

Species' traits and food-web complexity interactively affect a food web's response to press disturbance

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Abstract. Given current levels of biodiversity loss and environmental change, studies of how food webs respond to disturbance should broaden their focus beyond short-term disturbances to explore the effects of long-term, “press” disturbances. Press disturbances often disproportionately impact one or a few species, but these impacts invariably propagate to the remaining species in the food web. Additionally, the way species interact with each other within the food web influences the impact they have on the rest of the food web if it is disturbed. Here, we investigate the effect of species-level press disturbances in a large set of model food webs. We simulated disturbances as a reduction in growth rate of a single species within the food web, which is analogous to a targeted disturbance such as selective fishing. In these simulations, we were particularly interested in the resistance of the food web—the magnitude of disturbance it could tolerate before any species went extinct. We found that more highly connected and biodiverse food webs had lower resistance and were more likely to lose species at a low level of disturbance than sparsely connected food webs with few species. Food-web complexity also influenced which species were likely to go extinct due to the disturbance. At low species richness and/or low connectance, food webs could tolerate a large disturbance, and it was usually the focal species which went extinct. In contrast, webs were less stable at higher levels of complexity and a small disturbance rapidly propagated and caused the extinction of a non-focal species. Lastly, the disturbed species' traits were also important: Disturbance of a species with few interactions usually resulted in its own extinction, while disturbance of a species with many interactions more often caused the extinction of the disturbed species' predator(s). Likewise, the trophic level of the disturbed species influenced which species went extinct, although this was modulated by the complexity of the food web. Overall, our study indicates that both the traits of disturbed species and the complexity of the food web need to be considered in attempts to predict or manage the ecological impact of press disturbances.

Key words: degree; extinction; resistance; stability; trophic level.

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INTRODUCTION

Ecological communities are made up of interacting species and populations which, through time, are subject to periodic disturbances (Begon et al. 2006). These disturbances often remove

individuals and resources from the community and can significantly alter the structure and dynamics of the community as a result (Parker and Hurlbert 2006, Houseman et al. 2008). Disturbance, however, is a broad term, and different kinds of disturbances can cause different effects on

communities (Bender et al. 1984, Parkyn and Collier 2004, Parker and Huryin 2006, Houseman et al. 2008, Montoya et al. 2009). In an ecological context, there are two broad classes of disturbance: pulse disturbances and press disturbances (Bender et al. 1984). A pulse disturbance is best described as a short-term, discrete event, such as a storm. Although the event may be powerful, it subsides after a finite period of time. A press disturbance, on the other hand, is a long-term event, such as a change in nutrient level due to pollution or a change in temperature due to changing climate (Bender et al. 1984). Many theoretical studies of food-web disturbances focus exclusively on pulse disturbances (May 1972, Neubert et al. 2004, Allesina and Tang 2012, Tang and Allesina 2014); yet as ecosystems respond to ever-increasing anthropogenic impacts, press disturbances are becoming the norm for communities globally (Millenium Ecosystem Assessment, 2005; IPCC, 2014). As such, we desperately require a greater understanding of the effects of these kinds of disturbances.

It is not uncommon for press disturbances to affect one or a few species in the community disproportionately, for example, the harvesting of marine species (Sharp and Pringle 1990, Daskalov 2002, Benoît and Swain 2008, Estes et al. 2011). However, as species within a community interact in many ways, even species which are not directly affected by the disturbance can be impacted, in some cases even more severely than the originally disturbed species (Zavaleta et al. 2001, Sahasrabudhe and Motter 2011, Säterberg et al. 2013). This can lead to significant restructuring or even collapse of communities, as has occurred in a number of marine ecosystems due to overfishing of large consumer species (Sharp and Pringle 1990, Jackson et al. 2001, Daskalov 2002, Benoît and Swain 2008). Theoretical studies investigating the effect of press disturbances have largely focused on the robustness of food webs to species removal (Dunne et al. 2002, Estrada 2007, Dunne and Williams 2009, Curtsdotter et al. 2011), but a species does not have to be entirely removed to cause secondary or “non-focal” extinctions (Säterberg et al. 2013). In addition, many empirical press disturbances initially manifest themselves simply as a decrease in a species’ growth rate or increased mortality rate (Anderson et al. 2011, Graham et al. 2014). To effectively manage

communities, we therefore need to understand how the community will respond to sublethal disturbances and, more importantly, the point at which these disturbances actually cause extinctions.

An important factor underlying a community’s response to a disturbance is the complex network of interactions between the species within the community (Williams and Martinez 2000, Montoya et al. 2006, Neutel et al. 2007). Properties of this network, such as the number of interacting species and the density of interactions between them, can have a significant impact on the community’s response (Gardner and Ashby 1970, May 1972, Pimm 1984, Haydon 1994, Dunne et al. 2002, Wootton and Stouffer 2016). Similarly, the network traits (henceforth traits) of the disturbed species can influence how it affects other species within the community (Montoya et al. 2009, Curtsdotter et al. 2011, Donohue et al. 2013). Each species interacts uniquely within the food web—some interact with many species while others interact with few, and some are predators while others are producers. A generalist may be more likely to cause non-focal extinctions within the community than a specialist because generalists interact directly with a large proportion of species in the community (Curtsdotter et al. 2011). Top predators may be more likely to cause the non-focal extinction of species they do not directly interact with because top predators are important for regulating dominant and competitive species (Estes et al. 2011). If this is the case, having knowledge about the traits of the disturbed species may greatly increase our ability to predict the outcome of disturbance.

To gain insight into these questions, here we compared the response of simulated networks to incremental and sublethal press disturbances. We determined how the properties of food webs and the traits of a disturbed species affected how communities responded to species-specific press disturbances, such as those caused by overharvesting of a particular species. We focused on resistance as a measure of how a community responded to a press disturbance by quantifying resistance as the smallest magnitude of disturbance required to cause an extinction in the community (Ives and Cardinale 2004, Lake 2013). A more resistant community could withstand a larger disturbance than a less resistant

community. Notably, the extinction marking the end of the disturbance was not always the extinction of the disturbed species. We therefore also investigated whether these species-specific disturbances tended to result first in the extinction of the species being disturbed or in a non-focal extinction. Specifically, we investigated (1) how the parameters of the network affected the food web's resistance and (2) how the traits of the disturbed species affected the outcome of disturbance. The results of our study indicate that properties of the community and the species being disturbed interactively affect the outcome of the disturbance and shed new light on what properties of communities or species make them more or less resistant to press disturbances.

METHODS

Simulating model communities

To produce simulated networks with realistic structures, we used the niche model (Williams and Martinez 2000, Dunne and Williams 2009, Stouffer and Bascompte 2011) to generate networks with species richness $S \in [10, 100]$, at intervals of two species, and connectance $C \in [0.05, 0.4]$, at intervals of 0.05. Connectance is defined as the fraction of possible interactions which are actually observed in the community ($C=L/S^2$), where L is the total number of links between species in the network. For each of the 168 combinations of S and C , we generated 100 different networks, discarding any that contained species which shared no interactions with other species in the network, and checked their stability properties (see below) until we had a total of 100 stable networks for each combination of S and C . For some combinations of S and C , networks were less likely to be stable. In these cases, we generated new networks up to three times to try and obtain all 100 stable networks, although in some cases we still ended up with fewer than 100.

To define the dynamics of all networks, we randomly assigned per capita effects α_{ij} of all interactions from a normal distribution $N(0, 1)$. Each value α_{ij} quantifies the effect of an individual of species j on an individual of species i . Thus, when α_{ij} was a negative value, species j has a negative impact on species i , indicating that species j is the predator and species i the prey. To make

all interactions predator-prey, we set α_{ji} to a positive value when α_{ij} was a negative value and vice versa. Other than ensuring opposing sign, the values α_{ij} and α_{ji} were assigned independent of each other. We also set the diagonal values α_{ii} , the effect of species on themselves, to -1 . While the relationship of diagonal values to each other and to off-diagonal values is important for the stability of the food web and our choice of diagonal values affects this (Haydon 1994, 2000, Allesina and Tang 2012, James et al. 2015), we chose to use a common value for all diagonal values for simplicity, to remove an additional source of variability between networks and to make our results more directly comparable with previous work using the same assumption (e.g., May 1972, Novak et al. 2011, Allesina and Tang 2012).

To fully define the dynamic behavior of these communities, we used a system of generalized Lotka–Volterra dynamical equations (Pimm and Lawton 1978, Emmerson and Yearsley 2004):

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^S \alpha_{ij} X_i X_j \quad (1)$$

where X_i represents the population density of species i and r_i is the per capita growth rate of species i . Once biomasses and interaction coefficients were set, we could then solve for growth rate (r_i^*) in Eq. 1 when the community was at equilibrium. To ensure that all networks were feasible (i.e., all biomasses were positive) and to remove an additional source of randomness, we set all equilibrium biomasses $X_i^* = 1$. We also verified that all networks predisturbance were both locally stable and feasible. A community is locally stable if it returns to its original equilibrium point after a small disturbance based on the sign of the largest eigenvalue (May 1972, Pimm and Lawton 1977).

Simulating disturbances

We then subjected each network to simulated press disturbances to quantify their resistance. To do so, we individually decreased the growth rate of each species in every network in incremental steps of $0.001r_i^*$ (where r_i^* is their initial growth rate at equilibrium) and then, keeping interaction coefficients and all other species' growth rates constant, solved analytically to determine the new equilibrium biomasses and

whether the disturbed system was stable. We continued decreasing the growth rate of the focal species and resolving for the new equilibrium until any species' biomass dropped to or below 0, signifying an extinction. This extinction could be of the species being disturbed—a focal extinction—or the extinction of another species—a non-focal extinction (Säterberg et al. 2013). Across all simulated communities, this corresponded to over 1.7×10^8 simulated disturbances.

We quantified species-level resistance as the proportional change in growth rate required to reach the first extinction. Mathematically, this is expressed as $(r_i^* - r_i^b)/r_i^*$, and we call this quantity resistance as a more resistant network should tolerate a larger change in growth rate of the disturbed species before causing an extinction. When defined in this way, for example, a value of resistance of 0.5 indicates the food web can withstand the disturbed species' growth rate being decreased by half before causing an extinction. Note that it is possible for a species' growth rate to be decreased by more than 100% as that only implies that the growth rate is becoming more and more negative. If the biomass of a non-focal species dropped to or below zero (a non-focal extinction), we removed the extinct species from the food web entirely (growth rate, biomass, and all interactions set to zero) and then reassessed the food web's local stability without that species. As the largest eigenvalue was equal to zero at the point of extinction, we did this by decreasing the focal species' growth rate by up to five more steps of $0.001r_i^*$ and checked whether the network reached a new stable configuration.

As a result of these simulated press perturbations, we had S species-specific values of resistance for each network. To make this measure of stability analogous to network-wide properties like resilience and reactivity (Holling 1973, Neubert and Caswell 1997), we selected the minimum value of resistance for all species in each network to estimate the resistance for the entire network when considering the network as a whole. We chose to use minimum resistance as this was the most analogous to resilience, which concentrates on the dominant eigenvalue, and also because it provides the most conservative estimate. To check the effect of the decision, we repeated all of our analyses using the mean value of resistance for the network, and this did

not qualitatively change our results (results not shown here).

Network-level statistical analyses

To quantify how network resistance changed across size and connectance, we fit a generalized linear model with the `glm` function in R with Gaussian family and log link function. The model included terms for size, connectance and their interaction as predictors and the log of resistance as the dependent variable.

We also looked at the outcome of disturbance—whether the extinction was of the focal species or a non-focal extinction and, if it was a non-focal extinction, whether the network reached a new locally stable equilibrium once that species was lost. To consider how the outcome of disturbance changed across size and connectance, we used a binomial generalized linear model with each network's fraction of disturbances which resulted in a focal extinction as the dependent variable, and size, connectance, and their interaction as independent variables. Of those disturbances which resulted in a non-focal extinction, we were also interested in determining whether the network would be stable again without the secondarily extinct species. To do so, we again used a binomial generalized linear model with the same independent variables but with each network's fraction of non-focal extinctions that were stable post-extinction as the dependent variable. For each of the above models, R^2 values were calculated as $1 - (\text{residual deviance})/(\text{null deviance})$ (Faraway 2006).

Species-level statistical analyses

Finally, we investigated how the traits of the disturbed species impacted how a community responded to disturbance. The two traits we considered were trophic level—how high in the food web the species fed—and degree—how many interactions the species had with other species (Polis and Strong 1996). Here, degree included all interactions a species has with other species in the community, whether as predator or prey. Trophic level was quantified as the mean number of species through which energy passed, from primary producers to the focal species, weighted by per capita interaction strength as in Levine (1980). Thus, a primary producer had a trophic level of zero, a herbivore of one, and

predators and omnivores of successively higher numbers.

We first investigated how these traits affected whether a focal or non-focal extinction occurred. We then took the subset of disturbances which resulted in a non-focal extinction and investigated how the focal species' traits affected whether the secondarily extinct species was a species which interacted directly with the focal species or not. Finally, we took the subset of disturbances which resulted in the extinction of a directly interacting species and investigated how the focal species' traits affected whether the secondarily extinct species was a predator or prey of the focal species. We used three binomial mixed-effects models for each trait to examine these relationships between species' traits and the outcome of disturbance. For each model, the binary dependent variables indicated either focal (0) or non-focal (1) extinction; indirectly (0) or directly (1) interacting species; or prey (0) or predator (1) of the focal species. Network size, network connectance, trait (degree or trophic level of the focal species), and all possible interactions between them were the independent variables, plus a random effect for network. The random effect accounts for the fact that we have included multiple species from each network in the model, but those species are not independent as the local stability of the network is an emergent property of all species and all interactions therein. We used marginal (R_m^2) and conditional (R_c^2) R^2 values to assess the fit of our mixed-effects models (Nakagawa and Schielzeth 2013). R_m^2 explains the fit of the model when considering only fixed effects (in this case, size, connectance, and species' traits), while R_c^2 explains the fit of the model when considering both fixed and random effects.

When running the species-level models, we only included the appropriate subset of the total data for each successive model. Thus, the first model—focal vs. non-focal extinction—included all the data, as all simulated disturbances resulted in either a focal or non-focal extinction. The second model—directly or indirectly interacting species—only included those disturbances which resulted in a non-focal extinction. The third model—predator or prey—only included those disturbances which resulted in the non-focal extinction of a directly interacting species. While removing data that is surplus to

the specific question of interest allowed a finer understanding of what happened at each level, it can complicate trying to identify what is most likely to happen as the result of a disturbance of any particular species. For example, of those disturbances which result in a non-focal extinction, species with low degree may be more likely than species with high degree to cause indirectly interacting species to go extinct. There were, however, far fewer non-focal extinctions caused by species with low degree than high degree. When this is taken into account, species with low degree are much *less* likely to cause the non-focal extinction of an indirectly interacting species than species with high degree, not because they are more likely to cause the non-focal extinction of a directly interacting species (which is what our original model determined) but because they are more likely to cause a focal extinction. Therefore, to visualize what is actually likely to happen as the result of any given disturbance, we focus our analysis and results on the relationships which would be observed if all the data were included in each model as this gives a more accurate view of how likely each outcome of disturbance is, regardless of the other outcomes. Accordingly, we calculated the probability of a disturbance causing the extinction of an indirectly interacting species, $P(\text{indirect})$, as the probability of a disturbance causing a non-focal extinction, $P(\text{non-focal})$, multiplied by the probability that a disturbance *which caused a non-focal extinction* caused the extinction of an indirectly interacting species, $P(\text{indirect} | \text{non-focal})$; that is, $P(\text{indirect}) = P(\text{indirect} | \text{non-focal}) P(\text{non-focal})$. Similarly, the probability that a disturbance resulted in the extinction of the disturbed species' predator was given by $P(\text{predator}) = P(\text{predator} | \text{direct}) [1 - P(\text{indirect})]$. We have included an Appendix S1 containing the coefficients and their uncertainties for each of these models.

RESULTS

Network level

We were first interested in how resistance changed across size and connectance of a food web. We found that networks with the fewest species and lowest connectance had the highest resistance, while the most complex networks (those with high connectance and many species)

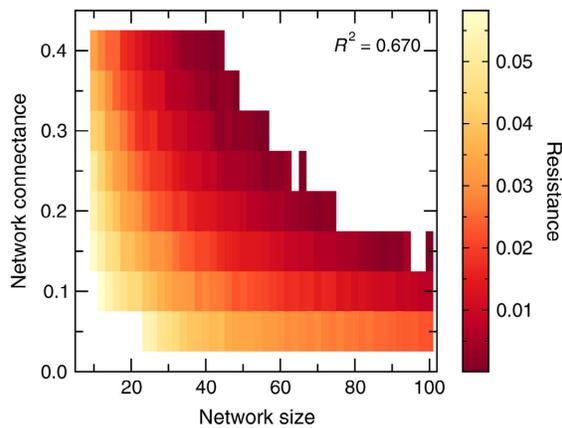


Fig. 1. Large and highly connected networks are the least resistant, while the simplest networks are the most resistant. Color represents the magnitude of resistance for a given combination of size and connectance, with red representing less resistant communities and yellow more resistant. Each cell shows an average of all values of resistance for simulated communities with that combination of size and connectance.

had the lowest resistance ($R^2 = 0.67$; Fig. 1). Across all disturbances, 59% resulted in a focal extinction (extinction of the disturbed species itself). Of those 41% which resulted in a non-focal extinction, 66% regained local stability after the secondarily extinct species was lost. At lower values of size and connectance, we found that press disturbances were much more likely to result in a focal extinction (approximately 80% of the time, $R^2 = 0.67$; Fig. 2a). Of those disturbances which did result in a non-focal extinction, the network was more likely to be stable without the secondarily extinct species at these low values of size and connectance ($R^2 = 0.37$; Fig. 2b). At higher levels of network complexity on the other hand, disturbances almost always resulted in a non-focal extinction, and it was rare that these networks were stable without the secondarily extinct species.

Species level

Having determined how the properties of the network affected the resistance, we then explored how the traits of the disturbed species affected the outcome of disturbance. In addition to the

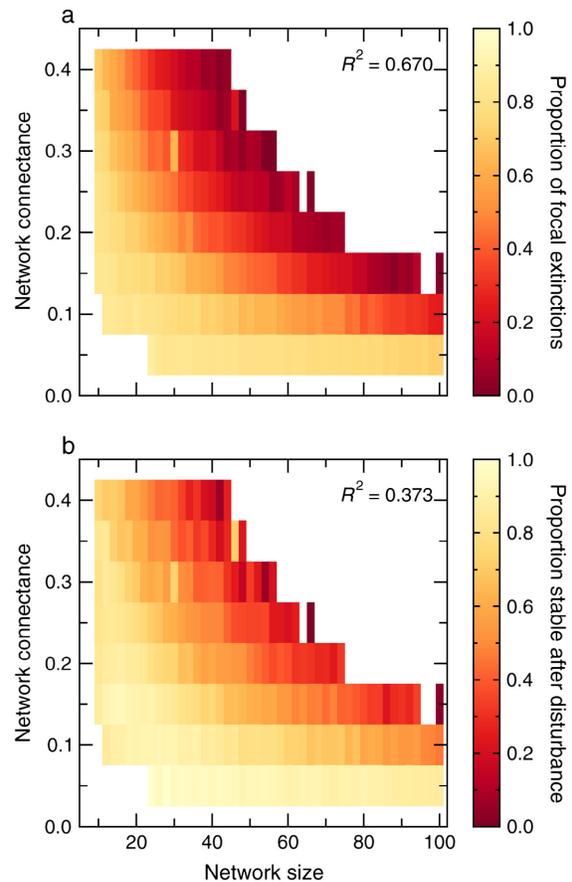


Fig. 2. The consequences of press disturbance depend on the size and connectance of the network. (a) At low levels of species richness and connectivity, most disturbances result in a focal extinction, while most disturbances result in a non-focal extinction in more complex communities. Red indicates a higher proportion of non-focal extinctions, whereas yellow indicates a higher proportion of focal extinctions. (b) Of those disturbances which result in a non-focal extinction, the community is stable without the lost species more frequently at low levels of size and connectance than it is in more complex communities. Red indicates a higher proportion of disturbances per network which are unstable when a species is lost, while yellow indicates a higher proportion of disturbances per network which are stable after a species is lost. Each cell shows the mean proportion of focal extinctions (panel a) or proportion of non-focal extinctions which were stable after the disturbance (panel b) across all simulated food webs with that combination of size and connectance.

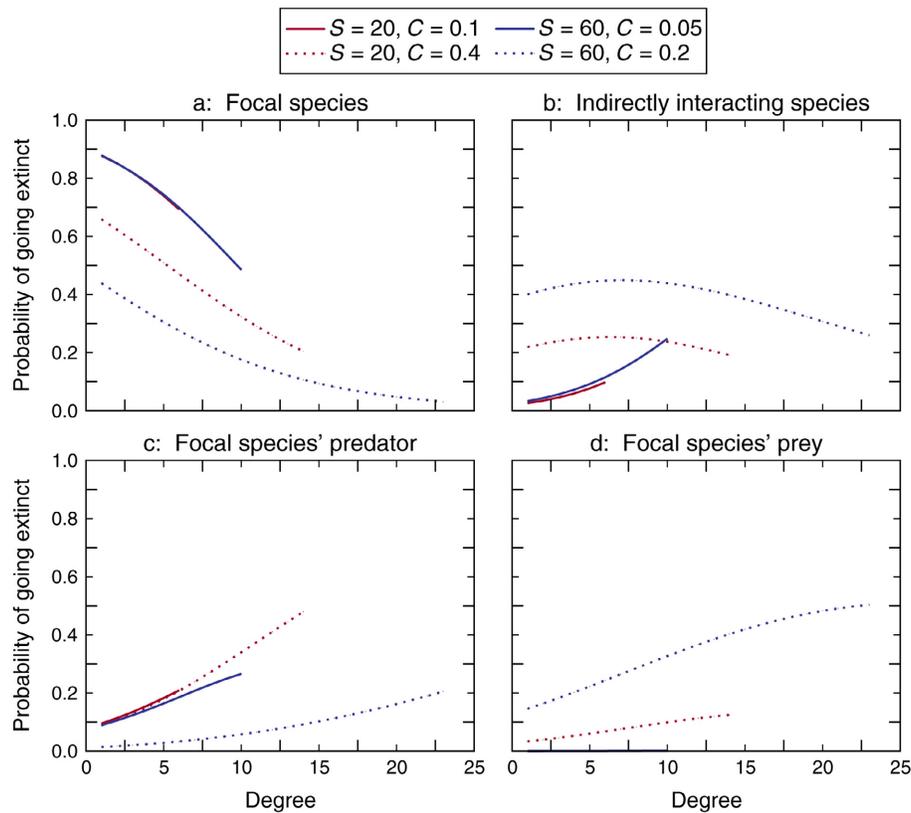


Fig. 3. The degree of the disturbed species affects the type of extinction and relationship of the extinct species to the disturbed species, as predicted by our binomial mixed-effects models. (a) When species with low degree are disturbed, they are more likely than species with high degree to go extinct themselves before causing a non-focal extinction. (b) Disturbance of species with intermediate degree is more likely to result in the non-focal extinction of indirectly interacting species, especially in food webs with high levels of connectance. (c, d) Species with high degree are more likely than species with low degree to cause the non-focal extinction of their predators or prey when disturbed. Lines in all panels are truncated to cover only those values of degree which occurred at the relevant levels of size and connectance.

59% of disturbances that resulted in a focal extinction, 24% resulted in the non-focal extinction of a species which did not interact directly with the focal species, 16% resulted in extinction of a predator of the focal species, and 1% resulted in extinction of a prey species of the focal species. Species with low degree (fewer interactions) were more likely to go extinct themselves when disturbed ($R_m^2=0.27$, $R_c^2=0.65$), while species with an intermediate degree were more likely to cause the non-focal extinction of a species they did not directly interact with, especially in food webs with high levels of connectance ($R_m^2=0.135$, $R_c^2=0.452$). Overall, species with high degree were more likely to cause extinction of their

predators, while in networks of high species richness and high connectance species with high degree were more likely to cause extinction of their prey ($R_m^2=0.33$, $R_c^2=0.78$; Fig. 3).

In food webs with low levels of connectance, species were most likely to cause a focal extinction when disturbed, particularly those species with a higher trophic level ($R_m^2=0.25$, $R_c^2=0.62$). In food webs with high connectance and low species richness, disturbance of high-trophic-level species was most likely to result in extinction of an indirectly interacting species ($R_m^2=0.18$, $R_c^2=0.53$), while disturbance of low-trophic-level species was more likely to result in extinction of their predators ($R_m^2=0.39$, $R_c^2=0.86$). It was rare

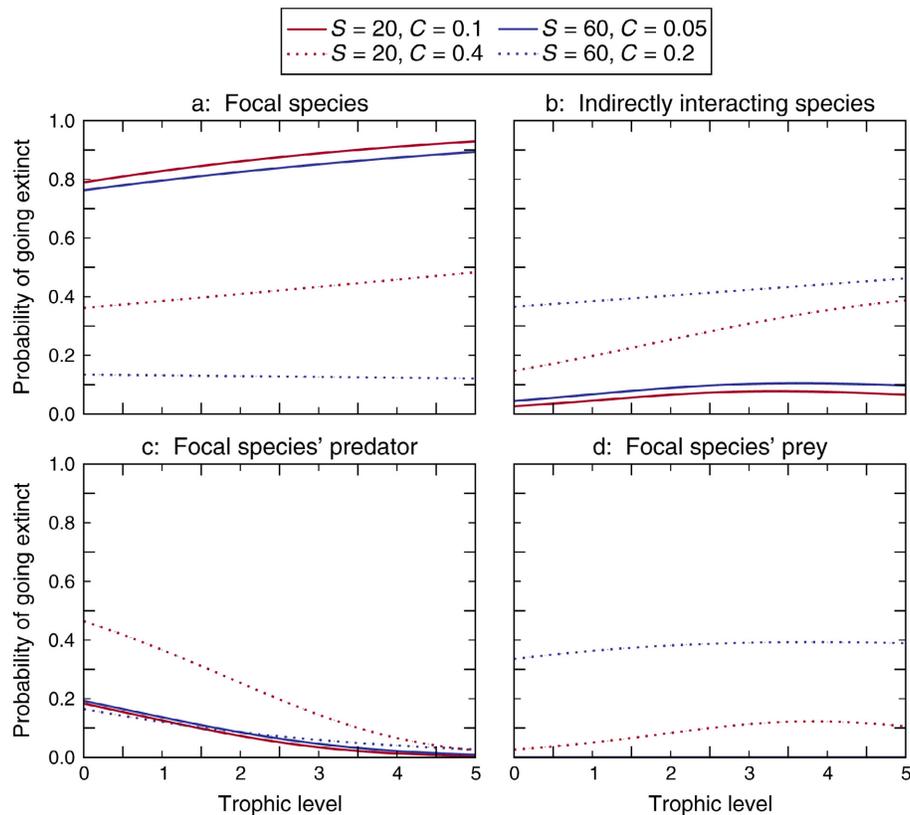


Fig. 4. The type of extinction and relationship of the extinct species to the disturbed species depends on the trophic level of the disturbed species, as predicted by our binomial mixed-effects models. (a) Disturbance of low-trophic-level species is slightly more likely to result in a non-focal extinction than disturbance of high-trophic-level species, particularly in communities with lower connectance. (b) Disturbance of high-trophic-level species is more likely to cause the non-focal extinction of indirectly interacting species, particularly in food webs with high levels of connectance. (c, d) Species with low trophic level tend to cause the extinction of their predators when disturbed, while species with high trophic level are more likely to cause the extinction of their prey species.

for a disturbance to result in extinction of the focal species' prey; however, this occurred most commonly in networks of high connectance and high species richness (Fig. 4).

DISCUSSION

We found that the resistance of a community to a single-species press disturbance decreased as communities increased in species richness and/or connectance. This agrees with other theoretical research on both press and pulse disturbances that has found an inverse relationship between complexity and stability (May 1972, Pimm and Lawton 1978, Yodzis 1981, Allesina and Pascual 2008). At high levels of species richness and

connectance, there are many direct and indirect interactions between species such that two species which are not directly connected may still have a large effect on each other (Yodzis 1988, Laska and Wootton 1998, Wootton 2002, Montoya et al. 2005, Stouffer and Bascompte 2011) and a small disturbance can propagate rapidly throughout the food web (Abrams 1992, Menge 1995, Montoya et al. 2009, Rohr et al. 2014). Indeed, we found that, as complexity increased, the number of disturbances which resulted in a non-focal extinction rather than extinction of the focal species increased to almost 100%. Clearly, while the disturbance was almost always insufficient to cause the focal species to go extinct, it was enough to disrupt the delicate balance

required to keep all interacting species at equilibrium and cause another species to go extinct. Frequently (>50%), the network was able to reach a stable configuration after this non-focal extinction; however, this occurred less often as complexity increased. This indicates that species in highly complex networks were simply too interdependent and could not continue to coexist when one was lost. The loss of the first species is also likely to lead to a cascade of further extinctions, an effect which has been documented in empirical and theoretical experiments (Petchey et al. 2008, Dunne and Williams 2009, Kaneryd et al. 2012, Sanders et al. 2013).

Clearly, the properties of the network as a whole give substantial insight into how the community will respond to a disturbance. We found, however, that for disturbances where only a single species bore the brunt of the disturbance, the network traits of that species also strongly affected the outcome of the disturbance. Disturbance of species with low degree usually resulted in a focal extinction. This is likely because the focal species either can no longer withstand predation when disturbed and goes extinct before its predator does, or, in the absence of predators, its prey are released from predation and thus will not go extinct before the disturbed species itself succumbs to its decreased growth rate. Species with higher degree, on the other hand, directly affect many other species which in turn can affect many others (Symondson et al. 2002, Orlando and Hall 2015). Disturbance of these species therefore may lead to a significant alteration in biomass of one of these interacting species, due to decreased predation or prey resources from the disturbed generalist, which in turn may lead to non-focal extinctions, even of those species which the focal species does not directly interact with (Quince et al. 2005, Curtsdotter et al. 2011). Other studies have also found that disturbance of generalists caused more non-focal extinctions than disturbance of specialists (Quince et al. 2005, Dunne and Williams 2009, Curtsdotter et al. 2011), although Montoya et al. (2009) found that disturbance of specialists had larger net effects on the rest of the food web than that of generalists. We also found that species with the highest degree tend to be most likely to cause the extinction of species they interact with directly. This is to some extent simply due to the fact that generalists also

cause more non-focal extinctions than specialists. When we considered only disturbances which resulted in a non-focal extinction, it became apparent that it is only in food webs with a high connectance level that species with high degree tend to cause extinction of their predators or prey. In these food webs, species with high degree are interacting directly with a large portion of the food web and it is therefore not surprising that the secondarily extinct species is usually one the focal species interacts with directly.

Species with a high trophic level are more likely to cause focal extinctions when disturbed, particularly in food webs with low species richness and connectance. In these food webs, most disturbances result in a focal extinction; however, when species with a low trophic level in these networks are disturbed, on the occasions when they cause a non-focal extinction, it is almost always of their predators. While it is not surprising that low-trophic-level species cause the non-focal extinction of their predators when disturbed, it is interesting that they very rarely cause the extinction of an indirectly interacting species such as an apparent competitor (Holt 1977). In these cases, it seems that the predator's loss of fitness due to the decreased biomass of their prey outweighs the impact of the disturbance on any other species. In food webs with high connectance, disturbances frequently result in the non-focal extinction of an indirectly interacting species, especially if the disturbed species has a high trophic level. Top predators are important for balancing competing species and preventing them from outcompeting each other (Paine 1992, Daskalov 2002, Rayner et al. 2007). When the top predator is disturbed, these competing species are released from this control. The increased biomass of one or both of these released species leads to extinction of their prey and/or competitors—species which are not directly interacting with the focal species (Paine 1966, Terborgh et al. 2001, Estes et al. 2011, Donohue et al. 2013). The few disturbances which result in extinction of the focal species' prey are caused by the disturbance of species in networks with high species richness and connectance when considering either degree or trophic level of the focal species. In these networks, there are many indirect interactions between species and which may allow another species to outcompete or overexploit the focal species' prey, despite the

decrease in predation from the focal species. In contrast, a disturbance essentially never caused the extinction of the focal species' prey in networks of low connectance. Here, there are insufficient indirect interactions to outweigh the effect of decreased predation by the focal species and cause the extinction.

In constructing our food webs, we made some assumptions which may have affected the results we observed and the implications of which could warrant future study. For example, to remove some of the variability between networks and thus focus more closely on the impact that varying levels of complexity have on food webs, we set all equilibrium biomass values $X_i^* = 1$ and all intraspecific interactions $a_{ii} = -1$. It is possible that such food webs behave differently than food webs with a more realistic biomass structure, where top predators had lower biomasses than species at lower trophic levels. In our simulations, predators may thus have a disproportionate impact on their prey due to their disproportionately high biomass. We tested the impact of this choice of biomass structure by repeating the analyses on food webs which had top predators with the lowest biomass and primary producers with the highest biomass. While we found that this did not qualitatively alter our results, further investigation of other more realistic biomass structures may yield different results, particularly when considering how traits such as trophic level affect the outcome of disturbance. Our second assumption, setting all intraspecific interactions to -1 , is a very common assumption for matrix models; however, it is also known to affect the behavior of the model in undesirable ways (Haydon 1994, 2000, Allesina and Tang 2012, James et al. 2015). For example, it can overestimate the stability of the system (James et al. 2015), and the stability of the system can be further enhanced simply by making the diagonal values more negative (Haydon 1994). Lastly, we worked with a linear model of species interactions and type I functional responses, a decision that we made to allow analytical tractability. On the other hand, empirical evidence is tipped in favor of more complex alternative models (Novak and Wootton 2008) and changes to the functional responses may yield different behavior and results. While we used these assumptions to allow for simplicity, mathematical tractability and comparison with

previous studies using similar assumptions (e.g., May 1972, Novak et al. 2011, Allesina and Tang 2012), there is scope for future studies to explore more realistic assumptions and determine how these affect these results.

CONCLUSIONS

Food-web complexity and species' traits interact in determining a food web's response to disturbances. This observation has important implications for conservation and management of natural systems undergoing press disturbances. While the harvest of some species may be more catastrophic than others, it is also important to maintain the structure of the food web as a whole to maximize resistance.

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