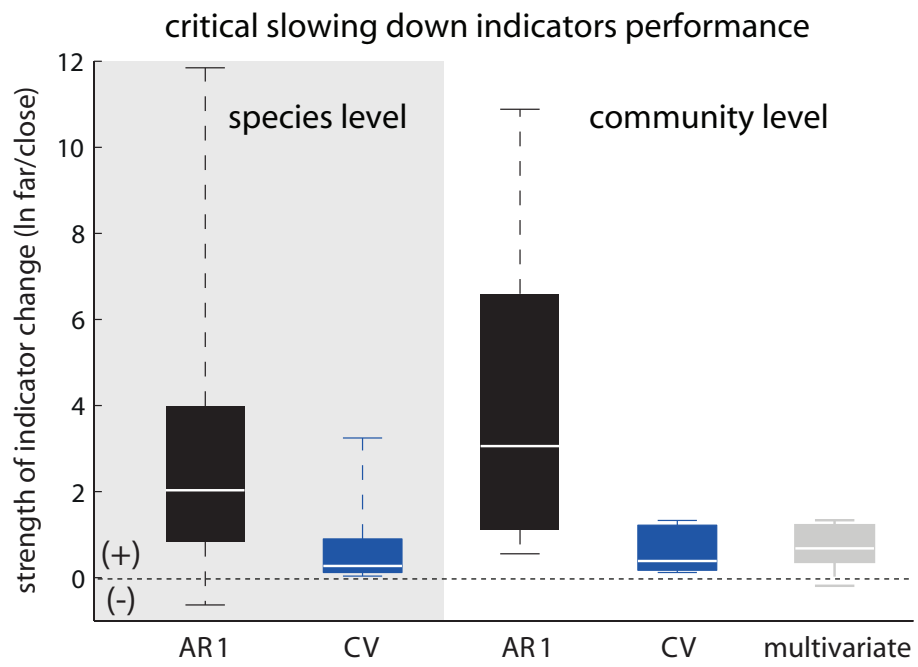


Figure 2



CSD species indicators ~ species-traits

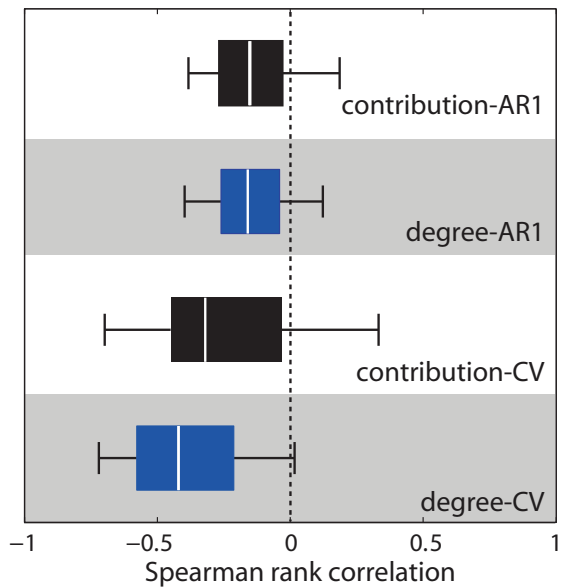


Figure 3

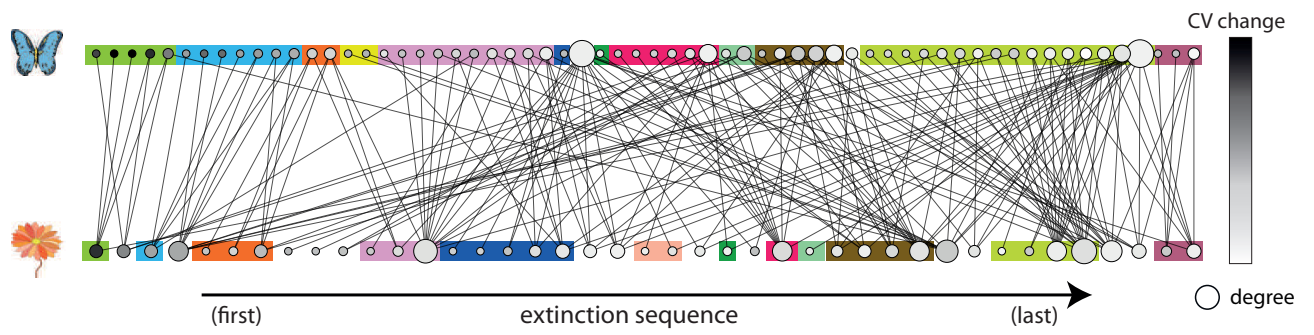


Figure 4

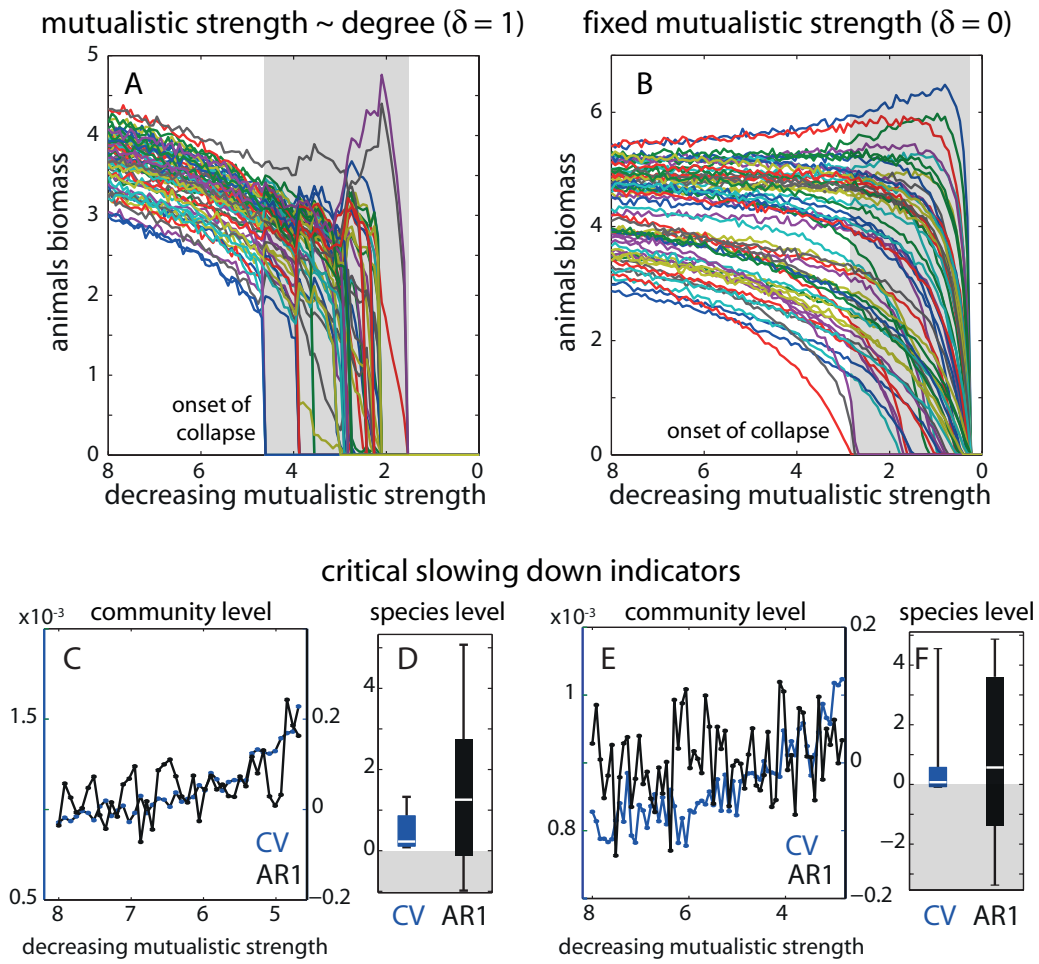


Figure 5