

The effects of network shape and perturbation on food web persistence

by

Cole Baird Brookson

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Department of Biological Sciences
University of Alberta

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Abstract

Global change is altering ecological communities and the food webs they support, reducing food web persistence. While a variety of features likely impact the dynamics of perturbed food webs, the relative importance of intrinsic factors (i.e. characteristics of the food web itself) and extrinsic factors (i.e. the type of perturbation experienced) is still unclear. Food web shape, which I define jointly by the species richness distribution and the biomass distribution across trophic levels, may be a useful tool in understanding persistence dynamics. I use a size-based food web model to investigate how 1) persistence dynamics vary across different food web shapes, and 2) how food web shape interacts with perturbation type (pulse, press, and periodic pulse) to influence species loss and biomass change over time. I show that while food webs in the natural world can take on all forms of biomass and species richness distribution, these shapes aren't likely stable without external forcing on the system, and that food webs with bottom-heavy species distributions are the most persistent. In addition, I show that when perturbed, the number of species lost and magnitude of change in biomass is driven jointly by endogenous mechanisms (i.e. food web shape), and exogenous mechanisms such as the trophic level of the perturbed species. These findings can be useful when forecasting how communities of interest may react to increasingly turbulent perturbation regimes caused by anthropogenic global change.

Acknowledgements

A special thanks to my advisor, Dr. Stephanie Green, for sticking with me through what I can only hope is the longest MSc degree you will ever have to advise. I thank you especially for letting me steer my own ship even when it didn't necessarily translate into productivity, it was an invaluable learning process for me. Thank you also for being supportive of my many various detours into other things that interested me, your willingness to let me engage broadly with research and the academy generally has helped me become a more focused researcher. Your patience has been appreciated more than you could know.

A huge thanks to my committee member, Dr. Mark Lewis, for providing extra support and somewhat of a second "home" lab during my time at UofA. I can't overstate how lucky I was to be able to engage with your research group and in your group meetings, during Steph's parental leave and afterwards. Thank you as well to Dr. Rolf Vinebrooke for agreeing to read and consider this thesis, and also for the stimulating discussions you always sparked during BIOL603. During my degree I was supported by an NSERC CGS-M scholarship, two Alberta Graduate Excellence Scholarships, and the University of Alberta Thesis-based recruitment scholarship.

I must also thank my bonus mentor and friend, Dr. Anne McLeod, without who's encouragement I doubt this thesis would ever have been completed. Thank you for helping with everything from code review to emotional support, it has meant the world.

Thank you to the members of the CHANGE lab, as well as the labs of Dr. Martin Krkošek and Dr. Marie-Josée Fortin for being my labs-away-from-home in Toronto.

Thanks as well to Drs. Sean Godwin and Andrew Bateman for being amazing colleagues and mentors, for giving me a break from my thesis when it was most needed, and for reminding me how much fun research can be. Thanks to my collaborators, many of whom are now friends, through all walks of science life, on the council of the Ecological Society of America, and the amazing folks at the Ecological Forecasting Initiative and its Canadian counterpart.

A huge thanks to all my friends, both in the academy and out, to my office mates both recent and past, Dr. Alex Davis and Courtney Stuart for being the best pandemic bubble I could ask for, and to Madeline Jarvis-Cross for reading anything I send you and being my absolute rock. Thank you as well to my ever-supportive family, none of what I do exists without you.

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Chapter 1

Introduction

Understanding how energy flows through ecosystems is one of the most important lines of ecological inquiry, dating back to the discipline's beginnings (Elton 1927; Lindeman 1942). As the basic unit upon which growth and reproduction is based, understanding how organisms obtain energy, and how that energy flows through a system is a challenging problem that still has many unanswered components (Pringle 2020). Researchers often attempt to understand how these energy fluxes may happen by modeling them as food webs; connected and often closed systems with the connections between different organisms representing the energy flowing from one organism to another, usually via consumption. Food webs are in turn then often represented as networks, with nodes quantified as species, and the flow of energy represented as the edges between the nodes. The study of food webs really blossomed in the 1970s when many ecologists began to focus on the structure of food webs (Cohen 1978; May 1973, 1983; Pimm 1982, and others). That is, beyond constructing single food webs such as the much-studied Benguela food web (Yodzis 1998), studying the processes and patterns common to many if not all food webs (May 1983).

While studying food web properties is an area of active basic research, it has important and timely implications for applied conservation as well. With anthropogenic change accelerating rates of biodiversity loss, preserving ecosystems and the functions they provide is paramount. The structure of the food web is known to con-

fer more benefits in terms of ecosystem services than simply the number of species present (Tylianakis et al. 2010). Given that some species will inevitably be lost as ecosystems change (McCarthy et al. 2012), the effects of loss on overall structure is essential, Insights from theoretical works can be of huge use in these efforts. For example, through simulation modeling McDonald-Madden et al. (2016), demonstrate that studying robustness (the ability of a food web to resist secondary extinctions when an initial extinction occurs) (i.e. Dunne et al. 2002) can reveal how and when food webs respond to changing conditions.

Among elements of food web theory that confer useful information to conservation initiatives, food web persistence, or the percentage of species remaining in a network following some event (Pascual & Dunne 2006), is a response measure that is generally used to measure the system's response to disturbance or perturbation. Persistence is a useful measure since it focuses on the discrete event of extinction. That is, a change in persistence is only recorded once a species fully goes extinct. Since the IUCN term of extinction and its precursors (i.e. threatened, endangered) are typically the unit of measure for conservation, persistence, is a helpful way to quantify those extinctions in a network food web.

Myriad additional metrics have been developed and used to try and quantify the structure of a food web, all of which are related to persistence. Connectance, or the proportion of realized trophic links vs. possible links in a food web, is perhaps the simplest. Connectance has been successfully used to predict persistence in model food webs (Gravel, Canard, et al. 2011; Rooney & McCann 2012), with higher connectance typically equating to higher persistence. In addition, modularity, a measure of how compartmentalized a food web is, has also been positively linked to persistence (Stouffer & Bascompte 2011). Beyond these two common network metrics McLeod & Leroux (2021) revealed that the prevalence of different omnivory motifs (i.e. small non-divisible units of omnivore interactions) impacted persistence both negatively and positively.

All these metrics are no doubt useful and likely relevant for well-resolved empirical food webs. Metrics such as modularity and the prevalence of omnivory motifs are challenging to utilize as predictors of persistence in food webs as they are perturbed by human activities. In particular, calculating such metrics rely on a relatively complete description of the food web prior to and during perturbation, which is notoriously difficult due to the scale and intensity of sampling required (Berlow et al. 2004). Given the limitations of current approaches, alternative ways to predict and persistence for empirical, complex webs are needed.

Numerous studies have hypothesized that the distributions of diversity (i.e. number of taxa) and biomass across trophic levels affects the structure of food webs over time. May (1973) proposed that one of the main things that could be driving food web stability (where stability is defined as the ability of a system to return to an equilibrium after perturbed, which is notably different from persistence, but related), could be trophic diversity, that is, the species richness across trophic levels. May (1983) further suggested that this simple and tractable metric could be a way to understand and model the persistence of food webs. Along with the number of species at different trophic levels, the amount of biomass at those different trophic levels is a measure of structure as well; possibly one that confers information about stability properties (Reuman et al. 2008). Previous studies have quantified how either the distribution of species richness or biomass across trophic levels affects dynamics over time in empirical and model systems (Fath & Killian 2007; McCauley, Gellner, et al. 2018; Turney & Buddle 2016). However, less attention has been focused on the extent to which these measures predict persistence.

Food webs do not exist in vacuums; they are affected by a number of different perturbations, which take a number of forms, varying in their duration, magnitude, and repetition (Arens & West 2008; Bender et al. 1984). We know that the frequency of these perturbations, as well as their intensity is increasing as a direct result of anthropogenic change (Ross et al. 2009). However, not every component of these per-

turbations is completely unpredictable. For instance, there are typically three types of perturbations: those that happen just once (pulse perturbations), those that occur cyclically (periodic pulse perturbations), and those that are a steady perturbation on the system (press perturbations). In addition, the effects of perturbations are usually focused on one trophic level (Kouki & Salo 2020), not dispersed across the entire system.

Here, I use simulation experiments to investigate how food webs with different “shape” – defined jointly by the distribution of species richness and biomass across trophic levels— persist over time in the face of various disturbance types. In Chapter 2, I construct size-based food web models that vary in consider both species richness and biomass distributions across trophic levels, taken jointly to be a measure of species shape, and investigate how these factors affect species persistence within the food webs over time. While food web architecture and structure have been evaluated before as factors that affect stability (Rooney & McCann 2012), I attempt to distill food shape down to these two simple distributions (richness and biomass) across trophic levels, and then show how these factors compare to other measures often linked to persistence such as connectance and modularity (Dunne et al. 2002; Stouffer & Bascompte 2011). This analysis also allows me to evaluate the extent to which the variety of food shapes observed in nature are likely to persist in the absence of disturbance or perturbation (i.e. such as from human sources of global change).

In Chapter 3, I extend this food web modeling to look at how food web shapes (again defined by richness and biomass distributions across trophic levels) respond to different perturbations. Specifically, I examine how different types of perturbations (Bender et al. 1984), and different targets of the perturbation (i.e. higher trophic levels vs. lower levels) may be important for persistence. These analyses allow me to determine whether endogenous factors such as food web shape, or exogenous factors such as type of perturbation or trophic level of perturbation are more relevant for predicting food web responses and persistence (Arens & West 2008).

Finally, in Chapter 4, I synthesize and discuss key findings from Chapters 2 and 3 — in particular, that species richness distribution can largely determine both short- and long-term persistence of food webs—and discuss next steps for future research.

Chapter 2

The persistence of size-based food webs and their shapes

2.1 Introduction

2.1.1 Ecological Persistence in the Anthropocene

Since the industrial revolution, degradation of ecological systems has continued to accelerate. From declining individual survival (Dusenge et al. 2019) to wholesale ecosystem collapse (Pinek et al. 2020), anthropogenic global change has been affecting the stability and persistence of ecological processes (Pettorelli et al. 2012). Protecting and managing ecological systems requires first better understanding the processes that structure them, and how these structures in turn affect stability over time. In particular, the structure of species interactions within an ecosystem, rather than just the number of species present, is likely more important for preserving ecosystem function (McCann 2007; McMeans, McCann, Tunney, et al. 2016; Tylianakis et al. 2010). Thus, a useful level of biological organization for understanding ecological persistence and stability is the food web, modeled as a set of predator-prey interactions (McCann 2011).

Many factors are thought to impact persistence (i.e. the proportion of extant species over time) of food webs including compartmentalization/modularity (Stouffer & Bascompte 2011), connectance (Dunne et al. 2002; Gravel, Canard, et al. 2011), and interaction strength (McCann et al. 1998). The effect of these attributes (in

both magnitude and direction) on food web stability has been debated for decades, myriad network metrics having been derived in the literature to try and find patterns in what determines persistence of food webs (Delmas et al. 2019). The success of this approach has been often successful, but still somewhat mixed, with large simulation-based studies recently adding some much needed clarity (Domínguez-García et al. 2019). However, determining the effects of these attributes on real food webs that are of management interest suffers from persistent challenges with empirical measurement (Berlow et al. 2004; Laska & Wootton 1998).

2.1.2 Food Web Shape

Food web *shape* may confer information about how persistent a given food web may be over time. In the literature, food web shape sometimes relates to the distribution of species richness (Turney & Buddle 2016), but also often is referred to with respect to the distribution of biomass across trophic levels (Jonsson 2017). These measures are less useful when referred to alone without the added context of the other, and are relevant in different ways for conservation and management of ecosystems. For example, maintaining food webs with high species richness contributes to food web stability (Zhao et al. 2019) directly by promoting redundancy in ecological niches (A. L. Downing & Leibold 2010; Loreau 2000), which is a key goal of biodiversity conservation. On the other hand, maintaining food webs with high biomass, often in the context of higher trophic levels, is of special interest in harvested systems such as fisheries or sport hunting.

Ecologists have long held consistent hypotheses about the distribution of species richness and biomass within food webs. Early theory by Elton (1927) and Lindeman (1942) suggested that food webs should have a pyramidal shape in both biomass and species richness, with large numbers of species and high proportions of biomass at low trophic levels, and fewer species/lower biomass at higher trophic levels. Lindeman's theory of ecological efficiency states that since energy transfer between trophic levels

is inefficient, there will tend to be progressively fewer species the further up the food chain the energy travels. This is well-founded as an observation in the literature (Bar-On et al. 2018; Hessen et al. 2004). A study of consumer-resource biomass, showed that predator biomass scales sub-linearly to their prey biomass (Perkins et al. 2022), generally resulting in a pyramidal shape (Trebilco et al. 2013). This makes sense in light of the fact that species-energy curves generally point to species richness increasing with more available energy (i.e. biomass) (Evans et al. 2005). Further, in a meta-analysis of this topic, Turney & Buddle (2016) show that across a set of published food webs from a variety of ecosystem types, the average proportion of species present across trophic levels, follows a generally pyramidal shape. However, empirical support for this hypothesis depends on how the “closed” system is defined in terms of space/time. For example, Tunney et al. (2012) showed that when a modeled system was joined across different habitat types, the trophic level with more biomass shifted to the higher trophic level, resulting in a top-heavy biomass distribution.

Moreover, in nature, multiple richness distribution shapes are common, ranging from top- to bottom-heavy. For example, Turney & Buddle (2016)’s findings are in contrast to a similar study that found that the majority of food webs across a variety of systems had a top-heavy richness distribution (Fath & Killian 2007). As Schmitz & Leroux (2020) point out, adaptations to enhance trophic transfer efficiencies can result in examples across ecosystems that demonstrate the opposite - that is, higher trophic levels are in fact more biomass-rich than lower ones (Bar-On et al. 2018; McCauley, Gellner, et al. 2018). A study of a large number of published food webs show that the more common distribution shape is a bottom-heavy one, that is, more species at lower trophic levels (Turney & Buddle 2016), there are still cases wherein food webs take the opposite shape (top-heavy), specifically in terrestrial systems (Turney & Buddle 2016).

2.1.3 Persistence and stability of food web shapes

While there are clearly a variety of food web shapes (i.e. biomass and richness distributions) in nature, it's not immediately clear whether some of these shapes are inherently more persistent. It could simply be that these different shapes have somewhat equal stability/persistence in the environment. However, endogenous mechanisms such as increasing biomass transfer efficiency across trophic levels suggest pyramidal shapes (McCauley, Gellner, et al. 2018; Slobodkin 2001). Conversely, conventional wisdom of classic Jacobian stability (i.e. whether or not a system returns to equilibrium when perturbed) would suggest that networks with top-heavy species richness would be more mathematically stable, since it's long been proposed that a larger number of weak interaction strengths leads to stability (Gilbert et al. 2014; McCann et al. 1998), and only species at higher trophic levels are capable of omnivory. Thus, maintenance of a variety of food web shapes in nature could be due to various exogenous mechanisms, such as temporal subsidization like mast tree fruiting (Curran & Leighton 2000; King 1983) or anthropogenic change, that alter food web shapes from some set of basal shapes that may exist in the absence of perturbation.

To test this idea, we simulated size-based food web models with all possible combinations of species richness and biomass distributions, producing nine food web shapes (Fig. 2.1 panel D). We then examined the extent to which food web shape affected properties such as modularity and connectance, and whether these properties in turn also affected persistence over time. Finally, we assessed the extent to which each shape persisted over time in the absence of perturbations, and evaluated whether each food web's original shape could be determined from the state of the system at the end of the simulations.

2.2 Methods

2.2.1 Food Web Shape and Network Construction

We considered three distinct distributions of species richness (i.e., top-heavy, uniform, and bottom-heavy) and three distinct distributions of biomass (i.e., pyramidal, uniform, and inverted) in a fully factorial design resulting in 1000 food webs in each of the 9 specific shapes (see Fig. 2.1).

Each food web contained 20 species, divided between resources and consumers. In order to accurately reflect a bottom- vs. top-heavy shape, we considered only consumers and resources as our trophic levels of interest (Note: omnivores would fall in between these two trophic levels). We considered a food web to be uniform if it has the equivalent number of consumers and resources, while a top-heavy food web had a 1.5:1 ratio of consumers to resources, and a bottom-heavy food web had a 1:1.5 ratio of consumers to resources (Fig. 2.1 A). We then assigned each species in a given web a body size based on a random draw from an exponential distribution with the rate parameter, λ (Millard 2013), from an analysis of empirical body size data in size-structured food webs (Brose, Archambault, et al. 2019) (Fig. 2.1 B, see Appendix A for more details).

Next, we assigned a biomass shape to the food web based on these body sizes. To model the distribution of biomass across trophic levels in our network food webs, we start with the definition that a system with more biomass as the top of the web (i.e. inverted pyramid) has more consumer (C) biomass than resource (R) biomass at multiple trophic levels (Sandin & Zgliczynski 2015). Species were divided into each group according to their body size, and the initial biomass of each species was drawn according to a truncated normal distribution where the mean of the random sample was a weighted value of the body size divided by the number of species (Fig. 2.1 C)). For example, for a given species with a body size in the upper third (large), the

biomass was drawn via a truncated normal distribution $[0.05, 1]$ where initial biomass

$$B \sim \mathcal{N}\left(\frac{v_l}{n_l}, 0.005\right),$$

where v_l is the weighted value v for large species l , and n_l is the number n of large l species. Thus, in this sample the mean, μ is given by $\frac{v_l}{n_l}$ and the standard deviation is $\sigma^2 = 0.005$. This network construction process resulted in 1000 connected networks per richness and biomass distribution combination (hereafter referred to as *shape*).

Simulation of Network Dynamics

To simulate biomass changes and persistence (the percentage of extant species) in these networks through time, we employ a consumer-resource model similar to that of Awender et al. (2021) and the classic model of Yodzis & Innes (1992). The biomass of all populations in the network is denoted as the vector \mathbf{X} , and each population, i has a biomass, X_i , which is modeled as

$$\frac{dX_i}{dt} = P_i(X_i) - \mu_i X_i + \mu_i X_i \sum_{j=0}^{N-1} \eta_i F_i(X_j) - \sum_{j=0}^{N-1} \frac{\eta_j \mu_j X_j F_j(X_i)}{e_{ji}}.$$

Here, $\mathbf{X} = (X_0, X_1, \dots, X_n)$ is the vector of biomass for n species, P_i is the production (growth) of species i , μ_i is the body-size specific metabolic rate, η_i is the maximum consumption rate relative to its metabolic rate. $F_i(X_j)$ is the functional response of species i consuming species j , and e_{ji} a measure of efficiency, is the fraction of biomass of j that is actually metabolized by species i . We further define the production P_i as

$$P_i(X_i) = \left\{ \begin{array}{ll} 0 & \text{if } \sum_{j=0}^{N-1} F_i(X_j) \neq 0 \\ r_i X_i \left(1 - \frac{X_i}{K_i}\right) & \text{if } \sum_{j=0}^{N-1} F_i(X_j) = 0 \end{array} \right\}.$$

where r_i is the growth rate, and K_i is the carrying capacity.

The functional response $F_i(X_j)$, is given calculated following Stouffer & Bascompte 2010 and McLeod & Leroux (2021).

$$F_i(X_j) = \frac{a_{ij}X_j}{\beta_0 + \sum_{n=0}^{N-1} a_{in}X_n}.$$

Here, a_{ij} is the interaction strength of species i consuming species j . We constructed our interaction matrices by random draws of possible interaction strengths between values 0.01 and 1.0 for all possible interactions (resources cannot eat consumers), then to ensure a food web that resembled food webs we see in nature, we re-sampled the number of interactions in the network down so that the network connectance was between 0.1 and 0.2, which is the range we see in nature McLeod, Leroux, et al. (2021).

Since the time-scale of the system is normalized to the mass-specific growth rate of the basal species, we can state all $r_i = 1$. Additionally,

$$\mu_i = \frac{a_x}{a_r} \left(\frac{M_i}{M_b} \right)^{-1/4},$$

and

$$\eta_i = \frac{a_y}{a_x}$$

where a_x , a_r , and a_y are allometric constants, and M_i is the body size of the i as described in Brose, Williams, et al. (2006), and $M_b = 1$. To allow for comparison with other works of similar intention, we use the same parameter values as Brose, Williams, et al. (2006) and Stouffer & Bascompte (2010) : $e_{i,j} = 0.85$; $K = 1$, $a_r = 1$, $a_x = 0.2227$, $a_y = 1.7816$.

2.2.2 Analysis of Networks

We simulated our 9000 networks over 25,000 time steps to ensure the initial transient dynamics stabilized. At the end of each time series we calculated a) the connectance (i.e. proportion of realized links), b) the modularity (i.e. compartmentalization), c) trophic level (defined as the average trophic level of a species' prey), and d) the predator:prey species richness and biomass proportions (See Appendix B for more

information on how each of these were calculated). In order to understand how persistence and other network metrics are affected by the network shape, we performed a series of regressions with responses of 1) consumer-resource biomass/richness proportions, 2) connectance, and 3) persistence. This served to help us ask two main questions. First, do the nine distinct food web shapes retain their distinct biomass and richness distributions over time? Second, how does the shape of a network impact its persistence?

To assess whether or not food webs retained their shapes, we calculated proportions of consumers to resources for both biomass and species richness, which are numerical measures of the distributions we use to generate our food web shapes. Taken together, they are a way to jointly measure the *shape* of each food web. To quantify change in overall food web shape through the course of the simulation, we performed a multivariate analysis of variance (MANOVA) on the joint measure of consumer-resource richness and biomass proportions at the beginning and the end of the timeseries to see if the 9 food web shapes remain distinct over the course of the timeseries.

Although food web stability has long been considered in the context of mathematical stability (Ives & Carpenter 2007; McCann 2000), there are multiple ways to define, measure, and understand their persistence and stability (Donohue et al. 2016). When food webs are considered as networks (Dunne 2006; Pascual & Dunne 2006), with nodes representing species and edges representing energy transfer between those two nodes, persistence can be understood as how many species in a network maintain some amount of biomass over the time span of interest (McLeod & Leroux 2021; Stouffer & Bascompte 2010). Connectance and modularity co-vary strongly with richness and biomass distributions, so to confirm that persistence patterns were not due to an effect of connectance, we conducted our persistence analysis in two steps. First, we separate out all nine food web shapes, and performed a regression on persistence with both modularity and connectance as explanatory variables. To look at the effect of biomass and richness distribution on end-of-simulation persistence, we performed

a simple factorial analysis of variance (ANOVA) with a crossed fixed effect between richness distribution and biomass distribution. All analysis was performed in Julia v1.8.1 (Bezanson et al. 2017) and R v4.2.2 (Team 2022).

2.3 Results

2.3.1 Persistence of Food Webs and their Shapes

After the initial transient dynamics of the food webs stabilized, the end persistence values ranged from just below 0.8 to 0.3, with species richness distribution but not biomass distribution determining the mean network end persistence (Fig. 2.2). Bottom-heavy networks with the majority of species in lower trophic levels were the most persistent, and experienced the shortest period of transient dynamics. Richness distribution across all three levels were significantly different from each other (F: 1149.02, p-value: $<2e-16$, Table 2.1), with top-heavy richness distributions experiencing the lowest persistence with a mean persistence of 0.31. Uniform richness distributions had a higher average persistence of 0.57, and bottom-heavy networks had a mean persistence of 0.75. Biomass distribution had no significant effect on persistence at any level (F: 0.19, p-value = 0.83, Table 2.1).

At the beginning of the timeseries, there are nine distinct consumer-resource proportion groupings, made up of the three species' richness distributions crossed with the three biomass distributions (Fig. 2.3 panel A, Table 2.2). However, by the end of the timeseries, only species' richness distribution is structuring the consumer-resource ratios (Fig. 2.3 panel B, Table 2.2). This shows that, on the timescale of these simulations, any effect of biomass distribution, or the interaction between biomass distribution and species' richness distribution, on the shape of the network is negligible. Instead, at the end of the timeseries, we can see three distinct shapes of networks arising determined by the species richness shape (Fig. 2.4). These three shapes do not have significantly different predator-prey biomass proportions, but do

in fact have different predator-prey richness proportions with the top-heavy food webs having a mean predator-prey richness proportion of ~ 0.28 , the uniform webs having a mean proportion of ~ 0.17 and the bottom-heavy webs of ~ 0.11 (Fig. 2.4, panels A, B, and C respectively).

All network shapes were significantly different from their starting values in both measures of species richness and biomass proportions (Fig. 2.3 panels A and B; Fig. 2.5), indicating a shift in shape across all networks. Across the three species richness distribution groups, the proportions of both biomass and species richness are different (i.e. the error bars between top-heavy, uniform, and bottom-heavy species richness distribution groups are non-overlapping, Fig. 2.5). Across the three biomass distribution groups however, there is little difference in the response of the richness and biomass proportions. That is, the error bars between pyramidal, uniform, and inverted pyramid biomass distributions are nearly all overlapping, indicating no significant difference between the groups (Fig. 2.5).

2.3.2 Relationship between shape and other measures

While we know richness distribution had an effect on the persistence and outcome of the webs, we wanted to see if other network metrics such as modularity and connectance had an effect as well. Our regression of the effect of connectance and modularity on persistence in each of the 9 different food web shapes showed that connectance had a significant effect in 8 out of the 9 shapes (Table 2.3). Since connectance had the least effect on networks with a pyramidal biomass distribution, we verified that biomass distribution as a categorical variable didn't have an effect on persistence at the end of the timeseries when tested with a separate ANOVA (Table 2.4). This result shows that connectance is statistically significant in predicting persistence, but, if we look at the model estimates and associated standard errors, we see that there is overlap between all of the groups. Therefore, the effects that we see of richness distribution on persistence are in fact not able to be explained

by connectance alone. Across all food web shapes, modularity had no effect on the persistence at the end of the timeseries.

2.4 Discussion

Decades ago, May (1973) noted a disparity between our theoretical models of food webs and what we see empirically. Despite nature being replete with examples of large complex networks, in theory, diversity in fact destabilizes community dynamics, and thus, complex networks should not exist in nature. Since then, researchers have been attempting to reconcile this paradox by trying to explore the architectural properties of food webs that may enhance food web stability and persistence. Previous work has highlighted how factors like omnivory (Gellner & McCann 2012), spatial dynamics (Gravel, Massol, et al. 2016), and modularity (Stouffer & Bascompte 2011) can all perhaps explain this mismatch between theoretical predictions and empirical reality. Here, we show how food web shape, conceptualized as the joint effect of species richness and biomass distributions across trophic levels, contributes to species persistence in simulated food webs. Our analyses demonstrate that bottom-heavy richness networks are the most persistent type of webs, while top-heavy richness webs are the least persistent. Moreover, the species lost in these simulations were not random; instead, we show that despite nine different initial shapes, all webs converged on a similar shape after transient dynamics stabilized. This shape is characterized by having a bottom-heavy species richness distribution, and an inverted pyramidal biomass distribution. In addition, we note that despite modularity being a well-documented boon to persistence in networks (Stouffer & Bascompte 2010), connectance was the network measure that had the largest effect on the persistence of networks aside from shape. It's worth noting as well that the connectance was not correlated across the starting shapes, and that each initial starting shape had an even distribution of the same connectance values.

The effects of species richness distributions on food web persistence we observed

through simulation mirror what we see in the real world. Empirically, many documented food webs display a bottom-heavy richness shape (Turney & Buddle 2016). Indeed, all our webs that started off with a top-heavy species richness, that structure disappeared, replaced by a bottom-heavy richness distribution (Fig. 2.4). Virtually no webs end up having a richness proportion higher than 0.5, despite all of the top-heavy webs starting above ~ 0.7 . This indicates that across all our different food web shapes, larger bodied consumers at higher trophic levels are likely the ones usually going extinct (Jacob et al. 2011). There may be many mechanistic reasons for what we see in our results. What is likely the case however, is that with respect to top-heavy species richness webs overall, there is simply not enough energy at the lower trophic levels to support top-heavy food webs.

Embedded in the idea of a interaction strength is the fact that a single organism will have a competitive ability to consume some set of organisms that will inevitably be greater or lesser to its competitors. We know that coexistence can be largely driven by variability in a system (e.g., Hallett et al. 2019), and in our system, we intentionally eliminated this variability, thus precluding the opportunity for competitive advantages to fluctuate. Thus, the explanation is likely that a) the rates of energy transfer from lower trophic levels to higher trophic levels are not sufficient to offset the inefficiencies in consumption, and b) often multiple consumers are competing for only a handful of resource species, and without any environmental or demographic stochasticity, there is no mechanism with which coexistence of multiple species can be maintained.

We saw a consistent pattern of consumer-resource biomass proportions moving towards high values over time, typically above 0.6 (i.e. $\geq 60\%$ of all biomass is concentrated in consumer species), across all food web shapes. In this configuration, the networks have shifted to a bottom-heavy species richness distribution, but smaller biomasses of each resource species—meaning there are a larger number of resource species with smaller biomasses supporting a few consumer species with high biomass levels. Ecologically, this configuration indicates a shortening and contracting of the

food web as a whole, with food chain length shortening (lower mean trophic level means the disappearance of higher trophic level consumers), and the networks gravitating to a bottom-heavy species richness distribution. This trend is also observed in real food webs; for example, in aquatic food webs, top-heavy biomass structure appears to be more common than previously thought.

There are some mechanistic reasons why this type of shape pattern may occur, particularly in marine ecosystems. Woodson et al. (2018), noted a high prevalence of two key phenomena in marine systems that can drive these patterns: first, generalist predators that can consume a variety of prey types, and second, large body-sized predators consuming low trophic level organisms can help in overcoming some of the traditional challenges to inverted pyramidal biomass distributions. These two mechanisms might speak to two factors at play in our simulations. First, when predators are more generalist, they are more likely to have more interactions that are therefore weaker (Closs et al. 1999), which can in turn lead to increased stability (McCann 2000). Second, presence of large-bodied organisms able to consume low-trophic level items may eliminate much of the lost trophic transfer efficiency (Lindeman 1942; Woodson et al. 2018) that can, if exhibited, result in pyramidal biomass distributions.

Top-heavy biomass distribution but bottom-heavy species richness is found in multiple systems. For example, in Lake Liambezi in Namibia, a recent study on the economically important fish ecosystem there described how tilapiine cichlids, the lowest trophic position in the fish community, were the most speciose group, but had very little biomass compared to fish species further up the food web (Peel et al. 2019). This shape is also consistent with patterns observed in many temperate North American lake systems (Del Giorgio & Gasol 1995) with ratios of heterotrophs to autotrophs, and large diversity of planktonic species compared to higher-trophic level fish species (Soininen et al. 2012).

Lakes are in fact a good real-world example of food webs that are well-described

by models like ours. They are relatively closed with respect to energy flow compared to, for example, marine systems, and have a limited number of species. Additionally, they can be considered well-mixed (though see McMeans, McCann, Humphries, et al. (2015) for a discussion of this), and have high resource turn-over rates (D’Alelio et al. 2016). For example, resources that are planktonic in nature exhibit this higher rate of turn-over, which is a mechanism that Wang et al. (2009) noted can create inverted biomass pyramids. These mechanisms in concert result in lake food webs that exhibit the “end-state” food web forms we show here.

It could be the case that anthropogenic activities are driving the occurrence of shapes that differ from what these results suggest is expected. On pristine coral reefs for example, biomass distributions are typically inverted pyramids, with higher proportions in higher trophic levels, such as sharks and other predatory fishes (Stevenson et al. 2007). However, over-fishing these large commercially valuable species can result in a shift of this biomass distribution, to take on pyramidal shapes with the majority of biomass at lower trophic levels (Sandin, Smith, et al. 2008). Anthropogenic climate change and its associated warming can also alter food web shape, but in the opposite direction, with warming in freshwater ponds resulting in food webs shifting from pyramidal to top-heavy with lower biomass in producer species (Shurin et al. 2012).

Anthropogenic stress is also causing significant change in species richness in a range of ecosystems. While in aquatic systems we generally predict higher proportions of bottom-heaviness of species richness (Turney & Buddle 2016), top-down fishing pressures can further reduce species diversity and biomass at higher trophic levels. In freshwater systems, stocking of a handful of top-predator fish species for sport fishing is a common occurrence, which reduces diversity due to competition between and/or predation on the native fish populations (e.g. Su et al. 2021), but can increase or maintain the biomass present at that trophic level due to the large influx of the stocked fish. Similarly, for invasive species such as Asian carp in the Mississippi river

basin, we know diversity of native sport fish plummets upon invasion (Chick et al. 2020), but the biomass of the Asian carp typically balloons, resulting in low diversity but high biomass in higher trophic levels. Our results suggest that this could in fact represent a persistent food web shape, but that finding would be conditional on the system not experiencing further upheaval.

Anthropogenic effects on food webs and ecosystems are only increasing. The models and associated analyses we present here provide a means to understand which pre-disturbance food web shapes are likely to be more resilient to future stress and perturbation. The capacity for a food web to be resistant or resilient to perturbation is likely also dependent on the type of perturbation the web is experiencing (Leroux & Loreau 2012; Montoya, Woodward, et al. 2009). It's not yet clear how the interaction between the shape of a food web and the type of perturbation that web is experiencing may jointly structure the response to perturbation, and given that we know food webs experience stressors ranging from consistent press perturbations (e.g. consistent fishing pressure) to periodic pulses (e.g. El Nino/La Nina events), it is paramount that we further develop our knowledge of how structure and perturbation jointly affect the persistence and stability of food webs.

2.5 Conclusion

With increasing interest in predicting the effects of various anthropogenic activities on food webs, our analyses highlight that food webs are not all created equal in terms of their long term persistence even in the absence of perturbation. We show here that while food webs in the natural world can take on all forms of biomass and species richness distribution, most shapes are not likely to be maintained over time without external forcing on the system. With a set of long time scale simulations we show that food webs tend to become bottom-heavy with respect to their species richness distributions, and have inverted pyramidal biomass distributions. Without consistent forcing, whether through changes, human interference, or both, specialist

consumer species likely become extirpated due to competition with generalists who can spread out their energy requirements across multiple prey items. Our results are most closely represented in nature by lake ecosystems which are likely more consistent with respect to our model assumptions including a lack of external inputs than other more open systems like oceanic marine food webs. Understanding how food web shapes arise mechanistically is important for subsequently understanding the impact of perturbations on those food webs. Effective understanding and forecasting of food webs as important ecosystem structures will require an approach that goes beyond consideration of only a single factor. Proactive management and conservation of these complex systems in the Anthropocene requires not only understanding how factors such as species richness and biomass distributions structure these webs in nature, but what these factors alongside others (e.g. perturbation type) can tell us about how food webs will react to change, which components of them are most sensitive, and how best we as stewards can mitigate these effects.

2.6 Tables

Persistence ANOVA (Categorical)					
Term	Deg. Free	Sum Sq	Mean Sq	F value	P-value
Biomass Dist.	2	0.004	0.002	0.19	0.827
Richness Dist	2	25.625	12.813	1149.02	<2e-16
Biomass * Richness	4	0.043	0.011	0.96	0.429

Table 2.1: Regression values from the categorical persistence regression. The end values persistence for each network were regressed against the categorical groups of the networks.

Consumer-Resource Ratios MANOVA						
Timepoint	Term	Deg. Free	Pillai-Bartlett Statistic	Approx F-Statistic	F deg. Freedom	P-value
Beginning	Biomass Dist.	2	0.9409	367.83	(4, 1656)	<2e-16
	Richness Dist	2	0.8785	324.28	(4, 1656)	<2e-16
	Biomass * Richness	4	0.4421	58.74	(8, 1656)	<2e-16
End	Biomass Dist.	2	0.0026	0.545	(4, 1656)	0.7031
	Richness Dist	2	0.542	153.89	(4, 1656)	<2e-16
	Biomass * Richness	4	0.007	0.723	(8, 1656)	0.6710

Table 2.2: Results of a Multivariate Analysis of Variance (MANOVA) performed on the two consumer-resource ratios performed at the *beginning* and separately at the *end* of the timeseries

Generalized Linear Regression of Shape Groups						
Biomass Dist.	Richness Dist	Term	Est.	Std Err	P-value	Sig.
Pyramid	Top-heavy	Connectance	-1.28	0.39	0.001	**
		Modularity	-0.68	1.03	0.51	
Pyramid	Uniform	Connectance	-0.78	0.34	0.024	*
		Modularity	0.05	0.93	0.958	
Pyramid	Bottom-heavy	Connectance	-0.03	0.40	0.94	
		Modularity	-0.30	0.87	0.73	
Uniform	Top-heavy	Connectance	-1.42	0.23	3.54e-10	***
		Modularity	-1.44	0.97	0.14	
Uniform	Uniform	Connectance	-1.56	0.18	3.0e-14	***
		Modularity	0.28	0.80	0.73	
Uniform	Bottom-heavy	Connectance	-1.51	0.17	5.9e-14	***
		Modularity	0.84	0.78	0.28	
Inverted	Top-heavy	Connectance	-1.41	0.23	1.9e-08	***
		Modularity	-0.43	1.19	0.72	
Inverted	Uniform	Connectance	-1.2	0.22	2.9e-07	***
		Modularity	-0.2	0.84	0.84	
Inverted	Bottom-heavy	Connectance	-1.13	0.27	6.6e-05	***
		Modularity	-0.7	0.97	0.46	

Table 2.3: Generalized linear regressions for each of the nine shape groupings of richness and biomass distribution. Each data grouping was regressed on connectance and modularity. The significance groupings are $0 < p < 0.001$: ***, $0.001 < p < 0.01$: **, $0.01 < p < 0.05$: *, and $p > 0.1$ does not get a marking.

Connectance ANOVA					
Term	Deg. Free	Sum Sq	Mean Sq	F value	P-value
Biomass Dist.	2	0.002	0.0001	0.224	0.800
Richness Dist	2	0.0379	0.0189	34.927	<2e-16
Biomass * Richness	4	0.0008	0.0002	0.393	0.814

Table 2.4: Factorial analysis of variance with connectance at the end of the timeseries as the response variable, and the two shapes, biomass and richness, as the fixed effects

2.7 Figures

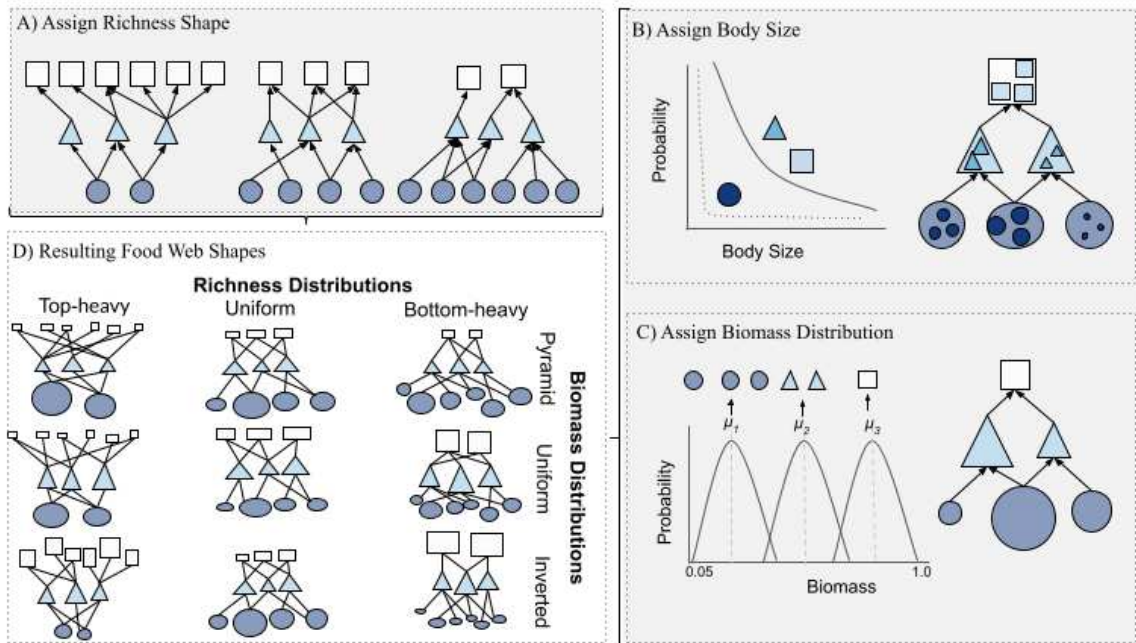


Figure 2.1: Conceptual diagram showing all possible food web shapes comprised of the three distinct biomass distributions and three distinct richness distributions. A) Describes how richness shapes were drawn, in three distinct distributions. B) Body sizes were drawn as random samples from an exponential distribution where the distribution was parameterized from the literature. C) Once body sizes were assigned, all organisms were divided into size (an approximation of trophic level), and each species was assigned a biomass based on a random draw from a truncated normal distribution, with mean dependent on body size.

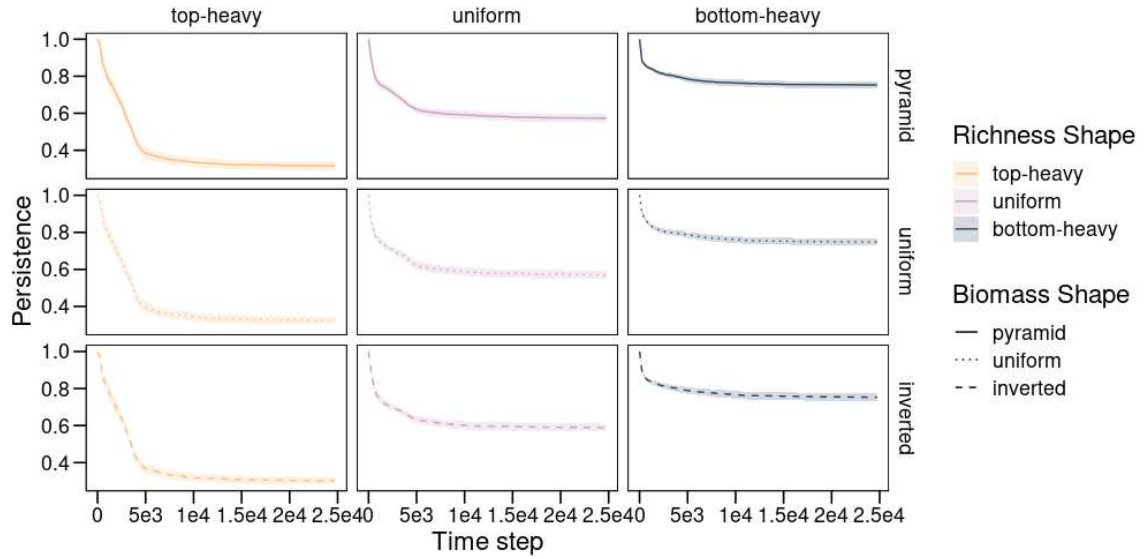


Figure 2.2: Mean network persistence across the timeseries simulated, grouped by each of the three types of richness and biomass distribution respectively.

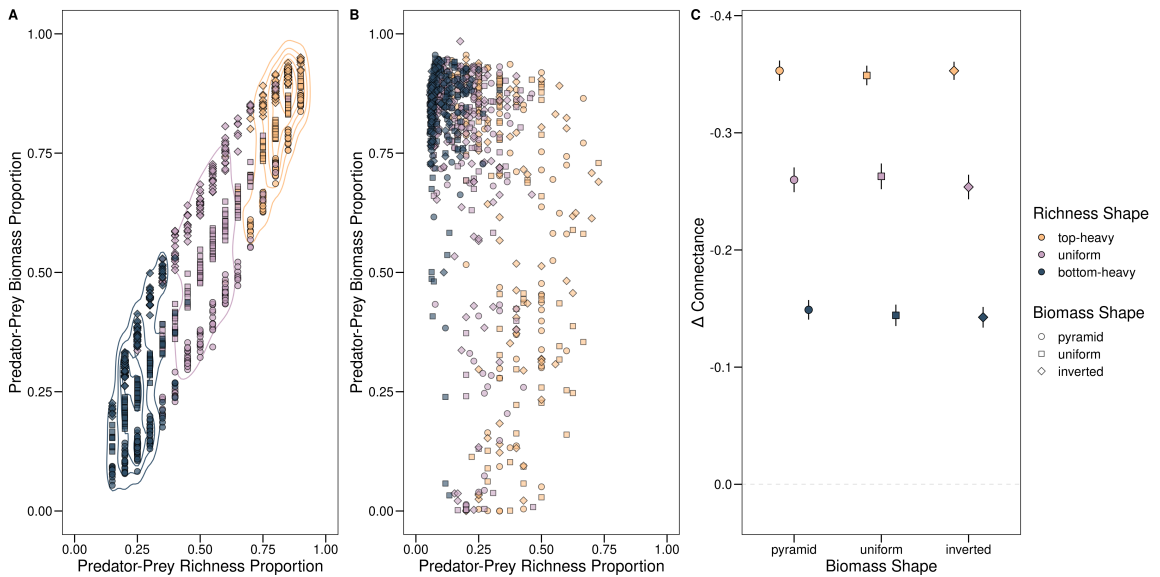


Figure 2.3: Beginning and end states for the consumer-resource proportions, along with connectance at the end state.

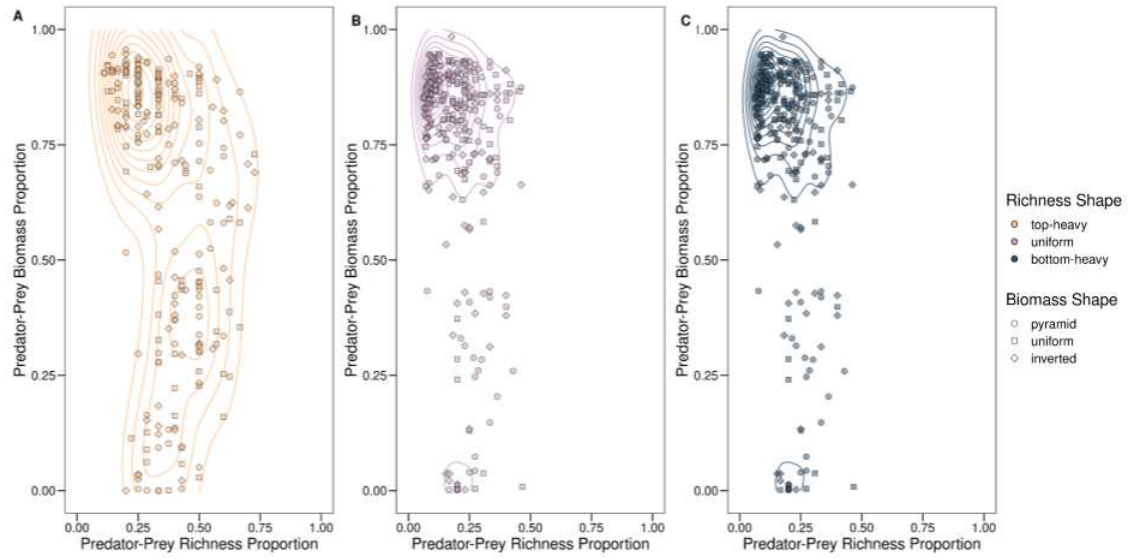


Figure 2.4: End states for consumer-resource richness and biomass proportions respectively.

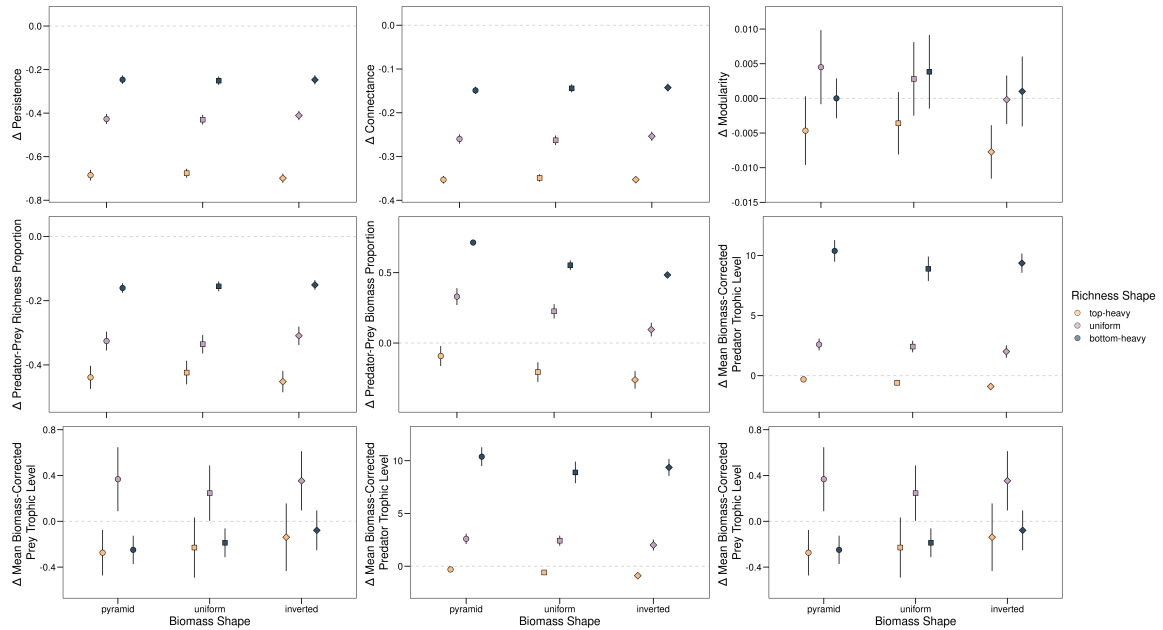


Figure 2.5: Change in all measured variables from the beginning of the timeseries to the end. zero represents the beginning value, and the points represent a distance from that initial value. Note that the confidence intervals here were calculated using standard error for difference which is defined as $\sqrt{SE_1^2 + SE_2^2}$

Chapter 3

Species richness across trophic levels mediates the outcomes of perturbations on food webs

3.1 Introduction

The timing, duration, and intensity of anthropogenic disturbances (i.e., perturbations) to ecological communities are increasing globally (Crain et al. 2008; O’Gorman et al. 2012). Understanding how ecosystems will respond to intensifying perturbation is crucial for maintaining services like water filtration, flood control, and fisheries stocks (Schmeller & Bridgewater 2021). Food webs are a standard way to measure flows of energy through ecological communities (Cohen et al. 2012), with research increasingly focused on understanding how their structure will be altered by changing perturbation regimes in order to inform conservation and management (Dietze et al. 2018; Lewis et al. 2023; Massoud et al. 2018). Responses to disturbance (measured through metrics like stability (May 1973; Pimm 1982), persistence (Montoya, Rodríguez, et al. 2003), and robustness (Dunne et al. 2002; Estrada 2007b)) may be driven by the characteristics of the food web itself (i.e., endogenous factors), the form of the perturbations on the food web (i.e., exogenous factors), and the interaction between the two.

How response to perturbation is measured is another key consideration. Anthro-

pogenic change often happens fast; species can be reduced to a fraction of their initial biomass incredibly quickly (e.g., passenger pigeons (Brooks 1955), bison (Boyd & Gates 2006), and cod (Bailey 2011)), but true extinction often takes much longer, and often likely occurs not from a continuation of the original pressure from humans, but from demographic stochasticity that occurs at low numbers (Cuenda et al. 2020). We often focus on cases where a species is completely lost from a system (Montoya, Pimm, et al. 2006), thus quantitatively changing the structure. While this is useful, the relative frequency of complete extinction in real systems is minuscule compared to scenarios where relative abundance (and therefore biomass) are affected. Since the 16th century, only 680 described vertebrate species have been pushed to extinction, whereas up to 1 million species were considered “threatened” by the IUCN as of 2023 (IUCN 2023), meaning that they have suffered $\geq 80\%$ abundance decline, which almost certainly has led to an even greater reduction in biomass (Birkeland & Dayton 2005; Jerardino et al. 1992; Raab 1992; Ricker 1981). Thus, it’s important to track both metrics of change (i.e. extinction and abundance decline) in a system when perturbed. While secondary extinctions can and do occur (Brodie et al. 2014), much of these secondary effects are reduced “performance” of other species following a primary extinction (Estes et al. 2011).

3.1.1 Endogenous Factors Affecting Persistence

Metrics such as connectance (Dunne et al. 2002) and modularity (Stouffer & Bascompte 2011) have been proposed to predict food web response to disturbance and also co-vary with factors like ecosystem type (Bramon Mora et al. 2018). However, such network metrics are hard to measure in empirical systems. Additionally, since these metrics are correlated across other types of food web information, it could be that these more accessible and simple measures of food web characteristics such as ecosystem type, species diversity across trophic levels, or biomass distribution across trophic levels, could give good measures of food web persistence or robustness (Mc-

Cauley, Gellner, et al. 2018; Zhao et al. 2019). Indeed, the distribution of species richness and biomass across trophic level, considered jointly as a food web’s “shape”, may be very useful in providing insight into whether or not food webs respond similarly to perturbations.

3.1.2 Exogenous Factors Affecting Persistence

When considering how food webs might respond to perturbations however, it is important to recognize that the endogenous mechanisms are not the only ones at play. Exogenous factors, most importantly the type of perturbation experienced, are also essential to consider (Bender et al. 1984). The timing, intensity, and length duration of perturbations likely all affect how food webs responds (Reice 1994; Wurff et al. 2007). Common types of perturbations include pulse perturbations (single, short, and typically high magnitude) such as droughts or disease, press perturbations, (single, long-term, low-magnitude) press perturbations such as harvesting, and periodic pulse perturbations, (cyclic short, medium-impact) such as forest fire regimes or El Nino/La Nina events (Jentsch & White 2019; Yang & Naeem 2008). While we know that both press and pulse perturbations can cause extinction events (Arens & West 2008), it has also been shown that type of perturbation can affect the transient dynamics of communities in model systems (Inamine et al. 2022). However, it’s still unclear how this exogenous factor interacts with the endogenous factors to impact not only extinction events but biomass dynamics in a whole community.

Persistence may also be affected not just by perturbation type, but by what part of the food web the perturbation acts on. Typically perturbations are linked to taxo- or functional group specific effects (Kouki & Salo 2020) and thus operate within a particular trophic level rather than across than multiple species at different trophic levels. Indeed, Dunne et al. (2002) as well as Estrada (2007a) have noted that anthropogenic impacts on food webs are non-random in terms of the trophic level they affect, and often affect either the top or the bottom of the food web, sending effects

cascading through the system. Indeed, the literature is replete with discussion of how top-down vs. bottom-up processes driven by perturbations structure food webs themselves (Kitching 2001; Marczak et al. 2011; Power 1992), such as exploitation of top predators in marine food webs causing cascading effects down the food web (Baum & Worm 2009), or the bleaching of corals (foundational species in reef food webs) caused by anthropogenic change (Pandolfi et al. 2011) which in turn impacts higher trophic level organisms such as fish by affecting resources available for foraging, shelter, and reproduction (Ruppert et al. 2013).

3.1.3 The Interplay of Endogenous and Exogenous Factors

We can consider the perturbation itself and the trophic level of the perturbation (consumer-affected or resource-affected) to be exogenous factors, and the shape of a food web, the species richness and biomass distributions as endogenous factors structuring food web response to perturbation.

The goal of this chapter is to explore how endogenous and exogenous factors contribute to extinction and changes in biomass in food webs subjected to perturbations. To investigate the exogenous and endogenous factors structuring food web responses to perturbations we considered two endogenous factors and one exogenous mechanism. Our endogenous factors were 1) the shape of the food web being perturbed, and 2) whether or not the perturbation happened at the top or the bottom of the food chains. Our exogenous mechanism was the type of perturbation the food web experienced. It is likely that multiple factors affect the response to perturbation, but it's less clear when different factors are more influential. Here, we ask what the relative impact of exogenous vs. endogenous mechanisms is in affecting food web responses to perturbations, and also attempt to unpack how these differences may play out when the focus shifts from species extinction to shifts in biomass distributions.

3.2 Methods

In the same manner as Chapter 2, we constructed a set of food webs with 20 species each, divided between consumers and resources, and simulated perturbations across all networks. During the simulations we tracked our variables of interest, and at the end of the simulations, used effect sizes from ANOVA analysis to determine which factors played a roll in affecting which outcomes.

3.2.1 Food Web Shape

We define food web shape as being described by the distribution of species richness across trophic levels and the distribution of biomass across trophic levels (See Chapter 2 for more detail). With respect to species richness, food webs could be composed mainly of consumers (3:2 consumer-resource ratio, termed top-heavy), an even number of consumers and resources (termed uniform), or the majority of species being resources (2:3 consumer-resource ratio, termed bottom-heavy). Our food webs were size-structured, so each species had a body size drawn from an exponential distribution with a separate rate parameter λ for consumers and resources. We parameterized our distribution with empirical data from body sizes in size-structured food webs documented in nature (Brose, Archambault, et al. 2019). Similarly for our biomass distributions, we consider a case where there is more resource biomass than consumer biomass, regardless of number of species (termed pyramid), a case with more consumer than resource biomass (termed inverted pyramid), and a case with even amounts.

3.2.2 Simulations

Once all food webs were constructed, we used a consumer-resource model based on that of Yodzis & Innes 1992 with additions from Awender et al. 2021. All biomass in the network across all species is denoted for n species as $\mathbf{X} = (X_0, X_1, \dots, X_n)$, and each species, i has a biomass, X_i . The model for the rate of change of biomass into

or out of species X_i is given by:

$$\frac{dX_i}{dt} = P_i(X_i) - \mu_i X_i - m_i X_i - \mu_i X_i \sum_{j=0}^{N-1} \eta_i F_i(X_j) - \sum_{j=0}^{N-1} \frac{\eta_j \mu_j X_j F_j(X_i)}{e_{ji}}. \quad (3.1)$$

Here, production (growth) of species i is given by the function P_i , with the body-size specific metabolic rate μ_i , m_i as the baseline mortality rate from perturbation (0 unless stated otherwise) and η_i as the maximum consumption rate relative to it's metabolic rate. The model is governed by the functional response $F_i(X_j)$ where species i is consuming species j . Not all biomass lost from j is consumed by i , and e_{ji} is the proportion actually metabolized. We further define the production P_i as

$$P_i(X_i) = \left\{ \begin{array}{ll} 0 & \text{if } \sum_{j=0}^{N-1} F_i(X_j) \neq 0 \\ r_i X_i (1 - \frac{X_i}{K_i}) & \text{if } \sum_{j=0}^{N-1} F_i(X_j) = 0 \end{array} \right\}. \quad (3.2)$$

Here, r is the growth rate, and K is the carrying capacity. The time-scale of the system is normalized to the growth rate of the resource species, so in our case for all i , $r_i = 1$. The functional response is a type II functional response of the form:

$$F_i(X_j) = \frac{a_{ij} X_j}{\beta_0 + \sum_{n=0}^{N-1} a_{in} X_n}. \quad (3.3)$$

The interaction strength here is a_{ij} . The interaction matrix of all species comes from a random draw of possible interaction strengths between 0.01 and 1.0 for any consumer-resource pairing. This matrix was then re-sampled down such that the connectance of the web was between 0.1 and 0.2. Connectance was given as the proportion of realized L vs possible S^2 possible interactions in a network, $\frac{L}{S^2}$.

For our metabolic rates an efficiency, we use the form of Brose, Williams, et al. 2006; Stouffer & Bascompte 2010

$$\mu_i = \frac{a_x}{a_r} \left(\frac{M_i}{M_b} \right)^{-1/4} \quad (3.4)$$

$$\eta_i = \frac{a_y}{a_x} \quad (3.5)$$

with allometric constants a_x, a_r , and a_y , the body size of species i given by M_i and $M_b = 1$. For other constants in our model we use consistent parameter values $e_{ij} = 0.85; K = 1, a_r = 1, a_x = 0.2227, a_y = 1.7816$.

These models were then simulated for 25,000 time-steps to allow the food webs to stabilize. To perform these simulations we used the deSolve package (Soetaert, Petzoldt, et al. 2010, 2015) in R 4.2.2 (Team 2022).

3.2.3 Perturbations

We simulated the food web for 25,000 time steps before subjecting the food webs to any perturbation to ensure that transient dynamics had died down. After 25,000 time steps, four species were randomly chosen from each food web - two resources and two consumers - as the species to be perturbed. The resources represented the bottom-up type perturbations, and the consumers represented the top-down. We then performed our second set of simulations, and here, each of the four randomly selected species was then subjected to three types of perturbations: pulse, press, and periodic pulse. That is, for each initial food web simulated, 12 additional simulations took place – three simulations (one each for each perturbation type), for each of the four species randomly drawn to be perturbed. To ensure that perturbations would be comparable, we standardized the quantity of perturbation per unit time following the method of Leroux & Loreau 2012. The perturbation was given as

$$C = zu\frac{1}{f} \tag{3.6}$$

where C is the constant quantity of perturbation per unit time, z is the pulse magnitude, u is the pulse duration, and $1/f$ is the frequency of the pulse. For our purposes, we chose $C = 4000$. u , in the pulse and periodic press simulations, had a set value of 100 time steps, and f was either equal to one for the press and pulse simulations, or 10 for the periodic pulse simulation. z then varied according to the values for each given situation. We then used the resulting values of z in place of m

in Eq. 1 to represent the mortality due to perturbation.

We simulated each of the scenarios (108,000 simulations in total. 9000 initial food webs, with 12 subsequent simulations for each initial web. One of each of the three perturbation types for each species drawn (4 species ere drawn) for 5000 time steps). Along the simulation, we tracked how many species went extinct (extinction was considered to be a biomass of $<1e-30$), when they went extinct along the timeseries, and how the biomass of the system changed on the whole, and also as a proportion between consumers and resources. We focused on percent change in biomass as our metric of interest as opposed to absolute biomass, as it better captures the departure (or lack thereof) of a system from it's previous state.

Since our data were conveniently factorial and satisfied basic assumptions, we performed analyses of variance (ANOVAs) on the number of species lost, the time of first and second extinction, and on the percent change in biomass at the end of the simulations. The explanatory variables included the variables associated with the endogenous factors which were food web shape (biomass and richness distributions) and the exogenous variable perturbation type. All analysis was performed in Julia v1.8.1 (Bezanson et al. 2017) and R v4.2.2 (Team 2022).

3.3 Results

As our model food webs were perturbed, we found that species loss and biomass changes occur over a significantly different time frames. While both diversity and biomass changed rapidly at the very beginning of the simulation, biomass dynamics stabilized relatively quickly (Fig. 3.1 panels C vs. D; after just 50 time steps for all perturbation types), whereas secondary extinctions continued to occur throughout the timeseries, with the second extinction coming after an average of 1988 time-steps (Figure 3.2). More than 99% of food webs lost at least one species, but not all food webs showed large changes in biomass. In those that did, magnitude of biomass loss varied widely; most food webs lost a relatively modest amount of biomass (15%),

some food webs lost more than 30% of their original biomass.

While our analysis of factors affecting the percentage of biomass lost during food web perturbation did not explain much variance ($R^2 = 0.07$), there were some patterns regarding which food webs were most affected. In particular, the interaction between species richness distribution type and trophic level of the organism being perturbed being the most important factor with respect to effect size (73% of explained variance; Table 3.1), followed by the trophic level of the perturbed species itself (17% of explained variance; Table 3.1). In fact, food webs where the perturbed organism was a consumer lost 11.9% of the network's biomass, while food webs with the resources perturbed lost 18.4% of their biomass (Fig. 3.2). The interaction between the trophic level of the perturbed species and the species distribution of the web was significant, but only in simulations where the resource was perturbed. In fact, the largest change by far was in simulations where a web with top-heavy species richness had a resource species that was perturbed. This resulted in, on average, a 28.7% decline in biomass. However, top-heavy food webs where the consumer was perturbed in fact had the lowest amount of biomass lost, an average of 6%, with that mean value not significantly different than zero (Fig. 3.2).

Overall, both exogenous and endogenous factors were important in determining food web responses to perturbation. However, the importance of each variable depended on the response we measured (Fig. 3.2). Number of species lost was explained to a slightly better degree by our model ($R^2 = 0.14$), with the endogenous factors being the most important. Here, species richness distribution accounted for 72% of explained variance (Table 3.2). Across all simulations, virtually every food web lost at least one species, but not all food webs lost more than one. At the end of the timeseries across all food webs, there were an average of 1.56 species lost. While the scenarios that lost the largest percent biomass (food webs with top-heavy species richness distributions and perturbed resources) were the same food webs who lost the most species (Fig. 3.2), the least-affected food webs were those with bottom-heavy

richness distributions, regardless of the trophic level of the perturbed species. Within that group, only food webs with perturbed resources were all significantly different than the other variable groupings (Fig. 3.2).

There was no effect of the type of perturbation on either the percentage of biomass lost, nor the number of species lost at the end of the simulations (Table 3.1, Table 3.2). There was however an effect on the time to first extinction. Again, only a moderate amount of variation in time to first extinction was explained by our model ($R^2 = 0.18$), and of that, 78% of it was explained by perturbation type. In fact, for food webs exposed to both pulse and periodic pulse perturbations, an extinction occurred near the beginning of the time series (Fig 3.3). Conversely, it took longer (on average, 146 time steps) for the first extinction to come about in food webs facing press perturbations. However, a second extinction, if it occurs, happened on average much later, after more than 1980 time steps. Trophic level of the perturbed organism most strongly influenced timing of the second extinction, accounting for 62% of the explained variance in that ANOVA ($R^2 = 0.18$).

3.4 Discussion

In the present work, we show that two key processes - extinction and biomass change - can happen on vastly different scales when a food web is perturbed. The effect of perturbations on a food web are felt near-instantaneously in terms of changes in species biomass; a result that is somewhat intuitive since our perturbation acts on the mortality term, decreasing biomass directly. The first extinction then follows relatively quickly. However, after the first extinction, the timescales of the two processes become somewhat divorced; after the initial decrease in biomass, we see little further change in biomass across the timeseries. Secondary extinctions on the other hand, occur much later in the timeseries. Thus, species destined to eventually go extinct have already had their biomass substantially reduced, and the decline from “functionally extinct” to fully extinct is what takes most of the time. Our analyses suggest a type

of extinction debt (Kuussaari et al. 2009) is at play, wherein the initial perturbation drives the perturbed species to extinction, and then the cascading effects are not felt for a significant period of time. Similarly, Arnoldi et al. (2018) demonstrate that long-term dynamics following pulse perturbations are more often controlled by rare species. Efforts to model habitat destruction as a pulse perturbation also showed that extinction debt can occur long after the habitat itself has been destroyed (Tilman & J. A. Downing 1994). Our results support growing bodies of work showing that the initial effects of perturbations are not likely to tell the whole story, and knock-on effects like extinction debt are essential to consider; an important effect when considering conservation and management action following ecosystem disturbance.

Across our different food webs, we saw a much stronger influence of species richness distribution than biomass distribution on response to perturbation. In particular, food webs with a top-heavy species richness distribution were the least able to withstand species loss following perturbation. Overall, we found that species richness distribution across trophic levels can act to buffer or exacerbate the effects of perturbation. This relates to the finding of Zhao et al. (2019) that horizontal diversity (the number of species at a given trophic level), confers stability to food webs subject to perturbation. However, these are the very types of stabilizing factors that anthropogenic change is having an effect on (Rooney, McCann, et al. 2006). Our results suggest that food webs with the top-heavy signature are not resilient to perturbations, regardless of the type of perturbation. These results are interesting when interpreted alongside our analysis in Chapter 2, which showed that top-heavy food webs are also the least persistent over time when when not perturbed. Indeed, food webs with bottom-heavy species richness are generally the most persistent in response to perturbation (i.e., they have the fewest species lost after perturbation). Thus, at least for species richness, strategies for persistence translate well; food webs that are generally more persistent in the absence of perturbations, are still more persistent when perturbed. Moreover, we found that top-heavy food webs lose significantly

more species than other food webs when resource species are perturbed, indicating that while top-heavy food webs may be less persistent in a system without perturbation, they do not have a reduced ability to buffer perturbations if the consumer is the one perturbed. Other works have described this phenomenon as well, in a set of modeling experiments McCauley, Gellner, et al. (2018) showed that top-heavy food webs were less stable than bottom-heavy food webs. Factors like weak omnivory (Gellner & McCann 2012) can actually stabilize top-heavy food webs, or if we consider a more open system, for example one with some kind of allochthonous subsidy (McCauley, DeSalles, et al. 2012), then this can also act to stabilize some of these less stable systems.

We found that the trophic level perturbed (exogenous) affected both the number of species lost and the amount of biomass lost from perturbed food webs, but only in the context of the food web shape (endogenous). This indicates that it is essential to consider both types of effects (i.e. endogenous and exogenous) concomitantly rather than separately to gain a full understanding of how food webs may be affected by perturbations. For example, when looking at biomass, we can see that the magnitude of loss in these top-heavy food webs can only really be understood if we also consider the trophic level perturbed. We show that when top-heavy food webs have a top-down perturbation, the loss in biomass is minimal (sometimes not significantly different than zero), but when the perturbation is bottom-up there is a much greater loss of biomass. This is logical since if the web has relatively few resource species, many consumer species are relying on only a few resources, and therefore the loss of just one will have a far more pronounced effect on how those consumer species are able to maintain higher levels of biomass.

Perhaps the most surprising result was the lack of effect of perturbation type on either biomass or species loss, potentially due to a combination of timing of the perturbations and a lack of capacity for the system to rebound. The average time to first extinction was 56 time-steps indicating that it happened very quickly. This

model does not include a mechanism for rebounding (e.g., nutrient influx or subsidy à la Leroux & Loreau (2012)), so the only way that a species experiencing a decline could rebound is through some form of release of consumption pressure, or an increase of available biomass to consume. An increase in available biomass to consume can happen in one of two ways either via direct increase in prey biomass from some sort of subsidy (Polis et al. 1997; Spiller et al. 2010; Yang & Naeem 2008), or reduced competition from the decrease in biomass of a competing predator (Chase et al. 2002). The type of perturbation did have a large effect on time to first extinction, which is not especially surprising, but since that effect is not present for the second extinction, it is likely that since the perturbed species does not often recover, the shape of the web and other factors play more of a role after the first extinction.

Often management objectives aim to preserve some aspect of a food web's structure to serve socio-economic purposes, such as a target species' biomass for harvesting (Bailey 2011) or the diversity of extant species that confer some separate cultural importance (Amberson et al. 2016). Understanding the extent to which components of the food web that actually confer the focal service are likely to be impacted by perturbation, given the food web's shape, can help to guide decision making. For example, our model systems indicate that if a bottom-heavy richness web experiences a top-down perturbation (i.e., consumer species is perturbed), then the number of species that will be less than the average number lost across other food web types, but the biomass lost from the system will be higher than average (~20%). That number of species lost might be manageable if maintaining diversity is the primary goal. However, if the goal is harvest-oriented, 20% of biomass lost, especially if that biomass is coming from the larger-bodied consumers, may be a significant blow to that market, and therefore worth exerting significant effort to try and avoid (e.g., Newfoundland cod fishery (Hutchings & Rangeley 2011)).

Perturbation frequency and intensity is increasing (Mann et al. 2017), and it is nearly inevitable that most food webs will experience some type of perturbation. At-

tempting to predict exactly when and where that will happen is perhaps a Sisyphean task, but predicting how a given food web will respond is something we can and should do to aid in effective adaptive management efforts by making preemptive efforts to understand how best to respond when these perturbations inevitably occur. Our results highlight that there is not a single best predictor of which food webs experience loss in species or biomass following perturbations; rather, there is a suite of factors, both exogenous and endogenous, that are impacting different facets of a food web's response to perturbation. Indeed, we likely must consider both types of factors in order to draw a clear picture of the overall response. Understanding how a food web is shaped, and knowing which trophic level may be most susceptible to a perturbation is an excellent, proactive step towards preventing, buffering, or containing negative effects.

3.5 Tables

Variance explained of each variable on change in biomass		
Parameter	η^2	% of Explained Variance
Biomass Dist.	0.0000826	0.00120
Richness Dist.	0.00388	0.0565
Perturbation Troph. Lev.	0.0118	0.172
Perturbation Type	0.0000000495	0.000000721
Biomass Dist. \times Richness Dist.	0.00111	0.0162
Biomass Dist. \times Perturbation Troph. Lev.	0.000512	0.00746
Richness Dist. \times Perturbation Troph. Lev.	0.0500	0.729
Richness Dist. \times Perturbation Troph. Lev. \times Biomass Dist.	0.00124	0.0180

Table 3.1: η^2 values, and the percentage of explained variance each variable accounts for, for each term in ANOVA performed on the regression of number of species lost. Percent of explained variance is calculated by dividing the η^2 value of a variable by sum of all η^2 values.

Variance explained of each variable on species lost		
Parameter	η^2	% of Explained Variance
Biomass Dist.	0.000453	0.00324
Richness Dist.	0.100	0.717
Perturbation Troph. Lev.	0.00128	0.00920
Perturbation Type	0.00000739	0.0000529
Biomass Dist. \times Richness Dist.	0.00130	0.00929
Biomass Dist. \times Perturbation Troph. Lev.	0.000922	0.00660
Richness Dist. \times Perturbation Troph. Lev.	0.0337	0.241
Richness Dist. \times Perturbation Troph. Lev. \times Biomass Dist.	0.00180	0.0129

Table 3.2: η^2 values, and the percentage of explained variance each variable accounts for, for each term in ANOVA performed on the regression of number of species lost. Percent of explained variance is calculated by dividing the η^2 value of a variable by sum of all η^2 values.

3.6 Figures

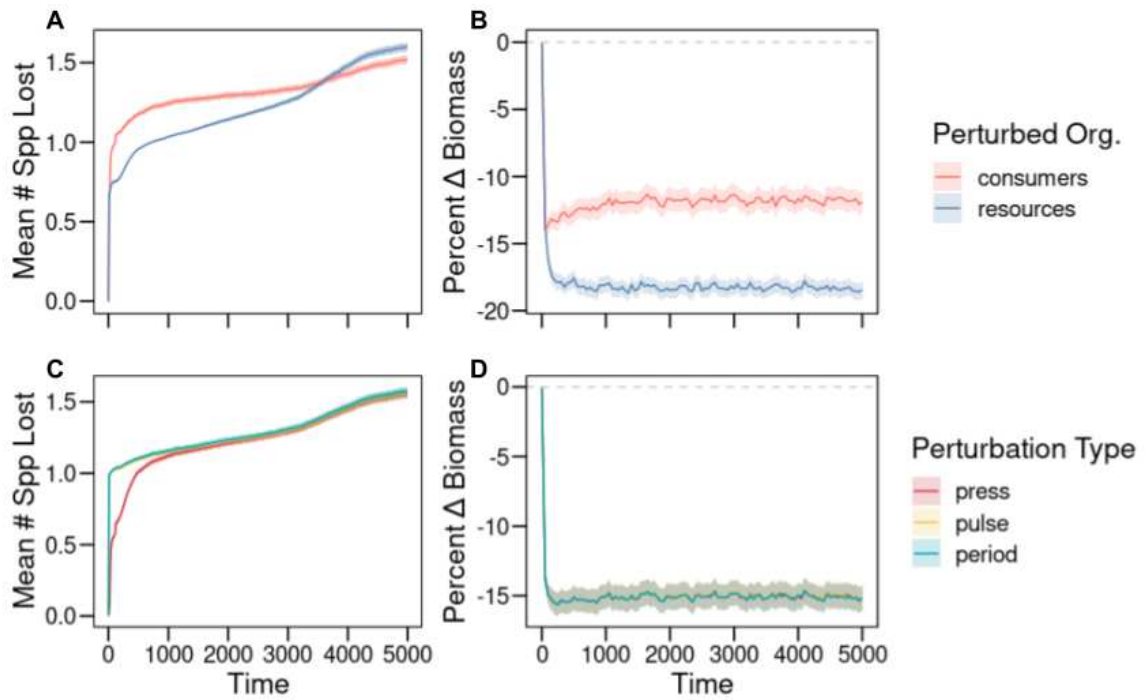


Figure 3.1: Timeseries of the simulations, showing the dynamics of both species lost and percent change in biomass between the trophic level of perturbed organism (consumers vs. resources) and the different types of perturbations.

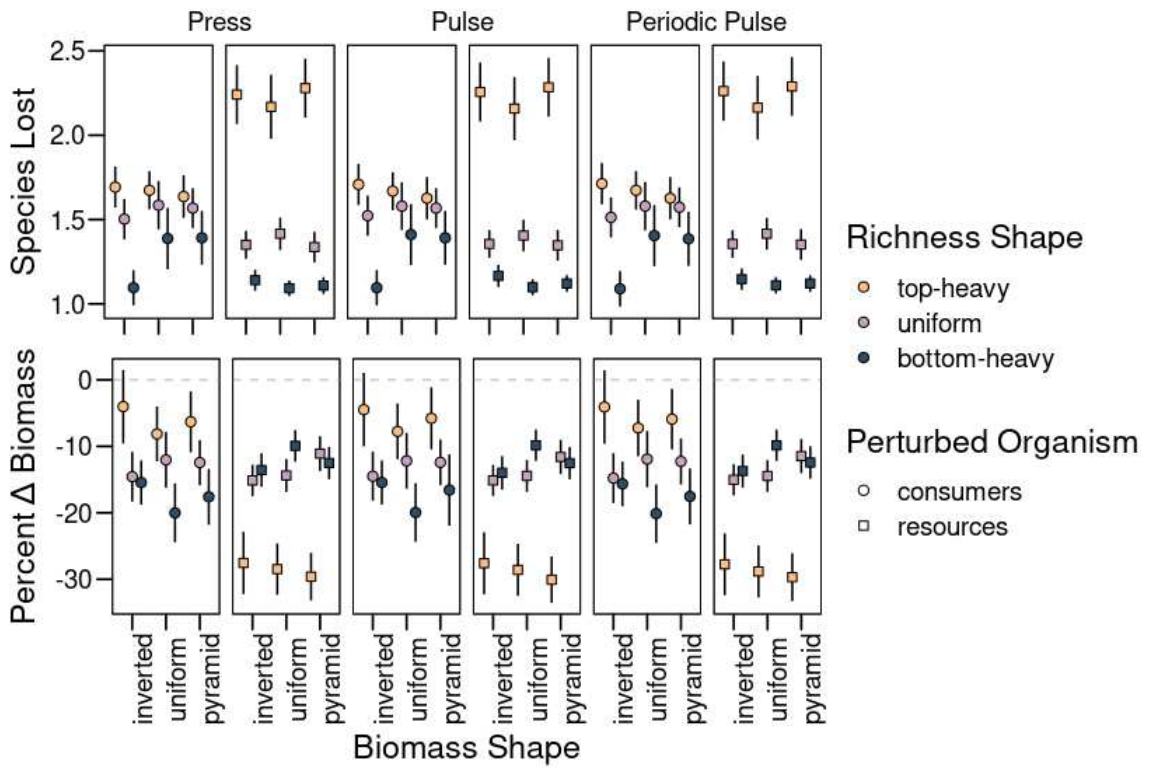


Figure 3.2: Measures of species lost and percent change in biomass across the two endogenous factors (food web shape divided between biomass and species richness distribution, and the trophic level of the perturbed organism), and the one exogenous mechanism (perturbation type).

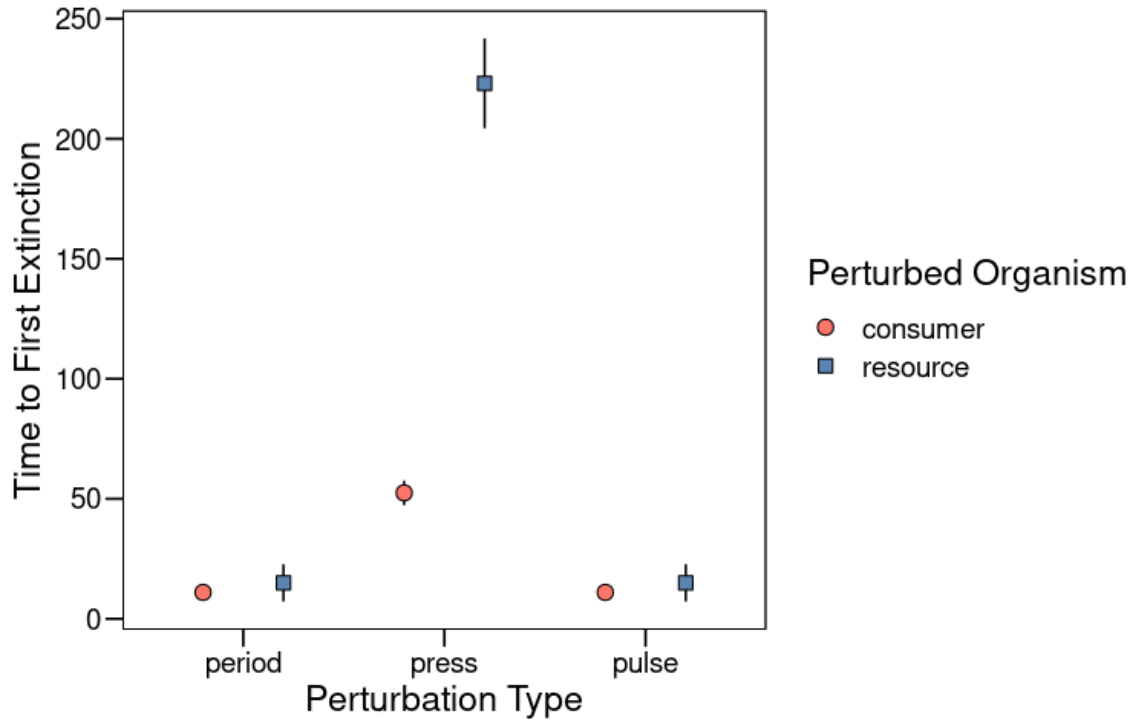


Figure 3.3: Measures of mean timing of first extinction based jointly on the trophic level perturbed, and the type of perturbation exacted on the system.

Chapter 4

Conclusions

My thesis explores of the effects of food web shape on persistence and response to perturbations. In Chapter 2, I used a simulation approach to explore how species richness distribution and biomass distribution across trophic level impacted persistence of food webs in the absence of perturbation, and showed how inherent instabilities tend to push these simulated food webs towards a somewhat universal shape that mirrors what we see in some natural food webs. In Chapter 3, I utilized the models I developed in Chapter 2 to explore relationships between food web shape and persistence under a range of perturbation types. I also showed that food web shape, an endogenous mechanism, combined with exogenous mechanisms to jointly structure the response of persistence.

I found that the distribution of species richness across trophic levels is an important factor in determining food web persistence, whether simulating food webs in a vacuum or under perturbation regimes. However, I also found that the trophic level perturbed (an exogenous factor) and the species richness distribution (an endogenous factor) jointly structured the food webs response in terms of the number of species lost as well as how biomass changed in food webs exposed to perturbations. Thus, even with a perfect understanding of a food web's structure, the outcome of a perturbation regime is still dependent to some extent on factors that are often less predictable prior to the event (Arens & West 2008; McDonald-Madden et al. 2016). The dependence

on both factors is not unexpected since when a perturbation happens at a trophic level that is relatively speciose, the food web itself is supported by that redundancy in species at the same trophic level, allowing it to buffer the effects from the perturbed species. This is in line with the findings of Sanders et al. (2018), who showed a similar result in an empirical study, demonstrating that secondary extinctions were less likely when trophic redundancy was high.

Additionally, I demonstrated how different types of responses to the perturbation play out over very different timescales. When looking at species loss, and secondary loss particularly, the extinction event itself tended to happen on a significantly longer timescale than biomass loss. Biomass loss stemming from the perturbation or its knock-on effects happened very quickly, typically within only a handful of time steps. However, the loss of a secondary species was much slower to occur, and even loss of an initial species took longer particularly under press perturbations. This indicated that across the different food web shapes, many webs experienced something akin to extinction debt (Kuussaari et al. 2009) wherein the majority of the biomass was lost quickly, but the species teetered on the edge before finally going extinct much later in the simulations. These timescales also were affected by the trophic level perturbed, where the time to first extinction, particularly in example of a press perturbation, took significantly longer when the species perturbed was a resource species compared to a consumer species.

Research on food webs in recent years has been primarily interested in understanding how stability, broadly termed, can be understood, specifically in the context of global change (Binzer et al. 2016; Emmerson et al. 2005). Much of this work has focused on trying to develop an understanding of which complex network measures can determine stability (or persistence) of those food web. In this thesis I ask if perhaps another approach, more easily estimated from empirical systems, could perform well in describing how persistence plays out in both long-term, stable systems, and in short-term systems subject to perturbation regimes. I show how species richness

distribution across trophic levels, first proposed by May 1983, may in fact be a useful measure that could be applied to conservation related questions.

There is room for further work, however. First, one of the dominant factors known to be a good predictor of food web stability and persistence is the number of species in the network (McCann 2007; Rooney & McCann 2012). Currently, it's not clear how the results shown here would hold when tested across a variety of food web sizes, but I suspect it is likely that the same patterns would remain. Additionally, persistence is just one response measure. Some studies take stability and parse it into resilience, which is how quickly a system returns to its reference state after a perturbation, and resistance, which is a measure of how resistant a system is to a large displacement, when it is in fact displaced from its reference state (Vallina & Le Quéré 2011). The results I present here are applicable to thinking about resistance, since persistence is conceptually similar, but it's not clear how food web shape would impact the *resilience* of a food web, if considered in its equilibrium state.

While in Chapter 3 I note that characterizing species richness across trophic levels is not a silver bullet solution to understanding persistence, this thesis attempts to inspect the use of this easily measurable, conceptually simple metric as a way to better inform food web models generally. As global change continues, it's less and less likely that food webs will become any easier to measure or predict, and so a flexible and adaptable set of approaches are needed to forecast what these webs will do in the future. Here I show that species richness distribution across trophic levels could provide a single, simple approach to understanding and predicting food web response to perturbations.

Bibliography

- Amberson, S. et al. (2016) “The Heartbeat of Our People”: identifying and measuring how salmon influences quinault tribal well-being. *Society & Natural Resources*, **29**. Publisher: Taylor & Francis, 1389–1404.
- Arens, N. C. & West, I. D. (2008) Press-pulse: a general theory of mass extinction? *Paleobiology*, **34**. Publisher: Cambridge University Press, 456–471.
- Arnoldi, J.-F. et al. (2018) How ecosystems recover from pulse perturbations: A theory of short-to long-term responses. *Journal of theoretical biology*, **436**. Publisher: Elsevier, 79–92.
- Awender, S., Wackerbauer, R. & Breed, G. A. (2021) Stability of generalized ecological-network models. *Chaos: An Interdisciplinary Journal of Nonlinear Science*, **31**. Publisher: AIP Publishing.
- Bailey, K. M. (2011) An empty donut hole: the great collapse of a North American fishery. *Ecology and Society*, **16**. Publisher: JSTOR.
- Bar-On, Y. M., Phillips, R. & Milo, R. (2018) The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, **115**. Publisher: National Acad Sciences, 6506–6511.
- Baum, J. K. & Worm, B. (2009) Cascading top-down effects of changing oceanic predator abundances. en. *Journal of Animal Ecology*, **78**, 699–714.
- Bender, E. A., Case, T. J. & Gilpin, M. E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology*, **65**. Publisher: Wiley Online Library, 1–13.
- Berlow, E. L. et al. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of animal ecology*, Publisher: JSTOR, 585–598.
- Bezanson, J. et al. (2017) Julia: A fresh approach to numerical computing. *SIAM review*, **59**. Publisher: SIAM, 65–98.
- Binzer, A. et al. (2016) Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Global Change Biology*, **22**. Publisher: Wiley Online Library, 220–227.
- Birkeland, C. & Dayton, P. K. (2005) The importance in fishery management of leaving the big ones. *Trends in ecology & evolution*, **20**. Publisher: Elsevier, 356–358.
- Boyd, D. P. & Gates, C. C. (2006) A brief review of the status of plains bison in North America. *Journal of the West*, **45**. Publisher: KANSAS STATE UNIVERSITY, 15.

- Bramon Mora, B. et al. (2018) Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications*, **9**. Publisher: Nature Publishing Group UK London, 2603.
- Brodie, J. F. et al. (2014) Secondary extinctions of biodiversity. *Trends in ecology & evolution*, **29**. Publisher: Elsevier, 664–672.
- Brooks, M. (1955). *The Passenger Pigeon: Its Natural History and Extinction*.
- Brose, U., Archambault, P., et al. (2019) Predator traits determine food-web architecture across ecosystems. *Nature ecology & evolution*, **3**. Publisher: Nature Publishing Group, 919–927.
- Brose, U., Williams, R. J. & Martinez, N. D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology letters*, **9**. Publisher: Wiley Online Library, 1228–1236.
- Chase, J. M. et al. (2002) The interaction between predation and competition: a review and synthesis. *Ecology letters*, **5**. Publisher: Wiley Online Library, 302–315.
- Chick, J. H. et al. (2020) Invasive silver carp is empirically linked to declines of native sport fish in the Upper Mississippi River System. en. *Biological Invasions*, **22**, 723–734.
- Clauset, A., Newman, M. E. & Moore, C. (2004) Finding community structure in very large networks. *Physical review E*, **70**. Publisher: APS, 066111.
- Closs, G. P., Balcombe, S. R. & Shirley, M. J. (1999). Generalist predators, interaction strength and food-web stability. *Advances in Ecological Research* (ed. by), pp. 93–126. Elsevier.
- Cohen, J. E. (1978) *Food webs and niche space*, Princeton University Press.
- Cohen, J. E., Briand, F. & Newman, C. M. (2012) *Community food webs: data and theory*, Springer Science & Business Media.
- Crain, C. M., Kroeker, K. & Halpern, B. S. (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology letters*, **11**. Publisher: Wiley Online Library, 1304–1315.
- Csardi, M. G. (2013) Package ‘igraph’. *Last accessed*, **3**, 2013.
- Cuenda, S., Llorente, M. & Capitán, J. A. (2020) Collapse and recovery times in non-linear harvesting with demographic stochasticity. *Applied Mathematics and Computation*, **380**. Publisher: Elsevier, 125236.
- Curran, L. M. & Leighton, M. (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**. Publisher: Wiley Online Library, 101–128.
- D’Alelio, D. et al. (2016) Ecological-network models link diversity, structure and function in the plankton food-web. en. *Scientific Reports*, **6**. Number: 1 Publisher: Nature Publishing Group, 21806.
- Del Giorgio, P. A. & Gasol, J. M. (1995) Biomass distribution in freshwater plankton communities. *The American Naturalist*, **146**. Publisher: University of Chicago Press, 135–152.
- Delmas, E. et al. (2019) Analysing ecological networks of species interactions. *Biological Reviews*, **94**. Publisher: Wiley Online Library, 16–36.

- Dietze, M. C. et al. (2018) Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences*, **115**. Publisher: National Acad Sciences, 1424–1432.
- Domínguez-García, V., Dakos, V. & Kéfi, S. (2019) Unveiling dimensions of stability in complex ecological networks. *Proceedings of the National Academy of Sciences*, **116**. Publisher: Proceedings of the National Academy of Sciences, 25714–25720.
- Donohue, I. et al. (2016) Navigating the complexity of ecological stability. *Ecology letters*, **19**. Publisher: Wiley Online Library, 1172–1185.
- Downing, A. L. & Leibold, M. A. (2010) Species richness facilitates ecosystem resilience in aquatic food webs. en. *Freshwater Biology*, **55**, 2123–2137.
- Dunne, J. A. (2006) The network structure of food webs. *Ecological networks: linking structure to dynamics in food webs*, 27–86.
- Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology letters*, **5**. Publisher: Wiley Online Library, 558–567.
- Dusenge, M. E., Duarte, A. G. & Way, D. A. (2019) Plant carbon metabolism and climate change: elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist*, **221**. Publisher: Wiley Online Library, 32–49.
- Elton, C. S. (1927) *Animal ecology*, University of Chicago Press.
- Emmerson, M. et al. (2005) Global change alters the stability of food webs. *Global Change Biology*, **11**. Publisher: Wiley Online Library, 490–501.
- Estes, J. A. et al. (2011) Trophic downgrading of planet Earth. *science*, **333**. Publisher: American Association for the Advancement of Science, 301–306.
- Estrada, E. (2007a) Characterization of topological keystone species: Local, global and “meso-scale” centralities in food webs. *Ecological Complexity*, **4**. Publisher: Elsevier, 48–57.
- Estrada, E. (2007b) Food webs robustness to biodiversity loss: the roles of connectance, expansibility and degree distribution. *Journal of theoretical biology*, **244**. Publisher: Elsevier, 296–307.
- Evans, K. L., Warren, P. H. & Gaston, K. J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**. Publisher: Cambridge University Press, 1–25.
- Fath, B. D. & Killian, M. C. (2007) The relevance of ecological pyramids in community assemblages. *Ecological Modelling*, **208**. Publisher: Elsevier, 286–294.
- Gellner, G. & McCann, K. (2012) Reconciling the omnivory-stability debate. *The American Naturalist*, **179**. Publisher: University of Chicago Press Chicago, IL, 22–37.
- Gilbert, B. et al. (2014) A bioenergetic framework for the temperature dependence of trophic interactions. *Ecology letters*, **17**. Publisher: Wiley Online Library, 902–914.
- Gravel, D., Canard, E., et al. (2011) Persistence Increases with Diversity and Connectance in Trophic Metacommunities. en. *PLOS ONE*, **6**. Publisher: Public Library of Science, e19374.

- Gravel, D., Massol, F. & Leibold, M. A. (2016) Stability and complexity in model meta-ecosystems. *Nature communications*, **7**. Publisher: Nature Publishing Group UK London, 12457.
- Hallett, L. M. et al. (2019) Rainfall variability maintains grass-forb species coexistence. *Ecology Letters*, **22**. Publisher: Wiley Online Library, 1658–1667.
- Hessen, D. O. et al. (2004) Carbon sequestration in ecosystems: the role of stoichiometry. *Ecology*, **85**. Publisher: Wiley Online Library, 1179–1192.
- Hutchings, J. A. & Rangeley, R. W. (2011) Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*, **89**. Publisher: NRC Research Press, 386–400.
- Inamine, H. et al. (2022) Pulse and Press Disturbances Have Different Effects on Transient Community Dynamics. *The American Naturalist*, **200**. Publisher: The University of Chicago Press Chicago, IL, 571–583.
- IUCN (2023). *The IUCN Red List of Threatened Species*.
- Ives, A. R. & Carpenter, S. R. (2007) Stability and diversity of ecosystems. *science*, **317**. Publisher: American Association for the Advancement of Science, 58–62.
- Jacob, U. et al. (2011). The role of body size in complex food webs: A cold case. *Advances in ecological research* (ed. by), pp. 181–223. Elsevier.
- Jentsch, A. & White, P. (2019) A theory of pulse dynamics and disturbance in ecology. *Ecology*, **100**. Publisher: Wiley Online Library, e02734.
- Jerardino, A. et al. (1992) Early coastal subsistence patterns in central Chile: a systematic study of the marine-invertebrate fauna from the site of Curaumilla-1. *Latin American Antiquity*, **3**. Publisher: Cambridge University Press, 43–62.
- Jonsson, T. (2017) Conditions for Eltonian pyramids in Lotka-Volterra food chains. *Scientific reports*, **7**. Publisher: Nature Publishing Group UK London, 10912.
- King, C. M. (1983) The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *The Journal of Animal Ecology*, Publisher: JSTOR, 141–166.
- Kitching, R. L. (2001) Food webs in phytotelmata: “bottom-up” and “top-down” explanations for community structure. *Annual review of entomology*, **46**. Publisher: Annual Reviews 4139 El Camino Way, PO Box 10139, Palo Alto, CA 94303-0139, USA, 729–760.
- Kouki, J. & Salo, K. (2020) Forest disturbances affect functional groups of macrofungi in young successional forests—harvests and fire lead to different fungal assemblages. *Forest Ecology and Management*, **463**. Publisher: Elsevier, 118039.
- Kuussaari, M. et al. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in ecology & evolution*, **24**. Publisher: Elsevier, 564–571.
- Laska, M. S. & Wootton, J. T. (1998) Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, **79**, 461–476.
- Leroux, S. J. & Loreau, M. (2012) Dynamics of Reciprocal Pulsed Subsidies in Local and Meta-Ecosystems. en. *Ecosystems*, **15**, 48–59.
- Lewis, A. S. et al. (2023) The power of forecasts to advance ecological theory. *Methods in Ecology and Evolution*, **14**. Publisher: Wiley Online Library, 746–756.

- Lindeman, R. L. (1942) The trophic-dynamic aspect of ecology. *Ecology*, **23**. Publisher: JSTOR, 399–417.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. en. *Oikos*, **91**, 3–17.
- Mann, M. E. et al. (2017) Influence of anthropogenic climate change on planetary wave resonance and extreme weather events. *Scientific reports*, **7**. Publisher: Nature Publishing Group, 1–12.
- Marczak, L. B. et al. (2011) Latitudinal variation in top-down and bottom-up control of a salt marsh food web. *Ecology*, **92**. Publisher: Wiley Online Library, 276–281.
- Massoud, E. C. et al. (2018) Probing the limits of predictability: data assimilation of chaotic dynamics in complex food webs. en. *Ecology Letters*, **21**. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ele.12876>, 93–103.
- May, R. M. (1973) Qualitative stability in model ecosystems. *Ecology*, **54**. Publisher: Wiley Online Library, 638–641.
- May, R. M. (1983) Ecology: the structure of food webs. *Nature*, **301**. Publisher: Nature Publishing Group UK London, 566–568.
- McCann, K. (2000) The diversity–stability debate. en. *Nature*, **405**. Number: 6783 Publisher: Nature Publishing Group, 228–233.
- McCann, K. (2007) Protecting biostructure. en. *Nature*, **446**. Number: 7131 Publisher: Nature Publishing Group, 29–29.
- McCann, K. (2011) *Food webs*, Princeton University Press.
- McCann, K., Hastings, A. & Huxel, G. R. (1998) Weak trophic interactions and the balance of nature. *Nature*, **395**. Publisher: Nature Publishing Group UK London, 794–798.
- McCarthy, D. P. et al. (2012) Financial Costs of Meeting Global Biodiversity Conservation Targets: Current Spending and Unmet Needs. *Science*, **338**. Publisher: American Association for the Advancement of Science, 946–949.
- McCauley, D. J., DeSalles, P. A., et al. (2012) From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. *Scientific reports*, **2**. Publisher: Nature Publishing Group UK London, 409.
- McCauley, D. J., Gellner, G., et al. (2018) On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities. en. *Ecology Letters*, **21**. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/ele.12900>, 439–454.
- McDonald-Madden, E. et al. (2016) Using food-web theory to conserve ecosystems. en. *Nature Communications*, **7**. Number: 1 Publisher: Nature Publishing Group, 10245.
- McLeod, A. M. & Leroux, S. J. (2021) The multiple meanings of omnivory influence empirical, modular theory and whole food web stability relationships. *Journal of Animal Ecology*, **90**. Publisher: Wiley Online Library, 447–459.
- McLeod, A. M., Leroux, S. J., et al. (2021) Sampling and asymptotic network properties of spatial multi-trophic networks. en. *Oikos*, **130**, 2250–2259.
- McMeans, B. C., McCann, K., Humphries, M., et al. (2015) Food Web Structure in Temporally-Forced Ecosystems. en. *Trends in Ecology & Evolution*, **30**, 662–672.

- McMeans, B. C., McCann, K., Tunney, T. D., et al. (2016) The adaptive capacity of lake food webs: from individuals to ecosystems. en. *Ecological Monographs*, **86**, 4–19.
- Millard, S. P. (2013) *EnvStats: An R Package for Environmental Statistics*, Springer, New York.
- Montoya, J. M., Pimm, S. L. & Solé, R. V. (2006) Ecological networks and their fragility. *Nature*, **442**. Publisher: Nature Publishing Group UK London, 259–264.
- Montoya, J. M., Rodríguez, M. A. & Hawkins, B. A. (2003) Food web complexity and higher-level ecosystem services. *Ecology letters*, **6**. Publisher: Wiley Online Library, 587–593.
- Montoya, J. M., Woodward, G., et al. (2009) Press perturbations and indirect effects in real food webs. *Ecology*, **90**. Publisher: Wiley Online Library, 2426–2433.
- O’Gorman, E. J., Fitch, J. E. & Crowe, T. P. (2012) Multiple anthropogenic stressors and the structural properties of food webs. en. *Ecology*, **93**, 441–448.
- Pandolfi, J. M. et al. (2011) Projecting coral reef futures under global warming and ocean acidification. *science*, **333**. Publisher: American Association for the Advancement of Science, 418–422.
- Pascual, M. & Dunne, J. A. (2006) *Ecological networks: linking structure to dynamics in food webs*, Oxford University Press.
- Peel, R. A. et al. (2019) Food Web Structure and Trophic Dynamics of a Fish Community in an Ephemeral Floodplain Lake. *Frontiers in Environmental Science*, **7**.
- Perkins, D. M. et al. (2022) Consistent predator-prey biomass scaling in complex food webs. *Nature Communications*, **13**. Publisher: Nature Publishing Group UK London, 4990.
- Pettorelli, N. et al. (2012) Tracking the effect of climate change on ecosystem functioning using protected areas: Africa as a case study. *Ecological Indicators*, **20**. Publisher: Elsevier, 269–276.
- Pimm, S. L. (1982) *Food webs*, Springer.
- Pinek, L. et al. (2020) Rate of environmental change across scales in ecology. *Biological Reviews*, **95**. Publisher: Wiley Online Library, 1798–1811.
- Polis, G. A. et al. (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology*, **78**. Publisher: Wiley Online Library, 1884–1897.
- Power, M. E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology*, **73**. Publisher: JSTOR, 733–746.
- Pringle, R. M. (2020) Untangling food webs. *Unsolved problems in Ecology*, Publisher: Princeton University Press, 225–238.
- Raab, M. L. (1992) The subsistence role of the abalone (*Haliotis cracherodii*) on aboriginal San Clemente Island. *California. Journal of Ethnobiology*, **12**, 63–80.
- Reice, S. R. (1994) Nonequilibrium determinants of biological community structure. *American scientist*, **82**. Publisher: JSTOR, 424–435.
- Reuman, D. C. et al. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. en. *Ecol-*

- ogy Letters*, **11**. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2008.01236.x>, 1216–1228.
- Ricker, W. E. (1981) Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**. Publisher: NRC Research Press Ottawa, Canada, 1636–1656.
- Rooney, N. & McCann, K. (2012) Integrating food web diversity, structure and stability. en. *Trends in Ecology & Evolution*, **27**, 40–46.
- Rooney, N., McCann, K., et al. (2006) Structural asymmetry and the stability of diverse food webs. *Nature*, **442**. Publisher: Nature Publishing Group UK London, 265–269.
- Ross, M. S. et al. (2009) Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. en. *Frontiers in Ecology and the Environment*, **7**, 471–478.
- Ruppert, J. L. W. et al. (2013) Caught in the Middle: Combined Impacts of Shark Removal and Coral Loss on the Fish Communities of Coral Reefs. en. *PLOS ONE*, **8**. Publisher: Public Library of Science, e74648.
- Sanders, D. et al. (2018) Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, **115**. Publisher: National Acad Sciences, 2419–2424.
- Sandin, S. A., Smith, J. E., et al. (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. en. *PLOS ONE*, **3**. Publisher: Public Library of Science, e1548.
- Sandin, S. A. & Zgliczynski, B. J. (2015) Inverted trophic pyramids. *Ecology of fishes on coral reefs*, Publisher: Cambridge University Press Cambridge, UK, 247–251.
- Schmeller, D. S. & Bridgewater, P. (2021). *The eighth plenary of the Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES-8): online, nexus, and transformative change*. Pages: 2857–2862 Publication Title: Biodiversity and Conservation Volume: 30.
- Schmitz, O. J. & Leroux, S. J. (2020) Food Webs and Ecosystems: Linking Species Interactions to the Carbon Cycle. *Annual Review of Ecology, Evolution, and Systematics*, **51**. eprint: <https://doi.org/10.1146/annurev-ecolsys-011720-104730>, 271–295.
- Shurin, J. B. et al. (2012) Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**. Publisher: Royal Society, 3008–3017.
- Slobodkin, L. B. (2001) The good, the bad and the reified. *Evolutionary Ecology Research*, **3**. Publisher: Evolutionary Ecology, Ltd., 91–105.
- Soetaert, K., Kones, J. K., et al. (2009) Package ‘NetIndices’, Publisher: Citeseer.
- Soetaert, K., Petzoldt, T. & Setzer, R. W. (2010) Solving differential equations in R: package deSolve. *Journal of statistical software*, **33**, 1–25.
- Soetaert, K., Petzoldt, T. & Setzer, R. W. (2015) Package ‘deSolve’. *Solving Initial Value Differential Equations, 2010d. deSolve vignette-R package version*, **1**.
- Soininen, J., Passy, S. & Hillebrand, H. (2012) The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. en. *Oecologia*, **169**, 803–809.

- Spiller, D. A. et al. (2010) Marine subsidies have multiple effects on coastal food webs. *Ecology*, **91**. Publisher: Wiley Online Library, 1424–1434.
- Stevenson, C. et al. (2007) High apex predator biomass on remote Pacific islands. en. *Coral Reefs*, **26**, 47–51.
- Stouffer, D. B. & Bascompte, J. (2010) Understanding food-web persistence from local to global scales. en. *Ecology Letters*, **13**, 154–161.
- Stouffer, D. B. & Bascompte, J. (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, **108**. Publisher: Proceedings of the National Academy of Sciences, 3648–3652.
- Su, H. et al. (2021) Stocking alien carp leads to regime shifts in native fish populations: Evidence from long-term observation and ecological modeling of a Chinese reservoir. en. *Ecological Indicators*, **132**, 108327.
- Team, R. C. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Tilman, D. & Downing, J. A. (1994) Biodiversity and stability in grasslands. *Nature*, **367**. Publisher: Nature Publishing Group UK London, 363–365.
- Trebilco, R. et al. (2013) Ecosystem ecology: size-based constraints on the pyramids of life. *Trends in ecology & evolution*, **28**. Publisher: Elsevier, 423–431.
- Tunney, T. D. et al. (2012) Food web expansion and contraction in response to changing environmental conditions. *Nature Communications*, **3**. Publisher: Nature Publishing Group UK London, 1105.
- Turney, S. & Buddle, C. M. (2016) Pyramids of species richness: the determinants and distribution of species diversity across trophic levels. en. *Oikos*, **125**. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/oik.03404>, 1224–1232.
- Tylianakis, J. M. et al. (2010) Conservation of species interaction networks. en. *Biological Conservation*, **143**, 2270–2279.
- Vallina, S. M. & Le Quéré, C. (2011) Stability of complex food webs: Resilience, resistance and the average interaction strength. *Journal of Theoretical Biology*, **272**, 160–173.
- Wang, H. et al. (2009) Modeling inverted biomass pyramids and refuges in ecosystems. en. *Ecological Modelling*, **220**, 1376–1382.
- Woodson, C. B., Schramski, J. R. & Joye, S. B. (2018) A unifying theory for top-heavy ecosystem structure in the ocean. en. *Nature Communications*, **9**. Number: 1 Publisher: Nature Publishing Group, 23.
- Wurff, A. W. G. van der et al. (2007) Type of Disturbance and Ecological History Determine Structural Stability. en. *Ecological Applications*, **17**, 190–202.
- Yang, L. H. & Naem, S. (2008) The ecology of resource pulses. *Ecology*, **89**. Publisher: Wiley Online Library, 619–620.
- Yodzis, P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. en. *Journal of Animal Ecology*, **67**, 635–658.
- Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *The American Naturalist*, **139**. Publisher: University of Chicago Press, 1151–1175.
- Zhao, Q. et al. (2019) Horizontal and vertical diversity jointly shape food web stability against small and large perturbations. *Ecology Letters*, **22**. Publisher: Wiley Online Library, 1152–1162.

Appendix A: Empirical Body Size Data

Since these body size distributions typically delineate between Consumers and Resources, we also divided organisms into these two groups. To assign each organism a body size, we drew from an exponential distribution with rate parameter λ . To get our value from our empirical data, we fit an exponential curve to the body size data present for each of those groups to get the rate parameter for each curve, λ . This was performed using the EnvStats package in R (Millard 2013). With these empirical parameters in hand, for every organism in all of our networks, we randomly drew a body size value from an exponential distribution, with rate parameter λ based on whether or not an organism was a consumer or a resource.

Appendix B: Network metrics

Connectance, C , is calculated as the proportion of realized L vs possible S^2 possible interactions in a network, $C = \frac{L}{S^2}$. Modularity was calculated using the iGraph package in R (Csardi 2013) following the approach of Clauset et al. 2004 wherein the modularity of a graph with respect to some particular division, measures how good the division is, or how separated are the different node types from each other. To calculate trophic level, we used the NetIndices package (Soetaert, Kones, et al. 2009), and calculated a trophic Level measure for each network of a) the average trophic level of all prey items (i.e. all organisms being consumed), and b) the average trophic level of all predatory items (i.e. all organisms consuming any other organism(s)). We then calculated a biomass-corrected version of each of these values. Last, we calculated the consumer-resource richness and biomass proportions. This is simply the proportion of the extant species richness or biomass that belong to predators vs. prey where a high consumer-resource proportion means that most of the species richness or biomass is concentrated in consumer species, whereas a low proportion indicates most richness or biomass is concentrated in resource species.