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Compensation masks trophic cascades in complex food webs

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Abstract

Ecological networks, or food webs, describe the feeding relationships between interacting species within an ecosystem. Understanding how the complexity of these networks influences their response to changing top-down control is a central challenge in ecology. Here, we provide a model-based investigation of *trophic cascades* — an oft-studied ecological phenomenon that occurs when changes in the biomass of top predators indirectly effect changes in the biomass of primary producers — in complex food webs that are representative of the structure of real ecosystems. Our results reveal that strong cascades occur primarily in small and weakly connected food webs, a result very much in agreement with empirical studies. The primary mechanism underlying weak or absent cascades was a strong compensatory response; in most webs predators induced large population level cascades that were masked by changes in the opposite direction by other species in the same trophic guild. Thus, the search for a general theory of trophic cascades in food webs should focus on uncovering the features of real ecosystems that promote or preclude compensation within functional guilds.

1 Introduction

Trophic cascades occur when changes in an ecosystem's top trophic level propagate down through the food web and drive changes in the biomass of primary producers (Hairston et al., 1960; Paine, 1980). Cascades have now been documented in virtually every type of ecosystem, but neither conceptual nor mathematical theories have been able to explain widespread variation in observed cascade strengths (Borer et al., 2005; Shurin et al., 2010); in some ecosystems, strong cascades impact several lower trophic levels while in others they diminish within a single trophic level (Heath et al., 2014). Indeed, *trophic trickles* (McCann et al., 1998) — weak or absent cascades in response to major changes to a food web's top trophic level — abound in nature (Brett and Goldman, 1996; Mikola and Setälä, 1998; Halaj and Wise, 2001). Given that human actions are disproportionately altering biomass of top predators (Estes et al., 2011), there is a pressing need to understand under what circumstances such changes will or won't cascade through complex food webs (Terborgh et al., 2010).

Food web structure has long been predicted to regulate cascade strength (Strong, 1992; Pace et al.,

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1999; Polis et al., 2000; Shurin et al., 2010) and the magnitudes of indirect effects in general (MacArthur, 1955; Yodzis, 1988). Indirect tests of this hypothesis have so far been accomplished by leveraging data on community features like functional or taxonomic diversity (Borer et al., 2005; Frank et al., 2006), in hopes that these proxies for web structure could provide clues to the features of ecological networks that influence the magnitude of cascading top down effects. However results have been mixed, with studies reporting both strong (Frank et al., 2006, 2007; Baum and Worm, 2009) and weak or noisy (Borer et al., 2005; Fox, 2007) associations between diversity measures and cascade strengths. Whether data support assertions that food web structure regulates cascade strengths remains unclear, and a coherent understanding of when relatively strong or weak trophic cascades occur is still lacking.

One impediment to progress is that extensions of cascade theory toward species rich and topologically complex food webs are needed to guide further empirical study. To date, cascade theory has focused largely on understanding variation in cascade strengths in model food chains (Oksanen et al., 1981; McCann et al., 1998; Heath et al., 2014; DeLong et al., 2015) and although extensions of cascade theory to alternate trophic modules exist (Bascompte et al., 2005; Fahimipour and Anderson, 2015), the mechanisms underlying variation in cascade strength in species rich and complex trophic networks remain poorly understood (Holt et al., 2010; Shurin et al., 2010).

Here we use a bioenergetic food web model to explicitly study the emergence of trophic cascades in species rich webs that are representative of the structure of real ecosystems following the invasion of a novel top generalist predator. We demonstrate that the strongest trophic cascades occur in small and weakly connected food webs — a result in agreement with some prior predictions (Pace et al., 1999; Polis et al., 2000; Fox, 2007; Shurin et al., 2010). Moreover, our results reveal that biomass compensation within producer and consumer functional guilds, whereby some species increase in biomass while others decrease proportionately, is the most common mechanism underlying weak or absent trophic cascades. Thus, the search for a general theory of trophic cascades in food webs should focus on uncovering the abiotic and biotic features of real ecosystems that promote or preclude biomass compensation and compensatory dynamics within functional guilds.

2 Methods

We generated food web topologies using an ecological niche model (Williams and Martinez, 2000) and simulated the dynamics of energy flows between species using a bioenergetic model (Yodzis and Innes, 1992; Brown et al., 2004; Brose et al., 2006b; Williams et al., 2007; Williams, 2008). The niche model is discussed in detail by Williams and Martinez (2000) and was used to generate topologies for 1200 food web simulations in a factorial design: initial species richnesses of $S = 10$, 15, 20 and 25 were crossed with directed connectance $C = 0.12$, 0.16 and 0.2 as niche model parameters (4 richnesses $\times$ 3 connectances $\times$

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100 iterations = 1200 webs total). These values of C were chosen because they encompassed a wide range of empirically observed connectance values (Dunne et al., 2002). Webs that deviated from the precise C values, contained disconnected nodes, or consisted of disconnected subgraphs were not considered.

Details of the energy flow model and parameters used are discussed by Williams et al. (2007) but briefly, an allometrically scaled nonlinear bioenergetic model (Yodzis and Innes, 1992) was used to study the dynamics of species biomasses and the occurrence of trophic cascades in niche model food webs when they are subject to the invasion of a new top predator. We report results from a single ecologically reasonable set of model parameters (see *Supplementary Materials*), though similar results were obtained with other model parameterizations. Biomass dynamics were represented as

$$\frac{dB_i}{dt'} = B_i G_i(B) - \sum_{j=consumers} \frac{x_j y_{ji} B_j F_{ji}(B)}{e_{ji}} \tag{1}$$

$$\frac{dB_i}{dt'} = -x_i B_i + x_i B_i \sum_{j=resources} y_{ij} F_{ij}(B) - \sum_{j=consumers} \frac{x_j y_{ji} B_j F_{ji}(B)}{e_{ji}} \tag{2}$$

for primary producers and consumers respectively. Here B_i is the biomass of species i. All k producers were assumed to have the same body mass, $M_k = 1$, and time t‘ was scaled with producer growth rate (Williams et al., 2007). The metabolic parameter x_i is the mass specific metabolic rate of species i relative to the time scale of the system and the non-dimensional constant y_{ij} is the ingestion rate of resource i by consumer j relative to the metabolic rate of i. The efficiency e_{ji} is the fraction of the biomass of resource i lost during consumption by consumer j, that is assimilated. The function $G_i(B)$ is the normalized growth rate of primary producer population i, which follows logistic growth, $1 - B_i/K_i$ where K_i is the carrying capacity of producer i. To control for effects of varying productivity on trophic cascade strength, we maintained constant productivity across simulations by assuming a system-wide carrying capacity K that is shared amongst i producer populations according to $K_i = K/n_p$, where n_p is the number of producer species in the web.

The function $F_{ji}(B)$ is the normalized multi-species functional response for consumer j and resource i, developed by Yodzis and Innes, 1992 and extended by others (Brose et al., 2006b; Williams et al., 2007; Williams, 2008). Adding consumer interference to a multispecies nonlinear functional can be represented as

$$F_{ji} = \frac{\omega_{ji} B_i^{1+q}}{B_0^{1+q} + d_i B_j B_0^{1+q} + \sum_k \omega_{jk} B_k^{1+q}}. \tag{3}$$

Here d_i is a positive constant that sets the amount of interference in the system and the sum in the denominator is over all k resources of consumer j. The parameter B_0 is the half saturation density. In order to avoid excessive extinctions or the collapse of webs following predator invasions, and permit the study of trophic cascades following major changes to web structure, we assumed that interference occurred but was weak ($d_i = 0.5$) and set the shape parameter $q = 0.2$, which slightly relaxed consumption at

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low resource biomasses — features that are both biologically realistic and likely too subtle to observe empirically (Williams, 2008). We assume passive resource switching, so $\omega_{ij} = 1/n_{ri}$ where n_{ri} is the number of resources consumed by species i. Additional model details are discussed by Williams et al. (2007) and in *Supplementary Materials*.

Simulations were run for 5000 model time steps at which point a top generalist predator invaded the food web. We assumed that the predator was a highly efficient generalist, with a fixed body mass consistent with a large secondary consumer (see *Supplementary Materials*) and a scaled attack rate twice that of other species in the system. We note that the augmented predator attack rate is still within the range of empirically observed values (Peters, 1983). Upon invasion, the predator had a probability of 0.5 of consuming any species in the web whose shortest path to a producer $P = 1$; the invader can consume herbivores or omnivores that are already present in the web, but not producers or other top predators. Following the predator invasion, each system was run for a further 5000 time steps for a total 10000 time steps. Cascade strengths were measured as log_{10} response ratios $log_{10}B_{post}/B_{pre}$, where B_{post} and B_{pre} are aggregate producer community biomasses (summed over all n_p basal species) averaged over the final 100 time steps after and before predator invasions respectively. Likewise, consumer level effects were calculated as log_{10} response ratios of aggregate consumer biomass, where the consumer guild was defined as all species that eat producers ($P = 1$, where P is the shortest path length to any producer species). Numerical integration of ordinary differential equations was accomplished using the *deSolve* package in R (R Core Team, 2015).

To study whether features of the initial network structure were strongly related to the response of systems to invading predators, we computed associations between the cascade strengths and a suite of common network properties (Williams and Martinez, 2004; Vermaat et al., 2009) using *ANOVA*. The network properties we considered were species richness, connectance, characteristic path length, the fraction of species that are basal, intermediate and omnivorous, clustering coefficient, mean maximum trophic similarity and Clauset-Newman-Moore modularity (Clauset et al., 2004). We note that the frequentist statistical hypothesis tests employed here were not used to assess statistical significance since p-values are determined by the number of simulations one chooses to run. Instead, we follow the suggestion of White et al. (2014) and use the statistical model described above as a framework for partitioning effect sizes and variance in these multifactorial simulations and comparing effect sizes among factors. We refer to these effects below using the notation $\beta_{variable}$ where for instance β_C is the connectance effect, which reflects the per unit impact of scaled (Gelman, 2008) C on the strength of cascades.

Finally, we sought to understand the mechanisms underlying weak trophic cascades, as these cascades would be least likely detected in empirical studies. We operationally defined *weak cascades* as a less than twofold change in aggregate producer biomass after predator invasions. One possibility is that weak

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cascades are caused by diffuse predator effects (*sensu* Yodzis, 2000), whereby predator consumption is spread over multiple resources leading to overall weak biomass responses at the population scales. In this scenario, species in each lower trophic level change only slightly in the same direction, and strong community level biomass responses fail to emerge. Alternatively, weak cascades could occur even in the presence of major changes to population biomasses if changes in strongly depressed species are offset by compensatory changes in the opposite direction by other species (i.e., biomass compensation; Gonzalez and Loreau, 2009) in the producer or consumer guilds. To quantitatively assess these possibilities, we present a measure μ that quantifies the degree of biomass compensation among populations i in a trophic guild as

$$\mu = 1 - \frac{|\sum_{i\epsilon s} B_{i,post} - B_{i,pre}|}{\sum_{i\epsilon s} |B_{i,post} - B_{i,pre}|} \tag{4}$$

where the sum is over all s species in a trophic guild (e.g., producers). This metric μ varies from 0 to 1, with 0 indicating that all species within a guild changed in the same direction (the biomass of all populations increased or decreased) and 1 indicating perfect biomass compensation. If weak trophic cascades are typically accompanied by small μ values, then we conclude that weak cascades usually occur because top down effects are too diffuse to effect strong changes in aggregate producer biomass. Conversely, if weak cascades are typically accompanied by large μ, then we conclude that compensatory changes in the opposite direction by species in the same guild lead to a small net changes in aggregate biomass. Herein, we refer to compensation in the producer and consumer guilds as μ_R and μ_N.

3 Results

Predator invasions had moderate effects on aggregate producer biomass in most food webs (Fig. 1). Producers changed by a factor of 1.7 on average across all simulations, and twofold changes in producer biomass occurred in only 31% of webs. Predator facilitation of producers was strongest in small and weakly connected webs (Fig. 2; $\beta_S = -0.111$, $\beta_C = -0.012$). Cascade strengths were also associated with other topological properties commonly used to describe web structure (Williams and Martinez, 2004; Vermaat et al., 2009). The strongest associations were observed between producer log response ratios and S, the fraction of basal species, the fraction of intermediate species and mean maximum trophic similarity (Table 1).

The magnitudes of consumer log response ratios were more strongly correlated with most food web properties (Table 1), suggesting that the sensitivity of a guild's log response ratio to initial network conditions may depend on trophic position; topology appears to exhibit relatively strong associations with changes in consumer level biomass following novel predator invasions compared to lower trophic levels. Depression of consumer biomass by invading predators was strongest in small and weakly connected networks (Fig. 2; $\beta_S = 0.741$, $\beta_C = 0.156$) with fewer basal species and less modular, more clustered

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network configurations (Table 1).

Producer compensation μ_R was negatively correlated with cascade strengths across all simulations (Fig. 3a; Pearson's $r = -0.34$), suggesting that biomass compensation among producers commonly masked cascades at the community scale (e.g., compare Figs. 3b & 3c). This result is recapitulated by the high frequency of simulations characterized by stronger trophic cascades and almost no producer compensation (Fig. 3a, dark shaded region). Indeed, of the webs that exhibited weak producer cascades (i.e., aggregate producer biomass increased by less than a factor of 2), 90% contained at least one producer population that more than doubled despite the absence of a strong community level cascade. Taken together this suggests that weak cascades were in large part caused by producer compensation, leading to a small net changes in aggregate biomass.

Compensation in the consumer guild increased strongly with S and C (Fig. 4), explaining the shift in consumer effect size distributions toward zero visible in Figs. 1e-h and Fig. 2. This suggests that two separate compensation mechanisms could explain weak cascades in webs. The first occurred primarily in smaller webs, when strong depression of consumers was transmitted to producer populations but failed to manifest at the guild scale because changes in some populations were offset by others in the opposite direction (i.e., *producer* compensation). The second occurred primarily in larger webs (Fig. 4), when top-down predator effects were immediately diminished in the consumer trophic guild due to *consumer* compensation. The strongest cascades occurred when the degrees of both producer and consumer compensation were low, which was most likely in small, weakly connected webs.

4 Discussion

Our modeling study found that strong trophic cascades at the scale of the producer community are more likely to occur in smaller, less connected ecological communities, a result that is in agreement with some previous interpretations of indirect effects and trophic cascades (MacArthur, 1955; Pace et al., 1999; Frank et al., 2006; Shurin et al., 2010). In most webs (90% of all simulations), at least one producer species doubled or more in biomass, yet strong community scale cascades occurred in only thirty percent of simulations. Strong population level cascades were often offset by an opposite biomass change in other species so that the overall producer community biomass wasn't strongly affected. Thus, restricting attention to trophic cascades as measured by changes in the overall biomass of producer species makes it much less likely that the effects of an invading species will be detected. Strong top-down effects still occur in large and complex ecological networks, but observing them requires finer-grained observations than simply measuring total plant biomass (Polis et al., 2000). In almost all communities, the introduced top species had a strong effect on both the relative biomass of species and the dynamics of the community. Shifts in relative species composition due to compensation within a community are more common than

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changes in the overall community biomass, and may be a potentially useful indicator for species invasions (Schmitz, 2006).

Weaker cascades in large highly connected webs have been attributed to weaker and more diffuse interactions among trophic levels in these systems (Leibold et al., 1997; Pace et al., 1999; Shurin et al., 2010). However, the observation that compensation frequently operated in multiple trophic guilds suggests a new hypothesis for the emergence of trophic cascades in complex food webs. Namely, changes at the top of webs have some chance of diminishing due to compensation within each trophic guild, as they cascade down to producers. If the trophic network is structured in a way that precludes compensation from occurring in any of these guilds, then a strong cascade will emerge. Alternatively, top-down regulation has the capacity to diminish within a single trophic level if the propensity for compensation is high in that particular system, which can result from particular network configurations or exogenous abiotic forcing in real ecosystems (Gonzalez and Loreau, 2009). Experimental tests of this hypothesis could be accomplished by adding conspecific generalist predators to replicate food webs with known topologies (e.g., experimentally assembled micro- or mesocosms) and measuring them repeatedly through time. However, replicated food web experiments with repeated measures are scant (Fahimipour and Hein, 2014) and to our knowledge no such data exist to test the results presented here.

The present study looks at the role of increasing web size and structural complexity on trophic cascades and the detection of the effects of species introductions. The model used, while more complex than those typically used in trophic cascade studies, is still highly idealized. The dynamics of real ecosystems often include many other non-trophic processes (Kéfi et al., 2015) which might dampen (or magnify) the cascading influence of top predators (Polis and Strong, 1996). One such example is that our study was restricted to models of closed systems. Evidence of cross-ecosystem cascades (Knight et al., 2005) and the influence of resource colonization rates on cascades (Fahimipour and Anderson, 2015) suggest that extensions of our model to open systems will be a promising enterprise for further theoretical study.

Identifying the abiotic and biotic features of ecosystems that regulate trophic cascades is a fundamental issue in ecology (Polis et al., 2000; Terborgh et al., 2010) and a practical problem for the management of invasive species, agricultural pests and zoonotic disease (Estes et al., 2011). While the present study identifies features of model food web architecture that influence cascades, the potential for compensation (Gonzalez and Loreau, 2009), complex indirect interactions and feedbacks (Yodzis, 2000) in real world networks together with insufficient data (Shurin et al., 2010) and issues of scale (Polis et al., 2000) combine to make the development of a predictive cascade theory of food webs a difficult problem.

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Acknowledgements

We thank Benjamin Baiser for useful discussions. This work resulted from the *Dynamics of and on Networks* workshop at the Santa Fe Institute in Santa Fe, NM. AKF was supported by the University of California Office of the President, the National Science Foundation under award no. 006741-002 and the Gordon & Betty Moore Foundation.

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Figure Captions

Fig. 1. (a—d) Stacked histograms of producer cascade strength frequency distributions for webs of different richness (panel columns) and connectance (green shading) values. The green dotted lines mark mean cascade strengths for reference. Smoothing was accomplished using a Gaussian kernel. (e—h) Stacked histograms of consumer cascade strength frequency distributions for webs of different richness (panel columns) and connectance (purple shading) values. The purple dotted lines mark mean consumer cascade strengths for reference. Smoothing was accomplished using a Gaussian kernel.

Fig. 2. Relationships between S, C and cascade strengths in the producer (green circles) and consumer (purple squares) guilds. Points and error bars represent mean cascade strength $\pm$ 2 *SEM* and lines show results of *loess* regression to raw simulated data. Panels (a), (b) and (c) correspond to C values of 0.12, 0.16 and 0.2 respectively.

Fig. 3. (a) Level plot showing the negative relationship between the producer cascade strengths and the degree of producer compensation, μ_R. Points represent individual simulations. The background is shaded according to a Gaussian kernel used for density estimation, where darker shades of green represent denser regions. A high density of stronger cascades with near-zero producer compensation is visible. (b) Example of a relatively strong cascade where compensation is weak. Colored green lines represent individual producer populations and the thick black line is the aggregate producer biomass. A dotted line marks the predator invasion. (c) Example of a weak cascade due to strong producer compensation.

Fig. 4. Relationships between S, C and compensation in the producer (green circles) and consumer (purple squares) guilds. Points and error bars represent mean compensation values $\pm$ 2 *SEM* and lines show results of *loess* regression to raw simulated data. Panels (a), (b) and (c) correspond to C values of 0.12, 0.16 and 0.2 respectively.

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Table Captions

Table 1. Results of *ANOVA* tests. The *Variable* column indicates the dependent variable to which statistics refer. The food web properties were species richness (S), directed connectance (C), characteristic path length (CPL), the fraction of species that are basal (*Frac.* B), intermediate (*Frac.* I) and omnivorous (*Frac.* Om), Clauset-Newman-Moore modularity, clustering coefficient and mean maximum trophic similarity. The β and *sums-of-squares* columns indicate the regression coefficients and model sums of squares respectively.

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Figure 1

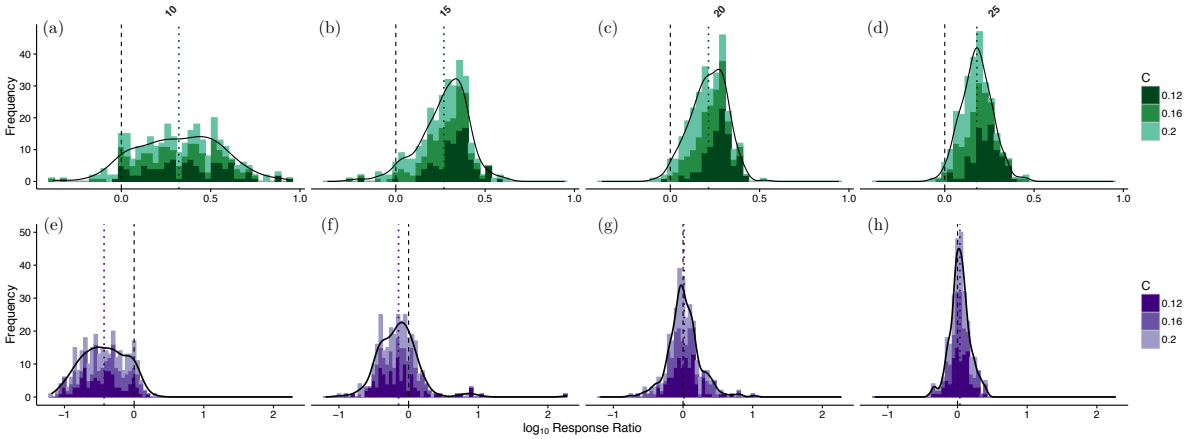

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Figure 2

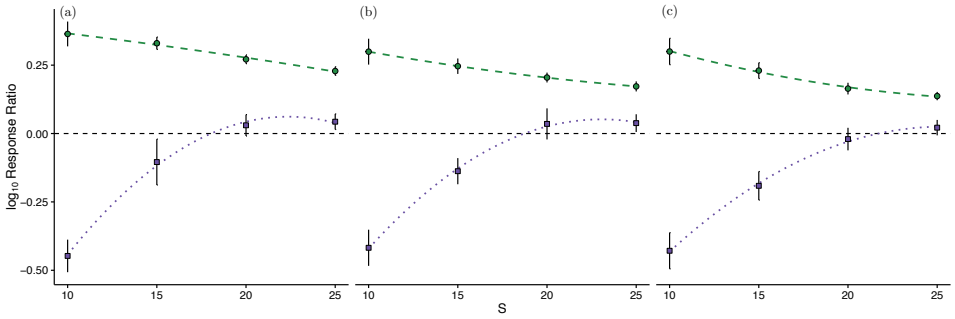

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Figure 3

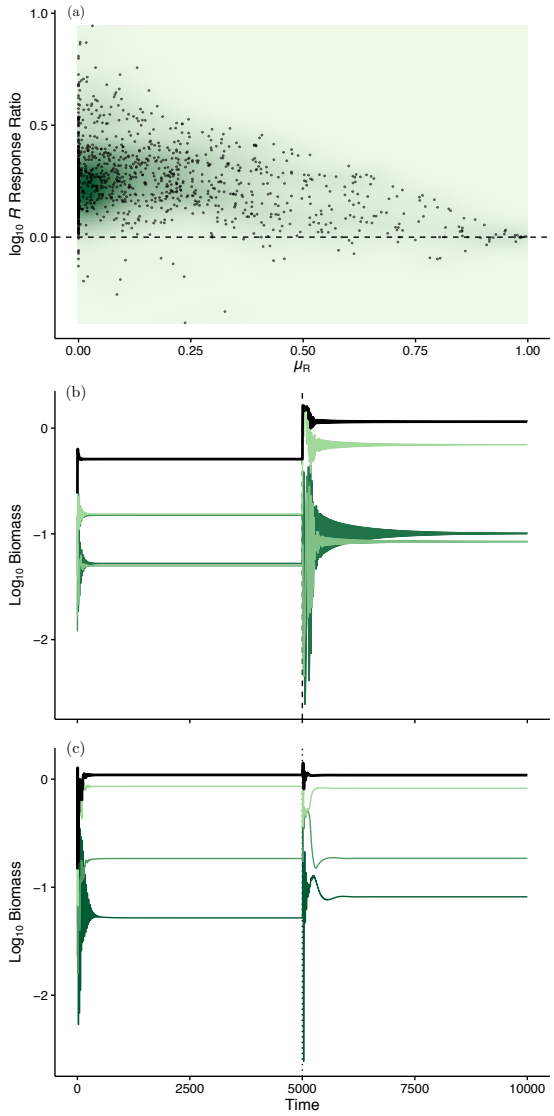

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Figure 4

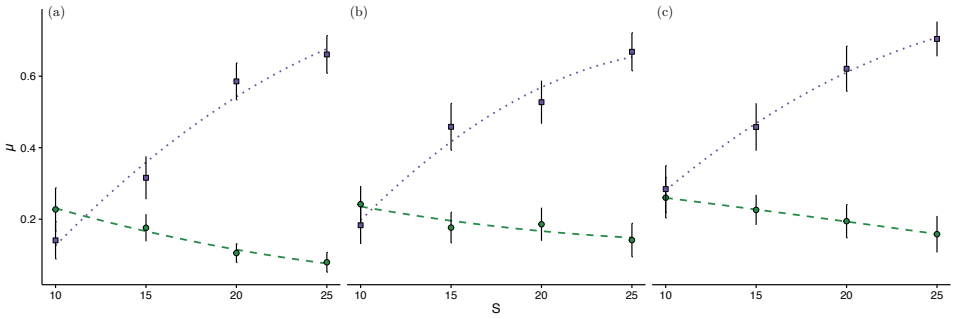

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Table 1: Results of *ANOVA* tests

Variable	Food Web Property	β	Sum-of-squares
Producer Response Ratio			
	S	-0.111	31.87
	C	-0.012	15.33
	CPL	0.08	0.53
	Frac. B	0.21	1.86
	Frac. I	-0.116	4.83
	Frac. Om	0.001	0.06
	Modularity	0.014	0.01
	Clustering Coefficient	0.009	0.19
	Mean Maximum Similarity	-0.095	1.48
Consumer Response Ratio			
	S	0.741	84.46
	C	0.156	0.58
	CPL	0.002	0.11
	Frac. B	0.218	4.24
	Frac. I	-0.084	6.95
	Frac. Om	0.014	0.03
	Modularity	0.077	0.55
	Clustering Coefficient	-0.084	0.93
	Mean Max Similarity	0.038	0.24

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Supplementary Methods

Metabolic parameters in the bioenergetic model (Yodzis and Innes, 1992; Brose et al., 2006b) are given by

$$x_i = \frac{a_{Ti}}{a_{rk}} \frac{M_k}{M_i}^{0.25} \tag{5}$$

$$y_{ij} = \frac{a_{ji}}{a_{Ti}}. \tag{6}$$

Here, M_i is the mass of an individual of species i and M_k is the mass of primary producers used for normalizing the time scale. The constants a_T, a_r and a_j ($mass^{0.25} \times time^{-1}$) were previously determined from empirical data on the allometry of metabolism, production, and maximum consumption respectively. We assumed that all species were invertebrates, and so $a_r = 1$, $a_T = 0.314$ and $y_{ij} = 8$ (see Brose et al. (2006b) for the derivation of these values). The assimilation efficiency $e_{ij} = 0.45$ for consumption of producers and $e_{ij} = 0.85$ for consumption of consumers. In order to reduce the size of the parameter space being explored, all species in a web were assumed to have a constant consumer-resource body size ratio Z so that the mass of species i was $M_i = M_k Z^P$ where P is shortest path length between species i and any producer. We report simulations in which $Z = 42$. This value represents the mean predator-prey body mass ratio reported by Brose et al., 2006a, although the results presented herein were not sensitive to the choice of Z across its biologically relevant range. We assumed that the predator had a fixed body mass consistent with a large secondary consumer $M_{pred} = Z^{2.5}$. To ensure predators were not entering webs in which many species had gone extinct prior to their arrival, we set a limit on the maximum allowable number of extinctions prior to invasions at two, using $B_i < 1 \times 10^{-15}$ as the extinction threshold. In the event of extinctions before predator arrival, we allowed the extinct taxa to reinvade the system at an initial biomass equal to the extinction threshold. We report results for systems in which $B_0 = 0.25$ and the system-wide carrying capacity $K = 5$. The initial biomass of each species was uniformly drawn from [0.01, 0.1] for all simulations.