

Fitting species into the complexity- stability debate

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*Dedicated to my family for their endless
support, love and encouragement*

Abstract

ECOLOGICAL COMMUNITIES — groups of interacting species — are subject to a variety of disturbances. Understanding responses to these disturbances is a primary goal of community ecology. The structural complexity of the community and the traits of the community's constituent species are both known to have a significant impact on a community's response to a disturbance. In this thesis, we investigated how these two scales — the community level and the species level — interactively affected community responses to both short and long term disturbances.

Our first hypothesis was that interaction strength would be weaker in species with many interactions when compared to species with fewer interactions. To test this hypothesis, we used simulated food webs and found that, in locally stable food webs, species with many interactions tended predominantly to have interactions with predators or with prey. While these many predator or prey interactions were weak, they tended to be balanced by a few interactions of the opposite type (with prey or predators) which were stronger than average. The structure of the network, where species had predominantly one type of interaction, was essential for this relationship between the number and strength of interactions to arise.

Our second study investigated how food webs of varying size and connectance respond to press and pulse disturbances. Many studies of food web stability only focus on the response to short term or "pulse" disturbances, however, as anthropogenic impacts on food webs increase, it is important to increase our understanding of food web responses to long term or "press" disturbances and determine whether they follow the same pattern as pulse disturbances. We found that more species rich and connected food webs were less stable to both types of disturbance and the more stable a food web was

to a pulse disturbance, the more stable it was to a press disturbance as well. We also found that the traits — trophic level and number of interactions — of the disturbed species impacted a food web's resistance to a press disturbance. Food webs were less resistant to the disturbance of species with many interactions or low trophic level than species with few interactions or high trophic level. The strength of species' effects on stability was also moderated by the structural complexity of the food web.

Together the work that makes up this thesis suggests that, to understand the stability of food webs to any kind of disturbance, we should consider both the structure of the network and the traits of the species embedded within it. While we found that networks were more vulnerable to disturbance of certain species than others, this observation also depended on the structure and complexity of the community they existed in. This has important implications for communities subject to disturbances, especially those disturbances which alter the way in which communities are structured and species interact.

Introduction

THE DIVERSE RANGE of species we observe in ecosystems around the world interact with each other in a variety of ways to form ecological communities. Some communities, such as coral reefs, are composed of many species while others, such as Arctic systems, contain few. In some communities, populations of each species remain relatively stable in size; in others they fluctuate wildly or collapse entirely, even in the absence of obvious external forcing (Murdoch, 1975). In addition to this intrinsic variation, communities are subject to natural and anthropogenic disturbances including fire, storms, and habitat destruction. There are many factors affecting a community's "stability" and response to disturbances. For example, complexity — the number of interacting species and how many interactions there are between them — and structure — how these interactions are arranged — of the community have strong effects on community stability (McCann, 2000; Rooney and McCann, 2012). The traits of the interacting species are also important, with some species having a larger effect on stability than others (Quince et al., 2005; Dunne and Williams, 2009; Curtsdotter et al., 2011), as is the type of disturbance (Bender et al., 1984; Glasby and Underwood, 1996), and even the definition of stability (Ives and Carpenter, 2007; Donohue et al., 2013). Disentangling these factors is one of the oldest threads of ecological research (Odum, 1953; MacArthur, 1955; Lewontin, 1969), but has renewed urgency as ecosystems face extreme levels of biodiversity loss and environmental change (Millenium Ecosystem Assessment, 2005; IPCC, 2014).

The complexity-stability debate

There are many aspects and definitions of stability, but collectively they refer to the ability of a community resist or recover from change (Ives and Carpenter, 2007). Diversity — the number of species in a community — is one of the most conspicuous ways in which communities differ and therefore one of the earliest aspects studied in relation to stability (Odum, 1953; Elton, 1958; Conrad, 1972; McCann, 2000). Early understanding of community stability held that diversity increased stability (Odum, 1953; MacArthur, 1955; Elton, 1958). This was the logical conclusion from observations of diverse communities, such as tropical forests, which remained constant in relative abundance over time while more species-poor communities often experienced wild fluctuations, such as insect outbreaks in boreal forests (Murdoch, 1975). MacArthur (1955) took those observations one step further and developed a mathematical framework to try and explain how diversity lead to increased stability. This framework used food webs — the network of predator-prey interactions describing who eats whom — to analyze both the number of species and the number of interactions between them. His concept was that if a species with many predators suddenly experienced a large increase in abundance, the effect of this overabundance on the predators would be diluted and the effect on any one predator species would be minimal. If, however, a species with only one predator experienced a large increase in abundance, that fluctuation would be passed on in full to the predator. Similarly, if a prey species became scarce, a predator with many prey would not suffer as strongly as a predator which fed exclusively on the scarce prey. Thus stability could be increased by increasing either the number of species in a community or the number of interactions between them. These two parameters — number of species and number of interactions between them — are collectively termed “complexity” (May, 1972; McCann, 2000). A more complex food web is one with a large number of species and many interactions between them while a simple food web is one with few species or interactions.

The early observations of diverse ecosystems and MacArthur’s framework were, however, based largely on observation and speculation (McCann, 2000). The first attempt to numerically determine the relationship between diversity and community stability revealed the exact opposite of these early studies (May, 1972). May (1972) used a mathematical model to simulate communities of varying species richness and connectance (the proportion of possible interactions

between species which actually occur) and determine their stability. He showed that the more diverse a community was and/or the more interactions between species, the *less* likely the community was to be stable. Other theoretical studies using similar approaches supported these findings (Gardner and Ashby, 1970; Pimm and Lawton, 1978). Clearly, however, many natural communities are very diverse and seemingly stable. As May's simulated communities were constructed at random, ecologists determined that natural communities must be structured in such a way as to allow them to persist despite an apparently destabilizing level of diversity (Yodzis, 1981; McCann, 2000). Yodzis (1981) supported this hypothesis by showing that by using realistic network structure and parameters stability of diverse communities was much easier to achieve. Many stabilizing structures have since been found, such that complexity is generally considered to increase stability when these aspects are accounted for (McCann et al., 1998; McCann, 2000; Kondoh, 2003; Emmerson and Yearsley, 2004; Stouffer and Bascompte, 2011).

*The importance of food webs **and** their species*

When investigating the stability of ecological communities, studies have largely focused on the complexity and structure of the food web (e.g. Ives, 1995; May, 1972; Chen and Cohen, 2001; Allesina and Tang, 2012) *or* the effect of one or a few species (e.g. McCann et al., 1998; Courchamp et al., 1999), and have largely overlooked how they interactively affect stability. Food-web stability has been shown repeatedly to depend on the structure and complexity of the food web (McCann, 2000; Stouffer and Bascompte, 2011; Rooney and McCann, 2012). This structure and complexity arises, however, from the interactions of multiple species, the traits of which can also influence stability beyond the influence of structure and complexity (Mouillot et al., 2013; Dehling et al., 2014; Olito and Fox, 2015). Equally, the influence of an individual species on the stability of the food web depends not only on the species' own traits, but also how that species interacts with other species and how they interact with each other (Sahasrabudhe and Motter, 2011; Peralta et al., 2014). In order to understand food-web responses to disturbances, it is essential to understand how each species contributes to stability in the context of the entire food web and the consequences for the rest of the community if they are impacted by a disturbance. This is particularly important with the current high levels of biodiversity loss and dis-

turbances which may alter the relationship of species to each other (Gilbert, 2009; Tylianakis et al., 2010; Rader et al., 2014).

In this thesis, we address the reciprocal effects of species' traits and network structure on stability in two parts. We first investigate how the distribution of links between species and the strength of those links affect network stability. It has frequently been assumed that species with many interactions should interact more weakly than species with few interactions (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Montoya et al., 2005; Wootton and Emmerson, 2005), but, to our knowledge, this has never been explicitly tested. Second, we investigate the response of food webs of varying complexity to press disturbances of individual species and how this response varies with network complexity and the traits of the disturbed species. Together these studies will help us to identify the traits of species which affect how food webs respond to disturbances as well as the interaction patterns among species which must be maintained to enhance stability.

Degree distribution and weak interactions

There are many aspects of food-web structure which are important for community stability. One of these is the degree distribution: how the number of interactions per species is distributed throughout the community (Dunne et al., 2002a; Arii and Parrott, 2004; Stouffer et al., 2005; Otto et al., 2007). Most food webs have an exponential degree distribution where the majority of species have few interactions and a minority have many interactions (Camacho et al., 2002; Stouffer et al., 2005; Digel et al., 2011; Sánchez-Carmona et al., 2013). This holds not only for the total number of links a species has, but also when the total is broken down into how many predators or prey a species has (Camacho et al., 2002; Digel et al., 2011). Indeed, the success of the niche model (Williams and Martinez, 2000) in reproducing many aspects of natural food webs is at least partly due to its assumption of an exponential degree distribution (Stouffer et al., 2005; Dunne and Williams, 2009).

Another important mechanism enhancing stability is the preponderance of weak interactions (McCann et al., 1998; Berlow et al., 2004; Pinnegar et al., 2005). In natural food webs, interaction strengths are skewed towards weak interactions and this has been shown to promote stability in both empirical and theoretical communities (Paine,

1992; Fagan and Hurd, 1994; Wootton, 1997; Sala and Graham, 2002; Berlow et al., 2004). McCann et al. (1998) used modules of 3 to 4 species to show that weak interactions are essential for stability by dampening the dynamic behavior of a potentially strong interaction. Modules where each strong interaction had at least one weak interaction to balance it were far more likely to achieve stability than modules with more strong interactions than weak. Successive studies have supported this finding and shown that loss of weakly interacting species can be detrimental to the stability of the community (Berlow, 1999; Emmerson and Yearsley, 2004; Bascompte et al., 2005).

Some studies have combined these two patterns — the distribution of degree and of interaction strength — to assume that species with many interactions will have weak interactions (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Montoya et al., 2005; Wootton and Emmerson, 2005; Montoya et al., 2009; Mougi and Kondoh, 2012). Intuitively, it makes sense that if a species interacts with many other species it will not affect, or be affected, as strongly by the interacting species as a species with few interactions. A generalist predator need not feed as heavily on each prey species as a predator with only one prey species, while a prey species with many predators will not withstand the same predation pressure from each predator that a prey species with only one predator can withstand. Indeed this assumption underpins MacArthur (1955)'s mathematical framework showing that increased complexity leads to increased stability. MacArthur's framework normalizes interaction strengths such that the sum of a species' incoming links equals one; in this way, a species with more interactions must have weaker interactions than one with few interactions (MacArthur, 1955). This then means that increased diversity tends to increase stability by increasing the number of weak interactions (MacArthur, 1955; McCann and Hastings, 1997). Despite the intuitive nature of this assumption, some empirical support for its existence (O'Gorman et al., 2010), its long history and repeated appearance in food-web models, it has to our knowledge never been experimentally tested.

Press disturbances and stability

There is a vast body of research investigating the relationship between complexity and stability. However, the focus of most of these studies is only on short term, discrete disturbances from which the community can recover once the disturbance subsides (e.g. May,

1972; Emmerson and Yearsley, 2004; Allesina and Pascual, 2008; Tang and Allesina, 2014). This type of disturbance is known as a **pulse** disturbance and examples include storms, fires, and floods (Bender et al., 1984). With increasing anthropogenic pressures on ecosystems globally, however, the vast majority of communities are experiencing disturbances, such as increased nutrient levels from pollution, which are long term changes that will not subside in the near term (Millenium Ecosystem Assessment, 2005; IPCC, 2014). These disturbances are known as **press** disturbances and can have vastly different effects on ecological communities than pulse disturbances (Bender et al., 1984; Glasby and Underwood, 1996).

Another issue muddying the waters around the stability-complexity debate is that of the definition of stability (Grimm and Wissel, 1997; Ives and Carpenter, 2007). Although the concept of stability is intuitively simple, there are many different aspects and thus definitions of stability, and each of these has a different relationship with complexity (Ives and Carpenter, 2007; Donohue et al., 2013). Many of these measures of stability only measure a response to pulse disturbances. It is unclear how results of studies using these measures will correspond to the stability of communities experiencing press disturbances. Studies focusing on press disturbances are increasing. However the relevant measures of stability are poorly characterized compared to those measuring stability to pulse disturbances (Glasby and Underwood, 1996; Grimm and Wissel, 1997). Many of these studies of press disturbance have focused on the effect of species removals and in particular the number of secondary extinctions they cause (Dunne et al., 2002b; Ebenman et al., 2004; Estrada, 2007; Dunne and Williams, 2009; Gilbert, 2009; Staniczenko et al., 2010). While understanding the effects of species removals is important given the current rate of biodiversity loss, many press disturbances do not fully remove a species, but merely impact its growth or death rate (Anderson et al., 2011; Gornish and Tylianakis, 2013; Graham et al., 2014). It is quite possible for a species to be “functionally extinct” and cause a secondary extinction when it still has positive biomass (Anderson et al., 2011; Säterberg et al., 2013).

Furthermore, many studies of species’ removals use a purely topological method, whereby a species only goes extinct when it loses all its prey species (Dunne et al., 2002b; Dunne and Williams, 2009; Staniczenko et al., 2010; Ebenman, 2011). This significantly overestimates how robust — how many secondary extinctions are caused as a result of a species’ removal — the network is to the loss of species (Curtsdotter et al., 2011) and precludes the ability to observe

secondary extinctions when the focal species is not itself extinct. The alternative is to use dynamic methods which include species interactions and allow for changes in biomass (due to predator release, for example) (Curtsdotter et al., 2011). This allows the study of community responses to disturbance to be extended to situations where the growth rate of the focal species is affected but does not cause complete extinction (Säterberg et al., 2013). Indeed, it would be particularly valuable to know how much different species in different communities can be impacted before becoming functionally extinct, and how this depends on the complexity of the community. This will have important ramifications for activities such as marine harvesting. For example, if species become functionally extinct when their growth rate is decreased by only a small amount, the harvesting limit needs to be above this threshold. To extend the discussion to those studies focused on species removals, it would also be beneficial to know whether a disturbed species will cause a secondary extinction before going extinct itself.

Species traits

Just as the complexity of a food web is likely to impact the response of the food web to press disturbances, it is also likely that the traits of the disturbed species will affect the food web's response to a sub-removal press disturbance. Here we use "traits" to describe how a species interacts with other species in a food web, for example, trophic level and the number of interacting partners a species has (degree). Species' traits are also shown to affect the number of secondary extinctions caused as a result of a species removal (Borrvall et al., 2000; Quince et al., 2005; Eklöf and Ebenman, 2006; Curtsdotter et al., 2011). It can therefore be expected that species' traits would also impact how much a species' growth rate can be decreased before an extinction occurs. It is perhaps unsurprising that targeted removal of the most connected species causes the most secondary extinctions in topological studies (Dunne et al., 2002b; Dunne and Williams, 2009) as species with many interactions with other species are more likely to be the only remaining prey item for another species than a species with few interactions. Dynamic studies have shown the same relationship between number of interactions and robustness of the community to loss of that species (Quince et al., 2005; Curtsdotter et al., 2011).

The trophic level of the disturbed species has also been shown to affect the robustness of the community to loss of species (Curtsdotter et al., 2011). Topological studies underestimate the importance of top-down control because species in these models can only go extinct when they lose all prey species (Dunne et al., 2002b). It is, therefore, impossible in those studies for removal of a top predator to cause a secondary extinction (Dunne and Williams, 2009; Curtsdotter et al., 2011). In reality, however, top predators are essential for controlling interactions between competitors and their loss can lead to population explosions and thus secondary extinctions (Paine, 1966; Estes and Palmisano, 1974; Elmhagen and Rushton, 2007). The loss of basal species can also be catastrophic as these form the basis of the entire community (Quince et al., 2005; Curtsdotter et al., 2011). Indeed, some studies have found that the community is least robust to the removal of basal species (Borrvall et al., 2000; Quince et al., 2005; Curtsdotter et al., 2011).

Aims and hypotheses

The overarching aim of this thesis is to explore how species fit into the complexity-stability debate and to extend the discussion to press disturbances. This will enable us to understand what aspects of food-web complexity, structure, and species' traits affect community stability and how communities will respond to different types of disturbances. We have broken this into two sections. The first concerns the relationship between interaction strength and degree in locally stable versus unstable food webs, while the second investigates the response of food webs to press disturbances.

It is frequently assumed that generalists (species with many interactions) should interact more weakly with each partner than specialists (species with few interactions) (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Montoya et al., 2005; Wootton and Emmerson, 2005). To our knowledge, however, this has never explicitly tested. The first part of this thesis tested this directly by comparing the relationship between a species' degree and mean interaction strength in locally stable versus unstable food webs. We asked whether species with many interactions did indeed have weaker interactions than species with few interactions. This brought together research on network structure and interaction strength to

determine the validity of an assumption underpinning multiple theoretical studies.

The second section investigated the response of food webs to incremental press disturbances of single species. The majority of the literature on the complexity-stability debate focuses on pulse disturbances (May, 1972; Neubert et al., 2004; Allesina and Tang, 2012; Tang and Allesina, 2014, e.g.). Those studies which investigate press disturbances mostly focus on the food web's response to species removals (Dunne et al., 2002b; Estrada, 2007; Curtsdotter et al., 2011, e.g.). Food webs are increasingly being exposed to press disturbances which, while they may not remove a species entirely, affect species' growth rates and can cause extinctions and restructuring of the food web (Anderson et al., 2011; Gornish and Tylianakis, 2013; Graham et al., 2014). For the complexity-stability debate to remain relevant, it is important to extend the debate to these types of disturbances. Specifically, we directly compared three measures of stability to press and pulse disturbances across varying levels of size and connectance to ask whether they all followed the same relationship with complexity. We hypothesized that the properties which convey stability to one type of disturbance may be different from those which convey stability to another type of disturbance, in which case our measures of stability would show different relationships with complexity. We then determined how the traits of the disturbed species affected the food web's response to disturbance. We hypothesized that food webs would be more vulnerable to disturbance of some species than others depending on their traits.

Together these studies investigated how species form stable communities and how the traits of these species and properties of the communities affected their response to different kinds of disturbances. Our results have implications for both research and the management of natural communities by showing that species need to be considered in the context of the community they exist in while networks cannot be studied without an understanding of the traits of species within.

Generalists have weaker and stronger interactions

Abstract

Ecological communities consist of generalists who interact with proportionally many species and specialists who interact with proportionally few. The strength of these interactions also varies, with communities typically exhibiting a few strong links embedded within many weak links. Historically it has been argued that generalists should interact more weakly with their partners than specialists and, since weak interactions are thought to increase community stability, that this pattern increases the stability of diverse communities. Here we studied model-generated predator-prey communities to explicitly investigate the validity of this argument. In feasible communities — those which were both locally stable and all species had positive biomass — we indeed found that species with many predators or prey are affected by them more weakly than species with few. This relationship, however, is only part of the story. While species with many predators (or prey) tend to be only weakly affected by them, these many weak interactions are balanced by a few strong interactions with prey (or predators). These few strong interactions are large enough that, when the effect of predator and prey interactions are combined, it seems that species with many interactions actually interact more strongly than species with few interactions. Though past research has tended to focus on either the arrangement of species interactions or the strength of those interactions, we show here that the two are in fact inextricably linked. This observation has implications for both the realistic design of theoretical models and the conservation of ecological communities, especially those in which the strength and arrangement of species' interactions are impacted by biodiversity-loss disturbances such as habitat alteration.

Introduction

In the face of increasing global biodiversity loss, understanding the effect of biodiversity on the stability of ecological communities is a pressing issue (Tilman and Downing, 1994; McCann, 2000; Loreau et al., 2003; Pereira et al., 2010; Cardinale et al., 2012). While early theoretical research suggested that diversity had a negative effect on stability (Gardner and Ashby, 1970; May, 1972; Pimm and Lawton, 1977, 1978), decades of successive research have largely come to support a positive relationship between biodiversity and stability (Tilman and Downing, 1994; McCann, 2000). The investigation of potentially important stabilizing mechanisms, however, remains an active area of research (Tilman and Downing, 1994; McCann et al., 1998; Worm and Duffy, 2003; Ives and Cardinale, 2004; Stouffer and Bascompte, 2010; Gravel et al., 2011; Stouffer and Bascompte, 2011; Rooney and McCann, 2012).

In their simplest form, studies of the network of interactions underlying an ecological community have focused primarily on the number of species and the number of interactions between those species as measures of network complexity (May, 1972). Subsequently, both theoretical and empirical studies have shown that higher order properties such as compartments or the distribution of species' degree—the number of interactions a species has—can also play a key role in enhancing stability (Dunne et al., 2002a; Arii and Parrott, 2004; Stouffer et al., 2005; Stouffer and Bascompte, 2010; Thébault and Fontaine, 2010; James et al., 2012). Other studies have also shown that the strength of interactions is important, and weak interactions in particular have been found to be very stabilizing (Paine, 1992; Fagan and Hurd, 1994; de Ruiter et al., 1995; Wootton, 1997; McCann and Hastings, 1997; McCann et al., 1998; Neutel et al., 2002; Otto et al., 2007; Tang and Allesina, 2014).

Combining the distribution of species' degree and the importance of weak interactions, it has long been speculated that species with many interactions should interact weakly while species with few interactions should interact strongly (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Montoya et al., 2005; Wootton and Emmerson, 2005). Such speculation makes intuitive sense since highly connected species should not need to interact as strongly with any one species of prey or be able to withstand high predation pressure from many predators (Montoya et al., 2005; O'Gorman et al., 2010). There is some evidence for this in

empirical studies (O’Gorman et al., 2010) and theoretical studies have incorporated this assumption when showing a positive relationship between biodiversity and stability (MacArthur, 1955; Mougi and Kondoh, 2012). Given how common this assumption is and the imprint it has left in the literature (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Montoya et al., 2005; Wootton and Emmerson, 2005; Mougi and Kondoh, 2012), we test it here directly. Furthermore, we consider both resilience and feasibility, instead of focusing exclusively on local stability. A more resilient community is one which returns to its original state more quickly after a disturbance, while a feasible community is one which is both locally stable and all species have a positive biomass. Finally, rather than concentrating on how an individual species affects those species it interacts with, we consider how an individual species is *affected by* the species it interacts with. Thus we test the hypotheses that, in feasible and/or more resilient food webs, species who have many prey are less reliant on each prey than those species with few prey, and that species with many predators are impacted less by each of their predators than those species with few predators.

Methods

Simulating model communities

We studied the properties of simulated communities across a range of species richness $S \in [4, 6, \dots, 48, 50]$ and a range of connectance $C \in [0.05, 0.10, \dots, 0.35, 0.4]$, where connectance represents the probability that any two species have a direct effect on each other. We chose these values of connectance to span the range commonly seen in natural food webs (Williams and Martinez, 2000; Dunne, 2006; Stouffer and Bascompte, 2011), whereas the sizes were constrained by the computational effort required for the subsequent calculations.

To introduce greater heterogeneity in the number of links per species (also known as degree) than would be observed in networks generated completely at random (Barabási and Albert, 1999; Dunne et al., 2002a; Stouffer et al., 2005), we randomly assigned each species i a probability p_i of interacting with other species, such that species with higher values of p_i will tend to have a higher degree. Studies of empirical networks indicate that an approximately-exponentially-decaying degree distribution, where a few species have many inter-

actions and many species have few interactions, gives a strong fit to that observed empirically (Dunne et al., 2002a; Camacho et al., 2002; Stouffer et al., 2005; Williams and Martinez, 2008). We therefore drew the species-specific values p_i at random from a beta distribution $\beta\left(1, \frac{1-c}{c}\right)$ (Williams and Martinez, 2000; Camacho et al., 2002; Stouffer et al., 2005). The probability that any off-diagonal value in the community matrix is non-zero was then given by $p_{ij} = \frac{p_i + p_j}{2}$ (Bascompte et al., 2003).

To characterize species dynamics within our simulated communities, we studied a system of generalized Lotka-Volterra equations (Williams, 2008; Allesina and Tang, 2012; Tang and Allesina, 2014)

$$f_i = \frac{dX_i}{dt} = r_i X_i (1 - X_i) + \sum_{j \neq i} \alpha_{ij} X_i X_j, \quad (1)$$

where X_i represents the total biomass of species i , r_i is the per capita growth rate of species i , and α_{ij} quantifies the per capita effect of species j on species i . Given an equilibrium solution X^* , the behavior of this community at or very near to equilibrium is provided by its community matrix M (Laska and Wootton, 1998; Allesina and Tang, 2012), whose elements $m_{ij} = \left. \frac{\partial f_i}{\partial X_j} \right|_{X^*}$. Substituting in Eq. 4 here gives

$$\begin{aligned} m_{ii} &= r_i(1 - 2X_i^*) + \sum_{j \neq i} \alpha_{ij} X_j^* \\ m_{ij} &= \alpha_{ij} X_i^*. \end{aligned} \quad (2)$$

We parametrized the community matrices M studied here as follows. First, we drew the non-zero off-diagonal elements m_{ij} from a normal distribution $N(0, 1)$. To ensure that our community only featured predator-prey interactions, we ensured that all interacting pairs m_{ij} and m_{ji} always had opposite sign structure (i.e., $m_{ij} > 0$ if $m_{ji} \neq 0$ and $m_{ji} < 0$). Second, we set all diagonal elements $m_{ii} = -1$. This latter condition has two immediate benefits: it imposes a reference time for self damping (Allesina and Pascual, 2008) and implies that differences between communities will only be due to the arrangement and strength of off diagonal elements (Allesina and Tang, 2012; Tang and Allesina, 2014).

With our generalized Lotka-Volterra model parametrized in this way, it is possible to directly solve for r_i and X_i^* when given the matrix M (Allesina and Tang, 2012). Having solved for X_i^* , the per capita effects α_{ij} can be calculated as

$$\alpha_{ij} = \frac{m_{ij}}{X_i^*}. \quad (3)$$

From the equilibrium densities X_i^* , we were able to determine whether the community matrix had a non-trivial, *feasible* equilibrium point such that all $X_i > 0$ (Tang and Allesina, 2014). Similarly, we also calculated the resilience of the community matrix—and hence this equilibrium point X^* —by quantifying its dominant eigenvalue (Pimm and Lawton, 1977).

Following the above methodology, we attempted to generate 100 feasible community matrices and 100 unfeasible community matrices for each combination of S and C , discarding any that contained species which did not interact with any other species. If we failed to reach these targets after generating 100000 candidate matrices, we kept the reduced number and moved onto the next combination. This gave us a total of 26786 matrices that we studied in greater detail as described below.

Statistical analysis

We first aimed to determine whether, in feasible and/or more resilient communities, species with many links are impacted less by the species they interact with than those with few links. To do so, we considered two values of interaction strength: per capita (α_{ij}) and per population (m_{ij}). The first, α_{ij} , therefore describes the effect of an individual of species j on an *individual* of species i while m_{ij} describes the effect of an individual of species j on the *population* of species i . For each species i , we calculated these as the mean of the absolute value of all interaction strengths for an individual of species j on an individual ($|\alpha_{ij}|$) or population ($|m_{ij}|$) of species i . To control for differences in size and connectance across networks, we used species' 'relative degree' as a measure of whether or not they had few or many interactions, where relative degree was calculated as a species' degree divided by the average degree for the network (k_i/z) and average degree (z) is given by the total number of interactions in the network divided by number of species $z = \frac{L}{2S}$. Note that the 2 in the denominator of this expression arises because each interaction contributes two "units" of degree, one to the predator and one to the prey.

Lastly, we focused on two measures of stability: resilience and feasibility. Resilience was quantified as the dominant eigenvalue, with a larger value indicating a less resilient network. Since a feasible network is one which was stable and where all species could co-exist

with a positive biomass at equilibrium; feasibility is a binary variable that indicates a network is either feasible or unfeasible.

Note that, by design, there should be no relationship between the number of interactions a species has and the strength of the effect of those interactions in our synthesized community since we assigned all interactions and interaction strengths at random. However, the stability of a network is an emergent property that can only be determined after all parameters are set. This means that any stabilizing relationship between the number of interactions a species has and the strength of those interactions could manifest itself more frequently in feasible or resilient networks than it does in unfeasible or less resilient networks. With this in mind, we used a linear mixed model to determine whether the data indicated a significant relationship with stability. Given our initial hypothesis, we were particularly interested in whether or not we would observe a negative relationship between relative degree and mean interaction strength which also depended on our measures of stability.

ORIGINAL NETWORKS

To compare across our original 26786 food webs, we used either mean $|\alpha_{ij}|$ or mean $|m_{ij}|$ as the dependent variable in the mixed model, relative total degree of species i ($k_i/2z$), a measure of stability (either resilience or feasibility), and their statistical interaction as independent variables, and we also included a random effect term for the network. Here 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 since the stability of the network is an emergent property of all species and all interactions therein. To investigate whether interactions with predators or prey contributed more to any eventual pattern we might find, we repeated the above analyses separately for each interaction type. To do so, we substituted in the mean negative ($|\alpha_{ij}^-|$ or $|m_{ij}^-|$) or positive ($|\alpha_{ij}^+|$ or $|m_{ij}^+|$) interaction strength as the dependent variable. In place of relative total degree, we likewise used k_i^-/z , the relative number of negative interactions (i.e., interactions with predators) or k_i^+/z , the relative number of positive interactions (i.e., interactions with prey). Note that we use $2z$ when considering interactions with both predators and prey combined, but only z when considering them separately.

CONTROLLING FOR TOPOLOGY

When comparing across networks, there can be structural variations, in terms of who interacts with whom, which can also affect stability. This “structure” is often referred to as network topology, and examples of topological patterns thought to influence stability include the degree distribution of the network (Dunne et al., 2002a; Arii and Parrott, 2004; Stouffer et al., 2005; Otto et al., 2007; Estrada, 2007), compartmentalization (Thébault and Fontaine, 2010; Stouffer and Bascompte, 2011), and the level of omnivory (McCann and Hastings, 1997; Holyoak and Sachdev, 1998; Tanabe and Namba, 2005; Gellner and McCann, 2012). It is possible that such patterns can have a stabilizing effect on networks which can outweigh the effect of the strength of interactions between species. Since we are most interested in the relationship between a species’ degree and how strongly it is affected by its interactions, we aimed to also control for potentially stabilizing or destabilizing effects of different topological structures. To do so, we took each of our 26786 networks and shuffled all m_{ij} values within the network while maintaining who was predator and prey in each interaction. Doing so consisted of randomly reassigning the positive and negative off-diagonal elements of the network separately in order to keep the sign structure of all predator-prey interactions identical. We repeated this process 100 times for each network to generate 26786 ensembles of 101 topologically-identical networks.

We then compared each of these sets to each other to determine whether, when controlling for the effect of topology, a significant relationship between relative degree and mean interaction strength still impacted stability. Here we again used a linear mixed model; however, we fit it separately to each of the 26786 sets of m_{ij} -shuffled networks. Again, either mean $|\alpha_{ij}|$ or $|m_{ij}|$ was the dependent variable, relative degree, a measure of stability (either resilience or feasibility), and their statistical interaction were the independent variables. This time we also included a random effect for species to account for pseudoreplication caused by the fact that the replicates of each species across the shuffled networks are not independent, as they will always have the same degree and interact with the same species. We then compared the results of these 26786 models by using a Chi square test to determine whether we observed a significant interaction between relative degree and stability more than we would expect at random at $\alpha = 0.05$.

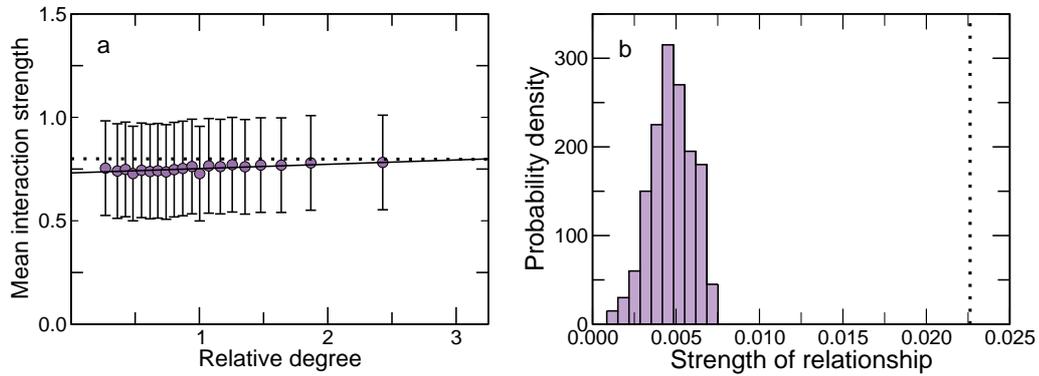


Figure 1: When all interactions are considered together, species with many interactions relative to other species in their food web have stronger interactions than species with few interactions. (a) The mean strength of all interactions ($|m_{ij}|$) increases with relative total degree ($k_i/2z$). Dashed lines show the equivalent relationship for unfeasible networks. (b) Although this relationship appears relatively weak, it is far stronger than what would be expected at random given the variation of interaction strengths imposed on the data. Here, we show the null distribution of the relationship in panel a but measured across 100 randomizations of the data. The dashed vertical line indicates the strength of the relationship observed in panel a.

Results

Original networks

Contrary to our initial hypothesis, we observed that species' relative degree is not related to its mean $|\alpha_{ij}|$ as a function of the resilience of the community matrix. When interactions were broken down into positive (prey) and negative (predator) interactions, we again found no relationship between the number of interactions and per capita interaction strength as a function of resilience. The above also held when testing for a relationship between mean $|\alpha_{ij}|$ and relative degree in either feasible or unfeasible simulated networks.

We similarly observed no relationship between mean $|m_{ij}|$ and relative degree when considering resilience as a measure of stability. In contrast, we observed a significant relationship between number of interactions and the impact of those interactions in feasible networks when mean $|m_{ij}|$ was our dependent variable. Intriguingly, it is in the opposite direction to what we hypothesized (Fig. 1). Here, the more interactions a population has, the *stronger* those interactions are. On the other hand, we found entirely contradictory patterns upon breaking this down into predator and prey interactions. When considering only predator or only prey interactions, the more interactions a species has, the *weaker* those interactions are in feasible networks (Fig. 2, Fig. 3). This occurs because species in feasible networks tend to have many predators and few prey or many prey and few predators (Fig. 4). In both cases, the many predators (or prey) impact the focal species weakly, giving rise to a negative interaction strength-degree relationship overall. The few prey (or predators), however, impact the focal species sufficiently strongly that,

when the effect of all interactions on the focal species' population are lumped together, species with many interactions are impacted *more strongly* by each species they interact with than species with few interactions. While the strength of the positive and negative relationships described above appear to be weak (Fig. 1a, Fig. 2a, Fig. 3a), they are far stronger than we would expect to observe at random (Fig. 1b, Fig. 2b, Fig. 3b).

Controlling for topology

Of the 26786 m_{ij} -shuffled sets of networks, very few exhibited a relationship between total degree and mean $|\alpha_{ij}|$ that was a function of feasibility (907; 3.4%) or resilience (1060; 4.0%) (Fig. 5). For predator and prey interactions, we found only 2.4% and 2.9% of networks, respectively, showed a significant interaction when feasibility was the measure of stability and 3.5% and 3.9% when resilience was the stability measure. In all cases, the proportion was significantly lower than would be expected at random in terms of false positives ($p > 0.05$). This would appear to imply that, even when controlling for network topology, a negative relationship between degree and mean per capita interaction strength does not contribute to increase resilience or feasibility of the community.

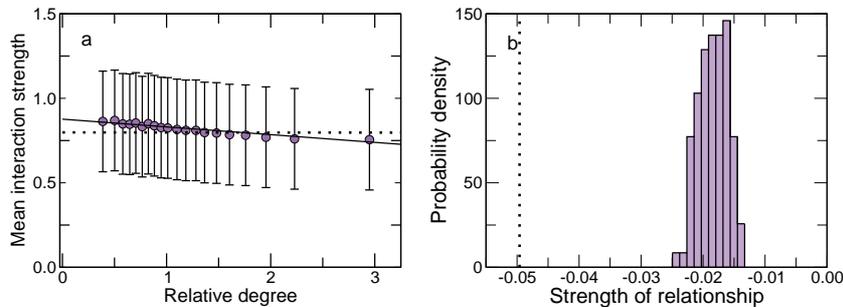


Figure 2: When considering only a species' interactions with prey, species which have many interactions with prey relative to other species in their food web have weaker interactions than species with few interactions. (a) The mean strength of interactions with prey ($|m_{ij}^+|$) decreases with relative degree (k_i^+ / z). (b) This relationship is stronger than would be expected at random. Symbols and calculation of null distribution follow Fig. 1.

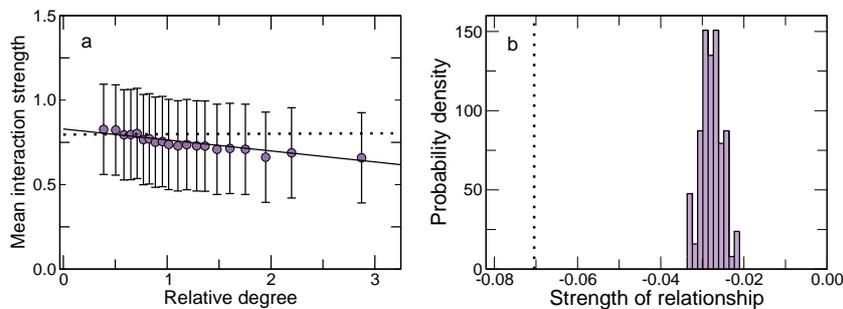


Figure 3: When considering only a species' interactions with predators, species which have many interactions with predators relative to other species in their food web have weaker interactions than species with few interactions. (a) The mean strength of interactions with prey ($|m_{ij}^-|$) decreases with relative degree (k_i^- / z). (b) This relationship is stronger than would be expected at random. Symbols and calculation of null distribution follow Fig. 1.

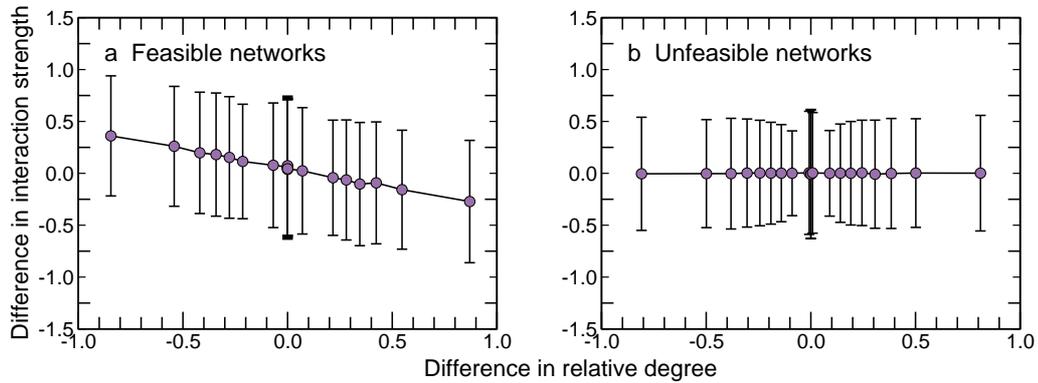


Figure 4: Feasibility depends on the strength and correct arrangement of a species' interactions. (a) When a species in a feasible web has more prey than predators, the effect of those prey on the population of species i is weaker than the equivalent effect of those predators on species i , and vice versa. (b) The same is not true in unfeasible food webs where no such relationship is observed. In both panels, the x-axis shows species' relative number of prey interactions minus the relative number of predator interactions $((k_i^+ - k_i^-)/z)$: species with positive values have more interactions with prey while species with negative values have more interactions with predators. The y-axis shows species' mean prey interaction strength minus the mean of predator interaction strength $(|m_{ij}^+| - |m_{ij}^-|)$: species with values above zero have stronger prey than predator interactions while species with values below zero have stronger predator than prey interactions.

When considering m_{ij} as our dependent variable, we saw a higher number of shuffle sets (1270; 4.7% for feasibility, 2066; 7.7% for resilience) with a significant effect of stability on the m_{ij} -degree relationship than we observed when mean $|\alpha_{ij}|$ was the dependent variable. When considering positive and negative interactions separately, we also see a higher number of significant interactions. Of course, these proportions still do not provide clear support for the stabilizing impact of a negative degree - m_{ij} relationship since they are again roughly consistent with what would be expected purely at random.

Nevertheless, we did find some evidence that the topology of the network alone can be important in determining stability: networks which are originally feasible are more likely to be feasible after shuffling than those which are not ($p < 0.001$). Importantly, it appears that the interplay between topology and the distribution of interaction strengths is most important for stability. We separated the m_{ij} -shuffled sets of networks into two categories: (i) those in which the original network was feasible and (ii) those in which it was not. The percentage of m_{ij} -shuffled sets which showed a significant effect of the interaction strength-degree relationship on stability was much higher in the originally feasible category than the originally unfeasible category (Fig. 5). This observation is most evident when studying mean $|m_{ij}|$ and feasibility. In this case, when positive and negative links are combined, we see only 4.7% of networks which exhibit a significant interaction. Conversely, when separated, we see that only 1.1% of the 18457 originally unfeasible networks exhibit this interaction, while 12.8% of those which were originally feasible have a significant interaction. Notably, this result holds whether mean $|\alpha_{ij}|$ or $|m_{ij}|$ is used as the dependent variable and whether stability is measured as resilience or feasibility (Fig. 5).

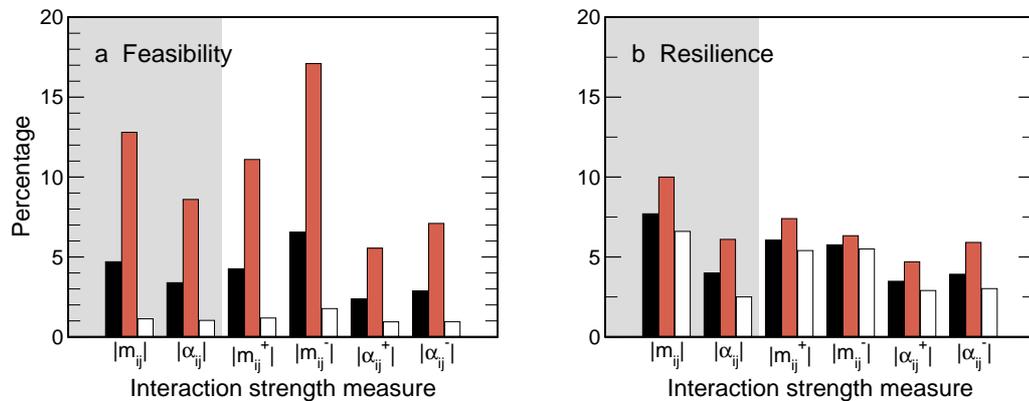


Figure 5: Bars show the percentage of m_{ij} -shuffled network sets which showed a relationship between degree and mean interaction strength that was a function of stability. A greater percentage of shuffle sets where the original network was feasible (orange bars) showed a significant relationship than those where the original network was unfeasible (white bars) or all networks together (black bars). This was true for both (a) feasibility and (b) resilience and both population (m_{ij}) and per capita (α_{ij}) interaction strength. The first two values in each graph — those shaded by the gray background — show the results for all interactions considered together, while the remainder show the results when interactions with predators ($|m_{ij}^-|$ and $|\alpha_{ij}^-|$) and prey ($|m_{ij}^+|$ and $|\alpha_{ij}^+|$) are considered separately.

Discussion

With the increasing support for the importance of weak interactions in stabilizing food-web dynamics (de Ruiter et al., 1995; McCann and Hastings, 1997; McCann et al., 1998; Neutel et al., 2002), and intuitive arguments that generalists should interact more weakly than specialists, it has long been assumed that a species with many interactions in a community should interact more weakly, on average, than a species with few interactions (MacArthur, 1955; May, 1972; Montoya and Solé, 2003; Wootton and Emmerson, 2005). While we found that this is indeed the case, the relationship between species' degree and mean interaction strength observed here is not as simple as we initially hypothesized. When considering both positive and negative links together, we find the feasibility of a network depends on the relationship between the number of interactions a species has and the strength of those interactions. However, in contrast to the negative relationship we expected, and which has been assumed in many previous studies, we found a *positive* relationship overall, namely, the more interactions a species has, the stronger those interactions are. Yet when we delved deeper and separated positive (interactions with prey) and negative (interactions with predators) interactions, we found the opposite relationship between mean population interaction strength and degree. For both positive and negative interactions, we specifically observed that specialists have stronger interactions than generalists. This result makes greater intuitive sense — generalists may be less efficient than specialists (Yamada and Boulding, 1998; Bernays et al., 2004; Terraube et al., 2011), species cannot withstand heavy predation from many predators (Gunzburger and Travis, 2004; Paterson et al., 2009; Rodriguez-Girones, 2012) etc. — and is the relationship we

originally expected to see. Nevertheless, it presents a paradox when compared with what we saw when positive and negative interactions are lumped together.

The solution to this conundrum lies in the interplay between network topology and interaction strength distribution. We found that species which have many interactions tend to have many positive or many negative interactions, but not both, and these tend to be weak but are balanced by a few strong interactions of the opposite type. What's more, these few strong interactions are sufficiently strong such that when we lump all interactions together it appears that species with many interactions have stronger interactions. Due to the trophic structure of natural food webs, it is likely that this is a pattern which is commonly found in nature; species near the bottom of the food web have many predators but few prey while those near the top have many prey and few predators (Williams and Martinez, 2000; Camacho et al., 2002). What is intriguing is that this pattern emerged in our feasible networks even when our networks were assembled in a random fashion with no predefined trophic structure.

We have focused on *feasible* food webs, where the biomass of all species must be positive as well as the network being stable, rather than focusing only on stability. Also, rather than examining how a focal species impacts other species, we have turned the tables and looked at how other species affect the focal species. In this way the distribution of interaction strengths with the topological pattern described above may have an intuitive and logical explanation; a species with many prey but few predators must be preyed on more heavily by those few predators or its population would increase to an extent that the network would no longer be feasible, while a species with few prey and many predators must prey heavily on those few prey to prevent being driven to extinction by its many predators. The stabilizing effect of weak interactions is well supported (de Ruiter et al., 1995; Wootton, 1997; McCann and Hastings, 1997; McCann et al., 1998; Neutel et al., 2002), and the reason for this is that weak interactions dampen the potentially chaotic effect of strong interactions (McCann and Hastings, 1997). Thus it may be that the pattern we observe here, with species having many weak positive or negative interactions countered by a few strong interactions of the opposite type, is an efficient way of ensuring that most strong interactions are sufficiently dampened by weak interactions.

Ultimately it appears that the combination of an asymmetric arrangement of a species' interactions and the strength of those interactions

is most important for feasibility. This conclusion is most strongly supported by the results we obtained upon shuffling interaction strengths. For very few networks which were originally unfeasible — and therefore were unlikely to show this asymmetric interaction pattern — was feasibility affected by the relationship between species' degree and mean interaction strength. In contrast, in networks which *were* originally feasible — and therefore likely *did* show this asymmetric interaction pattern — feasibility was far more likely to be dependent on the relationship between species' degree and mean interaction strength. Clearly, it is important to have a food-web structure which is conducive to feasibility before the stabilizing effect of a relationship between number and strength of interactions can be observed.

In conclusion, it seems that studies which have assumed that species with many prey (or predators) interact more weakly than those with few prey (or predators) have done so correctly. Nevertheless, this is only the tip of the iceberg. While the literature has tended to focus on either the topology of interactions or the strength of those interactions when studying food webs, our results indicate that these are two sides of the same coin and are too tightly interwoven to be treated independently. Thinking more broadly, this observation has clear impacts for the conservation and management of ecological communities (Brose, 2010; Tylianakis et al., 2010); while it is important to focus on conserving species and thus their interactions, it may also be important to focus on conserving the strength of those interactions. In particular, for a species with many prey, it may be more important to maintain the few predators which have a strong impact than the many prey it relies on weakly, and vice versa.

Responses to press disturbances: Effects of species' traits and food-web complexity

Abstract

With current high levels of biodiversity loss and environmental change, studies of food-web stability need to broaden their focus beyond short-term disturbances to include the effects of long-term “press” disturbances. Here we subjected simulated food webs to press disturbances by decreasing the growth rate of each species, individually, in the food web. We then compared the resilience and reactivity — measures of stability to short-term “pulse” disturbances — and resistance — a measure of stability to press disturbances — of each food web and found that stability of all types decreased as species richness and connectance increased. We found that resilience and reactivity were good predictors of resistance.

We also identified how the traits of the disturbed species affected a food web's response to disturbance. Our simulated food webs were less resistant to disturbance of generalists and basal species than specialists or top predators. These relationships depended on the complexity of the food web, being stronger at low levels of complexity. Thus, while the complexity of a food web largely determines its stability, for a given level of complexity the disturbance of some species can be more detrimental to the food web than others.

Introduction

Understanding how ecological communities will respond to disturbances is a central theme in both fundamental and applied ecology (MacArthur, 1955; May, 1972; McCann, 2000). 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, as a result, can significantly alter the structure and dynamics of the community (Parker and Huryn, 2006; Houseman et al., 2008; Takimoto et al., 2012). 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 Huryn, 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 natural communities are capable of withstanding or recovering from disturbances and returning to a state similar to that before the disturbance (Holling, 1973; Dale, 1991; Swift, 2002). This phenomenon is intuitively termed “stability”. There are, however, many different aspects and definitions of stability (Grimm and Wissel, 1997; Neubert and Caswell, 1997; Ives and Carpenter, 2007; Donohue et al., 2013). Many theoretical studies of food-web stability focus on measures of stability to pulse disturbances (May, 1972; Neubert et al., 2004; Allesina and Tang, 2012; Tang and Allesina, 2014, e.g.); yet as ecosystems respond to ever-increasing anthropogenic impacts, press disturbances are becoming the norm for communities globally (Millenium Ecosystem Assessment, 2005; IPCC, 2014). It is not uncommon for these 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). Unless we know whether or when a community stable to a pulse disturbance is also stable to a press disturbance, studies focused solely on pulse disturbances are of limited use in understanding how communities will respond to an increasing prevalence of press disturbances. Moreover, theoretical studies investigating the effect of press disturbances have largely focused on the robustness of food webs to species removal (Dunne et al., 2002b; Estrada, 2007; Dunne and Williams, 2009; Curtsdotter et al., 2011), but a species does not have to be entirely removed to cause secondary extinctions (Säterberg et al., 2013) and many of these press disturbances initially manifest themselves as a decrease in a species' growth rate or increased mortality rate (Anderson et al., 2011; Gornish and Tylianakis, 2013; Graham et al., 2014). To effectively manage communities we therefore need to understand how the community will respond to sub-lethal disturbances and, more importantly, at what point these disturbances actually cause extinctions.

Here we aimed to compare the stability of networks to pulse and press disturbances. We focused on three commonly used definitions of stability to pulse disturbances: local stability, resilience and reactivity. Local stability was the simplest mathematical definition as a community is locally stable if it returns to its original equilibrium point after a small disturbance (May, 1972). Resilience provided a way of quantifying stability, and measured the *rate* at which the community returned to equilibrium (Pimm and Lawton, 1977; Ives, 1995; Gunderson, 2000). A more resilient community was one that returns more quickly after a disturbance to its original state. Resilience is, therefore, an important property in the natural world where repeat disturbances can happen quickly. While resilience measures the long-term response to a pulse disturbance, many studies have shown that the transient dynamics - what happens in the period between the disturbance and the return to equilibrium - can be as or more important for the community's persistence (Chen and Cohen, 2001; Neubert et al., 2004; Caswell and Neubert, 2005; Fukami and Nakajima, 2011). Reactivity quantified this transient response to a disturbance and is defined as the maximum amplification rate of the disturbance (Neubert and Caswell, 1997). A highly reactive community was one in which a disturbance was rapidly amplified before decaying to the original state while an unreactive community was one in which the perturbation decayed immediately (Neubert et al., 2009). After quantifying a community's susceptibil-

ity to a pulse disturbance, we then used resistance as a measure of how a community responded to a press disturbance. Specifically, we quantified resistance as the 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. Note that the extinction marking the end of the disturbance was not always the extinction of the disturbed species (Säterberg et al., 2013). We, therefore, also investigated whether these species-specific disturbances tended to result first in the extinction of the species being disturbed or in a secondary extinction.

In addition to determining how the nature of a disturbance affected a community's response to the disturbance, we were also interested in how the properties of the food web and disturbed species affected a food web's response to disturbance (May, 1972; McCann, 2000; Quince et al., 2005; Montoya et al., 2009; Curtsdotter et al., 2011; Vallina and Le Quéré, 2011). 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; Miller et al., 2002; Montoya and Sol, 2002; 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 how a community responds to different kinds of disturbances (Gardner and Ashby, 1970; May, 1972; Pimm, 1984; Haydon, 1994; Dunne et al., 2002b).

While the properties of a food web can affect how vulnerable it is to a disturbance, species' traits can make a species more or less resistant to the disturbance or likely to affect other species within the community when disturbed (Montoya et al., 2009; Curtsdotter et al., 2011; Donohue et al., 2013). For example, a generalist may be more likely to cause secondary 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 able to withstand a reduction in growth rate before going extinct than a lower trophic species because a reduction in a predator's growth rate will likely lead to an increase in their prey species and thus their food resources (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.

Here, 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 over harvesting of a particular species. Specifically, we investigated (i) how well measures of stability to pulse disturbances can predict a community's response to a press disturbance, (ii) how the parameters of the network affected the food web's response to disturbance, and (iii) how the traits of the disturbed species affected the outcome of disturbance. The results of our study indicate how relevant studies of stability to pulse disturbances are to communities experiencing press disturbances, and 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) to generate artificial networks with species richness $S \in [10, 100]$, at intervals of 2 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 ($C = \frac{L}{S^2}$). For each of the 168 combinations of S and C , we generated many different networks, discarding any that contained species which shared no interactions with other species in the network, until we had a total of 100 networks for each combination of S and C .

For all networks, we randomly assigned per capita effects α_{ij} of all interactions from a normal distribution $N(0, 1)$. When α_{ij} (the effect of predator j on prey i) was a negative value, we set α_{ji} (the effect of prey i on predator j) to a positive value to make all interactions predator-prey. We also set the diagonal values α_{ii} , the effect of species on themselves, to -1 . Choosing a common value for all species imposed a reference time for self damping (Allesina and Pascual, 2008) and further implied that differences between communities were only due to the arrangement and strength of off-diagonal elements (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):

$$\frac{dX_i}{dt} = r_i X_i (1 - X_i) + \sum_{j \neq i} \alpha_{ij} X_i X_j, \quad (4)$$

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.4 when the community was at equilibrium. To ensure that all networks were feasible (all biomasses were positive) and to remove an additional source of randomness, we set all equilibrium biomasses $X_i^* = 1$. To test the impact of this decision, we also explored the behavior of networks with a more realistic biomass structure where top predators had lower biomasses than species at lower trophic levels, and this did not qualitatively alter our results (results not shown here). We ensured that all networks were initially locally stable (see next section for the exact definition) and feasible.

Resilience, reactivity, and resistance

For each network, we first quantified its resilience and reactivity — estimates of the network's stability to short-term disturbances. Resilience was measured as the dominant eigenvalue of the system and captured the *rate* at which a network returned to equilibrium after a disturbance (Pimm and Lawton, 1977). A negative eigenvalue meant that the network returned to its equilibrium and was locally stable. The greater the magnitude of the dominant eigenvalue, the faster the rate at which the network returned to equilibrium. Thus a more resilient network had a more negative eigenvalue. Reactivity is defined as the maximal initial amplification rate and, as such, measures the *transient* behavior of the network between the disturbance and return to equilibrium (Neubert and Caswell, 1997; Tang and Allesina, 2014). Reactivity was quantified as the largest eigenvalue of the symmetric part of the community matrix (Tang and Allesina, 2014). A negative value of reactivity meant that all perturbations decayed immediately while positive values indicated that some perturbations amplified before decaying. As such, a locally unstable network was always reactive; however, a locally stable network could be more or less reactive — or even “unreactive” in the sense that all perturbations decayed immediately — and it has previously been shown that two networks

with the same resilience can exhibit rather different values of reactivity (Tang and Allesina, 2014). Although networks can be unreactive, all our networks were at least slightly reactive. This is affected by the value of our diagonal entries. With more negative diagonal entries and thus stronger intraspecific interactions reactivity decreases (Tang and Allesina, 2014).

After quantifying how each network would respond to a short-term disturbance in terms of their resilience and reactivity, we subjected them to simulated long-term, press disturbances to quantify their *resistance*. To do so, we individually decreased the growth rate of every species in every network incrementally in steps of $0.001r_i^*$ (where r_i^* is their initial growth rate at equilibrium) until the system reached a bifurcation point. In all cases, this bifurcation coincided with the extinction of the species being disturbed—a focal extinction—or the extinction of another species—a secondary extinction (Säterberg et al., 2013). We quantified resistance as the change in growth rate required to cause this bifurcation. If the bifurcation was caused by a secondary extinction, we continued decreasing the growth rate of the focal species to determine whether the network reached a new locally stable configuration without the secondarily extinct species. Across all simulated communities, this corresponded to over 2×10^9 simulated disturbances.

We quantified resistance as the proportional change in growth rate required to reach an extinction; mathematically, this can be expressed as $(\frac{r_i^* - r_i^d}{r_i^*})$. We call this quantity resistance since a more resistant network could tolerate a larger change in growth rate of the disturbed species before causing an extinction. As a result of these simulated press perturbations, we had S values of resistance for each network. To make this measure of stability analogous to network-wide properties like resilience and reactivity, we used 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. For comparison, 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).

Statistical Analyses

Previous research has demonstrated that resilience and reactivity (henceforth measures of pulse stability) are strongly affected by size and connectance (Tang and Allesina, 2014), and we expected similar behavior for resistance. To quantify how resilience, reactivity and resistance changed across size and connectance, we used a generalized linear model for each measure of stability. The three models included terms for size, connectance, and their interaction as predictors and a measure of stability as the dependent variable. When reactivity or resistance were the measure of stability, we used the log of reactivity or resistance to obtain a better fit.

We next wanted to test whether resistance was predicted by our measures of pulse stability above and beyond any of the aforementioned effects of size and connectance. To do so, we used a generalized linear model with the log of resistance as the dependent variable and size, connectance, a measure of pulse stability, and all possible interactions between them as independent variables. As above, note that this corresponded to two separate models, one testing the relationship between resistance and resilience and one the relationship between resistance and reactivity. We used the log of resistance as the dependent variable to ensure that we never obtained predicted values of resistance below zero. When reactivity was the measure of pulse stability, we again used the log of reactivity.

We also looked at the outcome of disturbance — whether the extinction was of the focal species or a secondary extinction and, if it was a secondary 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 secondary 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 secondary extinctions that were stable post-extinction as the dependent variable.

Finally, we investigated how the traits of the disturbed species impacted how a community responded to disturbance. The 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. 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 energy passed through from primary producers to the focal species, weighted by link strength following Levine (1980). Thus a primary producer had a trophic level of zero, a herbivore of one, and predators and omnivores successively higher numbers.

We investigated how these traits affected the resistance of the network to disturbance, how they affected whether a focal or secondary extinction occurred, and, for those disturbances which caused a secondary extinction, whether the traits of the disturbed species were related to whether the network became stable again once the secondarily extinct species was lost. We used two separate mixed effects models to quantify how the traits of the disturbed species affected the resistance of the community to the disturbance, one for degree and one for trophic level. The log of resistance was the dependent variable and size, connectance, trait (degree or trophic level of the focal species), and all possible interactions between them were the independent variables. We also included a random effect for network. This random effect accounted for the fact that, while each species in a network was perturbed separately, they were not strictly independent because species in particular networks could tend to be more or less resistant for reasons not captured elsewhere in the model.

We then used binomial mixed effect models to determine whether the traits of the disturbed species affected the type of extinction caused and, for those disturbances which caused a secondary extinction, whether the network was stable again post extinction. For each network, the fraction of disturbances resulting in a focal extinction (as opposed to a secondary extinction) was the dependent variable while size, 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. When comparing how traits affected whether networks were stable without the secondarily extinct species, the independent variables were the same, however the dependent variable was the proportion of disturbances for each network which caused a secondary extinction and remained stable afterward (as opposed to those which caused a secondary extinction and became unstable afterwards).

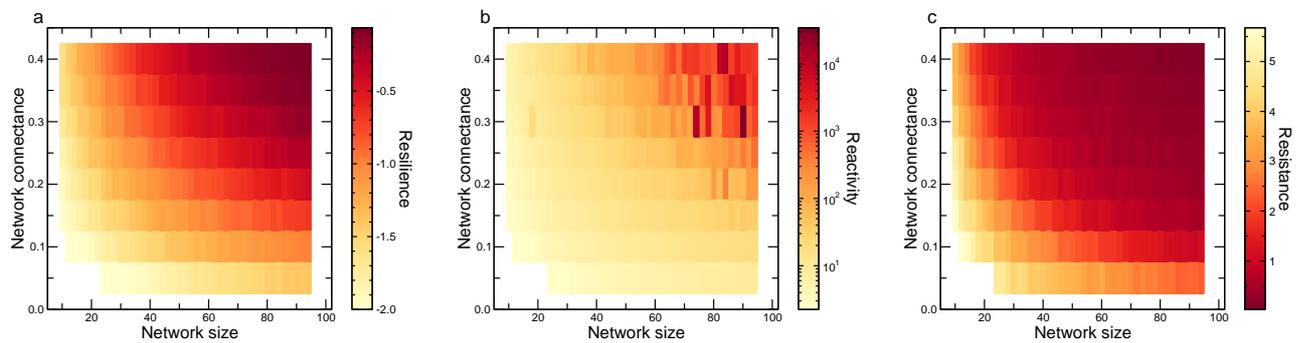


Figure 6: The relationship between different types of stability and size and connectance of the community. Colour represents the magnitude of stability for a given combination of size and connectance, with red representing less stable communities and yellow more stable. Each cell shows an average of all values of the relevant measure of stability for communities with that combination of size and connectance. (A) Resilience and (B) Reactivity: communities with low size and connectance are the most resilient and least reactive while large and highly connected networks are the least resilient and most reactive. (C) Resistance: large and highly connected networks are the least resistant while the simplest networks are the most resistant.

Results

We were first interested in determining and comparing how resilience, reactivity and resistance changed across size and connectance of a food web. Across all measures of stability (resilience, reactivity and resistance), we found that networks with the fewest species and lowest connectance were the most “stable” while the most complex networks (high connectance and many species) were the least “stable” (Fig. 6) (Resilience $R^2 = 0.836$, reactivity $R^2 = 0.839$, resistance $R^2 = 0.762$). The decrease in stability as complexity increased was particularly marked in both resilience and resistance and occurred at similar levels of size and connectance (Fig. 6a,c).

At lower values of size and connectance, we also found that press disturbances were much more likely to result in a focal extinction (approximately 80% of the time, $R^2 = 0.788$) (Fig. 7a). Of those disturbances which did result in a secondary extinction, the network was more likely to be stable without the secondarily extinct species at these low values of size and connectance (Fig. 7). At higher levels of complexity on the other hand, disturbances almost always resulted in a secondary extinction, and it was rare that these networks were stable without the secondarily extinct species ($R^2 = 0.316$). For the above models, R^2 values were calculated as $1 - \frac{\text{residualdeviance}}{\text{nulldeviance}}$ (Faraway, 2005).

We then directly compared each network’s response to a pulse versus a press disturbance to determine whether networks which were more resilient or less reactive (and therefore more stable to short-term pulse disturbances) were also more resistant and stable to long-term disturbances. At low values of size and connectance, where networks

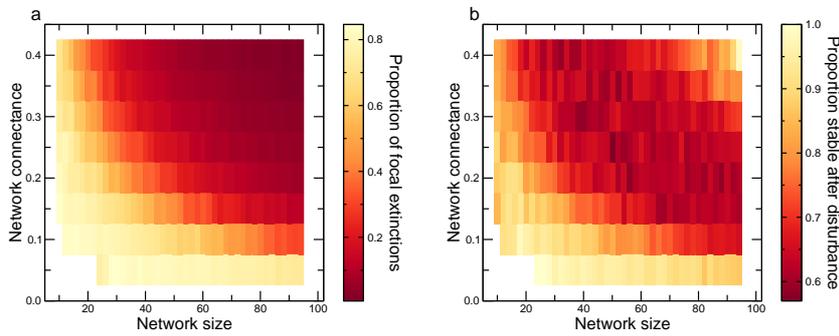


Figure 7: Whether a disturbance results in a focal or secondary extinction and, if it is a secondary extinction, whether the network reaches a stable state without that species, depends on the size and connectance of the network. (a) At low levels of species richness and connectance, most disturbances result in a focal extinction, while in more complex communities most disturbances result in a secondary extinction. Red indicates a higher proportion of secondary extinctions, while yellow indicates a higher proportion of focal extinctions. (b) Similarly, of those disturbances which result in a secondary extinction, the community is stable without the lost species more frequently at low levels of size and connectance than 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 secondary extinctions which were stable after the disturbance (panel b) for each food web with that combination of size and connectance.

tended to be most stable, we indeed found that resilience and reactivity were good predictors of resistance (resilience $R^2 = 0.804$, reactivity $R^2 = 0.794$) (Fig. 8). However, this relationship began to break down at higher levels of complexity to the extent that, at high levels of size and connectance, resistance was minimal regardless of resilience or reactivity.

Having determined how the properties of the network affected the response of the community to disturbance, we were then interested in determining how the traits of the disturbed species affected the outcome of disturbance. We used marginal (R_m^2) and conditional (R_c^2) R^2 values to determine the fit of our mixed 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 (the specific food web the species came from). The degree of the disturbed species affected the resistance of the network to press disturbances ($R_m^2 = 0.107$, $R_c^2 = 0.951$); networks were more resistant to the disturbance of species with few interactions (low degree) than those with many interactions (high degree), particularly at low species richness and high connectance or low connectance and high species richness (Fig. 9). The large difference between R_m^2 and R_c^2 indicates that the random effect — the particular network the species came from — explains a large amount of the results. In essence, this means that the properties of the network as a whole explain the baseline resistance (so some networks will be more resistant to disturbance of all species, regardless of the species' traits, than other networks). Species' traits then modify that baseline such that, within any particular network, resistance is lower to disturbance of generalists than specialists. Comparison of species from separate networks based on their traits, but without knowledge of the stability of the network they originate from, is far less informative.

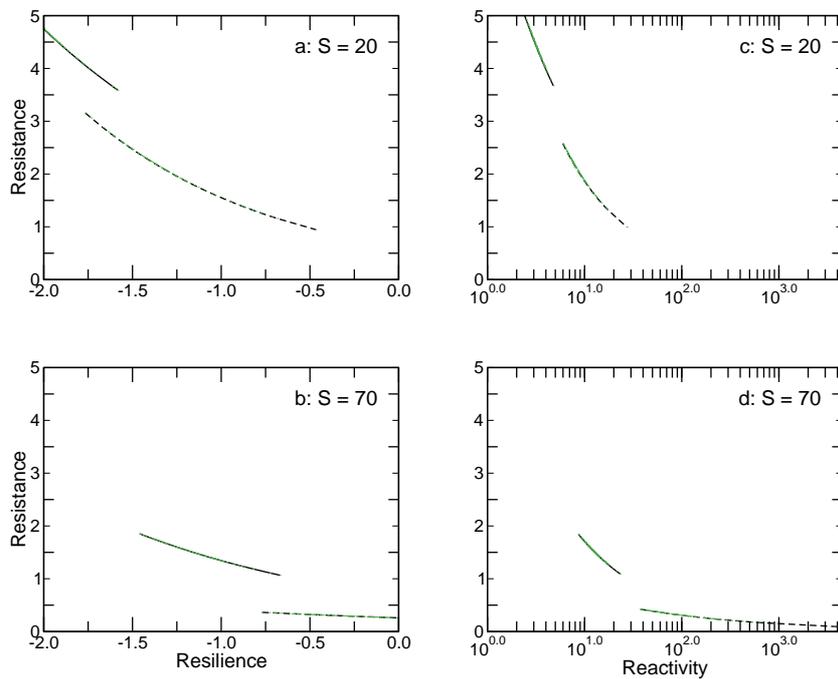


Figure 8: The ability of measures of stability to pulse disturbances (resilience and reactivity) to predict stability to press disturbances (resistance) depends on species richness and connectance, as predicted by our generalized linear mixed models. (a,b) Resilience is a good predictor of resistance at low levels of species richness and connectivity ($R^2 = 0.796$). This relationship weakens at higher levels of species richness and connectance. (c,d) Similarly the log of reactivity is a good predictor of resistance at low levels of species richness and connectance, but weakens at high levels of size and connectance ($R^2 = 0.768$). Panels a and c show the relationship for communities with 20 species, panels b and d show the relationship for communities with 70 species. Solid lines show the relationship for communities with a connectance of 0.1, while dashed lines show communities with a connectance of 0.3.

Although disturbing species with many interactions caused an extinction more quickly (the network was less resistant), they tended to cause secondary extinctions resulting in a new stable equilibrium rather than focal extinctions (Fig. 10). Species with few interactions, on the other hand, tended to go extinct themselves, and, when they did cause secondary extinctions, the network was unlikely to be stable without the secondarily extinct species. The relationship between degree and the community's response to disturbance was weaker at high levels of complexity.

Species with different trophic levels also had different effects on the rest of the community when disturbed ($R_m^2 = 0.149$, $R_c^2 = 0.959$). Networks were more resistant to disturbance of high trophic level species (top predators) than low trophic level species (primary producers) (Fig. 9). This relationship was strongest at lower levels of complexity. Again we see the large difference between R_m^2 and R_c^2 indicating that properties of the network set the baseline resistance and then species traits affect how far from this baseline resistance actually falls. Trophic level had little to no effect on whether disturbances result in a focal or secondary extinctions or whether the network was stable after a secondary extinction.

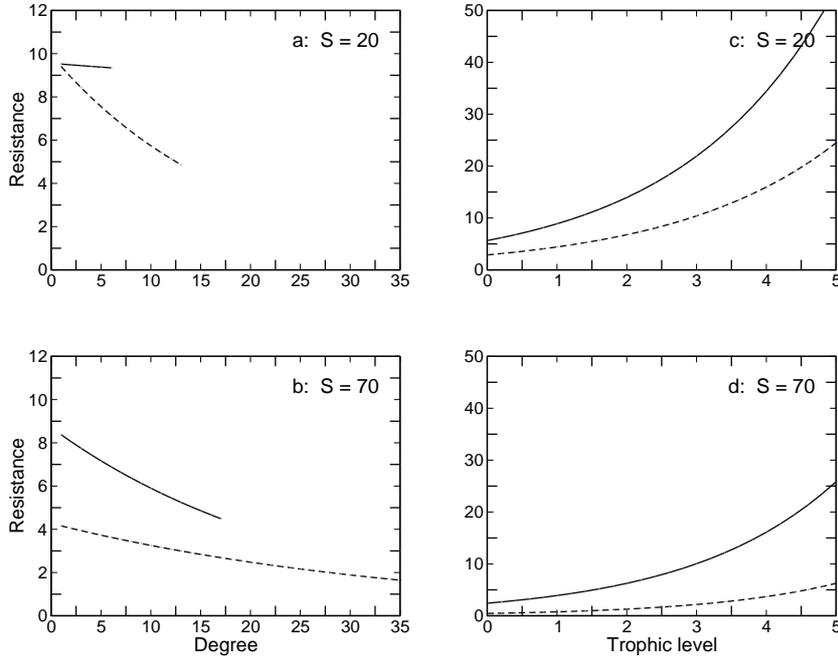


Figure 9: The resistance of the food web to a disturbance depends on the degree and trophic level of the disturbed species, as predicted by our generalized linear mixed models. (a,b) Communities are more resistant to disturbance of specialists than generalists, especially at high connectance and low species richness and low connectance and high species richness ($R_m^2 = 0.107, R_c^2 = 0.951$). (c,d) Communities are more resistant to disturbance of top trophic species than lower trophic species, especially at low species richness and low connectance ($R_m^2 = 0.149, R_c^2 = 0.959$). Panels a and c show the relationship for communities with 20 species, panels b and d show the relationship for communities with 70 species. Solid lines show the relationship for communities with a connectance of 0.1, while dashed lines show communities with a connectance of 0.3.

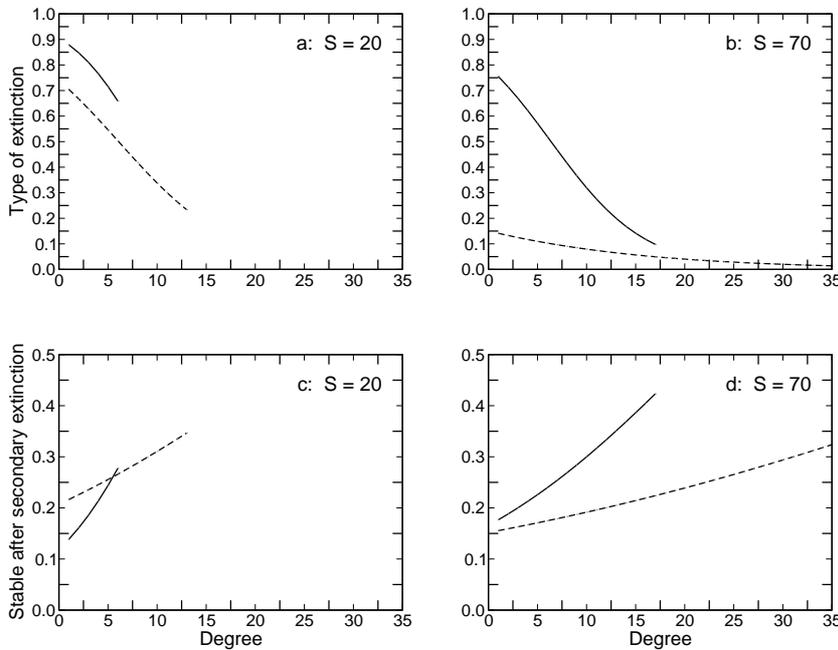


Figure 10: The outcome of disturbance depends on the degree of the disturbed species, as predicted by our generalized linear mixed models. (a,b) Disturbance of a specialist is more likely to result in a focal extinction (value of 1 on the y axis), while disturbance of a generalist is more likely to result in a secondary extinction (value of 0 on the y axis), although this is less evident in large, well connected networks ($R_m^2 = 0.453, R_c^2 = 0.770$). (c,d) Of those disturbances which result in a secondary extinction, if the disturbed species is a generalist it is more likely that the community will be stable after the loss of that species than if the disturbed species is a specialist ($R_m^2 = 0.019, R_c^2 = 0.251$). A value of 1 on the y axis means all disturbances causing secondary extinctions were stable after the disturbance, while a value of 0 means none were. Panels a and c show the relationship for communities with 20 species, panels b and d show the relationship for communities with 70 species. Solid lines show the relationship for communities with a connectance of 0.1, while dashed lines show communities with a connectance of 0.3.

Discussion

We found that the stability of a community to a single-species press disturbance followed much the same relationship with network complexity as the community's stability to pulse disturbances; as communities increased in species richness and/or connectance, they became less stable to both press and pulse disturbances. This agrees with other theoretical research 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, networks are very complex and there are many direct and indirect interactions between species such that two species which are not directly connected may 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). Indeed, we found that, as complexity increased, the number of disturbances which resulted in a secondary 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 secondary extinction; however, this occurred less often as complexity increased. This indicates that, in highly complex networks, species in stable and feasible webs were simply too interdependent and could not coexist when one was lost.

We also found that measures of stability to pulse disturbances were good predictors of resistance, beyond what was explained by the size and connectance of the network - the more stable a community was to a pulse disturbance (i.e., the more resilient or less reactive it was), the more stable it was to a press disturbance (i.e., the more resistant it was). This indicates that the properties which conferred stability to a pulse disturbance also tended to confer stability to a press disturbance. Many studies have found that elements of the structure of the network are important for stability, above and beyond species richness and connectance (McCann et al., 1998; Allesina and Pascual, 2008; Tylianakis et al., 2010; Stouffer and Bascompte, 2011; Allesina and Tang, 2012), and, indeed, this is why in the natural world we observe very diverse networks of species which are still stable (McCann, 2000;

Borrelli and Ginzburg, 2014; Borrelli, 2015). It is likely that the more stable food webs in our simulations exhibited more of these stabilizing mechanisms than less stable food webs. At high levels of size and connectance, however, the relationship between stability to press and pulse disturbances broke down. Here, as discussed above, communities appeared to be so delicately balanced that even the slightest perturbation was enough to cause an extinction; thus, regardless of how resilient or reactive a network was, it had minimal resistance.

Clearly, the properties of the network as a whole give some insight into how the community will respond to a disturbance. We found, however, that for disturbances where a single species bore the brunt of the disturbance, the traits of that species also affected the outcome of the disturbance. Specifically, when a species with few interactions was disturbed, the community could withstand a much larger disturbance before an extinction occurred than when a species with many interactions was disturbed. This is because generalists — species with many interactions — interacted directly with many other species in the food web (Symondson et al., 2002; Orlando and Hall, 2015). Disturbance to a generalist 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 secondary extinctions (Quince et al., 2005; Curtsdotter et al., 2011). Indeed, we found that, although communities could withstand a smaller decrease in growth rate to a generalist than a specialist before experiencing an extinction, we also found that disturbances of generalists tended to cause secondary extinctions, whereas disturbances of specialists tended to cause focal extinctions. Furthermore, when disturbance of a generalist resulted in a secondary extinction, the network was far more likely to be stable post-extinction than if the disturbed species was a specialist. When a specialist caused a secondary extinction, that species was likely the only, or one of few, predators or prey the specialist interacted with. This extinction likely therefore also caused the extinction of the specialist. In contrast, it is plausible that generalists tended to cause extinction of species which primarily interacted only with the generalist. As the generalist interacted with many other species, it was not strongly impacted by the lost species and neither were any other species. In a real-world context, this means that if a generalist species is disturbed, it is likely that secondary extinctions may occur at a relatively low level of disturbance, but that the network will likely remain stable without that lost species. In contrast, if a specialist is disturbed, the network may be able to withstand a larger disturbance before an extinction, but when one does occur it is likely to be the

specialist itself which goes extinct. Other studies have also found that disturbance of generalists caused more secondary 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 has larger net effects on the rest of the food web than generalists. This result may explain why, when a specialist caused a secondary extinction, the network was usually not stable post-extinction.

We found that the trophic level of the disturbed species also affected the outcome of disturbance; communities were less resistant to disturbance of primary producers than top predators. This is likely because a decrease in growth rate of top predators can have a positive impact on the biomass of their prey due to a release from predation (Montoya et al., 2009) and this in turn can feed back to bolster the biomass of the predator, to the extent that, in some cases, we found that the biomass of the predator actually *increased* at early stages of growth rate decrease. This phenomenon has been observed in natural systems, for example where trapping of wild cat populations actually led to an *increase* in wild cat populations (Lazenby et al., 2014). In contrast, we found that when a primary producer was disturbed, their growth rate was no longer sufficient to withstand the predation pressure of those above it, and the species rapidly went extinct. We found little to no effect of trophic level on whether the disturbance resulted in a primary or secondary extinction, in contrast to many empirical studies which find that loss of top predators cause more secondary extinctions than loss of primary producers (Donohue et al., 2013; Paine, 1966; Terborgh et al., 2001; Estes et al., 2011). The reason many of these studies find this result is due to competition between species, which we have not explicitly accounted for.

Food-web complexity and species' traits interactively affect a food web's response to disturbances. This has implications for conservation and management of natural systems undergoing press disturbances. While harvest of certain species may be more catastrophic than others, it is also important to maintain the structure of the food web as a whole in order to maximize resistance. Furthermore, our results indicate that the same properties which confer stability to pulse disturbances also confer stability to press disturbances. Further investigation of which stabilizing structures or mechanisms are most responsible for this relationship between press and pulse stability would be beneficial for attempts to maximize resistance by maintaining food-web structure.

Synthesis

In this thesis, we have investigated how network structure and complexity, species' traits, and disturbance type all relate to community stability. First we examined the relationship between species' degree and mean interaction strength and how this relationship affected local stability in networks with an exponential degree distribution. Secondly, we considered how network complexity and species' traits affected a food web's response to a press disturbance. Taken together, the results of these studies have several implications for the study of community stability and its applications.

Food-web complexity and structure

We found that food-web structure both affects stability directly and influences the effect of species with different traits on stability. We found that, while an exponential degree distribution increases stability (Arii and Parrott, 2004; Stouffer et al., 2005; Otto et al., 2007; Dunne and Williams, 2009), this needed to occur in such a way that species' interactions were predominantly incoming (from prey) or outgoing (to predators). That is, very few species with many interactions had both many prey and many predators. Further, the more numerous type of interaction tended to be weak while interactions of the rare type tended to be strong. While this relationship between species' degree and mean interaction strength is stabilizing, it can only be realized when this structure where species have predominantly in- or outgoing interactions occurs. Although it has frequently been assumed that species with many interactions should have weaker interactions, we have shown that it is not simply the *number* of interactions which is important but the number in each direction. To further test the importance of this structure, we randomly reassigned interaction strengths of each network while maintaining

the topology. We found that food webs which were initially stable and thus had this asymmetric link direction structure were more likely to be stable again after reassignment. This indicates that without this structure the stabilizing relationship between species' degree and mean interaction strength cannot occur and the network will not be stable no matter how interaction strengths are distributed.

We also found that the size and connectance of the network affects stability, not only to pulse disturbances but also to press disturbances. Stability to both disturbances decreased as complexity increased. In highly complex networks, there are many indirect interactions that allow a slight disturbance to any species to rapidly propagate and destabilize the network (Yodzis, 1988; Menge, 1995; Laska and Wootton, 1998; Wootton, 2002; Montoya et al., 2005; Stouffer and Bascompte, 2011). At this level of complexity, resistance to all press disturbances was so low that the traits of the disturbed species were irrelevant. At lower levels of complexity, however, the more stable a food web was to a pulse disturbance, the more stable it was to a press disturbance. This can be explained by structures of the food web — such as the asymmetric link structure discussed in the paragraph above — which enhance stability beyond what is accounted for by size and connectance (McCann et al., 1998; Allesina and Pascual, 2008; Tylianakis et al., 2010; Stouffer and Bascompte, 2011; Allesina and Tang, 2012). At high levels of complexity, food webs had minimal resistance to press disturbances regardless of their resilience or reactivity. It may be that at higher levels of complexity these stabilizing structures occur less frequently. This would help explain the decrease in stability with complexity. For example, it has been suggested that networks with higher connectance have a more uniform degree distribution (Dunne et al., 2002a). If the structural mechanism discussed in “*Generalists have weaker and stronger interactions*” indeed influences the stability of food webs in “*Response to press disturbances: Effects of species' traits and food-web complexity*”, a more uniform degree distribution at higher connectance levels may prevent the negative relationship between number and strength of interactions from occurring. This would contribute to the decrease in stability as connectance increases.

Species' interactions

The influence of a single species on stability, or the effect on the network if that species is disturbed, depends on how it interacts

with other species and on the structure and complexity of the food web as a whole. A number of studies have shown the importance of weak interactions for dampening the potential oscillations of strong interactions (Paine, 1992; Fagan and Hurd, 1994; Wootton, 1997; McCann et al., 1998; Sala and Graham, 2002; Berlow et al., 2004), and that strong interactions occur on two consecutive levels of a food chain less often than expected at random (Bascompte et al., 2005). Thus, it may be that a network structure where species have predominantly weak interactions in one direction and a few strong interactions in the other direction ensures that a strong interaction is usually followed by a weak interaction and that this pattern prevents disturbances from propagating. Equally, this means that if a neighboring species with whom the focal species interacts strongly is disturbed, the effect can be buffered by the focal species' many weak interactions in the opposite direction.

Species' traits affected a food web's response to a press disturbance. The structure and complexity of the network had a sufficiently large effect on the food web's resistance, however, that knowledge of the disturbed species' traits was most useful when comparing the effect of two species from the same food web. While the complexity of a food web set the baseline of stability to both press and pulse disturbances, the traits of the species within the food web affected how far from that baseline the response to a disturbance fell. How much a species' traits influenced stability depended on complexity of the network however; at high levels of complexity, species' traits had very little effect, while at low complexity they had a much greater effect. Thus the effect of an individual part depended on the structure of the whole.

Implications for theory and application

"Generalists have weaker and stronger interactions" draws together research on the importance of degree distribution (Dunne et al., 2002a; Arian and Parrott, 2004; Stouffer et al., 2005; Otto et al., 2007; Estrada, 2007), the distribution of links to predators and prey (Camacho et al., 2002; Stouffer et al., 2005), distribution of interaction strength, the importance of weak interactions for dampening strong interactions (McCann et al., 1998; Bascompte et al., 2005), some empirical support (O'Gorman et al., 2010) and a 60 year old argument for complexity enhancing stability (MacArthur, 1955) to show that a long held assumption, while true, only explained part of the story. We believe

that the finding that stability is influenced not only by the number and strength of interactions a species has but also the direction of those interactions gives a greater understanding of stabilizing mechanisms in empirical food webs and will thus enable more empirically accurate model generation for future research.

Comparison of stability-complexity relationships can be challenging, as stability can be quantified in a number of different ways (Grimm and Wissel, 1997; Ives and Carpenter, 2007; Donohue et al., 2013). In *“Response to press disturbances: Effects of species’ traits and food-web complexity”* we directly compared three measures of stability and included press as well as pulse disturbances. We found that all measures of stability showed the same relationship with complexity and, moreover, that food webs most stable to pulse disturbances were also most stable to press disturbances. This indicates that studies of food-web stability to pulse disturbances and the stabilizing mechanisms which increase stability — such as that which we investigated in *“Generalists have weaker **and** stronger interactions”* — may also be relevant to press disturbances, at least at a level of network realism employed here.

In a real-world context, our results show that it is important to consider species, not only for their intrinsic traits, but also how they interact with and relate to the community as a whole. Some species likely form more crucial elements of the community’s stability than others, but this also depends on the properties of the food web in which we find them (Power et al., 1996; Ebenman and Jonsson, 2005; Valls et al., 2015). These species may need greater protection for the sake of the whole community than some other species. For example, we found that food webs are least resistant to the disturbance of generalists, and that they tend to cause secondary extinctions when disturbed. Perhaps this is because generalists tend to have many weak interactions, and these interactions are known to be important for stability (McCann et al., 1998). Although generalists interact directly with many species, their influence on stability may be less a result of these direct interactions, and more a result of their contribution to a stable structure for the food web due to their weak interactions. To manage and conserve ecological communities subject to a variety of disturbances, perhaps we need to shift our focus to the protection and maintenance of those species and interactions which contribute the most to a stable network structure.

Future directions

There are a number of directions in which one could continue this research to draw a fuller picture of how species' interactions and network structure affect food-web stability to different disturbance types. For example, in both projects we only considered the impact of species' interactions in one direction; either the effect of the focal species on other species *or* the effect of other species on the focal species. Similarly there are a number of ways in which our simulated networks and disturbances were simplified relative to reality in order to make them mathematically tractable. Further studies using more realistic options may give a more accurate picture of how natural food webs may respond to disturbances. Finally, many of these threads of research were initially sparked by observation or experimentation of natural systems. To fully understand the implications of the studies presented here for natural systems, they should be investigated empirically.

In "*Generalists have weaker **and** stronger interactions*", we only considered the effect of interacting species *on* the focal species. The next step would be to extend this to examine how the focal species affects other species; i.e., do species with many interactions have weaker impacts on those species they interact with? We would not necessarily expect to observe the same relationship as we have when looking at how other species affect the focal species, as it has been shown in a number of cases that species can have strong effects on many species in the community, for example keystone or dominant species (Paine, 1992; Ebenman and Jonsson, 2005). This would also enable us to draw stronger inference about our perturbations experiment and why food webs are least resistant to the disturbance of generalists. In the case where the generalist is being disturbed it would be more informative to know the effect of generalist on other species and not only the effect of other species on the generalist.

In "*Response to press disturbances: Effects of species' traits and food-web complexity*", we considered how the traits of a disturbed species can affect the community's response to a disturbance. It would also be informative to study what traits make a species more or less vulnerable to a disturbance. For example, do specialists go secondarily extinct more frequently than generalists? Do secondarily extinct species usually have the same relationship (i.e., as prey or directly interacting) with the focal species? Frequently conservation and management is more interested in protecting a particular charismatic species rather

than determining the effect on the rest of the food web if a particular species is disturbed. While our current studies give us information about the latter, this proposed study would give important information about the former.

In order to obtain enough food webs to replicate across a wide range of size and connectance values, we have simulated networks. Although we have endeavored to make these as realistic as possible, by using the niche model (Williams and Martinez, 2000) and imposing a predator-prey interaction structure (Allesina and Pascual, 2008), there are still many elements of real networks which we will not have captured and will likely influence stability (James et al., 2015). For example, the level of accuracy in estimating interaction strengths is known to have a significant effect on stability (Novak et al., 2011) and we have set all our interaction strengths at random. We have hypothesized that the reason food webs most stable to pulse disturbances are also most stable to press disturbances may have to do with stabilizing features and structures of the food web, such as that which we observe in "*Generalists have weaker and stronger interactions*". In this case it may be that more realistic food webs may show a different relationship between stability to press and pulse disturbances than that which we observe here.

Similarly, to simplify our study of press disturbances, we only considered the effect of press disturbances on a single species at a time. In reality, these disturbances usually affect multiple species. While choosing which species to impact together, and by how much, to realistically investigate this would be a considerable challenge, it would give a more accurate understanding of how these disturbances would actually affect communities.

There has been at least one empirical study of the strength of species' interactions relative to the number of interactions (O'Gorman et al., 2010). To determine how common this pattern actually is in natural communities, however, further studies would be useful. In particular, these studies should also consider the number and direction of interactions, to determine whether the pattern of few strong and many weak interactions which we observe in "*Generalists have weaker and stronger interactions*" holds in natural communities.

While there are many empirical studies of the effect of press disturbances on communities, these tend to focus on disturbances which affect the community as a whole (such as a change in temperature) or focus on a species' removal (Zeng et al., 1997; Buonopane et al.,

2005; Guido and Pillar, 2015). These removal experiments, however, usually remove only one or a few species in the food web and do not compare the effect of removing one species compared to another. We found that the effect of species' traits on food-web resistance depends on the properties of the community and that this can occur without complete removal of the disturbed species. Experimental studies comparing the effect of decreasing the growth rate of a primary producer compared to a top predator — or a generalist compared to a specialist — within the same food web would give insight into the applicability of our results to natural communities.

Conclusions

While there is a wealth of research on the themes of community stability, network complexity and structure, species traits, disturbance types and how they all relate to each other, there are still a number of gaps in our knowledge. Here we have found that when these themes are brought together and studied directly they some times interact in surprising ways which could not be anticipated accurately by studying each theme in isolation. The relationship between species' degree and interaction strength are important for stability, but only when combined in an asymmetric structure which prevents the propagation of disturbances. Species' traits affect a food web's response to a disturbance, but only relative to the baseline set by the structure of the network, and the complexity of the network can make species' traits irrelevant. While there are still many studies to complete the reconciliation of these themes, the research presented here reveals some valuable insights into the stability of communities to different disturbance types and how this is influenced by the properties of the networks and species involved.

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