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Interactions among species and ecosystems determine their responses to scale-specific fluctuations

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Abstract

Interactions Among Species and Ecosystems Determine their Responses to Scale-Specific Fluctuations

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Ecosystems are highly connected systems with many interacting components. Understanding the

mechanisms creating ecosystem patterns requires an explicit consideration of the scales at which

interactions among species and their environments occur. This dissertation focuses on the scale of

temporal variability and how temporal variability is incorporated into communities' dynamics. I first

derive an abstract theory that describes the general patterns of variability propagation within

communities. Next, I explore the role of species' interaction strengths on community dynamics across

time scales. Finally, I study the impact of human-induced hydrological changes of the Guadalquivir River

on the European anchovy fishery in the Gulf of Cadiz.

Chapter 1 uses linear response theory to extend the top down and bottom up views of ecology across

time scales. Specifically, I study a tri-trophic food chain and how fluctuations in productivity filter up the

food chain. I find that variability follows the pattern predicted by top-down equilibrium-based theories

at slow time scales. However, at an intermediate time scale, consumers can both decrease and increase

the sensitivity of lower trophic levels to variability. For example, perturbations at intermediate

frequencies can excite the endogenous cycles of a community leading to resonance. Only at the fastest

time scales do top down effects begin to break down as variability becomes dampened at higher trophic

levels. This theory provides a robust new framework to interpret food web patterns resulting from

resource pulses and other bottom up perturbations.

Chapter 2 combines the metabolic theory of ecology and empirical examples of consumer-resource

interactions to ground the general theory developed in Chapter 1. Body size is not only a significant

determinant of vital rates and but also species interaction strengths. This approach allows me to focus on biologically relevant parameter space. I predict that predators can control herbivores and producers' variability at a time scale of days to years. This theory predicts that indirect effects actively shape communities' responses across a wide range of ecologically relevant time scales.

Finally, in Chapter 3, I explore the relationship between ecology and society by studying how agricultural water use is connected to the marine anchovy fishery in the Gulf of Cadiz. Using time series analysis, I explore the correlations between hydrology, the estuarine community, and anchovy recruitment to the Gulf of Cadiz. The Guadalquivir river's mean annual discharge and seasonality have decreased over the last 90 years due to increasing river regulation and extraction. European anchovies use the river estuary as a nursery. These hydrological changes have reduced anchovy recruitment to the Gulf of Cadiz, connecting terrestrial water use with the marine fishery. I then produce a water allocation theory for terrestrial agriculture and a marine fishery. I predict that even practices that improve water efficiency will not necessarily prevent terrestrial ecosystems from total water consumption. I find that the protection of downriver ecosystem services is only protected when the benefits to marine ecosystems are considered nonsubstitutable with terrestrial ecosystems.

The issue of scale – ecological and spatiotemporal – is at the heart of my thesis. My first chapter shows that the percolation of variability is not invariant across time scales. In my second chapter, I predict how body size drives differences in community responses to variability. These theories can provide new insights into how variability impacts communities. Finally, in my last chapter, I explore rivers and migration can create trade-offs between seemingly isolated ecosystems.

Interactions Among Species and Ecosystems Determine their Responses to Scale-Specific Fluctuations

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Introduction Ecological interactions

Ecological patterns are created by mechanisms operating across different temporal (Steele, 1985), spatial (Wiens, 1989), and organizational scales (Odum, 1971). For example, nutrient flux through an ecosystem is a function of community interactions (Ngai & Srivastava, 2006; Schmitz et al., 2010) and individual behavioral decisions (Kitchell et al., 1999; Plath & Boersma, 2001). As ecologists, our understanding of processes interacting across multiple timescales is still developing. Creating a synthesis across time scales is uniquely challenging due to the practical difficulty of collecting long-term high-resolution time series (e.g., Gosz et al., 2010) and limitations in the mathematical approaches used to derive ecological theory (Holt, 2008). In Chapter 1, I develop a theory on how ecosystems filter temporal variability across time scales. In Chapter 2, I use allometric scaling to explore how species interaction strengths and time scale mismatches drive population dynamics. In Chapter 3, I combine ecological and socio-economic approaches to establish the consequences of human water use on marine fishery yields.

Species interactions are a fundamental determinate of community dynamics. For example, a producer population's dynamics are dependent on the strength of herbivory. At the same time, herbivores need producers as a resource. Thus, species interactions determine the flow of nutrients and energy through an ecosystem. In communities of three or more species, species may interact indirectly (Wootton, 1994). For example, a predator can increase a producer's biomass by consuming herbivores, thereby releasing the producer from herbivory (Ripple et al., 2016). Indirect effects can fundamentally alter community structure upon losing even a single species (Mills et al., 1993). Species interactions can propagate temporal disturbances throughout the community (Ostfeld & Keesing, 2000). However, although species interactions are crucial determinates of community dynamics, the overwhelming number of possible indirect interactions can make it challenging to assess one species' impact on another (Yodzis, 1988).

Simple food web motifs are the building blocks of highly reticulated natural food webs (Wootton, 1994). Common motifs found in nature are intraguild predation, linear food chains, apparent and direct competition (Pimm & Lawton, 1978). Linear food chains simplify food webs by aggregating species into discrete feeding guilds (Elton, 1927). In the first two chapters of this thesis, I focus on the propagation of variability up food chains. I use food chains to study predators' effects on lower trophic levels (top-down effect) and the indirect effects of primary production on the variability of higher trophic levels (bottom-up effects).

Once at the center of considerable debate, ecologists have adopted a synthetic view of top-down and bottom-up effects and the ecosystem properties that determine their relative importance (Powers, 1994). In ecosystems with strong bottom-up control, an increase in primary productivity will have diminishing impacts up a food chain due to thermodynamic loss of energy (Lindeman (1942). Thus, a food chain with bottom-up control should be a food pyramid with more biomass at the bottom of a food chain (Elton, 1927). Hairston, Smith, & Slobodkin (1960) proposed that consumers can control the biomass of lower trophic levels. The effect of predators on producer biomass would later become known as a trophic cascade. The exploitative ecosystem hypothesis mathematically formalized the top-down perspective (Fretwell & Barach, 1977; Oksanen et al., 1981; Oksanen & Oksanen, 2000). Carpenter & Kitchell (1984) found that lake ecosystems showed an alternating pattern of top-down control in four trophic level systems. Later, studies have synthesized these two approaches and investigated which ecosystem properties control the relative impact of top-down versus bottom-up control (Borer et al., 2005, 2002; DeLong et al., 2015; McCann et al., 1998; Power, 1992; Shurin et al., 2002). My first chapter aims to expand these equilibrium-based theories to predict how top-down control impacts the percolation of variability up food chains across time scales.

Frequency response theory provides a general approach to studying how communities will respond to recurring fluctuations. In nature, communities experience recurring disturbances such as El Nino to

diurnal fluctuations. Recurring disturbances can be modeled as a sum of sinusoids occurring along a

spectrum of frequencies (Weatherhead, 1986; Vasseur & Yodzis, 2004). Frequency response theory

predicts how communities will amplify or dampen environmental disturbances across the frequency

spectrum. Traditionally, a community's response to disturbance has been characterized by its long-term

recovery back to equilibrium following a singular disturbance. If disturbances are recurring, communities

will not reach their asymptotic behavior before being perturbed again. It is anticipated that rapid

fluctuations will not induce feedbacks between species. Thus, the impacts of rapid fluctuations are

predicted to dissipate as they spread through the community. However, recent studies have shown that

resource pulses elicit ecosystem-wide impacts on food webs (Ostfeld & Keesing, 2000; Yang et al., 2010),

and resource pulses can even be amplified up food chains (Yang et al., 2010). Thus, there remains a gap

in the ecological literature on the interplay between indirect effects and community dynamics across

time scales (Holt, 2008). I will contribute to a growing body of literature on how the time scale of

disturbances alters how variability is filtered into a population's dynamics (Ives & Jansen, 1998; Ripa &

Ives, 2003).

In my third chapter, I expand my research beyond ecological interactions to explore the relationship

between human society and ecological communities. For example, an ecosystem is the collection of all

of the interactions between biotic and abiotic actors (Tansley, 1935). A social-ecological system (SES)

extends this concept by including the relationship within and among an ecosystem and society (Berkes

et al., 2000). Social-ecological systems are complex, adaptive, and delimited by spatial or functional

boundaries surrounding particular ecosystems and societal structures (Dearing et al., 2010). Water

basins are an example of an SES system and argued by some managers to be a fundamental unit of

management (Warner et al., 2008); however, the sharing of technology, water, trade, and the

movement of animals can create connections beyond the water basin (Liu et al., 2016). These

connections beyond the water basin present challenges for managing water use equitability (Yuan et al., 2020).

Water is central to biodiversity and human well-being (Vörösmarty et al., 2010). Human society uses water for mutually exclusive activities, such as irrigation, manufacturing, and residential use (Babel et al., 2005). Economists have used economic efficiency principles to determine water allocation (Kay et al., 1999). However, not all of the benefits provided by water are readily reduced to economic efficiencies, such as values of equity, health, and biodiversity (Peterson et al., 2010). For example, jobs in different communities are not substitutable to the people who live there, and stakeholders prioritize local benefits over distal benefits (Zia et al., 2011, 2015). The development of holistic water policies, such as the ecosystem approach (Kay et al., 1999) and the telecoupling framework (Liu et al., 2016), aims to balance the diverse values within and across socio-ecological systems.

Outline of chapters

In Chapter 1, using frequency response theory, I develop an ecological theory that predicts the percolation of variability up a linear food chain. I define the ability of consumers to control the variability of lower trophic levels a "variation cascade." I find that variation cascades are not invariant across frequencies. Specifically, the community dynamics at low frequencies follow the equilibrium theory of the exploitative ecosystems hypothesis governs, at intermediate frequencies, the community can resonant, and at high frequencies, the community will average across disturbances. This study is an essential step in understanding how environmental variation percolates through communities and the role of top-down effects on the variability of lower trophic levels.

Chapter 2 combines allometric scaling and empirical information on consumer-resource interactions to develop a biologically informed theory to predict the time scales in which communities are the most susceptible to environmental variability. In this study, I use allometric scaling and frequency response

theory to derive the time scales at which communities transition from amplifying and dampening disturbances. I find that species interaction strength controls the patterns of variability and that the abstract patterns in Chapter 1 occur in biologically relevant parameter space.

Chapter 3 explores the consequences of terrestrial water policy on a marine fishery using multi-decadal time series analysis and socio-ecological theory. Terrestrial water use is shaping the hydrology of the Guadalquivir River estuary – a nursery for European anchovies. Anchovies have lower recruitment from the estuary when discharge is low or aseasonal. I then create an allocation model for terrestrial and marine socio-ecological systems and examine the impact of different institutional norms around water policy and the outcomes for socio-ecological systems.

Summary and synthesis

The issue of scale is at the heart of my thesis, from addressing how communities filter temporal variability and finding a connection between marine and terrestrial socio-ecological systems. Overall, I hope my thesis introduces more rigor towards studying how time scale shapes the interactions between species.

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Chapter 1 Variation cascades: resource pulses and top-down effects across time scales

Abstract

Top-down and bottom-up theories of trophic control have been fundamental to our understanding of community dynamics and structure. However, most ecological theories focus on equilibrium dynamics and do not provide predictions for the response of communities in temporally fluctuating environments. By deriving the frequency response of populations in different trophic communities, we extend the top-down and bottom-up theories of ecology to include how fluctuations in potential primary productivity percolate up the food chain and are re-expressed as population variability. Moreover, by switching from a time-based representation into the frequency domain, we provide a unified method to compare how the time scale of perturbations determines the responses of communities. We define the top-down effects of consumers on the variability of lower trophic levels as a variation cascade. At low frequencies, primary producers and secondary consumers have the highest temporal variability, while the primary consumers are relatively stable. Similar to the exploitative ecosystem hypothesis, top-down effects drive an alternating pattern of variability; however, this qualitative pattern does not extend to higher frequencies. Instead, at intermediate frequencies, variation cascades amplify temporal variation up the food chain. At high frequencies, variation cascades disappear, and fluctuations are attenuated up the food chain. In summary, we provide a novel theory for how a community responds to fluctuations in productivity, and we show that indirect species interactions play a crucial role in determining community dynamics across the frequency spectrum.

Introduction

Indirect effects are a significant determinant of a community's structure and function (Carpenter & Kitchell, 1988). In addition to mediating the response to long-term changes, indirect effects play an important role in mediating the response to short-term changes, even when these changes enter the community at singular points (e.g., resource pulses) (Ostfeld & Holt, 2004). For example, during El Nino, high rainfall generates temporary increases in plant growth, which supports higher rates of growth in secondary consumers (Previtali et al., 2009). Although secondary consumers have a fundamental role in shaping communities, such bottom-up effects are predicted to dominate when resource pulses are fast (Schwinning & Sala, 2006). However, many systems experience recurrent resource pulses along a spectrum of time scales (e.g., daily, annually, decadal, etc.). If resource pulses are recurrent, the impact of one resource pulse can carry over to the next pulse (Noy-Meir, 1973), as recovery back to equilibrium is commonly prolonged (Hastings, 2004). In such cases, the propagation of variability through the community is mediated by the set of positive and negative feedbacks on each population. We develop a novel theory that extends our understanding of how these feedbacks, classified as top-down and bottom-up control in trophic systems, determine the response of populations to fluctuations in primary productivity. Early work in this area suggested that community dynamics and structure were primarily determined by resource availability. Lindeman (1942) predicted that thermodynamic constraints (i.e., energy lost to metabolism and the inefficiency of ingestion and digestion) should cause increases in resource availability to have diminishing returns up the food chain. Extending this idea to resources pulses, pulse-reserve (Noy-Meir, 1973) and hierarchy theory (Schwinning & Sala, 2006) both predict the attenuation of resource pulses, as they are transferred via interactions throughout the community. Bottom-up fluctuations would, therefore, tend to produce less population variability in consumers relative to their producers. In contrast, a recent meta-analysis found that, on average, the populations directly utilizing a resource pulse have a smaller response than their consumers, who are only indirectly

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experiencing the pulse (Yang et al. 2010). Despite the fact that resource pulses feed directly into the bottom trophic levels, bottom-up theories are insufficient to explain the amplification of variability up food chains.

Recognizing that consumers can impose top-down control on resources, resource pulses could yield responses that are amplified in higher trophic levels. For example, secondary consumers can increase producer biomass by releasing producers from herbivory in a trophic cascade (Oksanen et al., 1981; Oksanen & Oksanen, 2000). For this study, we define potential primary productivity (PPP) as the biomass of producers in the absence of herbivory. The exploitative ecosystem hypothesis (EEH) predicts an alternating pattern of top-down regulation within food chains that changes with food chain length (Oksanen et al., 1981; Oksanen & Oksanen, 2000). For example, in a two trophic level system, increases in resource availability will increase primary consumer biomass and not producer biomass. Following from this, if resources fluctuate, variability could be amplified up the food chain, as the producer will have low variability, and the primary consumer will be highly variable. Yet, EEH is built upon the assumption that alterations in resource availability are long term and sustained (Bender et al., 1984; Schmitz, 1997; Yodzis, 1988) and might not be the best predictor of acommunity's response to rapid fluctuations in resource availability. Thus, we develop a theory of top-down control in fluctuating environments to determine if top-down control can explain the empirical pattern of amplification of variation up food chains.

Using a frequency based approach, we can calculate the interplay between resource pulses and top-down control. When switching from the time domain to a frequency-based representation, processes changing slowly are represented by low frequency sinusoids and those changing quickly by high frequency sinusoids. Resource availability can fluctuate hourly to multi-annually, and the frequency content of all these fluctuations is known as the frequency spectrum. Frequency response is a general mathematical approach that predicts how communities respond to sinusoidal perturbations across the

frequency spectrum (Nisbet & Gurney, 1976; Ripa et al., 1998). A community's response to sinusoidal

disturbances is also a sinusoid of the same frequency but with a different amplitude and phase lag.

Furthermore, complex environmental fluctuations can be modeled as a sum of sinusoids, using Fourier

Series. Thus by combining frequency response and Fourier series, we are not limited to modeling simple

sinusoidal perturbations but instead can model a community's response to complex environmental

forcings. For example, Ripa et al. (1998) used the frequency response to derive a theory of how two

interacting species filter environmental noise. By focusing on frequency responses, we provide a unified

method for studying how communities amplify or dampen perturbations across the frequency

spectrum.

Here, we develop a novel theory for how resource pulses impact the dynamics of a food chain. We

explore how the community shifts from tracking its equilibrium response, to averaging across high

frequencies by determining when populations amplify and attenuate fluctuations in potential primary

productivity. Furthermore, we extend the concepts of top-down and bottom-up control across the

frequency spectrum. Finally, we demonstrate how to combine Fourier series with amplitude responses

to model complex community responses to episodic disturbances with long interpulse intervals. In

summary, we present a theory of how top-down and bottom-up effects control across time scales.

Methods

The model derivation

Following Pimm (1982), we model a tri-trophic food chain where biomass enters the community via

primary production by the producer (R), which is then consumed by a primary consumer (H), and

ultimately eaten by a secondary consumer (P).

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - a_{RH}\,R\,H + \; r\,B\,\mathrm{Cos}(2\pi\omega t)$$

$$\frac{dH}{dt} = H(c_{RH}a_{RH}R - a_{HP}P - d_H)$$

$$\frac{dP}{dt} = P(c_{HP}a_{HP}H - d_P)$$

Eq 1

We assume that the producer exhibits linear negative density dependence, characterized as logistic growth to a carrying capacity (*K*) in the absence of herbivory. A sinusoidal function $rBCos(2\pi\omega t)$ generates fluctuations in PPP where ω is the frequency, and *B* is the amplitude of the additive change in PPP. The intrinsic rate of increase of the producer (r) is also included in the forcing term since faster-growing populations can take greater advantage of an increase in resources. Similar to Pimm (1982), the two consumers have linear (Holling Type I) functional responses with attack rates (a_{RH} and a_{HP}) and assimilate biomass according to their conversion efficiencies c_{RH} and c_{HP}. The consumers do not have intraspecific interference competition, and as such, have density-independent per-capita death rates d_H and d_P.

This model produces three non-trivial equilibrium communities ξ, defined as the following sets denoting which populations have positive (non-zero) abundance {R, R-H, and R-H-P}. We report the equilibrium abundances in the Supplement (A 1-2, A 1-3, & A 1-4). The asymptotically stable equilibrium of the producer-only community (ξ = R) is a stable node. In contrast, the more diverse communities can exhibit either a node or focus, depending on parameters (Figure 1-1 a & b).
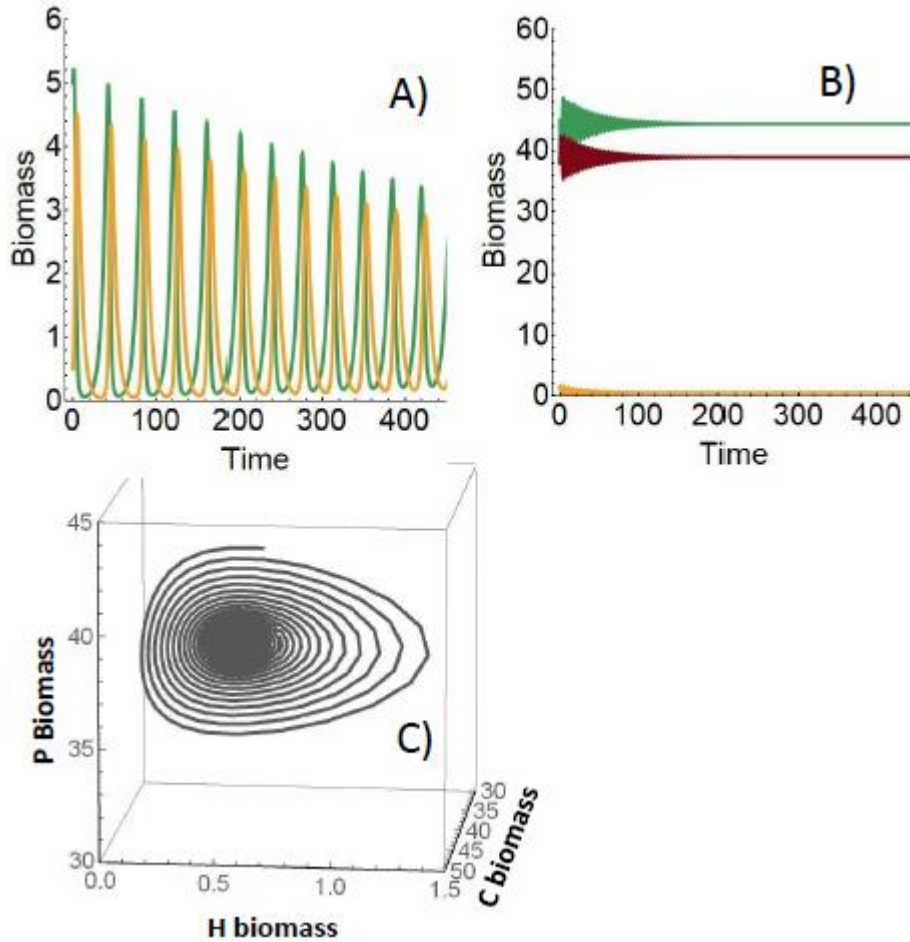
Figure 1-1. The time-series of the biomass dynamics of a food chain with either A) two or B) three trophic levels in a constant environment. C) The phase volume of the tri-trophic food chain spiraling towards its stable equilibrium. The three trophic levels are differentiated by colour such that green = R, yellow = H, and red = P. All of the solutions were solved using Runge-Kutta algorithms in Mathematica using the following parameters r = 0.2, d_H = 0.21, d_P = 0.21, a_{RH} = 0.2, a_{HP} = 0.2, K = 100, c_{RH} = 0.9, & c_{HP} = 0.9.

Model Analysis

We use frequency response theory to determine how fluctuations in PPP are incorporated into the population dynamics of each trophic level (Nesbit & Gurney, 1982). The frequency response G(iω) (see Nisbet & Gurney, 1982) represents the ratio of a given population's oscillation in biomass Y(iω) at frequency ω (radians), to those of the driving environmental signal S(iω):

$$G(i\omega) = \frac{Y(i\omega)}{S(i\omega)}$$

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Eq 2.

In practice, Y(iω) is unknown because Eq 1 cannot be analytically solved. We, therefore, resort to approximating the frequency response G(iω) by linearizing equation 1 using the Jacobian matrix J, where J^{ξ} gives the Jacobian matrix for the equilibrium ξ, and then solving the following relationship:

$$G(i\omega)_j^{\xi} = Y(i\omega)|(i\omega I - J^{\xi})^{-1}|S(i\omega)$$

Eq 3,

where j is the identity of the focal trophic level (R, H or P), Y is the output vector corresponding to the identity of the focal trophic level (e.g., {1, 0, 0} for j = R) and S is the input vector that determines where the perturbation enters the community. By varying the output vector and equilibrium, we use Eq 3 to calculate the frequency response for each of the three communities. We focus on the situation when the producer experiences an additive sinusoidal perturbation with amplitude rB, assuming that $B=1$, giving S = {r, 0, 0}.

For example, for ξ = R, $J^{\xi} = J^R = r$, and the solution of Eq 3 is:

$$G(\omega)_R^R = \{1\}(i\omega I - r)^{-1})\{r\}$$

$$G(\omega)_R^R = \frac{r}{r + i\omega}$$

Eq 4.

Thus, the frequency response for a producer, in the absence of other trophic levels is dependent on its intrinsic rate of increase (r) and the frequency of the resource pulses (ω).

It is worth noting that this analysis can be completed with a generalized Jacobian matrix describing any species interaction (e.g., competition, mutualism, and predation; see Ripa et al. 1998). In this study, we focus on the specific case of resource pulses and their impacts on a tri-trophic food chain.

Metrics

Amplitude response

The amplitude response $A(\omega)_j^{\xi}$ measures the deviation of the jth population's dynamics around its equilibrium relative to the amplitude of fluctuation in PPP (Nisbet & Gurney, 1976; Nisbet & Gurney, 1982). The amplitude response is equal to the magnitude of the frequency response $G(i\omega)_j^{\xi}$. A population amplifies a resource pulse when the amplitude response is greater than one, while a value less than one represents dampening.

Efficiency of transfer

We quantify the relative variability of two adjacent trophic levels using the efficiency of transfer (ET_{jk}^{ξ}) (Ripa et al., 1998). For the equilibrium community ξ, we define (ET_{jk}^{ξ}) as the log-ratio of the amplitude response of a focal trophic level (j) and the adjacent lower trophic level's (k):

$$ET_{jk}^{\xi}(\omega) = Log\left(\frac{A_j^{\xi}(\omega)}{A_k^{\xi}(\omega)}\right)$$

Eq 5.

Negative values indicate that the amplitude of fluctuations decreases up the food chain (attenuation), while positive values indicate that the higher trophic level has a greater amplitude (amplification). The efficiency of transfer is a very similar metric to the one used by Yang et al. (2010) to measure the amplification of resource pulses between trophic levels, except that (ET_{jk}^{ξ}) captures how amplification changes with the frequency of the resource pulse.

Variation cascades

We measure the impact of the population (k) on the amplitude of fluctuations expressed by a lower trophic level (j) by calculating the log-ratio of the amplitude response of a population (j) in the presence and absence of population (k). We call the effect of the population (k) on the amplitude of population (j) the variation cascade (VC_j^k):

$$VC_j^k(\omega) = Log\left(\frac{A_j^{\xi+k}(\omega)}{A_j^{\xi}(\omega)}\right)$$

Eq 6

If the VC_j^k is positive the addition of a new trophic level (k) increases the amplitude of population (j), while if the VC_j^k is negative the addition of population (k) decreases the amplitude of population (j). If the VC_j^k is zero the consumer (k) does not affect the focal species (j) and thus, there is no top-down effect, at that frequency. Using the variation cascade, we can assess the consumers' indirect effects across the frequency spectrum.

Results

Amplitude response

Frequency response – Producer only community (ξ = R)

In the absence of the primary consumer, the producer (R) exhibits logistic growth in a constant environment (Figure 1 - 2a, b, & c); however, if PPP is fluctuating, then the producer will oscillate around the equilibrium (Figure 1 - 2a, b, & c). The amplitude of theproducer's oscillations decreases as the frequency increases (Figure 1 - 2d) according to:

$$A_R^R(\omega) = \sqrt{\frac{r^2}{\omega^2 + r^2}}$$

Eq 7.
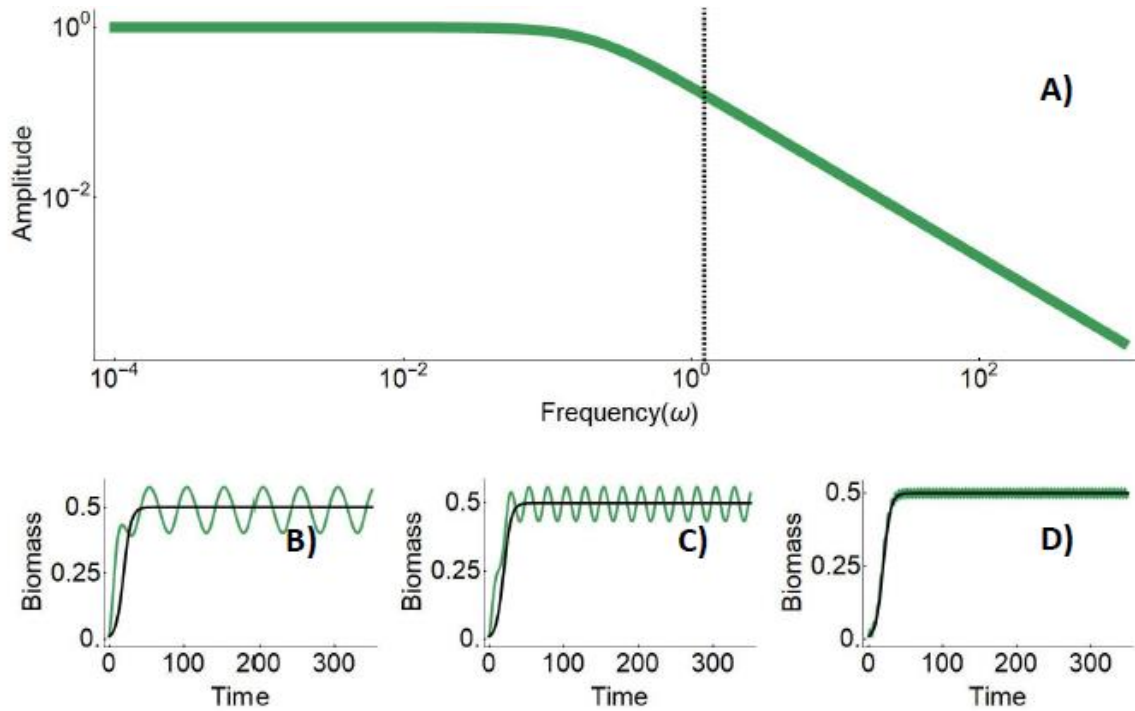
Figure 1 - 2. A) Log-log plot of the amplitude response of the primary producer (A_R^R (ω)). The amplitude response determines how a sinusoidal disturbance will be amplified or dampened. The primary producer's biomass grows to carrying capacity in a constant environment (black); however, when the productivity is fluctuating with frequency (B) ω = 1/10, (C) ω = 1/30, & (D) ω = 1/60 (where r = 1/5 & K = 1/2) the producers switch from tracking the fluctuation to averaging across the perturbation.

At low frequencies, nearly all of the variation in PPP is translated into variability in the producer's biomass. At high frequencies, A_R^R declines toward zero. Faster fluctuations offer less time for thepopulation's biomass to adjust to the changing conditions and causes the transition from the

behavior known as ''tracking' to that known as ''averaging' (Nisbet and Gurney 1976). Averaging across

fluctuations is a significant contributor to the autocorrelation or redness of population dynamics (e.g.,

Vasseur & Yodzis (2004)). Consistent with previous work (May, 1973; Vasseur, 2007), one can define the

threshold frequency at which populations switch from averaging to tracking behavior as $\omega^* = r = \lambda$,

where λ is also the dominant eigenvalue of the system (Holling, 1973). At frequencies above λ

fluctuations are dampened by more than (approximately) 70%.

Frequency response producer and primary consumer community

With the addition of a primary consumer, the amplitude response of the producer becomes

$$A_R^{RH}(\omega) = \sqrt{\frac{r^2 a_{RH}{}^2 c_{RH}{}^2 K^2 \omega^2}{d_H{}^2(d_H{}^2 + \omega^2)r^2 + 2a_{RH}c_{RH}d_H{}^2 Kr(\omega^2 - d_H r) + a_{RH}{}^2 c_{RH}{}^2 K^2(\omega^2 - d_H d_H r)^2}}$$

Eq 8

and changes in two significant qualitative ways. The producer's abundance is less sensitive to low

frequency fluctuations (as the numerator approaches zero), and the producer's amplitude response now

has a local maximum at an intermediate frequency (Figure 3a). At low frequencies, the primary

consumer decreases the producer's amplitude response by suppressing (consuming) the additional

producer biomass during times of high PPP (Fig 1 - 3a and A 1-18 for analytical solution). As the

frequency increases, the producer's amplitude response increases to a local maximum, such that

fluctuations at these frequencies are amplified (Figure 3b). The amplification of perturbations at

particular frequencies is known as harmonic or coherence resonance (McKane & Newman, 2005;

Spagnolo, Fiasconaro, & Valenti, 2003). The producer's resonant frequency is

$$\omega_{Rmax} = \frac{\sqrt{d_H}\sqrt{a_{RH}c_{RH}K - d_H}\sqrt{r}}{\sqrt{a_{RH}}\sqrt{c_{RH}}\sqrt{K}}$$

Eq 9.
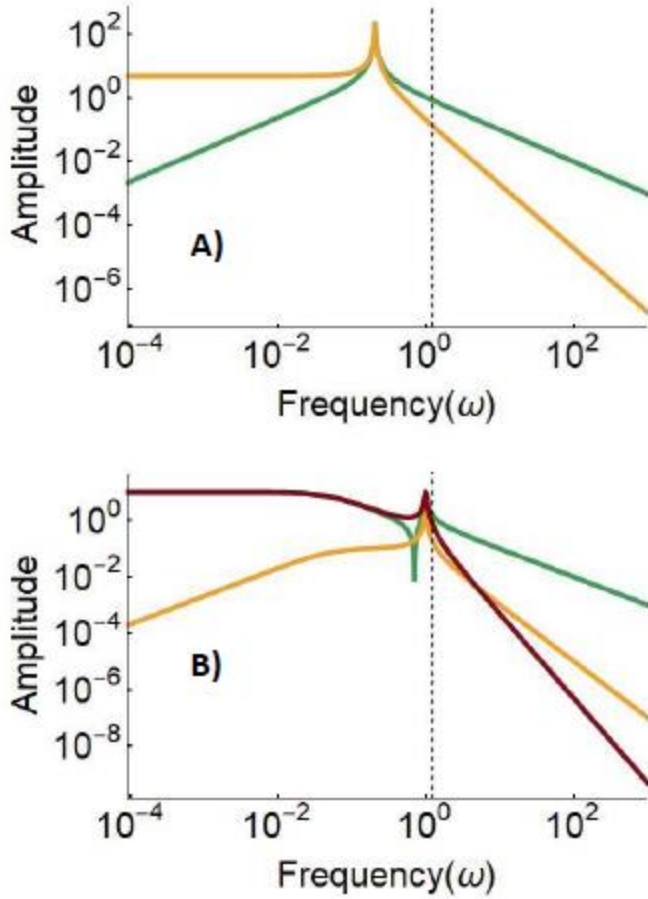
Figure 1 - 3. Log-log plots of amplitude responses of two and three trophic level food chains. (A) The amplitude response of community R-H-P (A_R^{RHP}, A_H^{RHP}, & A_P^{RHP}). B) The amplitude response of the producer and primary consumer's amplitude responses in a two trophic level food chain (A_R^{RH} & A_H^{RH}). The amplitude responses of R = green, H = yellow, and P = red. The amplitude responses are parameterized using r = 0.2, d_H = 0.21, d_P = 0.1, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 1, c_{HP} = 1.

The amplification by the producer exhibits at ω_{Rmax} is

$$max_R(A_R^{RH}(\omega)) = \frac{a_{RH}c_{RH}K}{d_H}$$

Eq 10.

We find that the maximum amplification by the producer (Eq 10) is proportional to the consumer's interaction strength (A 1-5). Thus, consumers that have a higher impact on the mean biomass of the producer will also increase the producer's maximum response to fluctuations in PPP. However, at high frequencies, the amplitude response decreases; here, primary consumers do not affect the producer's response to temporal fluctuations in PPP, as all trophic levels average across fast fluctuations (Figure 1-2a vs. 3a).

Amplitude responses in the full community

The introduction of the secondary consumer causes a shift in top-down control at low frequencies and introduces novel dynamics at intermediate frequencies. The producer is responsive to low frequency fluctuations in PPP (Figure 3b). The primary consumer is unresponsive to low frequency temporal fluctuations and has a local maximum at intermediate frequencies (Figure 1-3b). The secondary consumer is responsive at low frequencies and dampens high frequency perturbations (Figure 1-3b). At low frequencies, the food chain has a cascading pattern, from bottom to top trophic level, of high amplitude, low amplitude, high amplitude fluctuations, which is consistent with EEH. However, this alternating pattern does not persist up the frequency spectrum. We include each of the analytical solutions of the producer's, primary consumer's, and secondary consumer's amplitude responses in the Supplement.

Efficiency of transfer

The efficiency of transfer between the producer and the primary consumer (ET_{RH}^{RH}) (Figure 1-4c) is a log-linear function of the resource pulse frequency:

$$ET_{RH}^{RH} = -Log\sqrt{\frac{(d_H - a_{RH}c_{RH}K)^2\omega^2}{a_{RH}{}^2K^2}}$$

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Eq 11.

The slope of ET_{RH}^{RH} is always negative. Therefore, as the frequency increases, the primary consumer

becomes less variable than the producer (Ripa et al., 1998). The lower temporal variability of the

consumer at higher frequencies is not due to thermodynamic limitation constraints as the only change

in the system is the frequency of the perturbations. Instead, the dampening is due to producers and

consumers dynamically averaging across perturbations.
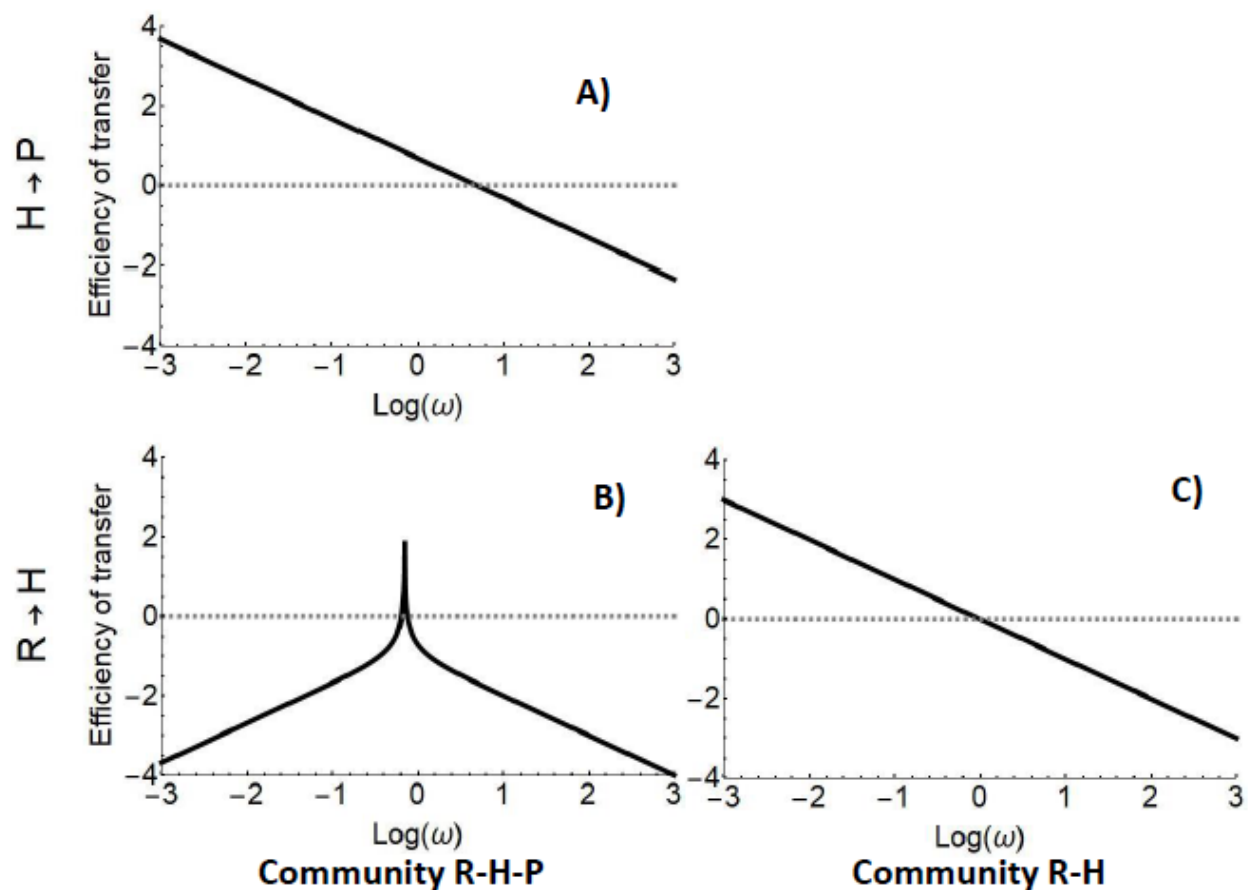
Figure 1 - 4. Plots of the efficiency of transfer of A) the primary producer to primary consumer's in the

R-H-P community ET_{RH}^{RHP}, B) primary producer to primary consumer's in the R-H community ET_{RH}^{RH}, and

C) primary consumer to secondary consumer's in the R-H-P community ET_{HP}^{RHP}. The efficiency of

transfers is parametrized using r = 0.2, d_H = 0.21, d_P = 0.1, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 1, c_{HP} = 1.

The introduction of a secondary consumer changes the ET of the producer to the primary consumer (ET_{RH}^{RHP}) from a decreasing log-linear function to a log-quadratic function (Fig 1-4a). The ET_{RH}^{RHP} will always be negative at low and high frequencies; because the numerator is a lower order polynomial than the denominator with positive leading coefficients. Thus, the primary consumer will experience lower amplitude fluctuations than the producer at low and high frequencies (Figure 1-4c). At intermediate frequencies, the ET_{RH}^{RHP} exhibits a local maximum (Figure 1-4a) and the ET_{RH}^{RHP} can even become positive such that temporal variability is amplified (as seen in Figure 1-4a).

As the frequency increases, the primary consumer's amplitude increases log-linearly relative to that of the secondary consumer. Eventually, at high frequencies, the food chain transitions such that secondary consumers will have a relatively lower amplitude than the primary consumers.

Variability across the frequency spectrum

We classify the variability of the community into one of four modes depending on which trophic levels are amplifying or attenuating a resource pulse. If ET_{RH}^{RH} and ET_{HP}^{RHP} are both positive (negative), amplitude increases (decreases) from the bottom to the top of the food chain. Using this scheme, we define the relative variability of a food chain based on the sign of its ETs (ET_{RH}^{RHP}, ET_{HP}^{RHP}): 1) (+, +) a pattern of increasing amplitude with trophic level, 2) (-, -) a bottom-up pattern of decreasing amplitude with trophic level, 3) (-, +) a cascading pattern where primary consumer and secondary consumers have the largest fluctuations and 4) (+, -) a humped shaped pattern where the primary consumer is the most variable.
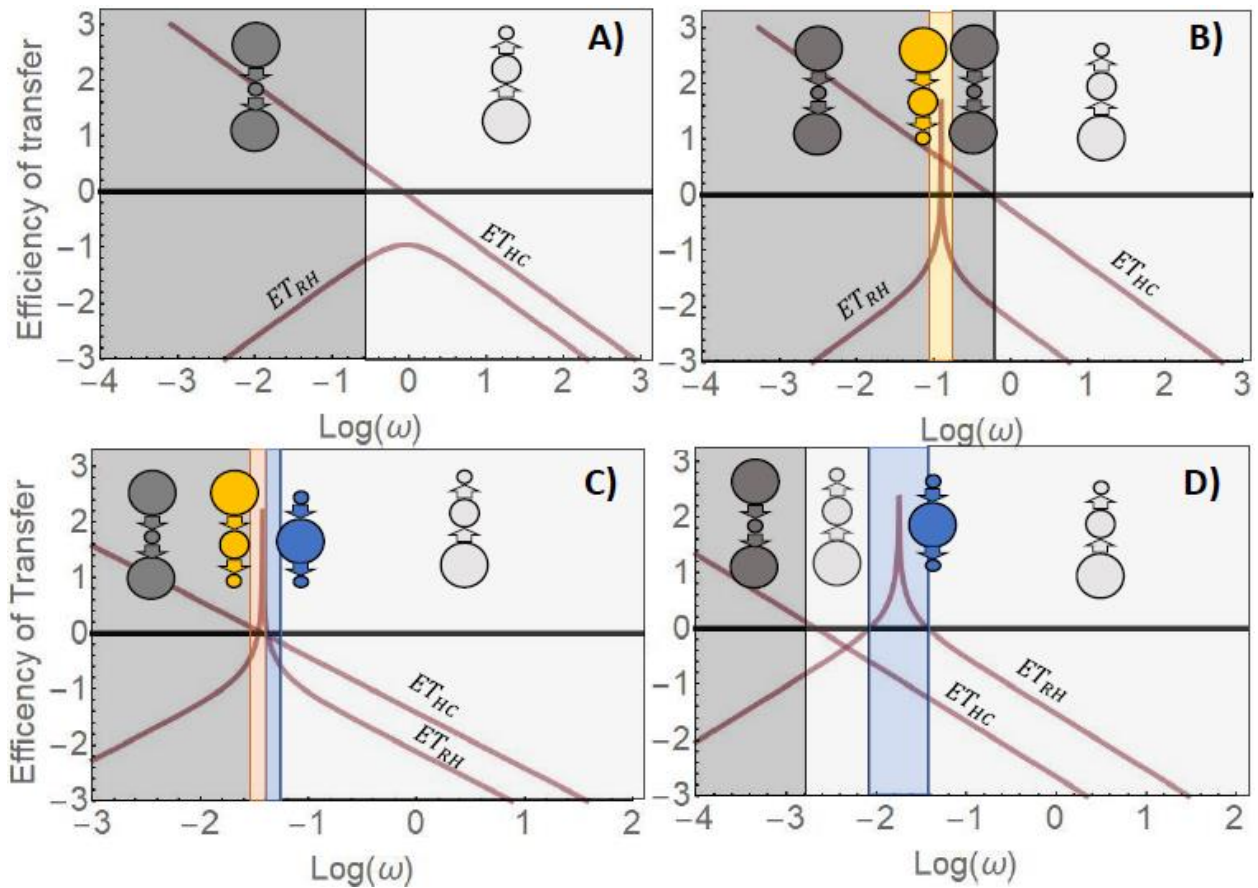
Figure 1 - 5. There are four different scenarios for the pattern of variability modes across the frequency gradient. The four scenarios can be differentiated using the efficiency of transfer ET_{RH}^{RHP} and ET_{HP}^{RHP}. The signs of the ETs determine the relative variability mode of the food chain. (+,+) (orange), (-,-) (light grey),(-,+) (dark grey), (+,-) (blue). The four scenarios their variability from low to high frequency are A) (-,+) to (-,-) B) (-, +), (+, +), (-, +), and finally (-, -), C) (-, +), (-, -), (-, +), and finally (+, +) D) (+, -), (+, +), (-, +), and finally (+, +). The changes in shading represent when the food chain shifts from one relative stability mode to another. The food chains represent the relative stability of the food webs such that a large diameter implies a larger amplitude. All food webs qualitatively acted the same at high frequencies and at low frequencies. In this food chain the producer is at the bottom of the food chain and the secondary consumer is at the top. The shading for (-, +), (+, +), (+, -). The parameter values for each regime are: A)

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d_H = 0.21, d_P = 0.001, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 0.2, r = 0.2, c_{HP} = 0.0068, b) d_H = 0.21, d_P = 0.001, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 0.2, r = 0.2, c_{HP} = 0.0267, C) d_H = 0.21, d_P = 0.01, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 0.2, r = 0.2, c_{HP} = 0.356, & D) d_H = 0.21, d_P = 0.1, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_{RH} = 0.2, r = 0.2, c_{HP} = 0.1

Communities will transition among these different modes across the frequency spectrum (Fig 1-5). Consistent with EEH, at low frequencies, all communities have an alternating pattern of variability (-,+). However, as the frequency increases, the secondary consumer becomes less variable than primary consumers (-,-). At high frequencies, the amplitude of fluctuations decreases with trophic position. All the communities respond similarly at high and low frequencies (Fig 1-5). We also find three other general scenarios in which the primary consumer amplifies resource pulses at intermediate frequencies (matching the empirical pattern seen by Yang et al. (2010). The amplification between the producer and primary consumer will only occur at intermediate frequencies. The order that the intercept of the ET_{HP}^{RHP} and the intercepts of ET_{RH}^{RHP} occur differentiates these three other scenarios (Fig 1- 5b, c, & d). We modeled the dynamics of scenario 2 in Fig 1-6, which reveals the changing mode of variability across time scales. Overall, amplification can occur at any trophic level, and communities will experience different variability modes across the frequency spectrum.
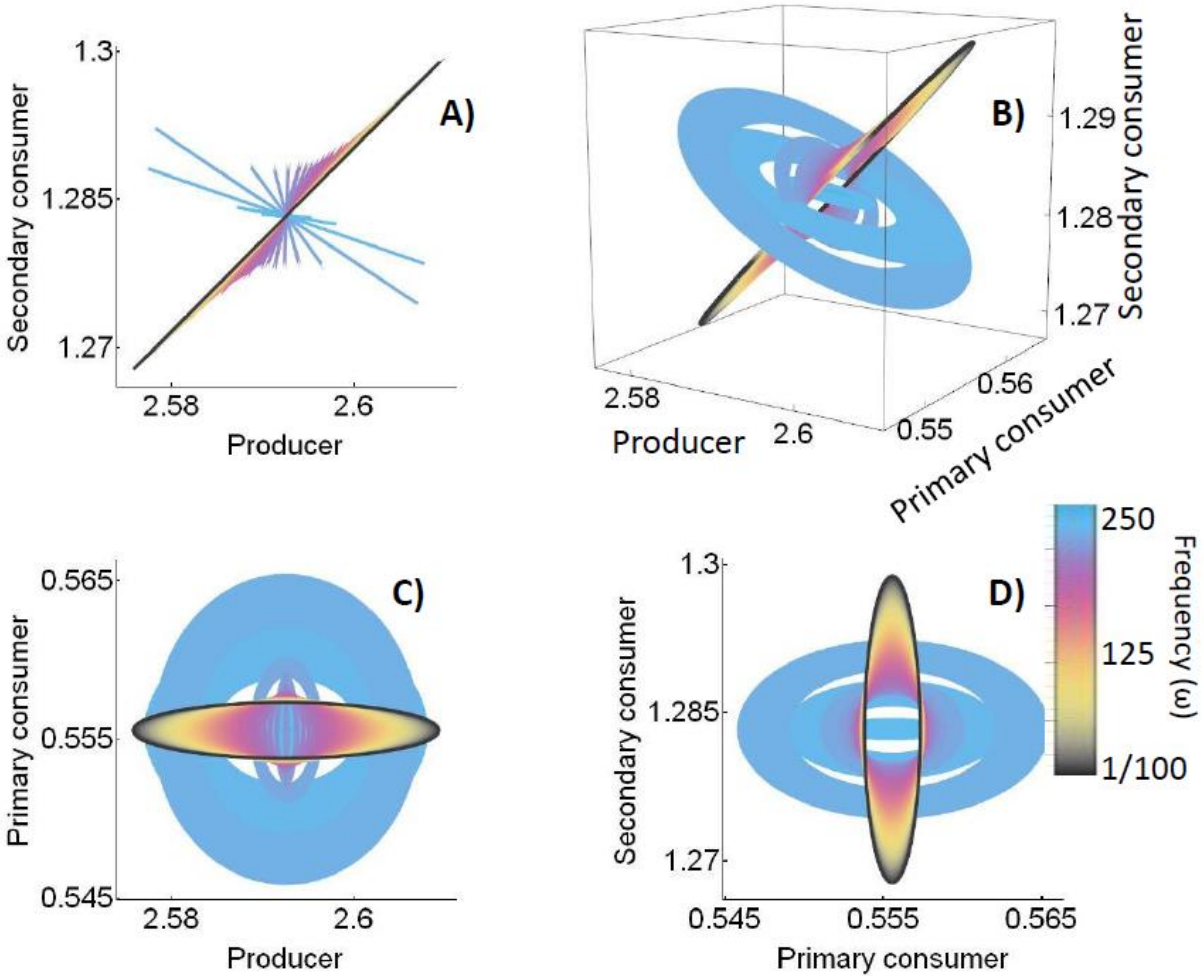
Figure 1 - 6. The dynamics of the tri-trophic food web across the frequency spectrum. A) phase-plane of the producer and secondary consumer B) phase-volume of the tri-trophic food chain C) phase-plane of producer and primary consumer D) phase-plane of the primary consumer and secondary consumer. The frequency is allowed to vary from 1 (black) to 1/350 (blue). The parameters used for the numerical simulations are $d_H = 0.21$, $d_P = 0.1$, $K = 10$, $r = 0.15$; $a_{RH} = 0.2$, $a_{HP} = 0.2$, $c_{RH} = 0.9$, $c_{HP} = 0.9$, $B = 1/10$. The numerical simulations were completed in Mathematica 11.3 using NDSolve and Runge-Kutta.

Variation cascades: Top-down effects on community variability

Primary consumer

The variation cascade is the impact of top-down effects on lower trophic levels' variability, across the frequency spectrum. The producer has its variability reduced by the primary consumer (Figure 1-7b), at low frequencies. At intermediate frequencies, the producer's biomass increases during periods of high PPP, which stimulates a delayed increase in the primary consumer. After PPP begins to fall, the consumer's biomass will continue to grow for a short time. Thus, the primary producer's biomass is influenced both by lower resources and elevated consumption during times of low PPP. However, when producer biomass is low the primary consumer's biomass will collapse, once again releasing the producer from herbivory. This recurrent dynamic causes resonance at these frequencies. Finally, at high frequencies, feedbacks between the producer and the primary consumer breakdown. Therefore, the top-down effect of primary consumers shifts from stabilizing to destabilizing before eventually breaking down at high frequencies.
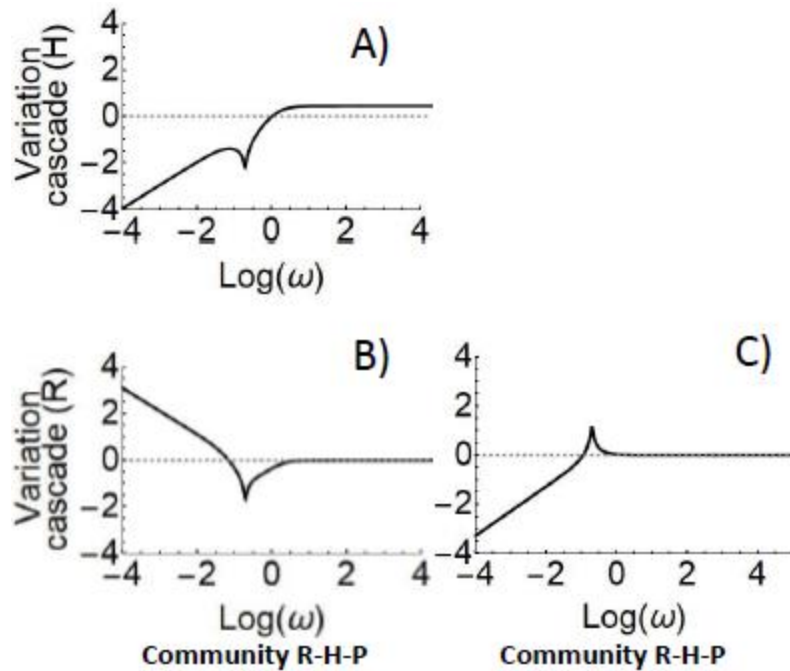
Figure 1 - 7. Plots of the variation cascades across the frequency spectrum. A) the effect of the secondary consumer on the primary producer's amplitude response VC_H^P B) the effect of the primary consumer on the producer's amplitude response VC_R^H C) the effect of the secondary consumer on the primary consumer's amplitude response VC_H^P. r = 0.2, d_H= 0.21, d_P = 0.1, a_{RH} = 0.1, a_{HP} = 0.1, K = 100, c_R = 1, c_H = 1

Secondary consumer

The secondary consumer has three significant effects on the producer's amplitude response: 1) they make producers sensitive to low frequency resource pulses, 2) they can stabilize the producer at intermediate frequencies, and 3) they change the resonant frequency. At low frequencies, analogous to trophic cascades, the secondary consumer makes the producers sensitive to changes in resource availability (Figure 1-7a). Here the secondary consumer also increases the producer's variability. At

intermediate frequencies, the primary and secondary consumers reduce producer variability by

absorbing the resource pulses into their biomass while exhibiting resource-consumer cycles of their own

Figure 1-6c. Secondary consumers also change the frequency at which resonance will occur. Finally, at

high frequencies, the secondary consumer does not affect the producer's amplitude. By moving beyond

a dichotomy, we find that the impact of consumers changes continuously across the frequency

spectrum. Furthermore, increasing frequency does not merely cause a breakdown of top-down effects

(Figure 1-7c). Instead, the consumers can greatly increase the producer's temporal variability is at

intermediate frequencies (Figure 1-7). Thus by considering the recurring nature of the perturbations, we

show consumers have strong indirect effects on lower trophic levels across a large swathe of the

frequency spectrum.

Modeling community responses to complex perturbations

Combining frequency response theory with Fourier series representation of perturbations yields a

flexible and powerful toolkit capable of modeling the response of communities to complex and realistic

disturbances. For example, episodic perturbations with long inter-pulse intervals are a standard model

of resource pulses and can be approximated by the summation of a small number of sinusoids (Figure 1-

8a & b; A1-27). In such cases, the community's response can also be represented as a series of sinusoids

that individually behave according to the patterns described above (see A1-28) but sum to determine

population dynamics (e.g., Figure 8c). Similarly, sums of sinusoids (Fourier series) can be used to model

$1/f$ noise and other complex disturbances (Cohen et al., 1999), allowing our framework to address both

deterministic and quasi-deterministic perturbations. Frequency response can be used to study the

impacts of nonadditive perturbations as well. For example, fluctuations in resource carrying capacity (K)

can be modeled explicitly by including an additional differential equation to represent the dynamics of K

or by using a chemostat model of resource availability (e.g., Clodong & Blasius, 2004). Introducing

variation in this manner can filter the amplitude response of resources and higher trophic levels in a

myriad of ways; this is an exciting avenue for future research. Overall, frequency response provides a

powerful tool for modeling a community's response to environmental disturbances.
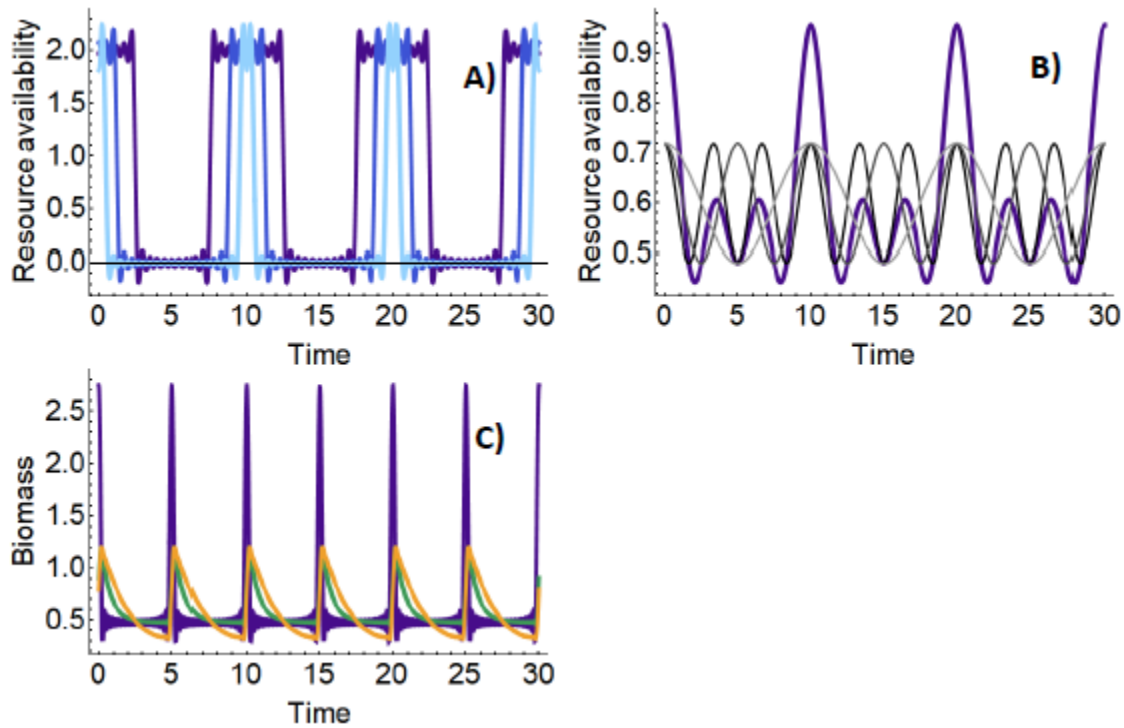
Figure 1-8. Time series of episodic resource pulses and a community's response to complex dynamics. A)

Time series of three rectangular waves using their first twenty harmonics. h = 2, L = 10, purple (δ = 5),

blue (δ = 2.5), and light blue (δ = 1). B) An approximation of a rectangular wave (using its first five

harmonics) and the first five terms of its Fourier series (Purple). The first five harmonics of the

rectangular wave. C) The response of a producer and herbivore recreated using Fourier series and

frequency response (h = 1, δ = 0.5, L = 2, d_H = 0.1, k = 10, c_H = 0.2, r = 0.5, a_{RH} = 0.1).

Discussion

Bottom-up and top-down control interact to determine how patterns of attenuation and amplification occur across trophic communities in response to resource pulses. Across the frequency spectrum, a community's response can be divided into three general categories. At low frequencies, a community tracks its equilibrium. At high frequencies, top-down effects break down and communities average across perturbations. At intermediate frequencies, variation cascades can both stabilize and destabilize the community. Despite the changing nature of top-down control across the frequency spectrum, the efficiency of transfer reveals a simple relationship between the frequency of resource pulses and the propagation of variability through food chains. For example, in a two trophic level food chain, the efficiency of transfer between a producer and consumer is always a linear function of frequency. By extending the Exploitative Ecosystem hypothesis (EEH), from an equilibrium-based theory, we have created a new testable theory of the impact of fluctuations in PPP and top-down effects on the temporal variability of food chains.

In general, a low frequency resource pulse will produce a cascading pattern of variability where the top trophic level is highly variable. In a two trophic level food chain, an increase in PPP will cause the primary consumer's abundance to increase without affecting the producer's biomass and hence, amplification of variability (Fig 1-3b & 4b). Secondary consumers make the producer more variable, as the secondary consumer can suppress the primary consumer releasing the producer to increase during times of high PPP. Our theory reveals that EEH well approximates a community's response to low frequency resource pulses.

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At the high end of the frequency spectrum, the community dynamics exhibit a bottom-up pattern as fluctuations are dampened up the food chain (Fig 1-5 & 6). The decreasing pattern is not caused by classical expectations such as energetic constraints (Lindeman, 1942), nonlinear thresholds (Noy-Meir, 1970), or stochastic averaging (Wooton, 1994). Instead, the bottom-up dampening pattern is due to the dynamical averaging at each successive trophic level; each trophic level introduces an additional layer of averaging when expressing the variation of its experiences in its resource. The vital rates of each member population are essential for determining the thresholds at which averaging occurs. At high frequencies, only events of extreme magnitude or those generating discontinuous effects on population growth will produce substantial ecosystem-wide effects at fast time scales. The bottom-up pattern of variability at high frequencies aligns with conceptual models of resource pulses by showing that top-down effects are limited at high frequencies.

At intermediate frequencies, the food chain experiences the broadest range of dynamics due to the interplay between top-down and bottom-up effects. For instance, when the intrinsic dynamics match the time scale of the fluctuations, resonance will amplify temporal variability at all trophic levels (Benincà et al., 2011; McKane & Newman, 2005; Orland & Lawler, 2004). We demonstrate that top-down effects can theoretically create the empirical pattern of amplification up food chains, seen in Yang et al., (2008). However, resonance may also be constrained to only particular trophic levels (Fig 1-6d). For example, large fluctuations emerge between the primary and secondary consumers (e.g., Fig 1-5d) while the producer's biomass remains static. Furthermore, how vital rates determine the pattern of the temporal variation is an area deserving of further research (e.g., using allometric scaling (Innes & Yodzis, 1992)). Despite the richness of dynamics at these intermediate frequencies, the efficiency of transfers provides a tractable method for studying the propagation of variation through communities.

Understanding how variability percolates through communities opens up many future directions for research. Benicia et al. (2011) found that phytoplankton populations' resonant frequencies match the

variation in their environments. Communities near resonance frequencies have been shown to be more

susceptible to invasion (Greenman & Norman, 2007; Greenman & Pasour, 2012) and it is possible that

fluctuations near resonant frequencies could support a longer food chain similar to autocorrelated noise

inflating population size (Bell & Gonzalez 2000). Furthermore, resource pulses are often localized in

space; understanding how spatial variation in the amplitude of resources pulses leads to aggregate

responses at the community level is an important area for future work. Organismal behavior also

represents an important mechanism whereby responses to fluctuations can be mediated at the

population level. These and other mechanisms can be embedded into our current framework for

studying the frequency response provided that they do not introduce discontinuities or temporal

dependencies into model equations or parameters.

Variation cascades clarify the role of top-down control across the frequency spectrum. For example, our

theory demonstrates that the variability in producer biomass in response to resource pulses can only be

understood in the context of the broader community (e.g., their primary and secondary consumers). We

demonstrate that secondary consumers may cause primary producers to be more susceptible to slow

changes in resource availability while also reducing the producer's response to faster variation. Re-

evaluating the strength of top-down effects in the light of time scale dependence of variation cascades

could explain the variability in the strength of top-down control seen in nature (e.g., Power, 1992).

Moreover, given that large carnivores are being lost from ecosystems at a much greater rate than other

groups, we may see dramatic shifts in the expression of biomass variability at other trophic levels as

extinctions occur.

Using a linear approximation to estimate the frequency response is a limitation of our approach,

especially since ecological systems are noted for their nonlinearities (May, 1970); however linear

approximations can be a good predictor of ecological dynamics (Ives, 1995). Linear approximations are

more accurate if perturbation sizes are sufficiently small, and/or when the equilibrium is sufficiently far

from a bifurcation point. If the system is in a highly non-linear region of space, or close to a bifurcation, then oscillations in PPP will have a different effect than predicted by this approach (e.g., Rinaldi et al., 1993). Promisingly, food chains experiencing resource pulses show an essential property of linear systems where the magnitude of a community's response is proportional to the magnitude of the resource pulse (Yang et al. 2010). We believe that linear methods provide a substantial first step forward in developing a theory that predicts how temporal variability percolates through communities.

In summary, we have developed a novel theory that predicts how indirect effects control the impact of perturbations across trophic levels and time scales. We find that variation cascades can cause amplification and attenuation of temporal variability in surprising ways in different parts of the frequency spectrum. Furthermore, by providing an analytical prediction for communities' responses to environmental forcing, we provide new rigor to our understanding of the mechanisms that generate community structure, dynamics, and function.

Acknowledgments

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Chapter 2. Time scale dictates the impact of species interactions – stability relationship

Abstract

Past studies have shown that weak species interactions stabilize communities by deflecting or absorbing variability. However, species interactions' impact on community stability is traditionally studied at equilibrium despite communities being embedded in fluctuating environments. Thus, we create a theory using frequency response theory to explore how species' interaction strengths impact community stability across time scales. We propose two complementary hypotheses for determining a community's stability across the frequency spectrum 1) weak species interactions will stabilize communities, and 2) that time scale mismatches between species prevent resonance. Using a tri-trophic food chain as a case study, we find that weak species interactions between herbivores and predators can dissipate the producer's variability. Furthermore, using the allometrically scaling of populations' vital rates, we predict that a food chain's resonance frequency lowers with larger predator and herbivore sizes. Finally, using empirical consumer-resources examples, we find communities can track variability at the time scale of months – years. Thus, we predict the time scales at which equilibrium dynamics operate in natural ecosystems. In summary, this theory presents an exciting step towards understanding how species interactions drive community dynamics across time scales.

Introduction

Environmental fluctuations are critical drivers of population and community dynamics. For example, El Nino causes recurring periods of high rainfall, temporarily supporting massive growth in plants, herbivores, and predators (Previtali et al., 2009). Yet, most ecological research has focused on the consequences of mean changes in the environment, even though climate change is predicted to make heat waves and droughts more severe (IPCC, 2014). A focus on equilibrium dynamics and mean changes in the environment leaves us ill-prepared to predicts climate changes impacts (Vasseur et al., 2014; Felton & Smith, 2017; Ghosh et al., 2020). Excitingly, frequency response theory provides a new opportunity to extend ecological theories of stability across time scales.

Frequency response theory characterizes a community's response to environmental variability across the frequency spectrum (Nesbit & Gurney, 1978). The frequency spectrum is the distribution of the amplitudes and phases of each frequency of an environmental forcing. Using Fourier series and transforms, a time-based representation can be transformed into a frequency-based representation of variability. In essence, slow oscillations are represented by low frequencies and fast oscillations as high frequencies. In general, communities will track low frequency perturbations and average across high frequencies (Fig 2-1). However, communities can exhibit a rich set of dynamics at intermediate frequencies, such as resonance (Simon & Vasseur, 2021). Resonance amplifies variability and is a putative mechanism for the ubiquity of population cycles seen in natural systems (Nesbit & Gurney, 1976). Tri-trophic food chains have two distinct patterns at intermediate frequencies: 1) all trophic levels amplify variability, and 2) producers become highly insensitive to variability (Fig 2-1 B). Simon & Vasseur (2021) found that these dynamics are not universal across all communities, and only specific parameterizations exhibit these intermediate dynamics (See Figure 2-1 A & B). However, the abstraction of previous theories obfuscates whether these intermediate dynamics are occurring in ecologically relevant parameter space or time scales.
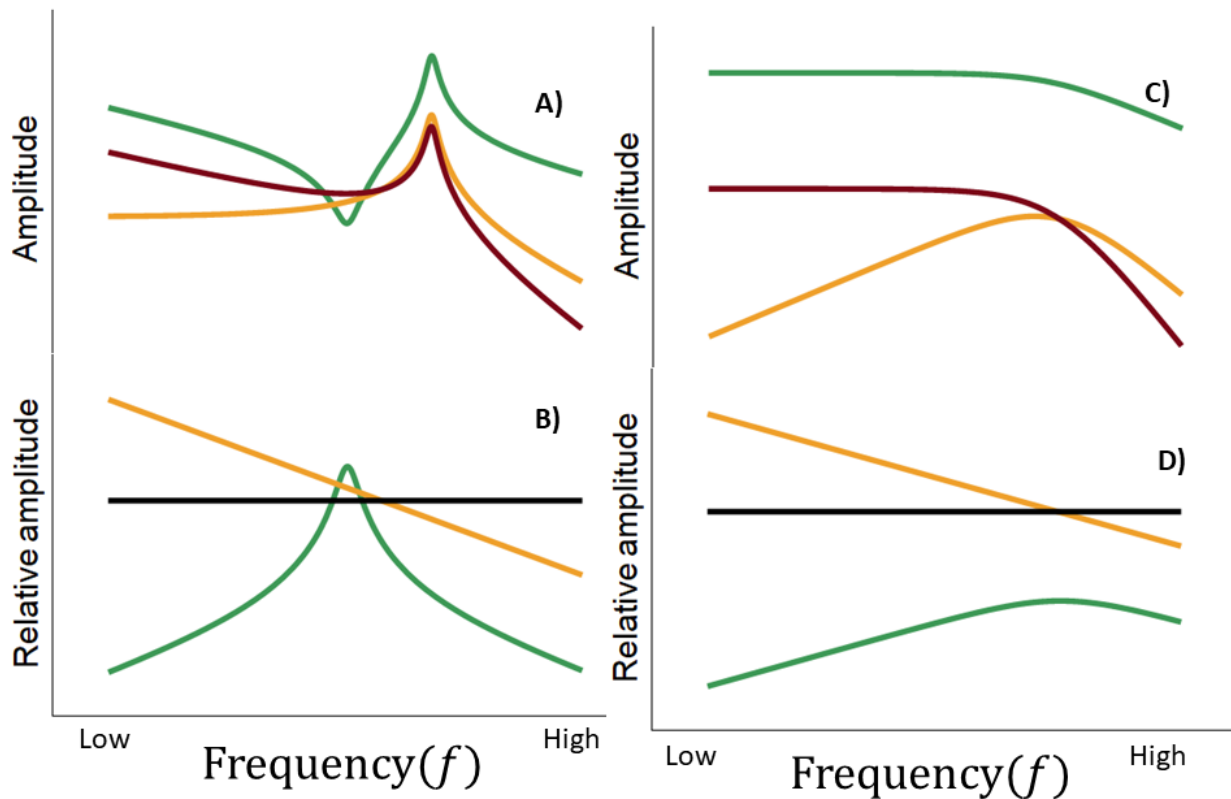
Figure 2-1. Generalized amplitude responses (A & C) and efficiency of variability transfers (C & D) of a tri-trophic community to fluctuations in the producers' productivity. Amplitude response measures the amplification or dampening of a trophic level to a disturbance (green = producer, yellow = herbivore, red = predator).. At the same time, the efficiency of variability transfers predicts the relative amplitude response between two adjacent trophic levels (green = producer-herbivore, yellow = herbivore-predator). When the efficiency of variability transfer is above (below), the black line represents the higher trophic level being more (less) responsive to variability. All communities track their equilibrium dynamics at low frequencies and average across high frequencies. Consequently, for a tri-trophic food chain, the community has a cascading top down pattern (Oksanen & Oksanen, 2000). In contrast, at high frequencies, each trophic level will sequentially dampen variation up the food chain. However, communities' intermediate time scales are not universal. Instead, only some communities will resonant A) or have their producers' variability be dampened at intermediate dynamics (A & B).

We propose two complementary hypotheses for determining a community's stability across the

frequency spectrum 1) weak species interactions will stabilize communities, and 2) that time scale

mismatches will prevent resonance. For example, we predict that the high stability of producers at

intermediate frequencies is caused by weak species interactions between the herbivores and predators, dissipating variability in producers. If time scale matching determines the stability of communities, then intermediate dynamics (e.g., resonance) will be seen at intermediate species interaction rates, turnover rates, and body sizes. We predict that communities with matching time scales and strong interaction effects will have the strongest resonance.

Using allometric scaling (Yodzis and Innes, 1992), we parameterize a linear food chain to study how populations filter variability. Allometry is the relationship between populations' vital rates scale and body size (i.e., large organisms have slower growth rates than smaller species). Allometric scaling constrains our analysis to biologically plausible parameter space. Additionally, a food chain's body size distribution determines species' interaction strengths (Emmerson & Raffaeli, 2004). Thus we can test whether a body size distribution that creates weak species interactions dampens variability and if large body size differences will limit resonance due to time scale mismatches. Thus allometric scaling provides a straightforward method to determine the time scales at which resonance-like phenomena could occur in nature and to test our two hypothesizes.

We have two goals in this manuscript 1) to identify the mechanisms that stabilize communities and 2) to find the time scales at which communities transition among tracking, resonating, and averaging over environmental oscillations. Thus, we derive a general theory for a linear food chain to explore how species interaction strengths determine the relative variability of each trophic level. Then using allometric scaling, we determine how communities' frequency response scales with body size, turnover time, and species interaction strength. We follow up with an exploratory analysis using the Consumer Resource Database (Brose, 2005) to find biologically plausible patterns of variability of food chains. In summary, we derive a general but biologically informed theory of how temporal variability moves through communities and the role of time scale in determining communities' responses.

Methods

Model description

We model a tri-trophic food chain using differential equations describing changes in biomass density

(kg/year),

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{(1-\delta_H)J_H RH}{R_0+R} + rCos(2\pi ft)$$
$$\frac{dH}{dt} = H(\frac{J_H RH}{R_0+R} - \frac{(1-\delta_P)PJ_P}{H_0+H} - T_H)$$
$$\frac{dP}{dt} = P(\frac{HJ_P}{H_0+H} - T_P)$$

Eq 1,

where R, H, and P are the biomass densities of the primary producers, herbivores, and predators,

respectively. We assume that consumption is described by a Holling Type II functional response with

half-saturation rates R_0 & H_0 and maximum consumption rates given by J_H and J_P. Biomass is removed

from the herbivore and predator populations at the per-capita rates T_H and T_P. In the absence of

herbivores, producers would grow logistically with an intrinsic rate of increase r and carrying capacity K.

The parameters δ_H, and δ_P denote the fraction of biomass consumed that is not assimilated by the

herbivores and predators, respectively. Table 2-1 summarizes all of the model parameters.

The endogenous stability of the unforced model has been well studied (e.g., Hastings & Powell, 1991)

and can produce a range of dynamics, including stable equilibria, limit cycles, and quasiperiodic chaos.

This community has three biologically relevant equilibria ξ = {R, R-H, R-H-P}. In this manuscript, we focus

only on R-H-P. We report the equilibrium solutions in Appendix S2-1. For this analysis, we focus on

stable parameter space defined by negative real eigenvalues and nonnegative densities. This

assumption keeps the community away from chaotic parameter space where our methods may not reliably reproduce the population dynamics.

Although perturbations, such as resource pulses, can directly affect any trophic level, we focus on those impacting the producer population. We generate fluctuations in producers' productivity by including the term $rCos(2\pi ft)$ in Eq 1. We assume a sinusoidal perturbation with frequency f in cycles/year and magnitude proportional to the producer's intrinsic rate of increase.

Amplitude response

Frequency response theory predicts that a population's response is sinusoidal when forced by a sinusoidal oscillation, with the same frequency as the external forcing. The amplitude response describes the relative amplitude of the population (i)'s fluctuations to the forcing's amplitude $A(f)_i$. The amplitude response can be derived following Simon & Vasseur (2021). For example, to find the producer's amplitude response, we first derive its transfer function from its state-space representation using the following transformation,

$$G(s)_R = \{1, 0, 0\}(sI - Jac)^{-1})\{r, 0, 0\}$$

Eq 2.

where I is the identity matrix, and Jac is the Jacobian matrix. The amplitude response is found by setting s = $i2\pi f$ and taking the magnitude of $G(i2\pi f)_i$.

$$A(f)_R = |G(i2\pi f)_R|$$

Eq 3.

A community's Jacobian is found by linearizing around its equilibrium. The Jacobian matrix is a matrix of

the species' per capita interaction strengths where $\frac{d_i}{dj} = z_{ij}$

$$Jac = \begin{matrix} z_{RR} & z_{RH} & z_{RP} \\ z_{HR} & z_{HH} & z_{HP} \\ z_{PR} & z_{PH} & z_{PP} \end{matrix}$$

Eq 4.

We provide the tri-trophic food chain's amplitude response regarding its interaction strengths in

Appendix S2-2.

Allometric scaling of population vital rates

Allometric scaling improves ecological theory's interpretability and biological realism following (Yodzis &

Innes,1992). We parameterize Eq. 1 by using the relationship between the vital rates (r, T, ($1-\delta_x$)) and

their body size and metabolic type. The vital rates scale exponentially within these groups with body size

to the -¼ power (Brown et al., 2004).

The intrinsic rate of increase r is defined as,

$$r = a_r M_r^{-1/4}$$

Eq 5.

The biomass lost due to metabolism of consumer x is,
$$T = a_T M_x^{-1/4}$$
Eq 6.

Consumer x's maximum rate of energy assimilation is,
$$(1 - \delta_x)J = a_J M_x^{-1/4}$$
Eq 7.

We differentiate between three general metabolic types: invertebrate ectotherms, vertebrate ectotherms, and vertebrate endotherms. These groups represent shared characteristics described by differences in the intercepts of their allometric scaling (Table 2-2.). The allometrically scaled differential equations are reported in Appendix S2-2.

To aid in translatability to natural systems, we choose not to nondimensionalize our model by biomass or time scale. Thus a frequency of 1/10 cycles/year is a decadal perturbation (North Atlantic Oscillation), one cycle/year is annual (seasonal), and a cycle of 12 cycles/year is closer to occurring monthly (lunar cycles).

Parameter	Description	Value	Units
R	Producer biomass	--	kg/area
H	Herbivore biomass	--	kg/area
P	Predator biomass	--	kg/area
f	Natural frequency	--	Cycles/year
J	the mass-specific ingestion rate	--	kg/(kg year)
T	The mass-specific respiration rate	--	kg/(kg year)
r	The intrinsic rate of increase	--	kg/(kg year)
K	Carrying capacity	1	kg/area
R_0, H_0	the half-saturation density of ingestion of herbivores and predators	free	kg/area

δ_H, δ_P	The fraction of ingested energy that is lost to feces or urine	0.55,0.15	--

Table 2-1. Parameter and variable definitions. Based on the model derived by Yodzis & Innes (1992).

Name	Phytoplankton	Invertebrate	Endotherm	Ectotherm
a_J	--	9.7	89.2	8.9
a_T	--	0.5	54.9	2.3
a_r	0.386	--	--	--

Table 2-2. The empirically derived intercepts of the allometric relationships for a_J & a_T and a_r from Yodzis and Innes (1992) in kg (kg year)$^{-1}$ kg$^{0.25}$.

Allometry of frequency response

Interaction strength and turnover rate
We derive the allometric scaling of per capita interaction strength from the Jacobian matrix, using Eq 4.

Turnover time is calculated as the equilibrium biomass divided by the flow rate into or out of a particular

biomass pool.

The allometry of frequency response
We completed a sensitivity analysis of a community's amplitude response to alterations in R_0, M_R, M_H,

and M_P.

Yodzis and Innes (1992) demonstrated that in a two-trophic level system, that the ratio of R_0/K

determined the strength of top-down control of consumers on resources (and other dynamical behavior

that resulted). Without loss of generality, we set K=1 and examine how changes in R_0 impact our findings

via sensitivity analysis. As R_0/K increases, consumers exert less control over their resources because

their consumption rate diminishes. Conversely, at low values of R_0/K, consumers exert strong top-down

pressure and can generate cyclical dynamics due to overconsumption of resources.

The efficiency of variability transfer

We use the efficiency of variability transfer to establish how variability is propagated up the food chain. The efficiency of variability transfer is defined as the relative amplitude response of a lower trophic (j) and a higher trophic level (k) and is defined mathematically as

$$EVT(f)_{jk} = \left(\frac{A(f)_k}{A(f)_j}\right)$$

Eq 8.

Variability is amplified if $EVT(f)_{jk} > 1$ and damped when $EVT(f)_{jk} < 1$. When the $EVT(f)_{jk}$ equals one, the amplitude is equal between trophic levels.

We parameterized a family of $EVT(f)_{jk}$'s using Brose et al. (2005)'s database of pairwise consumer-resource interactions. The consumer-resource database contains the body size, metabolic type, species interaction type, and ecosystem type of consumer-resource pairs (Brose et al., 2006). We created a family $EVT(f)_{jk}$'s using predator-prey interactions from the consumer-resource database to parameterize Eq 9. We performed a sensitivity analysis of the $EVT(f)_{RH}$ & $EVT(f)_{HP}$ to R_0 and producer body sizes. However, we report all 10 000 interactions in Appendix 2-7. Included in the figures in the main text are 100 terrestrial, 30 fresh water, and 48 marine consumer-resource pairs. We included only a subset of the 10 000 invertebrate-invertebrate predataor-prey interactions for clarity..

Results

Allometric scaling of equilibrium biomass, turnover rate, interaction strength

Food chains with small producers had high producer and predator biomasses (Figure 2-2).

Increased producer body size decreased the interaction strength between predators and

herbivores and the impact of herbivores on themselves (Figure 2-2).
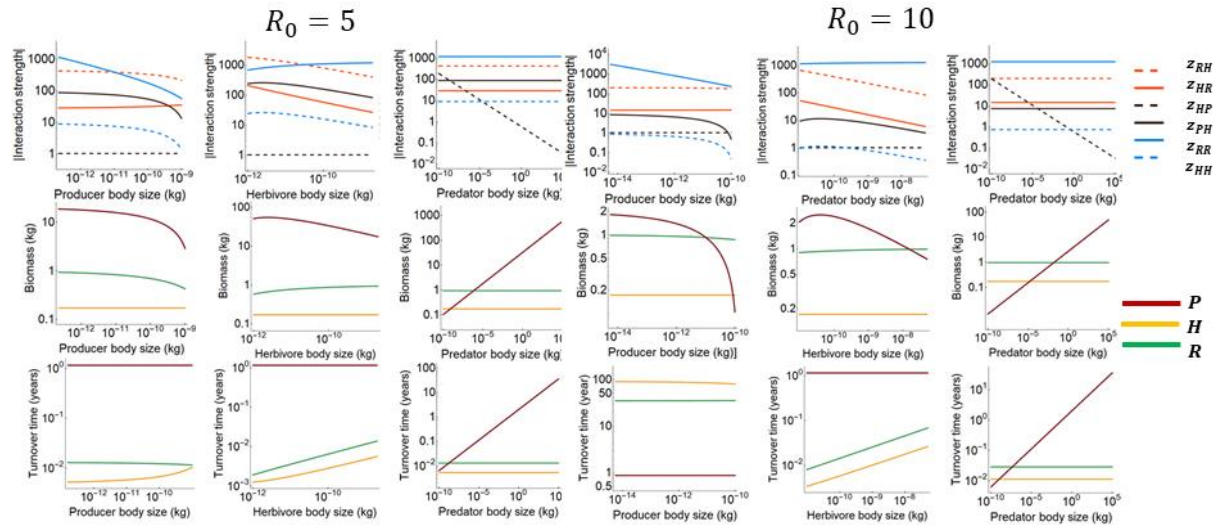
Figure 2-2. The sensitivity of species' interaction strength, equilibrium biomass, and turnover time to changes in R_0 and the body size of producers, herbivores, and predators.

Communities with large herbivores had lower predator biomass and higher producer biomass (Figure 2-

2). The turnover time of producers and herbivores increased with herbivore body size. Increasing

herbivore body sizes led to weaker interactions up the food chain (Figure 2-2).

Large predators had high population biomass and high turnover times (Figure 2-2). Increased predator

body size decreases the per capita interaction strength between predators and herbivores (Figure 2-2).

The turnover time of the predator also decreased with predator body size.

Allometry of amplitude responses

Small producers led to the community resonating, while larger producers had their variability dampened

at intermediate frequencies (Fig 2-3). The analytical solution of the producers as a function of

interaction strength is

$$A(f)_{\mathrm{HP}} = \frac{\sqrt{z_{PH}{}^2 z_{HP}{}^2 + z_{HH}{}^2 (2\pi f)^2 + z_{PH} z_{HP}(2\pi f)^2 + (2\pi f)^4}}{\sqrt{D}}$$

Eq 9.

The numerator drives the cross trophic level difference because the denominator (D) is shared across all

trophic levels (Full equations in Supplement S2 - 6). Furthermore, the numerator is the source of

dampening seen in the producer when it is less than one. We performed a sensitivity analysis of the

numerator to changes in z_{HH} and z_{HP} in Fig 2-5. We found that weak interactions between the herbivore

and predator could dissipate variability; however, high levels of dampening required the herbivore to

have a low impact on itself. We find that dampening emerges at larger producer body sizes only if z_{HH} is

weak, e.g. Figure 2-3 weak z_{HH} versus 2-4 strong z_{HH})

Figure 2-3. Sensitivity analysis of the (A,B,C) predators' amplitude response, (D,E,F) herbivores amplitude response, and (G, H, I)producers amplitude response to M_R, M_H, and M_P changes. Parameterized with R_0 = 5.
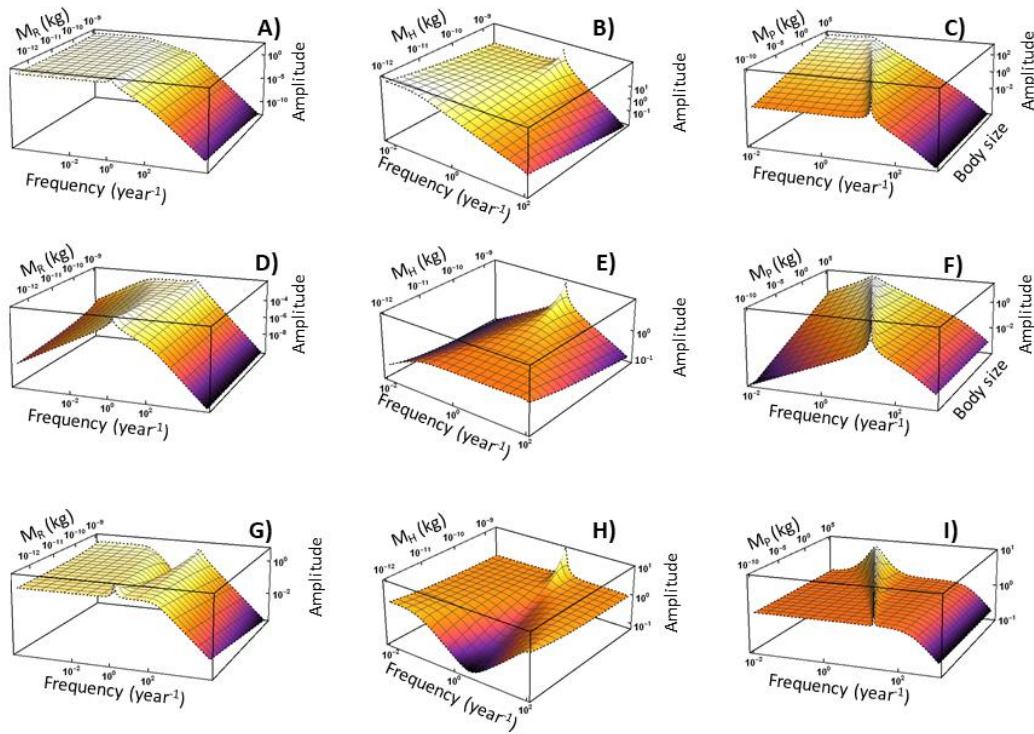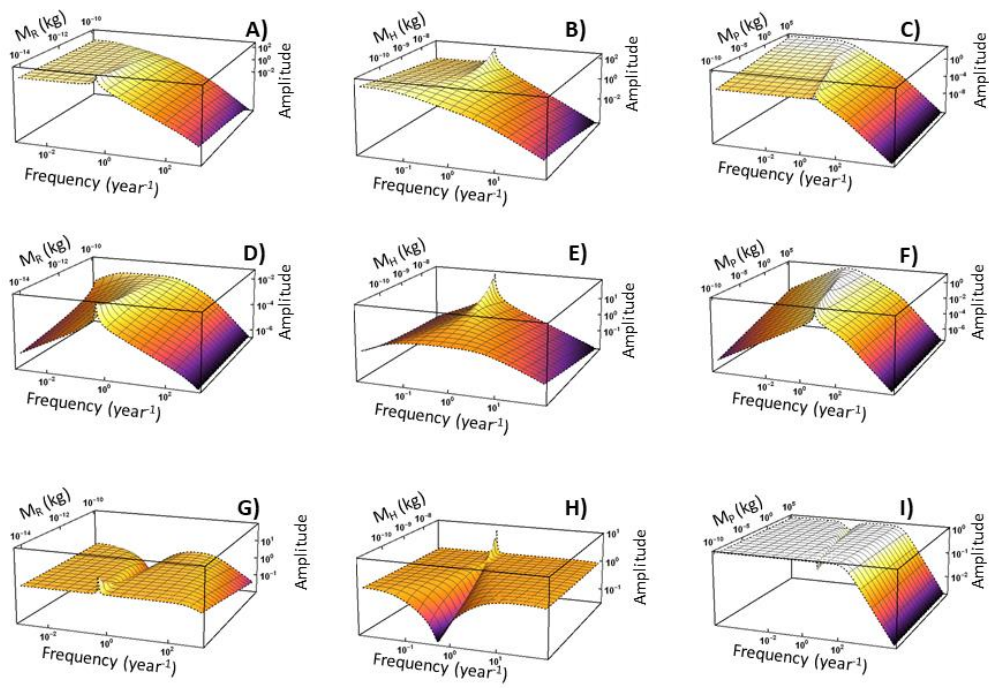
Figure 2-4. Sensitivity analysis of the (A,B,C) predators' amplitude response, (D,E,F) herbivores amplitude response, and (G, H, I)producers amplitude response to M_R, M_H, and M_P changes. Parameterized with $R_0 = 10$.
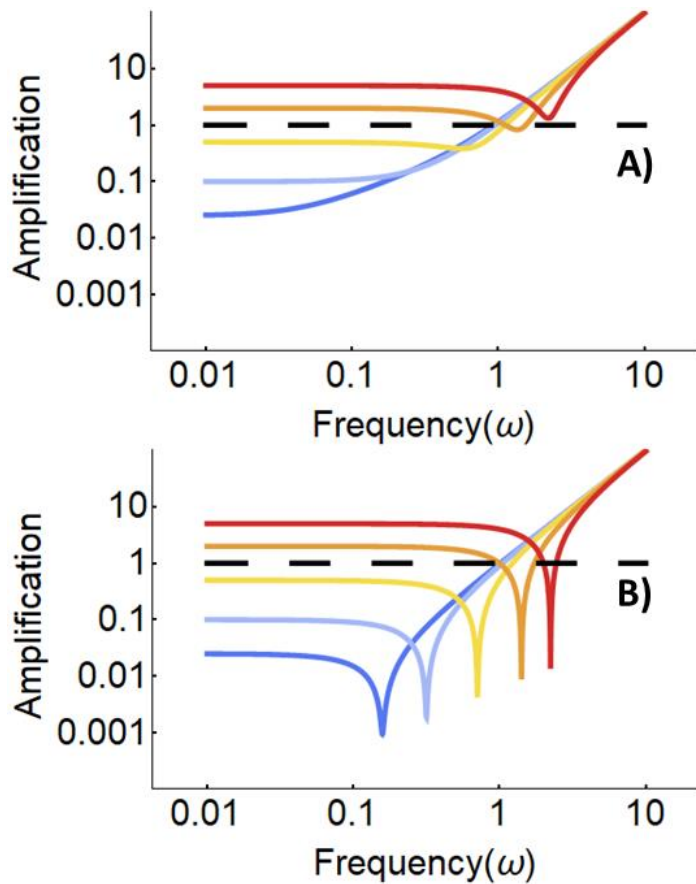
Figure 2-5 The sensitivity of producers dampening factors to z_{HH} and z_{PH} ($z_{PH}=0.5$ dark blue, $z_{PH}=2$ light blue, $z_{PH}=$ yellow, $z_{PH}=$ orange, & $z_{PH}=$ red). Weaker z_{PH} leads to greater dampening at low frequencies. However, for dampening at intermediate frequencies, z_{HH} must be small. We parameterized Eq 3 using $z_{PH} = -0.05$ and A) $z_{HH} = 0.6$ B) $z_{HH} = 0.006$

Smaller herbivores dampened producer variability (Fig 2-6), while larger herbivores amplified the

communities variability. Large herbivores had weaker z_{HH}, z_{HP}, and z_{PH}, however dampening outweighed

by amplification caused by weaker z_{RH} and z_{HR}. Thus, when all species interactions were weak, the

strength of resonance increased because the dampening factors are outweighed by the emergence of

resonance across all trophic levels.

Increasing predator body size either led to amplification (Fig 2-3) or dampening (Fig 2-4) at intermediate

frequencies. If R_0 was high, the herbivore's impact on itself is weak (Fig 2-2); dampening by the weak

interactions between the predator and herbivore overcomes amplification in the producer. However,

the herbivore and the predator still resonated across all predator body sizes (Fig 2-4). Thus, the

mechanisms that create amplification and dampening are conflicting forces combined to determine the

dynamics of communities.

Handling time sensitivity

The communities amplitude responses were sensitive to alterations in herbivore and predator half-

saturation rate (Fig 2-6). Herbivores with intermediate R_0 had the strongest resonance. Herbivores with

high R_0 had weak interactions and low z_{HH}, leading to dampening. Increasing H_0 led to a shift to

dampening in producers as z_{HH} is weakened (Fig 2-6).
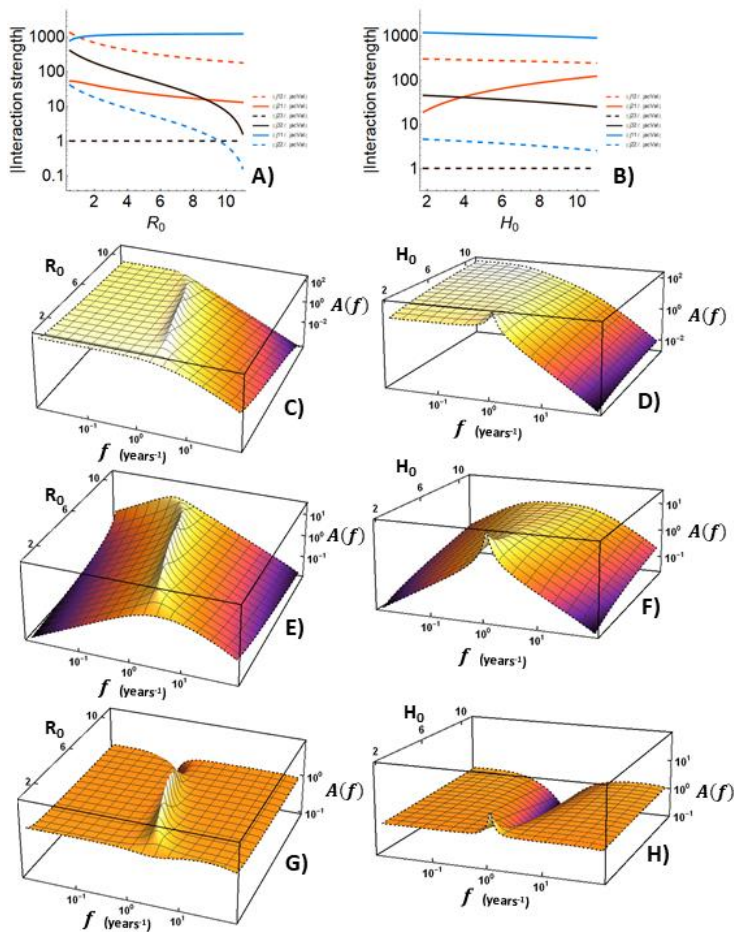
Figure 2-6. The sensitivity analysis of the community's amplitude responses to changes in R_0 and H_0.

The efficiency of variability transfer

The efficiency of variability transfer between herbivores and predators as a function of interaction

strengths is

$$EVT(f)_{HP} = z_{HP}2\pi f$$

Eq 10.

Thus the stronger z_{HP}, the higher the relative variability of the predator.

The EVT_{RH} is

$$EVT(f)_{HP} = \frac{\sqrt{z_{HR}^2(2\pi f)^2}}{\sqrt{z_{PH}^2 z_{HP}^2 + z_{HH}^2(2\pi f)^2 + 2z_{PH}z_{HP}(2\pi f)^2 + (2\pi f)^4}}$$

Eq 11.

The leading term of the denominator is positive; thus, the denominator is largest at high and low

frequencies. Therefore, variability is always dampened up the food chain at low and high frequencies.

We have already modeled the denominator in Figure 2-5, as it is the numerator of the producer's

amplitude response and dampening in the producer. Thus dampening in the producers leads to

amplification up the food chain, i.e., when z_{HH}, z_{HP}, and z_{PH} are weak.

Allometry of EVT

The relative variability of trophic levels is changing at ecologically relevant time scales. Amplification

between producers and herbivores occurs at intermediate producer body sizes (Fig 2-7). Interestingly,

we find that the EVT_{RH} (Fig 2-7) and EVT_{HP} (Fig 2-8) appeared to be differentiated by ecosystem type. The

frequency of the peak sensitivity of herbivores is lowest in marine and highest in freshwater ecosystems. Predators could transition from being more variable than herbivores at time scales of weeks up to several decades (Fig 2-8). In the consumer resource data, marine predators are larger; thus, the predator-herbivore transition is at a lower frequency in marine ecosystems than in terrestrial or freshwater ecosystems. Marine herbivores were more likely to amplify variability and became less sensitive at high R_0.
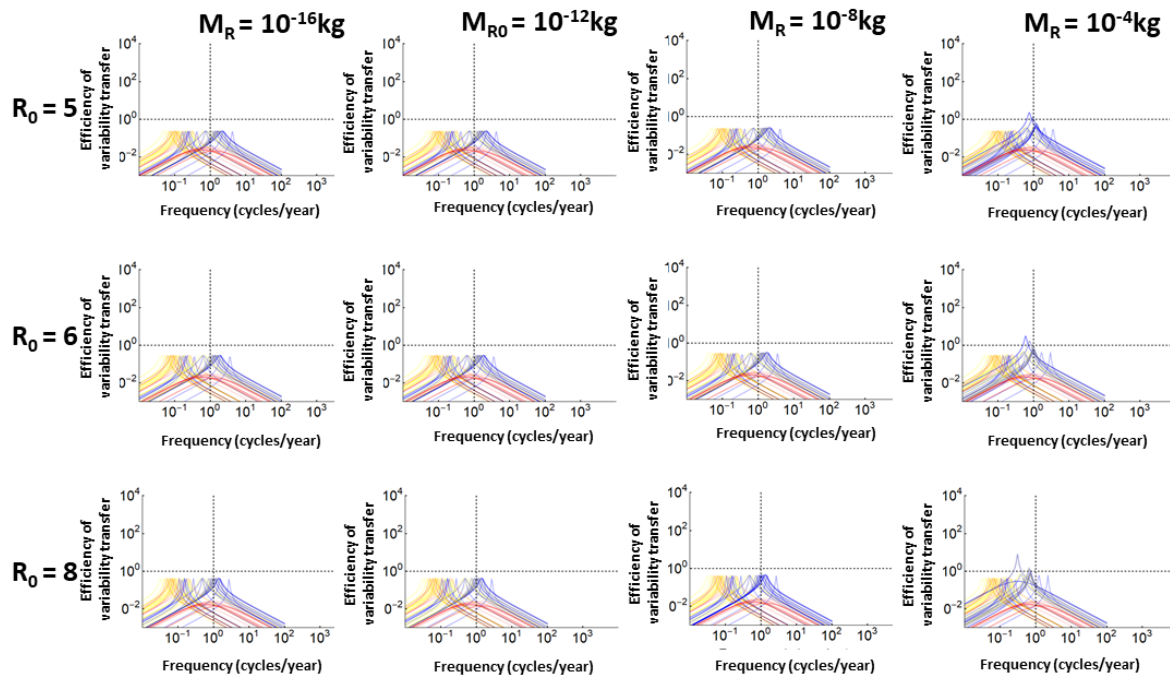
Figure 2-7 The efficiency of variability transfer between the herbivore and producer in marine (yellow), terrestrial (red), and freshwater (blue). Variability is transferred more efficiently to marine and freshwater herbivores than terrestrial herbivores. Larger producers in marine ecosystems led to the greatest amplification up the food chain.
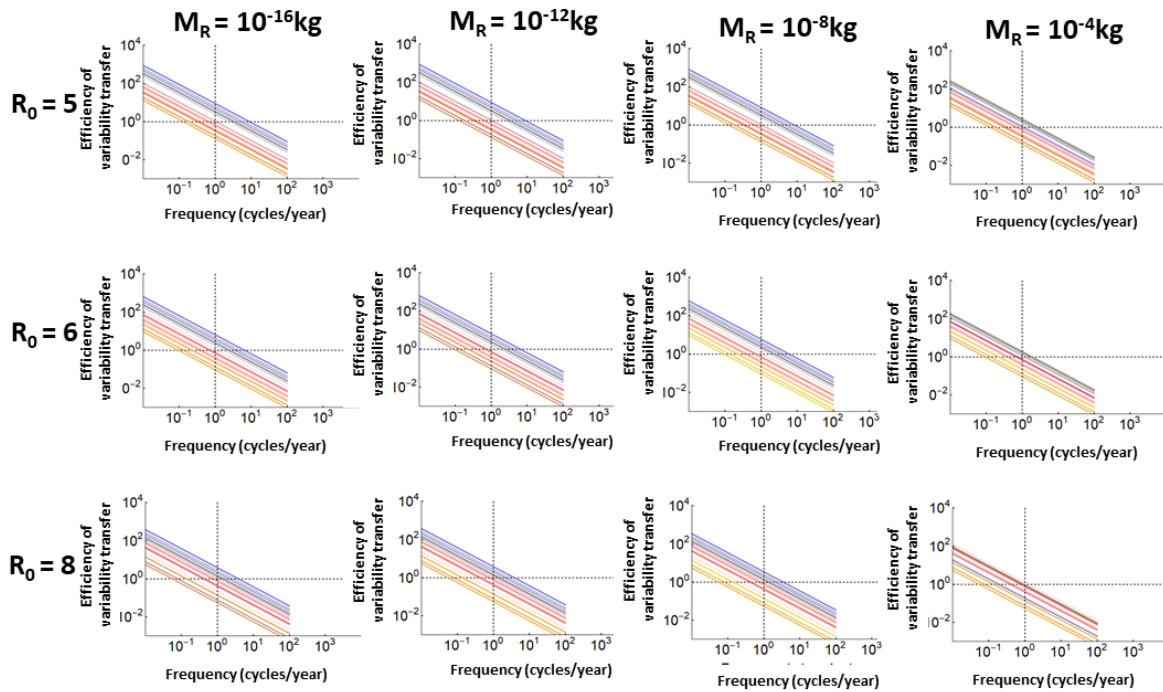
Figure 2-8 The efficiency of variability transfer between the predator and herbivore in marine (yellow), terrestrial (red), and freshwater (blue). Freshwater predators consistently appeared to amplify variability at higher frequencies than the other ecosystems. Variability was amplified up the food chain at the time scales of months to decades. Larger producers caused amplification up the food chain to occurs at lower frequencies.

Discussion

In agreement with Menge & Sutherland (1976), we predict indirect effects are not relegated to arbitrarily long times scales; instead are shaping communities' responses at time scales of weeks to years. Larger predators and herbivores lower a community's resonance frequency—providing theoretical support for Calder (1994)'s hypothesis that the period of population cycles of herbivore-predator cycles lengthens with herbivore body size. Time scale matching may lead to resonance; however, it did not appear ubiquitous. However, weak interactions between herbivores and predators do dissipate variability in the producer. In summary, we have created a novel theory that predicts communities variability across time scales as a function of species interaction strengths and body size.

By defining a community's amplitude responses and efficiency of variability transfers as functions of species interaction and body size, we have created an opportunity to compare across ecosystems. For example, we predict that weak interactions between predators and herbivores dampen variability in the producer. However, weak species interactions between predators and herbivores can also create resonance, increasing the community's variability. The beneficial impact of weak species interactions depends on the distribution of species interaction strength as dampening in producers requires the herbivores have a weak effect on themselves. We find some evidence time scale matching as intermediate saturation rates created the strongest resonance. However, intermediate body sizes did not lead to resonance. However, the feasibility of equilibria constrained the observable body size ratios; therefore, body size mismatches may not be significant enough to cause the breakdown of resonance. Overall, the strength of species interactions and their distribution governs the dynamics of communities across time scales.

Steele (1985) suggested that terrestrial and marine ecologists studied different ecological processes because marine systems' population dynamics are more autocorrelated than terrestrial dynamics. For example, when time scale mismatches are significant, a dichotomous model of tracking versus averaging is a sufficient description of community dynamics (e.g., Sala & Schwinning, 2004). However, in some ecosystems, disturbances at intermediate time scales create novel dynamics. (Table 2-3. Hastings 1998; Simon & Vasseur 2020). Our theory predicts that variability can be amplified from producers to herbivores, unlike equilibrium theories of top-down control (Powers, 1992) when predators and herbivores have weak species interactions. Thus we predict that top-down forces can operate at the time scales required for resource pulses to be amplified up food chains (Yang et al., 2008). We predict that large predator sizes should lead to more amplification up food chains. Our sensitivity analysis suggests that marine herbivores will be more likely to amplify variability in food chains. Food chains

differ in their variability across the frequency spectrum; however, we propose a theory of how species interactions and body size drive community differences.

We assumed homogenous and distinct trophic levels with no spatial structure; however, future studies can study more complex communities subject to multiple stressors. Food webs are composed of strongly interacting motifs connected by weak interactions (McCann et al., 1998). For example, many species feed across multiple trophic levels, e.g., omnivores and intraguild predators. Omnivory is traditionally found as destabilizing (Tanabe, & Namba, 2005); however, omnivores provide a tractable example of the incorporation of variability through multiple paths. Potentially, like ripples in water, variation in food chains could interfere with itself constructively and destructively. At the same time, connections between food chains (e.g., between terrestrial and marine ecosystems) present an opportunity to determine how motifs resonant and damping frequencies will interact with each other. We believe that time scale research is at an exciting threshold that could rapidly advance our understanding of ecological systems.

We have derived a new synthetic theory of population dynamics across time scales. Our approach formalizes conceptual theories, such as pulse-reserve theory (Noy-Meir, 1970). By studying variability across time scales, we have grounded ecological theories derived at equilibrium from being abstractions, occurring at arbitrarily long time scales, to ecologically relevant theories by predicting the time scales at which communities will track their equilibria. We also predict novel ecological dynamics occurring at time scales of interest for ecologists. Thus, we have created new testable hypotheses for communities' variability across time scales. Furthermore, the mathematical machinery of frequency response theory provides a generalizable approach to study dynamics across time scales (Ripa et al., 1998). In summary, this theory offers predictions at the time scales at which ecologists investigate population dynamics, hopefully creating a foundation for predicting the impact of heatwaves and droughts created by climate change.

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In Table S2-1., we summarize the qualitative patterns of variability across the frequency spectrum.

	Continuum	Slow	Intermediate	High
General	- The relative variability of trophic levels changes continuously with frequency	- Track equilibrium	- Possibility of resonance and dampening	- Dynamical averaging
Three trophic levels	- The relative variability of predators and herbivores is a linearly decreasing function of frequency. - The relative variability of producers and herbivores is a quadratic concave up function of frequency	- Predators and producers are the most variable trophic levels	- Possible resonance in any trophic level - Possible dampening in the producer	- Dynamical averaging
Two trophic levels	- Relative variability of herbivores and producers is a linearly decreasing function of frequency	- Herbivores more variable than producers	- Possible resonance in both the producer and herbivore	- Dynamical averaging
One trophic level	- The producer tracks environmental disturbances and then averages across disturbances at high frequencies	- Producers track environmental differences	- No resonance or dampening	- Dynamical averaging

Table S2-2. The general pattern of food chains across the frequency spectrum. We break the continuum into three rough timescales based on a community's response, which discusses when equilibrium theories apply (Slow), disturbances interact with the natural frequencies of the system to producer resonance and dampening (intermediate), the populations average across perturbations (fast). The slow, intermediate, and fast time scales are course but provide a way of framing our view of ecological disturbances on ecosystems.

Appendix 2

for the dynamics of a tri-trophic food chain.

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{(1-\delta_H)J_H RH}{R_0 + R} + rCos(2\pi ft)$$

$$\frac{dH}{dt} = H\left(\frac{(1-\delta_R)J_H RH}{R_0 + R} - \frac{(1-\delta_P)PJ_P}{H_0 + H} - T_H\right)$$

$$\frac{dP}{dt} = P\left(\frac{HJ_P}{H_0 + H} - T_P\right)$$

S2-1

We report the equilibrium solutions for S2-1 in the Table below:

Equilibrium	
Producer only	$R^* = K$
Producer-Herbivore	$$R^* = -\frac{R_0 T_H}{(-J_H + T_H + J_H \delta_H)}$$ $$H^* = \frac{rR_0(\delta_H - 1)(-J_H K + KT_H + R_0 T_H + J_H K \delta_H)}{K(-J_H + T_H + J_H \delta_H)^2}$$
Producer-Herbivore-Predator community	$$R^* = 1/2\frac{(K - R_0 \pm \sqrt{4H_0 J_H T_P K + r(K + R_0)^2(T_P + J_P(-1 + \delta_P))})}{\sqrt{r}\sqrt{(-J_P + T_P + J_P \delta_P)}}$$ $$H^* = -\frac{H_0 T_P}{(T_P + J_P(-1 + \delta_P))}$$ P^* $$= \frac{1}{2KT_P(T_P + J_P(-1 + \delta_P))}(-2H_0 KT_P(T_H + J_H(-1 + \delta_H))$$ $$+ \sqrt{r}R_0(-1$$ $$\pm \delta_H)\sqrt{4H_0 J_H KT_P + r(K + R_0)^2(T_P + J_P(-1 + \delta_P))}\sqrt{T_P + J_P(-1 + \delta_P)}$$ $$+ rR_0(K + R_0)(-1 + \delta)(T_P + J_P(-1 + \delta_P)))(-1 + \delta_P)$$

Table S2-2. The equilibrium values of the tri-trophic food web and its sub-nested communities.

The jacobian of S2-1 is defined as:

$$Jacobian = \begin{array}{ccc} \frac{\partial R}{\partial R} & \frac{\partial R}{\partial H} & \frac{\partial R}{\partial P} \\ \frac{\partial H}{\partial R} & \frac{\partial H}{\partial H} & \frac{\partial H}{\partial P} \\ \frac{\partial P}{\partial R} & \frac{\partial P}{\partial H} & \frac{\partial P}{\partial P} \end{array} = \begin{array}{ccc} z_{RR} & z_{RH} & z_{RP} \\ z_{HR} & z_{HH} & z_{HP} \\ z_{PR} & z_{PH} & z_{PP} \end{array}$$

S2-2

Using the Jacobian, we derive a general theory for a tri-trophic food chain three species interacting in a theory where the producer is directly experiencing the disturbance, and species H & P are indirectly experiencing the resource pulse.

$$A(f)_R^{RHP} = r \sqrt{\frac{z_{HP}{}^2 z_{PH}{}^2 + z_{HH}{}^2 \omega^2 + 2 z_{HP} z_{PH} \omega^2 + \omega^4}{D}}$$

S2-3

$$A(f)_H^{RHP} = r \sqrt{\frac{z_{HR}{}^2 \omega^2}{D}}$$

S2-4

$$A(f)_P^{RHP} = r \sqrt{\frac{z_{HR}{}^2 z_{PH}{}^2}{D}}$$

S2-5

Where,

$$D = -2 z_{RR} z_{RH} z_{HR} z_{HH} \omega^2 + z_{RR}{}^2 (z_{HP}{}^2 z_{PH}{}^2 + z_{HH}{}^2 \omega^2 + 2 z_{HP} z_{PH} \omega^2 + \omega^4) + \omega^2 (z_{RH}{}^2 z_{HR}{}^2$$
$$+ z_{HP}{}^2 z_{PH}{}^2 + z_{HH}{}^2 \omega^2 + 2 z_{HP} z_{PH} \omega^2 + \omega^4 + 2 z_{RH} z_{HR} (z_{HP} z_{PH} + \omega^2))$$

S2-6

For the analysis in the manuscript, we parameterize S2-3, S2-4, S2-5 with a linearized form of S2-1.

Abstract

Climate change is decreasing water supplies globally while water demand is rising, making water access, distribution, and management essential for equity and efficiency. In response, water management has shifted towards practices that improve water efficiency. However, links between geographically separated socio-ecological systems, known as telecouplings, obscures the evaluation of water policy's potential outcomes. This study focuses on a connection between terrestrial water use and marine fisheries. First, we analyze multidecadal time series from southern Spain to find a relationship between the Guadalquivir river estuary's hydrology and the European anchovy (*Engraulis encrasicolus*) 's recruitment to the Gulf of Cadiz. Then using hydro-economic modeling, we explore the outcomes of different water policies on the telecoupled socio-ecological systems. We find that current best practices lead to increased water use by rising water efficiency incentivizing agricultural expansion. Thus, if water management continues under a business as usual model, water basins are likely to continue to allocate water for terrestrial use, and water savings are unlikely to be passed on to the marine realm

Introduction

The management of the earth's fresh water is one of the most significant challenges facing humanity. Climate change alone is expected to decrease freshwater availability globally by 20 – 40% (IPCC, 2014). Water is needed within a water basin for multiple exclusive demands (e.g., water for agricultural versus residential use (Babel et al., 2005)). Telecouplings, causal links between geographically separated socio-ecological processes (Liu et al., 2003, 2013, & 2016), can complicate the evaluation of the trade-offs among ecosystem services. For example, hydroelectric installations can alter a river's hydrology leading to reduced fishery yields hundreds of kilometers downriver (Sabo et al. 2017). Rivers are likely the source of many telecouplings due to their rivers' ribbon-like form leading them to transect multiple socio-ecological systems. However, river termini can be estuaries that marine species frequently use as

nurseries (Ray, 2005). We wish to address if agriculturally-driven hydrological changes and migration into estuaries can telecouple terrestrial agriculture and marine fisheries.

A river's hydrology directly impacts riverine species but a river's influence could be exported by migrating marine species (Drake et al., 2002; Fernández-Delgado et al., 2007). Hydrology can alter a river's salinity (Ruiz et al., 2006), temperature (Preece & Jones, 2002), nutrient loads (Maavara et al., 2020), connectivity (Barbarossa et al., 2020), and atmospheric gas exchange (Galy-Lacaux et al., 1997). Riverine species are hypothesized to perform better when hydrology matches the river's unregulated historical discharge (Marmulla, G., 2001). Dam removals can benefit river biodiversity; however, hydrological regimes may also be designed to mitigate the impact of regulation or potentially improve fisheries' productivity (Sabo et al., 2017). Water policy already tries to balance numerous ecosystem services (Apitz et al., 2006). Despite estuary reliance by many species (Ray, 2005), there is limited knowledge of the linkage between estuary hydrology and marine species' recruitment (an exception Lenanton & Potter., 1987), likely due to the challenges of studying species across life-stages and ecosystems. Discovering the environmental drivers of recruitment could play a crucial for protecting existing fisheries and the recovery of already collapsed stocks (Hodgson et al., 2020).

If terrestrial water use and marine species are connected, we think it becomes crucial to reflect on how water policy, technology, and practices shape water use. For example, water basins are viewed as the fundamental unit of water management (White, 1957; Teclaff, 1967; Newson, 1997); thus, even if marine fisheries benefit from the water, they are omitted when deciding water policy. Thus marine fisheries of estuary-reliant species could be placed at greater risk of expanding water use. Yet, practices such as deficit irrigation that improve irrigation water efficiency could passively benefit marine species by creating water savings (English, 1990) without restructuring water policy. Deficit irrigation is based on

the observation that irrigation has diminishing return rates for crop yields, and rising irrigation rates incur rising costs (English, 1990). Thus, maximum agriculture net returns occur at intermediate irrigation rates resulting in water savings. Yet, if more land is available for irrigation, potential water savings can be used to irrigate more land (Berbel, 2015) instead of being passed onto the estuary. Thus, we wish to explore how water policies can prevent runaway water use and the implications of water policy for coastal communities.

In this manuscript, we develop a case study in southern Spain of the telecoupling of terrestrial water use to marine fisheries and then create a water allocation theory for such telecoupled SESs. Using multidecadal time series, we explore the impact of agriculture's industrialization (Berbel, 2012 & 2015) on the Guadalquivir river estuary. The estuary is an essential habitat in the life cycle of European anchovies (*Engraulis encrasicolus)*and their main prey the mysid and around another 30 marine fish species, (Drake et al., 2007; Ruiz et al., 2009; González-Ortegón et al., 2012;González-Ortegón et al.. 2015). We explore how the estuary's hydrology controls the estuarine community and the recruitment of European anchovy to the Gulf of Cadiz*.* We then present a model of telecoupled marine-terrestrial socio-ecological systems (SESs) and explore the outcome of different institutional norms for the telecoupled SESs. We aim to address two main issues 1) whether the recruitment of a marine species from estuaries can telecouple terrestrial water use with marine fisheries and 2) the implications of water policy for telecoupled marine and terrestrial SESs.

Methods
Case study description

Starting in 1931, a series of reservoirs were built along the Guadalquivir river. The total area irrigated has dramatically expanded to over 850 000 ha (Berbel et al., 2015, Fig 3-1a). Water demand has risen due to the expansion of agriculture (Berbel, 2015). When full, the reservoirs can store over 8000 hm^3,

sufficient to irrigate crops for a full year of drought (Berbel et al., 2012). Terrestrial demand now exceeds the average supply of renewable water through the hydrological cycle (Berbel et al., 2015)

In the Gulf of Cadiz, European anchovies spawn from April to September in the coastal fringe between the mouths of the Guadiana and the Guadalquivir Rivers over the 50 m to 100 m isobaths, where eggs are found in large concentrations and adults are mainly fished (Rodríguez-Roda, 1977; Millan, 1999; Baldó et al., 2006). Early larvae, which feed on phytoplankton and zooplankton, are primarily found close to the Guadalquivir River mouth (Baldó et al., 2006; Ruiz et al., 2006). During the summer and fall, juvenile anchovies are found mainly in the Guadalquivir estuary (Drake et al., 2007), where mysids are the main contributors to their diet (Baldó & Drake, 2002). The estuary's warm temperatures and higher food availability promote faster larvae growth than in open waters. In the fall, juveniles migrate offshore, where the anchovy fishery is highly dependent on these age-zero recruits, making the fishery vulnerable to year-to-year fluctuations in recruitment. Across Europe, many anchovy fisheries have been closed due to dwindling stocks (Taboada & Anadón, 2016). Discovering the causes of anchovy stock collapses is crucial for protecting the few existing fisheries and the future recovery of the already collapsed stocks.

The estuarine community has been surveyed in a monthly suprabenthos-nekton survey in the Guadalquivir estuary since 1997.

Anchovy recruitment and adult biomass indices in the Gulf of Cadiz were obtained from the ICES stock assessment (2017).

Hydrological and meteorological data

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Freshwater discharges from the Alcalá del Río dam were obtained from the Regional River Authority

(Confederación Hidrográfica del Guadalquivir) database located at

https://www.chguadalquivir.es/saih/DatosHistoricos.aspx. Meteorological data for Huelva, Spain, were

obtained from *https://www.ncei.noaa.gov/*.

Data transformation

The environmental variables (discharge and precipitation) and the biotic variables (adult anchovy

biomass, juvenile anchovy biomass, and mysid biomass). The monthly discharge, precipitation, juvenile

anchovy, and mysid biomass data were all decomposed using classical seasonal decomposition by

moving averages into three components: a smoothed long-term trend, an average seasonality, and sub-

annual (short-term) deviations (base R package stats 3.5.1).

Hydrology

We relied on the high natural interannual variation in discharge to evaluate hydrology's impact on

anchovy recruitment.

We quantified the coupling of precipitation and discharge by decomposing them using the Morlet

function and then calculating their annual coherence in *R wavecomp* package.

We quantified discharge's historicity using the coherence of the average seasonality during a time of low

regulation (1931-1951) and the detrended discharge from (1991-2019). Historicity is low if modern

discharge had a low magnitude or discharge is mismatched in timing with the historical seasonality.

Hydrology

We used linear regression to describe the long-term trend in the $\log_{10} (x + 1)$ transform discharge and

precipitation.

Estuary

Using linear regression, we tested for a relationship between the short-term deviations in anchovies and

mysids. We also used linear regression to determine the relationship between monthly discharge and

mysid summer biomass (Jun-Aug).

Recruitment

We quantified the relationship between $\log_{10}$ (anchovy recruitment + 1) and $\log_{10}$ (detrended annual

mean discharge + 1), historicity, $\log_{10}$ (the previous year's adult anchovy biomass + 1) in the Gulf of

Cadiz and all three first-order interactions.

Hydro-economic model construction

In the below section, we develop a theoretical examination of water use in telecoupled marine and

terrestrial socio-ecological systems (schematic of the telecoupled socio-ecological systems, Figure 3-1).
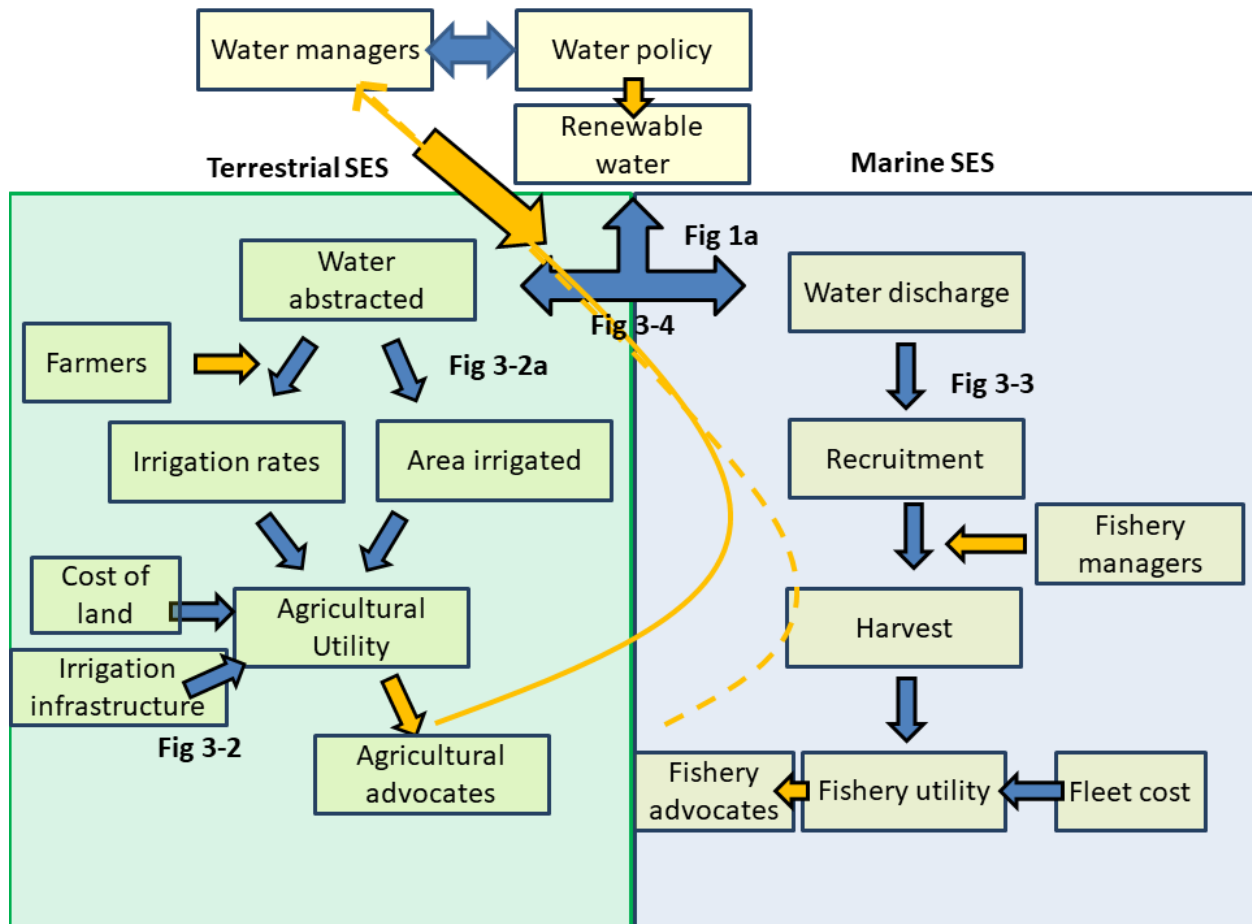
Figure 3-1. A schematic of telecoupled marine and terrestrial SESs. Every year managers allocate renewable water for abstraction or discharge. Water allocation by water managers is then a function of their objective function. Individual stakeholders in agriculture can choose to invest in irrigating more land or having a higher irrigation rate per unit area. The cost of irrigation, land, and benefits from yields will be communicated to advocates, informing water managers to have their water needs. The water that is discharged to the estuary mediates marine fish recruitment. Based on recruitment and stock numbers, fishery managers can determine the sustainable yield of the fishery. Fishery advocates then use the fishery harvest to advocate for water from water managers.

We begin with the assumption that the telecoupled SES has a total annual water budget (W_{total}) and that water use is exclusive to either terrestrial use (W_L) or marine use (W_M).

$$W_{total} = W_L + W_M$$

Eq 1.

The water extracted (W_L) will mainly transpire to the atmosphere and not return to the river during the same period (Berbel et al., 2015). The estuary is the river's terminus, and thus once discharged, water will become unavailable for terrestrial use on the time scale of interest.

Institutional norms are created from a combination of tradition, values statements, practicality, legislated policy, and scientific knowledge (Meyer & Rowan, 1977). A foundational water policy norm is that water basins are a fundamental water management unit (White, 1957; Teclaff, 1967; Newson, 1997). We explore the consequences of altering this norm by comparing management approaches that maximize the economic efficiency of either the terrestrial SES, marine SES, and the total efficiency of the SESs. Following this, we explore the water use when balancing local efficiency and equity between SESs, a common approach allocating water under local regions within water basins.

Agriculture's objective function

Agriculture's economic value $U_L(A_I, I)$ is the balance of the value of the agricultural products sold versus the costs of land and irrigation; $U_L(A_I, I)$ is a function of is the area irrigated A_I and irrigation rate I.

$$U_L(A_I, I) = \varphi_y H(I) A_I - \varphi_L A_I - \varphi_W W_L$$

Eq 2

Thus, agriculture's objective function ($\max\{U_L(A_I, I)\}$) is based on the selling price of the crop φ_y, the cost per unit area of irrigable land φ_L, and the per-volume cost of irrigation infrastructure φ_W. The yield per acre *H(I)* as a function of irrigation rate is

$$H(I) = \frac{I}{h + I}$$

Eq 3,

and h is the irrigation rate at which the yield is half its maximum yield.

Since $W_L = IA_I$ we can expand $U_L(A_I, I)$ to

$$U_L(A_I, I) = \varphi_y \frac{I}{h+I} A_I - \varphi_L A_I - \varphi_W A_I I$$

Eq 4.

Marine objective function

We focused this analysis only on the benefits fisheries provide for coastal communities, such that the objective of water policy is to maximize the sustainable harvesting rate $C(r)$, while minimizing the cost of maintaining the fishery. Formally, the value of the fishery as a function of discharge is,

$$U_M(A_I, I) = \varphi_C C(r(W_M)) - \varphi_{fleet},$$

Eq 5.

where $C(r)$ is set at the maximum sustainable yield (Fig 3-4D). The market price of the catch is φ_C and the cost of maintaining the fishing fleet is φ_{fleet}. Following the observation that discharge benefits fishery stocks (Gillson, 2011), we assume recruitment $r(W_M)$ is proportional to discharge W_M –see Fig 3-4C: therefore,

$$C(W_M) \propto W_M.$$

Eq 6.

Maximizing efficiency in telecoupled SESs

If the economic benefits of terrestrial and marine are viewed as interchangeable, the objective function for a telecoupled SES is

$$\max\{U_{L+M}(A_I, I)\} = \max\{U_L(A_I, I) + U_M(A_I, I)\}$$

Eq 7.

Thus, the goal is to improve the total economic efficiency of the telecoupled system irrespective of the distribution of benefits between SESs.

Balancing local efficiency with equity

If we suppose the marine and terrestrial objective functions are nonsubstitutable due to their local contributions to jobs or cultural value, a joint objective can be modeled via the Douglas-Hobbs function (Allen, 1934).

$$\max\{U_{LM}(A_I, I)\} = \max\{U_L(A_I, I)U_M(A_I, I)\},$$

Eq 8.

Maximizing $U_{LM}(A_I, I)$ should result in improving the economic efficiency of both SES utility while simultaneously balancing utility between SESs (Fig 3-4F & S22).

Model analysis

For each scenario, we calculated the local unconstrained maximums of the objective function and the constrained maximums. We searched for possible local maxima using gradient criteria that $\frac{\partial U}{\partial A_I} = 0$ & $\frac{\partial U}{\partial W_L} = 0$. The constrained maxima were found using the Lagrangian Method. Optima limited by water represents either 1) basin closure ($W_L = W_{total}$), or 2) a halt to abstraction ($W_M = W_{total}$). A mixed water allocation strategy occurs if W_L & $W_M > 0$. An optimum located on the constraint $A_I = A_{total}$ represents all available land being irrigated.

Results

Case study

Precipitation has decreased by 5% since 1951 (Fig 3-2b); however, the discharge has been reduced by 40% since 1951 and 70% of historical levels seen in 1931 (Fig 3-2a).
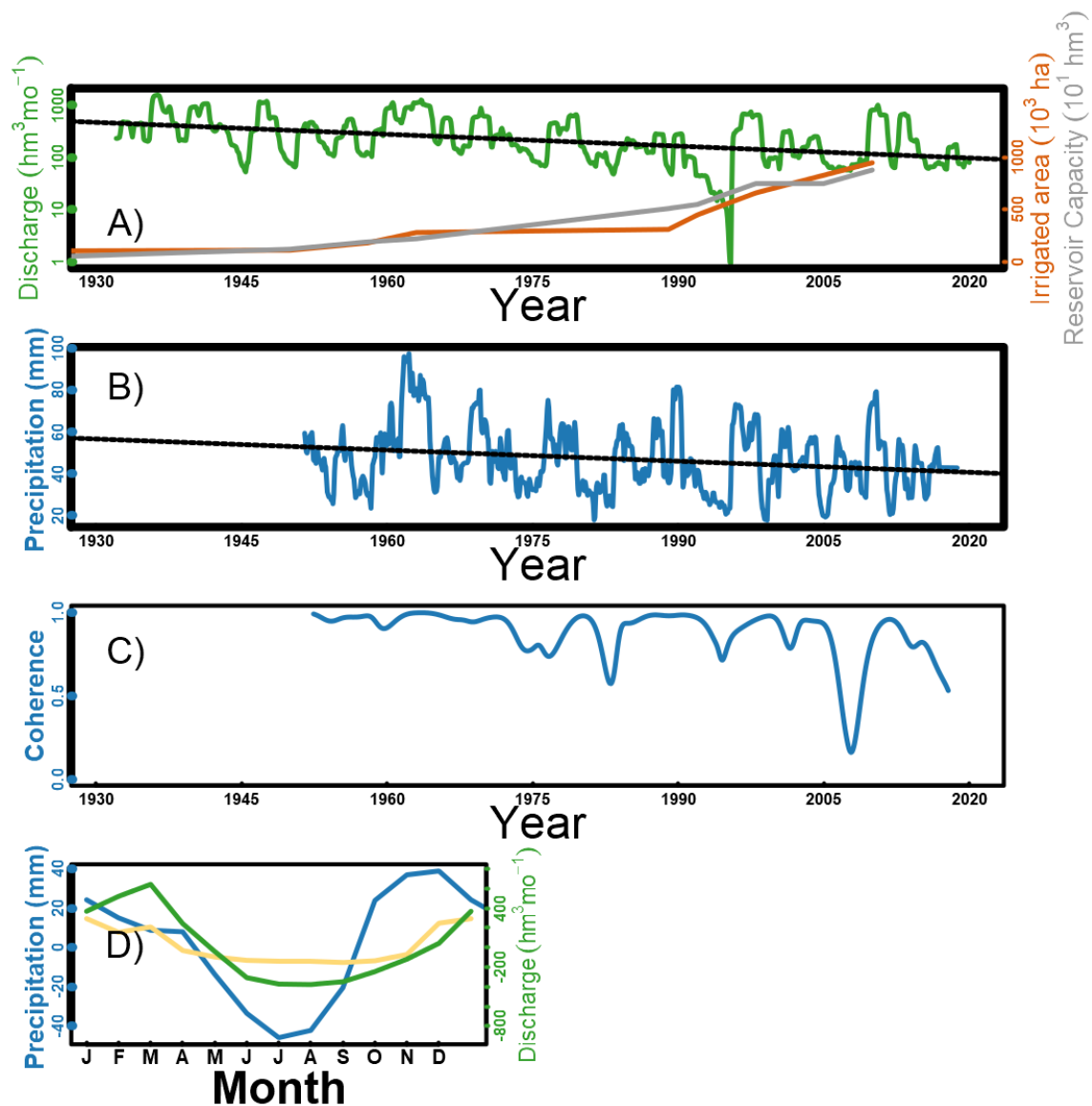
Figure 3-2. A series of reservoirs have been built along the Guadalquivir river for storing water. The hydrology of the estuary is determined by rainfall, regulation, and water abstraction. A) The time series of the monthly detrended discharge from the Alcalá del Río reservoir (blue), the area of land irrigated (brown), and the volume of water abstracted for irrigation (green). Monthly discharge has decreased by 70% from 1931-2018 linear regression (black). Meanwhile, the area of land irrigated and the volume of water abstracted has similarly increased. B) The time-series plot shows that monthly detrended precipitation (blue) has decreased by 5% since 1951, trend line (black), and is highly variable between years. C) The strength of annual coherence (blue) between precipitation and discharge. Historically precipitation and discharge were highly synchronized. However, increasing reservoir capacity and abstraction appears to have led to a decoupling of precipitation and discharge. D) The average seasonality of precipitation (blue), a historical discharge (1931-1955), and modern discharge (1988-2018). Modern discharge (yellow) is less seasonal than the historical discharge of the Guadalquivir river.

Southern Spain receives the majority of its precipitation during the winter (Fig 3-2d), and historically, the Guadalquivir river showed high winter discharge and low summer discharge. The average seasonality of discharge has decreased since 1931-1951 (Fig 3-2d) and has become decoupled from precipitation (Fig 3-2c).

Juvenile anchovies and mysids enter the estuary in the early spring and migrate to the Gulf of Cadiz in the summer - early fall (Fig 3-3d). We find that sustained discharge during Jan-Mar is linked to greater mysid summer biomass (For a summary of the results, see Table 1; $p = 0.005$, $R^2 = 0.57$, Fig 3-3c). From Jan-Mar gravid females with high reproductive potential migrate from the coastal sea to the estuary, and hydrological changes could disrupt migration into the estuary. *Mesopodopsis slabberi* biomass is positively correlated with juvenile anchovies ($p = 0.00001$, $n = 204$, $R^2 = 0.31$, Fig 3-3b). Thus, hydrological disruptions of mysid migration may lead to fewer resources (mysids) for juvenile anchovies before anchovies migrate into the Gulf of Cadiz.
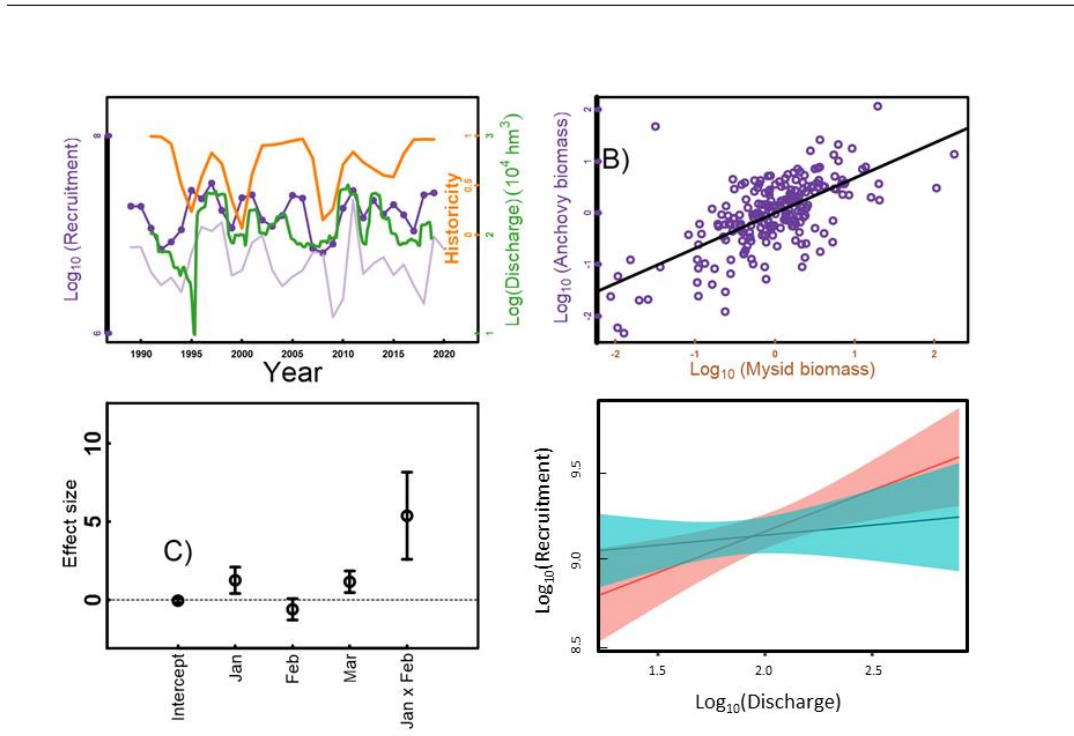
Figure 3-3. The links between hydrology of the estuary and the recruitment of anchovies to the Gulf of Cadiz. A) The time series plot of recruitment (purple circles), adult spawning abundance (light purple), the historicity of discharge (orange), and annual discharge (green). B) The scatterplot of mysids and anchovies shows that increased mysids in the estuary lead to more juvenile anchovies (n = 570, p < 0.0001, R^2 = 0.65). C) The plot of effect sizes for monthly discharge on mysid summer biomass. The spring peak biomass of mysids benefits from high sustained discharge through Jan-Mar (n = 24, p < 0.0001, R^2 = 0.40). D) The interaction of historicity and mean monlthly discharge. The highest recruitment requires both high historicy and discharge. The benefit of increasing discharge is low without a high historicity.

The best fit model for recruitment included adult biomass, discharge, and historicity, and all of their interaction terms (p=0.0114, R^2 = 0.46: See supplement Table 3-2 for a summary). We find that low monthly discharge and low seasonality are correlated with reduced recruitment of anchovies to the Gulf of Cadiz. The largest recruitment events are created when monthly discharge and historicity are high (Figure 3-3).

SES model

We detail the results for finding the maxima of agriculture's objective function and then repeat this analysis for the other management models in Appendix Eq S1-30 and highlight the main findings below.

Agriculture

The objective function of the terrestrial SES does not have a global maximum (S1). Thus the objective

function's optima occur when either land or water is constraining.

When land is constraining, the optima will occur at

$$A_I = A_{total},$$

Such that the irrigation rate is

$$I = -h + \frac{\sqrt{h}\sqrt{\varphi_y}}{\sqrt{\varphi_W}}$$

eq 9

and

$$U_L^w(A_I, I) = A_{total}(-\varphi_L + (-\sqrt{h}\sqrt{\varphi_W} + \sqrt{\varphi_y})^2)$$

eq 10

However, deficit irrigation will only produce water-savings

if $W_{total} > -h + \frac{\sqrt{h}\sqrt{\varphi_y}}{\sqrt{\varphi_W}}$

Eq 11

This constraint represents when the system will switch from being land to water constrained (Fig 3-4e &

f, S12). If Eq 11 does not hold all water will be extracted ($W_L = W_{total} = IA_I$) such that the optimum occurs

at

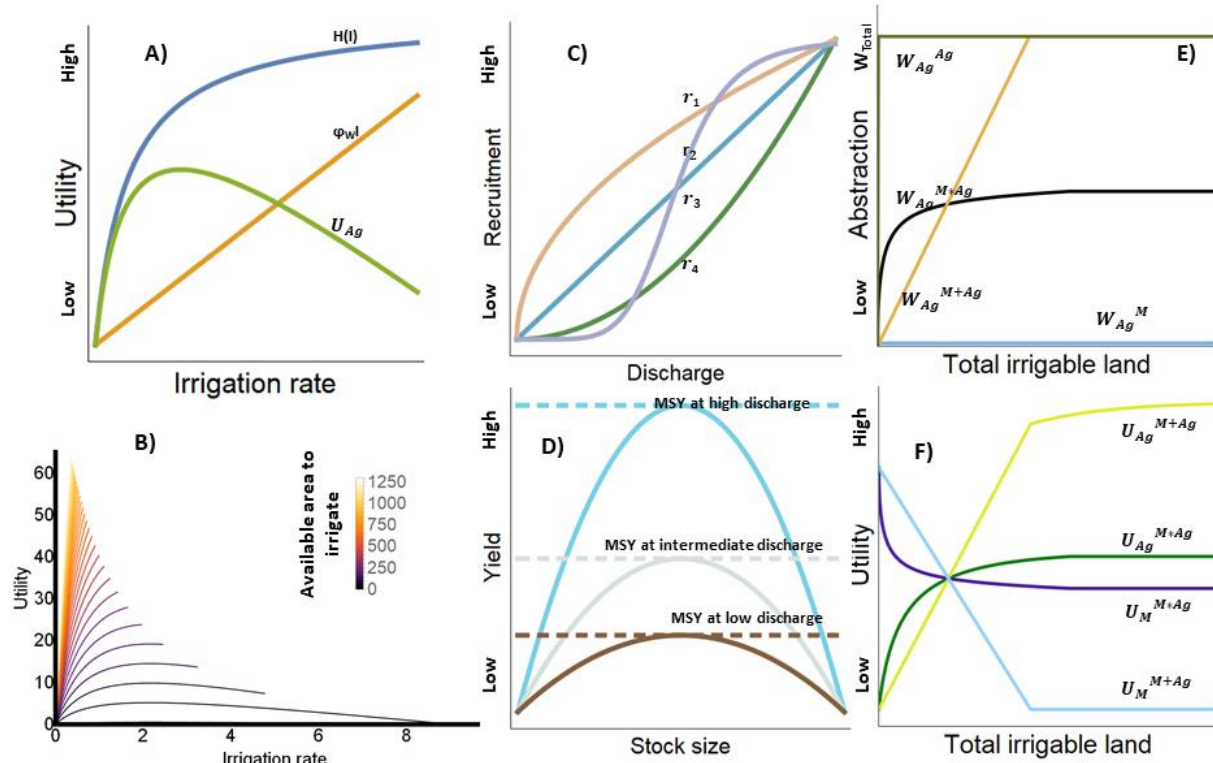$$A_I = \frac{W_{total}(-1 + \frac{\sqrt{\varphi_y}}{\sqrt{\varphi_L}})}{h},$$

eq 11

$$I = \frac{h\sqrt{\varphi_L}}{-\sqrt{\varphi_L} + \sqrt{\varphi_y}}$$

eq 12

$$U_L^w(A_I, I) = \frac{W_{total}(\varphi_L - h\varphi_W - 2\sqrt{\varphi_L}\sqrt{\varphi_y} + \varphi_y)}{h}$$

eq 13.

If Eq 11 does not hold agricultural expansion continues until the SES has reached basin closure (Fig 3-4a).

Figure 3-4. The dynamics of telecoupled terrestrial and marine SESs.

a) A plot of the utility function based on English (1990)s original derivation of deficit irrigation. In this model, productivity is a diminishing function of the irrigation rate (blue). Irrigation costs increase linearly with irrigation rates (yellow). The balance of the cost and benefits of irrigation (green) causes an optimum utility at intermediate irrigation rates.

b) A plot of the sensitivity of economic utility function of agriculture to total irrigable land available. When total irrigable land is high, the local optima is no longer accessible and, the optimal strategy is to abstract all water. On the other hand, when the objective of water policy is to maximize U_L the model predicts only land-limited systems will result in the prevention of basin closure.

c) The link between discharge and recruitment appears to be monotonic however could be 1) linear, 2) sigmoidal, 3) accelerating, or 4) deaccelerating.

d) A stock versus yield curve of fisheries under different discharge regimes. Harvesting above MSY will lead to the collapse of the fishery; however increased discharge improves the MSY by increasing the intrinsic rate of increase (r).

e) The plot of the optimal abstraction rate versus the total available irrigable land under different objective functions: 1) We find that maximizing terrestrial SES's utility function leads to the abstraction of all of the water until the area of land is limiting. 2) If the norm is to maximize marine SES's utility function, all of the water will be released. 3) If the goal is to maximize the total efficiency of the telecoupled SESs water savings will only be passed onto fisheries in land-limited systems, 4) Finally, a utility that balances efficiency and equity of the marine and terrestrial SESs leads to water being allocated to both terrestrial and marine SESs.

f)   The utiltiy function of marine and terrestrial SESs as a function of total irrigable land. Under the telecoupled SESs we determine what the utility will be for each SES. Maximizing the total efficiency of the telecoupled SESs leads to high utility in terrestrial systems and low utility in marine systems when there is a high amount of total irrigable land. However, when balancing the utility of telecoupled SESs we find that both marine and terrestrial ecosystems can have relatively high utilities despite the total amount of irrigable land.

Fishery

The fisheries' objective function is a positive monotonic function of discharge. Thus, fisheries' objective function allocates all water to the marine SES (Fig 3-4).

Maximizing the economic efficiency of a telecoupled system

We find that allocating water based on maximizing the total economic utility of the fishery and agricultural sectors $\max(U_{L+M})$ will not necessarily create a mixed water allocation, as land must still be a limiting factor to prevent agricultural expansion. However, the amount of land needed to constrain agricultural expansion is less (Fig 3-4 e & f), resulting in mixed allocations more frequently.

Balancing terrestrial and marine economies

In managing telecoupled SESs, the Douglas-Hobbs function results in a balance between efficiency and equity. Each SES will independently maintain high utility (Fig 3-4f) as water will always be allocated water to both SESs regardless of land versus water limitation (S22) (Fig 3-4f). Thus if the local economic benefit is nonsubstitutable, water allocation will be a mixed strategy (Fig 3-4e & f).

Conclusion and Implications

We find that defining water basins as a fundamental water management unit has significant implications for coastal ecosystems and communities. While river hydrology is known to impact inland fisheries, we find that a short-distance migration into the estuary is sufficient to connect migratory marine species with upriver processes. This telecoupling combined with our socio-ecological modeling suggests that a continued focus on improving water and economic efficiencies alone will not necessarily provide equitable and sustainable water allocation for coastal communities. Excitingly, we find that marine fisheries yields can be enhanced by recreating more historical hydrology (Fig 3-3) that reflects the

ecology of anchovies (Fig 3-2d). Studying telecouplings is an opportunity to improve the equity and integrity of SESs, as telecouplings reveal stakeholders beyond the water basin.

Animal movement is a crucial connector of socio-ecological systems. For example, the migration to and from freshwater by anadromous fish can move nutrients from the marine ecosystem into terrestrial ecosystems. Anadromous fish rely on connected river networks to reach their spawning sites as they migrate great distances upstream (Mattocks et al., 2017). For anadromous species, estuaries are a transition point at which they are sensitive to environmental stressors (Hodgeson et al., 2020). However, we find that an estuarine-reliant marine species needs only to travel the relatively short distance to the estuary to telecouple coastal ecosystem services with terrestrial water use. As recruitment for short-lived species is highly variable, we argue that estuarine hydrology may play a key role in developing more sustainable and resilient fisheries. The sensitivity of anchovy recruitment to upstream processes may explain the anchovy stock collapse in the Mediterranean Sea by 70%, following the Nile River's damming in the 1960s (Aleem, 1972). We suggest that telecouplings between marine and terrestrial SESs could play a previously unattributed role in recovering fishery stocks and securing coastal communities' livelihoods that rely on fisheries in their Economic Exclusive Zones.

Under the original model, deficit irrigation is sufficient to prevent basin closure; however, this result is inconsistent with the observation that basin closure is occurring in multiple water basins that have already adopted deficit irrigation (Feuillette, 2001; García-Mollá, 2000; Moench et al., 2003). Under the water allocation model used by English (1990), farmers set the irrigation rate for a fixed amount of available land by weighing the cost and benefits of different irrigation rates. Irrigating crops enhanced yields but at a diminishing rate of return, such that a reduction in the irrigation rate at high levels of water application maintains comparable levels of yield (Fig 3-4a). Under this model, the maximum utility occurs at intermediate water usage (English, 1990; reproduced in Fig 3-4a). However, analyses that include flexible land use shows that improved efficiency drives increasing land usage (Berbel, 2015).

Deficit irrigation, therefore, does not prevent basin closure in the long term unless limited land prevents

agricultural expansion. Thus, while deficit irrigation is a critical tool for managing water use, it must be

part of a more holistic water policy strategy to prevent basin closure.

We suggest extending water policy scope beyond the water basin level and developing a new concept of

the fundamental water management unit (White, 1957; Teclaff, 1967; Newson, 1997) is critical for

creating more resilient and robust coastal fisheries. Water policies have already been expanded to

protect inland and some aspects of coastal ecosystems (Gren et al., 2000; Howarth et al., 2002).

Meanwhile, there is growing evidence that rivers, adjacent coasts, and marine ecosystems are

connected with terrestrial ecosystems (de Carvalho-Souza *et al.*, 2018; Hodgson *et al.*, 2020; Lotze,

2010). For anchovies and other marine fisheries that use estuaries, solely developing and evaluating

policy based on the direct impacts to inland waters is not sufficient because this leads to the financial

costs of extraction being passed on to coastal communities. Globally, a movement towards basin

closure, e.g., the Colorado River rarely reaches the ocean, is occurring despite the adoption of water-

efficient practices. Some regions are implementing administrative basin closure to protect biodiversity

and the integrity of transport along the river (Berbel, 2015). Creating an efficient, equitable, and

sustainable water policy is paramount as climate change reduces available water availability.

An opportunity to reduce conflict in telecoupled systems considers balancing intra and inter-annual

variation in supply and demand. For example, reservoirs improve the reliability of the water supply for

terrestrial use. We have found that storing water during the critical months reduces anchovy

recruitment. However, we could identify months in which to store water and discharge water in order to

reduce conflicts between agriculture and fisheries. Moreover, this kind of optimization can be expanded

to include many of the additional demands for water. We believe that intra annual variation is key to

balancing efficiency and equity with the reliability and resilience of both SESs.

In closing, the water discharged into the ocean is not a missed opportunity but provides an essential

resource for the marine ecosystem.

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Contributions

Acknowledgments

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Appendix 3

In this supplement, we summarize the source, collection, and analysis of the empirical data used in this manuscript and the development and analysis of the theoretical model.

Mysid summer biomass

We explored the impact monthly log cumulative discharge of Dec, Jan, Feb, Mar, April, and their 1st order interaction terms on the seasonal deviations of mysids using AIC. The best model was

Regressor	Value	SD	t - value	p - value	DF	R^2_{Adj}
Intercept	-0.00819	0.137	-0.060			
Jan discharge	1.55	0.473	3.28			
Feb discharge	-0.70	0.370	-1.89			
March discharge	1.29	0.397	3.25			
Jan * Feb discharge	2.92	0.723	4.04			
Total				0.005	12	0.57

Table 3-1. The impact of monthly discharge on mysid spring biomass. We find that mysids benefit from continuous discharge from Jan – March. If discharge starts in Jan and then ends in Feb, summer biomass is reduced. Thus high summer biomass relies upon a high flow rate throughout the winter.

Regressor	Value	SD	t - value	p - value	DF	R^2_{Adj}
Intercept	- 0.76	2.2	-0.34	0.73	--	--
Annual discharge	6.0	2.1	2.9	0.0090	--	--
Historicity	7.2	3.21	2.2	0.038	--	--
Annual discharge x historicity	6.1	2.6	-2.4	0.028	--	--
Total				0.011	DF=22	R2Aj=0.31

Table 3-2. The summary table of anchovy recruitment regression. We find that increased annual discharge combined with a historical pattern of discharge improves anchovy recruitment

```
Call:
lm(formula = recruitY ~ biomass + season + discharge + season *
    discharge + biomass * discharge + biomass * season)

Residuals:
    Min     1Q  Median     3Q     Max
-0.28283 -0.09639 0.01431 0.13823 0.24857

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)      17.6981    3.0290  5.843 7.04e-06 ***
biomass          -1.2653    0.4588 -2.758  0.0115 *
season           -4.6484    3.1739 -1.465  0.1572
discharge        -6.6918    3.6239 -1.847  0.0783 .
season:discharge  0.9257    0.5229  1.770  0.0905 .
biomass:discharge 0.9939    0.5451  1.823  0.0819 .
biomass:season    0.6098    0.4755  1.282  0.2131
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1682 on 22 degrees of freedom
Multiple R-squared:  0.4683,      Adjusted R-squared:  0.3233
F-statistic: 3.23 on 6 and 22 DF,  p-value: 0.01979
```

Appendix 3-2 Theoretical model development and analysis

We model four scenarios under different objective functions: *I*) to maximize the economic utility of agriculture, *II*) to maximize the economic utility of the fishery, *III*) to maximize the total economic utility of the fishery and agriculture, and *IV*) to balance total efficiency with equity between SESs. Under each scenario, the objective function is constrained by limited total available water ($W_L + W_M <= W_{total}$), limited irrigable land ($A_I <= A_{total}$), and abstraction and discharge must be nonnegative ($W_L >= 0$ & $W_M >= 0$).

Objective functions

Fishery utility

The fishery's economic utility is a balance of the value of fish harvested versus the cost to maintain the fishing fleet.

$$U_M = \varphi_C C(r(W_M)) - \varphi_{fleet}$$

Eq S3-1.

φ_C is the market price for fish. We assume no elasticity in anchovy market price. φ_{fleet} is the cost of maintaining the fleet.

If $r(W_M) = W_M$ between discharge and recruitment, Eq S4 simplifies to

$$U_M = \varphi_F(W_M) - \varphi_{fleet}$$

Eq S3-2.

Also as $r(W_M)$ appears to be a monotonically increasing function even with different concavities the optima will always be at $W_M = W_{total}$

Since $W_{total} = W_L + W_M$ & $W_L = IA_I$,

$$U_M = \varphi_C(W_{total} - IA_I) - \varphi_{fleet}$$

Eq S3-3

Objective functions of a telecoupled system
These models can be placed into a multi-objective decision-making framework using additive and multiplicative utility functions to combine the two. The additive utility function will maximize total economic output while multiplicative balances equality and maximum output.

Additive Joint utility
The total economic utility of the telecoupled system is the sum of the two utility functions.

$$U_{M+L} = U_M + U_L$$

Eq S3-4

Multiplicative joint utility
The socio-economic utility balances the equality between the two SES, such as it protects one region's utility from reaching zero.

$$U_{ML} = U_M * U_L$$

Eq S3-5

Model analysis and results
Agriculture utility function
Unconstrained local maxima
The unconstrained agricultural objective function does not have a global maximum.

Constrained maxima
The constrained maximum of the terrestrial SES under water constraints is

Total water

$$A_I = \frac{W_{total}(-1 + \frac{\sqrt{\varphi_y}}{\sqrt{\varphi_L}})}{h},$$

Eq S3-6

$$I = \frac{h\sqrt{\varphi_L}}{-\sqrt{\varphi_L} + \sqrt{\varphi_y}}$$

Eq S3-7

$$U_L^w(A_I, I) = \frac{W_{total}(\varphi_L - h\varphi_W - 2\sqrt{\varphi_L}\sqrt{\varphi_y} + \varphi_y)}{h}$$

Eq S3-8

Total land
The constrained maximum for agriculture, when constrained by total area of irrigable land, is

$$A_I = A_{total}, I = -h + \frac{\sqrt{h}\sqrt{\varphi_y}}{\sqrt{\varphi_W}}$$

Eq S3-9

$$U_L^w(A_I, I) = A_{total}(-\varphi_L + (-\sqrt{h}\sqrt{\varphi_W} + \sqrt{\varphi_y})^2)$$

Eq S13-0

Fishery utility function
The fishery does not have an unconstrained maximum, but as discharge has to be nonnegative, we find that the fishery is at a maximum whenever all of the available water is discharged.

$$W_M = W_{total}$$

Eq S3-11

$$U_L^w(A_I, I) = \varphi_F W_{total} - \varphi_{Fleet}$$

Eq S3-12

Additive joint utility

Unconstrained maxima
The joint utility of the fishery and agriculture has critical points at

$$A_I = 0,$$

Eq S3-13

and

$$I = \frac{-\varphi_L - h\varphi_C - h\varphi_W \pm \sqrt{-4h\varphi_L(\varphi_C + \varphi_W) + (\varphi_L + h\varphi_C + h\varphi_W - \varphi_y)^2} + \varphi_y}{2(\varphi_C + \varphi_W)}$$

Eq S3-14

Thus one potential solution is a maximum at $W_M = 0$. This will occur if the fishery is more profitable than agriculture. Along Wm=0, agricultural will not invest in land such that that A₁=0.

Constrained maxima

Water constraint

The constrained maximum for agriculture, when limited by the available water, is at

$$A_I = \frac{W_{total}\left(-1 + \frac{\sqrt{\varphi_y}}{\sqrt{\varphi_L}}\right)}{h},$$

Eq S3-15

$$I = \frac{h\sqrt{\varphi_L}}{-\sqrt{\varphi_L} + \sqrt{\varphi_y}}$$

Eq S3-16

The maximum utility along the water constraint is

$$U_L^{Max}(A_I, I) = \frac{W_{total}(\varphi_L - h\varphi_W - 2\sqrt{\varphi_L}\sqrt{\varphi_y} + \varphi_y)}{h}$$

Eq S3-17

Thus the more water available, the greater the utility.

Land constraint

The constrained maximum for agriculture, when constrained by total area of irrigable land, is

$$A_I = A_{total},$$

Eq S3-18

$$I = h\left(-1 + \frac{\varphi_y}{\sqrt{h(\varphi_F + \varphi_W)\varphi_y}}\right)$$

Eq S3-19

$$U_L^{Max}(A_I, I) = W_{total}\varphi_C + A_{total}(-\varphi_L + h(\varphi_C + \varphi_W) + \varphi_y - 2\sqrt{h(\varphi_C + \varphi_W)\varphi_y}$$

Eq S3-20

Multiplicative joint utility

Unconstrained

$$A_I = \frac{(\sqrt{\varphi_y} - \sqrt{\varphi_L})(-\varphi_{fleet} + \varphi_C W_{total})}{2 \varphi_C \sqrt{\varphi_L} h}$$

Eq S3-21

$$I = \frac{\sqrt{\varphi_L} h}{\sqrt{\varphi_y} - \sqrt{\varphi_L}}$$

Eq S3-22

$$U_{M*L}^{Max}(A_I, I) = \frac{((\varphi_y - 2\sqrt{\varphi_y}\sqrt{\varphi_L} + \varphi_L - \varphi_W h)(\varphi_{fleet} - \varphi_C W_{total})^2)}{4 \varphi_C h}$$

$$W_M = \frac{1}{2}(W_{total} - \varphi_C \varphi_{fleet})$$

Eq S3-23.

Under the multiplicative utility, the maximum utility does not incentivize using more water. For example, if the cost of the fleet is small, then half the water should be discharged and half abstracted. However, if the amount of area is low enough, then the land can be constraining, and more water should be discharged (see below).

$$U_{ML} = 0$$

Eq S3-24

Water constrained

$$U_{ML} = 0$$

Eq S3-25