Check for updates

Ecology, 0(0), 2021, e03277
© 2021 by the Ecological Society of America

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

Franz W. Simon[1] and David A. Vasseur

Department of Ecology and Evolutionary Biology, Yale University, New Haven 06520 USA

Citation: Simon, F. W., and D. A. Vasseur. 2021. Variation cascades: resource pulses and top-down effects across time scales. Ecology 00(00):e03277. 10.1002/ecy.3277

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 have focused on equilibrium dynamics and do not provide predictions for communities' responses 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 temporal 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 communities' responses. At low frequencies, primary producers and secondary consumers have the highest temporal variability, while the primary consumers are relatively stable. Similar to the Exploitation Ecosystem Hypothesis, top-down effects drive this alternating pattern of variability. We define the top-down effect of consumers on the variability of lower trophic levels as a variation cascade. However, at intermediate frequencies, variation cascades can amplify temporal variation up the food chain. At high frequencies, variation cascades weaken, and fluctuations are attenuated up the food chain. In summary, we provide a novel theory for how communities will respond to fluctuations in productivity, and we show that indirect species interactions play a crucial role in determining community dynamics across the frequency spectrum.

Key words: *bottom-up control; exploitation ecosystem hypothesis; food chain; frequency response; press perturbation; pulse perturbation; resilience; resistance; trophic cascade.*

Introduction

Species interactions are a significant determinant of a community's structure and function (Carpenter and Kitchell 1988) and can transmit variability throughout a community (Ostfeld and Holt 2004). For example, during El Nino, high rainfall temporarily generates rapid plant growth fueling large fluctuations in herbivore biomass (Previtali et al. 2009). Short term increases in resource availability are known as resource pulses (Yang et al. 2008). Although consumers have a fundamental role in shaping communities, top-down effects are predicted to breakdown when resource availability fluctuates rapidly (Schwinning and Sala 2004). However, many ecosystems experience recurrent resource pulses along a spectrum of time scales (e.g., daily, annually, decadally, 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). Understanding the propagation of variability will help determine populations' vulnerability to shifts in community composition and climate (Piovia-Scott et al. 2017). We develop a novel theory that extends our understanding of how feedbacks, classified as top-down and bottom-up control in trophic systems, determine the populations' responses to primary productivity fluctuations.

Early work in this area suggested that community dynamics and structure were primarily determined by resource availability. Lindeman (1942) predicted increases in resource availability should have diminishing returns up the food chain due to thermodynamic constraints (i.e., energy lost to metabolism and the inefficiency of ingestion and digestion). Pulse-reserve (Noy-Meir 1973) and hierarchal theory (Schwinning and Sala 2004) predict that variability, created by resource pulses, is attenuated as it is propagated throughout the community. Bottom-up fluctuations would, therefore, tend to result in less population variability in consumers relative to producers. In contrast, a recent meta-analysis found a mix of attenuation and amplification of variability up food chains (Yang et al. 2010). On average, the populations directly utilizing a resource pulse have a smaller response than their consumers, who indirectly experience the pulse (Yang et al. 2010). Thus, although resource pulses feed directly into bottom trophic levels, bottom-up theories are insufficient to explain the amplification of variability up food chains.

Manuscript received 28 May 2020; revised 6 August 2020; accepted 6 October 2020; final version received 12 November 2020. Corresponding Editor: Caz M. Taylor.
[1] E-mail: Franz.simon@yale.edu

If consumers can impose top-down control on lower trophic levels, then the variability could be amplified up food chains. For example, in a two trophic level food chain, increases in resource availability will increase primary consumer biomass and not producer biomass. Following from this, if resource availability fluctuates, variability could be amplified up the food chain, as the producer will have low variability, and the primary consumer will be highly variable. The Exploitation Ecosystem Hypothesis (EEH) predicts an alternating pattern of top-down regulation within food chains as a function of food chain length (Oksanen et al. 1981; Powers 1992; Oksanen and Oksanen 2000). Thus, in tri-trophic food chains, secondary consumers will release producers from herbivory via trophic cascades (Hairston et al. 1960; Oksanen et al. 1981; Oksanen and Oksanen 2000). Yet, EEH is built upon the assumption that alterations in resource availability are long term and sustained (Bender et al. 1984, Yodzis 1988, Schmitz 1997) and might not be the best predictor of a community's response to rapid fluctuations in resource availability. Therefore, we develop a theory of top-down control across time scales 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 a community's response to sinusoidal perturbations across the frequency spectrum (Nisbet and 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 (Chatfield 1975). Thus by combining frequency response and Fourier series, we are not limited to modeling simple sinusoidal perturbations but 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. Using frequency response theory, 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 food chains. 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 (PPP). For this study, we define PPP as the biomass of producers in the absence of herbivory. Furthermore, we extend the concepts of top-down control by finding the impact of consumers on the response of lower trophic levels to resource pulses across the frequency spectrum. We call this top-down effect a variation cascade. 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 describing how fluctuations in primary productivity are expressed as temporal variability and the role of top-down control in regulating communities' response to bottom-up forcing across all 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)

$$\begin{aligned}\frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right) - a_{\mathrm{RH}}\mathrm{RH} + \mathrm{rBCos}(\omega t)\\ \frac{dH}{dt} &= H(c_{\mathrm{RH}}a_{\mathrm{RH}}R - a_{\mathrm{HP}}P - d_{\mathrm{H}})\\ \frac{dP}{dt} &= P(c_{\mathrm{HP}}a_{\mathrm{HP}}H - d_{\mathrm{P}})\end{aligned} \quad . \qquad (1)$$

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(ωt) 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 with positive (non-zero) biomass {R, R-H, and R-H-P}. For the rest of this analysis, we use ξ to denote the focal community/equilibrium. We report the equilibrium biomasses in Appendix S1: Eqs. S2–S4). 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 (Fig. 1a,b). In this model, increasing mean productivity leads to bifurcations that increases the length of food chains that can persist at equilibrium. Oksanen and Oksanen (2000) used this pattern to argue that top-down effects will

change along the productivity gradient as food chains lengthen. Our analysis focuses on viable communities and contrasts the populations' variability when trophic levels are sequentially added. This approach provides similar insight into top-down and bottom-up effects and focuses on the fluctuations' frequency as the key parameter of interest.

Model analysis

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

$$G(i\omega) = \frac{Y(i\omega)}{S(i\omega)}. \tag{2}$$

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

$$G(i\omega)_j^{\xi} = Y(i\omega)\left|\left(i\omega I - J^{\xi}\right)^{-1}\right|S(i\omega) \tag{3}$$

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, see Data S1: TransferFunctionDerivation.nb. 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 $\xi = R$, $J^{\xi} = J^{R} = r$, and the solution of Eq. 3 is

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

$$G(\omega)_R^R = \frac{r}{r + i\omega}. \tag{4}$$

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 food chains.

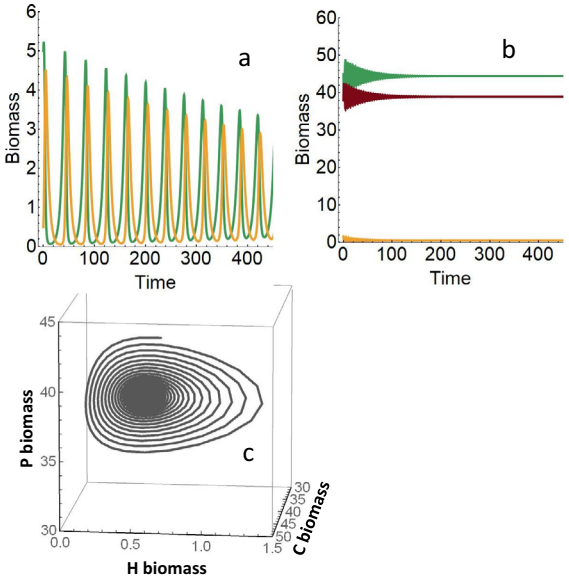

FIG. 1. The time series of the biomass dynamics of a food chain with either (a) two or (b) three trophic levels in a constant environment. (c) The phase volume of the tri-trophic food chain spiraling toward its stable equilibrium. The three trophic levels are differentiated by color such that green is the producer R, yellow is the primary consumer H, and red is the secondary consumer P. All of the solutions were solved using Runge-Kutta algorithms in Mathematica using the following parameters: intrinsic rate of increase $r = 0.2$, per capita death rates $d_H = 0.21$ and $d_P = 0.1$, attack rates $a_{RH} = 0.2$ and $a_{HP} = 0.2$, carrying capacity $K = 100$, and conversion efficiencies $c_{RH} = 0.9$ and $c_{HP} = 0.9$. Biomass and time unit are in arbitrary units.

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 fluctuations in PPP (Nisbet and Gurney 1976, 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 responses of the focal trophic level (j) and the adjacent higher trophic level (k)

$$ET_{jk}^{\xi}(\omega) = \log\left(\frac{A_k^{\xi}(\omega)}{A_j^{\xi}(\omega)}\right). \tag{5}$$

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) in their meta-analysis on natural ecosystems to measure the amplification of resource pulses between trophic levels, except that (ET^{ξ}_{jk}) captures how amplification changes with the frequency of the resource pulse.

Variation cascades.—We define consumers' top-down effect on lower trophic levels' amplitude response as a "variation cascade." While analogous to trophic cascades, trophic cascades quantify the mean change of the producer's biomass by the introduction of a secondary consumer. Formally, 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). Thus, the variation cascade (VC^{k}_{j}) of population (k) on population (j) is

$$VC^{k}_{j}(\omega) = \mathrm{Log}\left(\frac{A^{\xi+k}_{j}(\omega)}{A^{\xi}_{j}(\omega)}\right). \quad (6)$$

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

Results

Amplitude response

Frequency response: producer-only community ($\xi = R$).—In the absence of the primary consumer, the producer (R) exhibits logistic growth in a constant environment (Fig. 2b–d); however, if PPP is fluctuating, then the producer will oscillate around the equilibrium (Fig. 2b–d). The amplitude of the producer's oscillations decreases as the frequency increases (Fig. 2a) according to

$$A^{\mathrm{R}}_{\mathrm{R}}(\omega) = \sqrt{\frac{r^2}{\omega^2 + r^2}}. \quad (7)$$

At low frequencies, nearly all of the variation in PPP is translated into variability in the producer's biomass. At high frequencies, $A^{\mathrm{R}}_{\mathrm{R}}$ declines toward zero (Fig. 2a). Faster fluctuations offer less time for the population's biomass to adjust to the changing conditions and resulting in the transition from the behavior known as "tracking" to "averaging" (Nisbet and Gurney 1976). Averaging across fluctuations is a significant contributor to the autocorrelation or redness of population dynamics (e.g., Vasseur and Yodzis 2004). Consistent with previous work (May 1976, 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

$$A^{\mathrm{RH}}_{\mathrm{R}}(\omega) = \sqrt{\frac{r^2 a^2_{\mathrm{RH}} c^2_{\mathrm{RH}} K^2 \omega^2}{d^2_H\left(d^2_H + \omega^2\right) r^2 + 2 a_{\mathrm{RH}} c_{\mathrm{RH}} d^2_{\mathrm{H}} K r(\omega^2 - d_{\mathrm{H}} r) + a^2_{\mathrm{RH}} c^2_{\mathrm{RH}} K^2 (\omega^2 - d_{\mathrm{H}} d_{\mathrm{H}} r)^2}}. \quad (8)$$

Now, the producer's biomass 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 (Fig. 3 b). 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. 3b and Appendix S1: Eq. S18 for analytical solution). As the frequency increases, the producer's amplitude response increases to a local maximum, such that fluctuations at these frequencies can be amplified (Fig. 3b). The amplification of perturbations at particular frequencies is known as harmonic or coherence resonance (Spagnolo et al. 2003, McKane and Newman 2005). The producer's resonant frequency is

$$\omega_{\mathrm{R}\max} = \frac{\sqrt{d_{\mathrm{H}}}\sqrt{a_{\mathrm{RH}} c_{\mathrm{RH}} K - d_{\mathrm{H}}}\sqrt{r}}{\sqrt{a_{\mathrm{RH}}}\sqrt{c_{\mathrm{RH}}}\sqrt{K}}. \quad (9)$$

The amplification by the producer exhibits at $\omega_{\mathrm{R}\max}$ is

$$\max_{\mathrm{R}}\left(A^{\mathrm{RH}}_{\mathrm{R}}(\omega)\right) = \frac{a_{\mathrm{RH}} c_{\mathrm{RH}} K}{d_{\mathrm{H}}}. \quad (10)$$

We find that the producer's maximum amplification (Eq. 10) is proportional to the consumer's interaction strength (Appendix S1: Eq. S5). Thus, consumers who have a higher impact on the producer's mean biomass 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 PPP's temporal fluctuations,

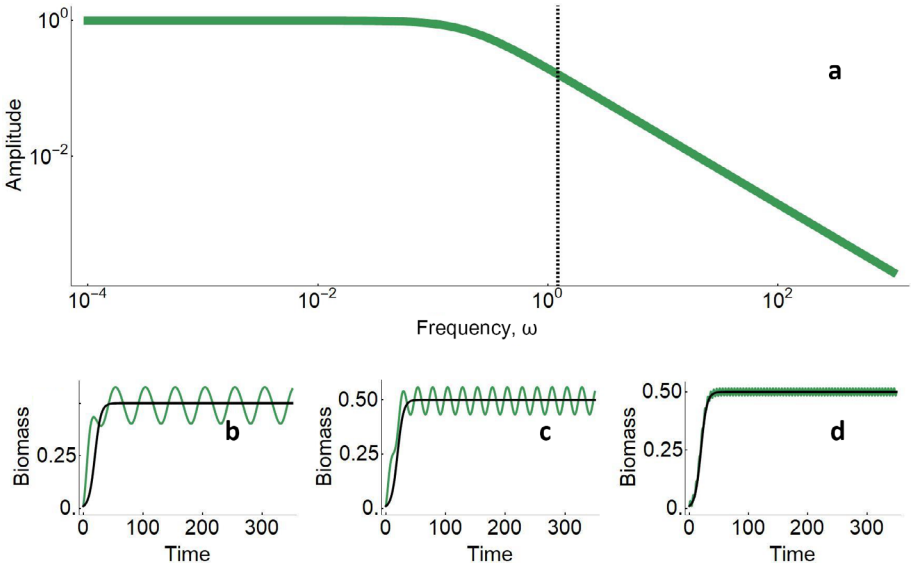

FIG. 2. The response of a primary producer to sinusoidal disturbances. (a) Log-log plot of the amplitude response of the primary producer ($A_R^R(\omega)$). The amplitude response determines how a sinusoidal disturbance will be amplified or dampened. The primary producer's biomass grows to carrying capacity in a constant environment (black); however, when the productivity is fluctuating with frequency (b) $\omega = 2\pi/10$, (c) $\omega = 2\pi/30$, and (d) $\omega = 2\pi/60$ (where $r = 1/5$ and $K = 1/2$), the producers switch from tracking the fluctuation to averaging across the perturbation. Biomass and time are in arbitrary units.

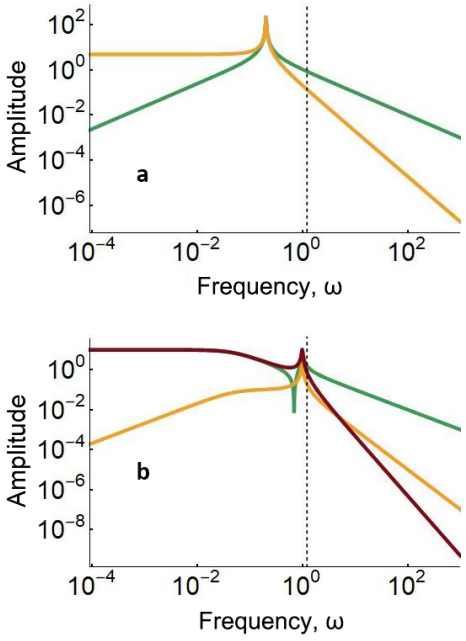

FIG. 3. Log-log plots of amplitude responses of two- and three-trophic-level food chains. (a) The amplitude response of community R-H-P (A_R^{RHP}, A_H^{RHP}, and A_P^{RHP}). (b) The amplitude response of the producer and primary consumer's amplitude responses in a two trophic level food chain (A_R^{RH}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

as all trophic levels will average across fast fluctuations (Figs. 2a vs. 3b).

Amplitude responses in the full community.—The secondary consumer's introduction 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 (Fig. 3 b). The primary consumer is unresponsive to low-frequency temporal fluctuations and has a local maximum at intermediate frequencies (Fig. 3a). The secondary consumer is responsive at low frequencies and dampens high-frequency perturbations (Fig. 3a). 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 (Fig. 3a). We include the analytical solutions of all of the amplitude responses in Appendix S1.

Efficiency of transfer.—The efficiency of transfer between the producer and the primary consumer (ET_{RH}^{RH}; Fig. 4c) is a log-linear function of the resource pulse frequency

$$ET_{RH}^{RH} = -\log\sqrt{\frac{(d_H - a_{RH}c_{RH}K)^2\omega^2}{a_{RH}^2K^2}}. \qquad (11)$$

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.

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

As the frequency increases, the secondary consumer's amplitude response decreases log-linearly relative to that of the primary consumer ET_{HP}^{RHP}. The food chain transitions such that secondary consumers will always have a relatively lower amplitude than the primary consumers at high frequencies (Fig. 4a).

Variability across the frequency spectrum

We classify the community's variability into one of four modes depending on which trophic levels are amplifying or attenuating a resource pulse. For example, if ET_{RH}^{RHP} 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 the producer and secondary consumers have the largest fluctuations; and (4) (+,−) a humped-shaped pattern where the primary consumer is the most variable.

Communities will transition among these different modes across the frequency spectrum (Fig. 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 always decreases with trophic position. All the communities respond similarly at high and low frequencies (Fig. 5). We find three other general scenarios in which the primary consumer amplifies resource pulses at intermediate frequencies (matching the empirical patterns seen by

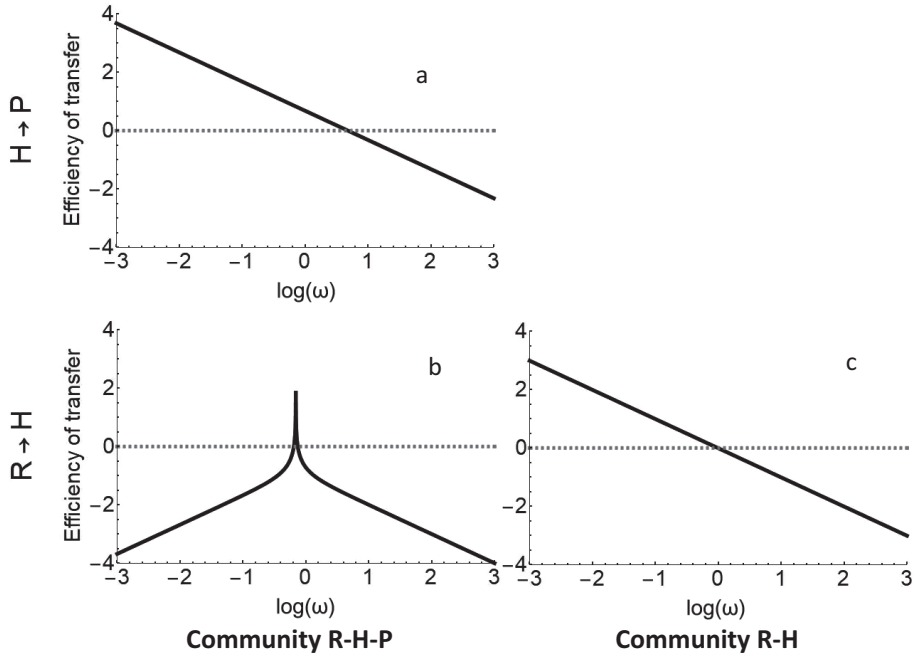

FIG. 4. Plots of the efficiency of transfer of (a) the primary consumer to the secondary consumer in the R-H-P community ET_{HP}^{RHP}, (b) primary producer to the primary consumer in the R-H-P community ET_{RH}^{RHP}, and (c) primary producer to the primary consumer in the R-H community ET_{RH}^{RHP}. The efficiency of transfers is parametrized using $r = 0.2$, $d_H = 0.21$, $d_P = 0.1$, $a_{RH} = 0.1$, $a_{HP} = 0.1$, $K = 100$, $c_{RH} = 1$, $c_{HP} = 1$.

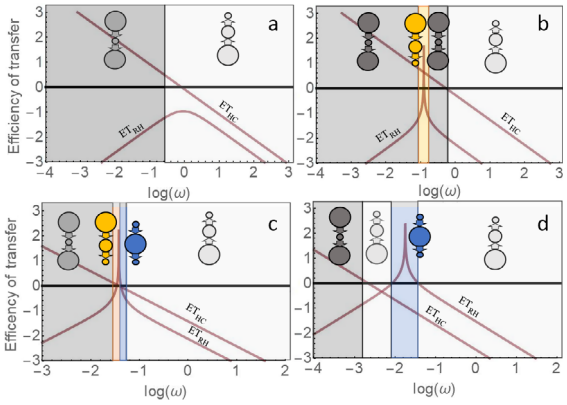

FIG. 5. There are four different scenarios for the pattern of variability modes across the frequency gradient. The four scenarios can be differentiated using the efficiency of transfer ET_{RH}^{RHP} and ET_{HP}^{RHP}. The signs of the ETs determine the relative variability mode of the food chain: +, + (orange); −, − (light gray); −, + (dark gray); +, − (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 parameter values for each regime are (a) $d_H = 0.21$, $d_P = 0.001$, $a_{RH} = 0.1$, $a_{HP} = 0.1$, $K = 100$, $c_{RH} = 0.2$, $r = 0.2$, $c_{HP} = 0.0068$, (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) $d_H = 0.21$, $d_P = 0.01$, $a_{RH} = 0.1$, $a_{HP} = 0.1$, $K = 100$, $c_{RH} = 0.2$, $r = 0.2$, $c_{HP} = 0.356$, and (d) $d_H = 0.21$, $d_P = 0.1$, $a_{RH} = 0.1$, $a_{HP} = 0.1$, $K = 100$, $c_{RH} = 0.2$, $r = 0.2$, $c_{HP} = 0.1$.

Yang et al. (2010). The variability amplification between the producer and primary consumer will only occur at intermediate frequencies. The ordering across the frequency spectrum of the intercept of the ET_{HP}^{RHP} and the intercepts of ET_{RH}^{RHP} differentiates these three other scenarios (Fig. 5b–d). In Fig. 6, we model a community's dynamics across the frequency spectrum of resource pulses. Overall, amplification can occur at any trophic level, and communities will shift among variability modes across the frequency spectrum.

Variation cascades: Top-down effects on community variability

Primary consumer.—The variation cascade is the impact of consumers on lower trophic levels' amplitude response. At low frequencies, the producer has its amplitude response reduced by the primary consumer (Fig. 7 c). At intermediate frequencies, the variation cascade is destabilizing because of the feedbacks between trophic levels and the disturbances' recurrent nature. Resonance emerges as the intrinsic cycling of the producer-primary consumer matches the frequency of the resource pulses. As during high PPP periods, the producer grows rapidly while escaping herbivory. Eventually, high producer biomass will fuel growth in the primary consumer, increasing the rate of primary consumption. If the decrease in PPP coincides with this increased consumption, then the producer's collapse will be driven by the combination of low resources and high consumption resulting in overcompensation. Once the producer's biomass is low, the primary consumer's biomass will begin to starve, releasing the producer from herbivory, starting the process again. This recurrent dynamic will result in wilder fluctuations swings than if the primary consumer were absent. Finally, at high frequencies, feedbacks between the producer and the primary consumer breakdown (Fig. 7c). In summary, primary consumers' top-down effect shifts from stabilizing to destabilizing before eventually breaking down at high frequencies.

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 community's resonant frequency. At low frequencies, the secondary consumer makes the producers sensitive to PPP's variability (Fig. 7b), analogous to a trophic cascade. At intermediate frequencies, the primary and secondary consumers reduce the producer's variability (Fig. 7b) by absorbing the resource pulses into their biomass while exhibiting resource–consumer cycles of their own (Fig. 6). Secondary consumers also change the frequency at which resonance will occur (Figs. 7a, b). Finally, at high frequencies, the secondary consumer does not affect the producer's amplitude response (Fig. 7b). By moving beyond a dichotomous view of time scale, we find that top-down effects do not merely breakdown at high frequencies (Fig. 7a, b); instead, we show secondary consumers have strong indirect effects on the producer 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 communities' responses to complex and realistic disturbances. For example, episodic perturbations with long interpulse intervals are a standard model of resource pulses and can be approximated by the summation of a small number of sinusoids (Fig. 8a,b; Appendix S1: Eq. S27). 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 Appendix S1: Eq. S28) but sum to determine population dynamics (e.g., Fig. 8c). Similarly, sums of sinusoids (Fourier

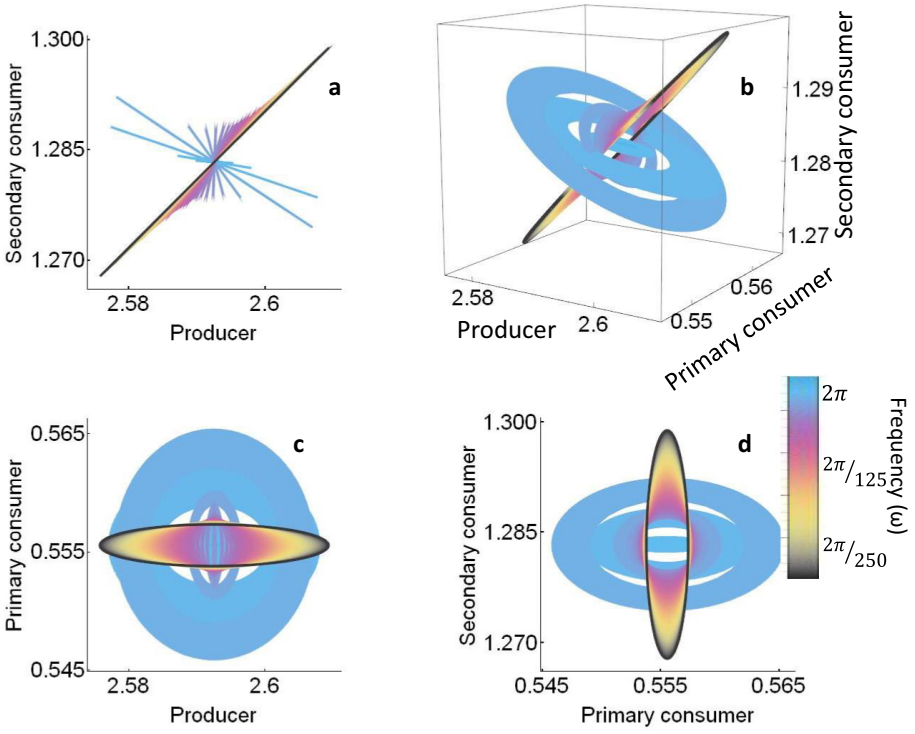

FIG. 6. The dynamics of the tri-trophic food web across the frequency spectrum. (a) Phase plane of the producer and secondary consumer, (b) phase volume of the tri-trophic food chain, (c) phase plane of producer and primary consumer, and (d) phase plane of the primary consumer and secondary consumer. The frequency is allowed to vary from $2\pi/250$ (black) to 2π (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. Biomass is in arbitrary units.

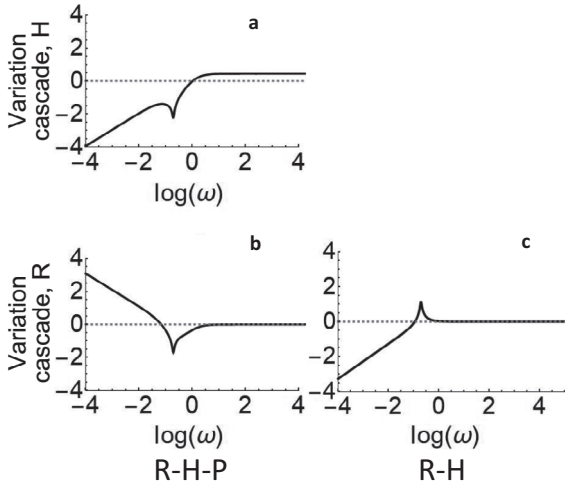

FIG. 7. Plots of the variation cascades across the frequency spectrum. (a) The effect of the secondary consumer on the primary consumer's amplitude response VC_H^P, (b) the effect of the secondary consumer on the primary producer's amplitude response VC_R^P, and (c) the effect of the primary consumer on the producer's amplitude response VC_R^H. Parameters are $r = 0.2$, $d_H = 0.21$, $d_P = 0.1$, $a_{RH} = 0.1$, $a_{HP} = 0.1$, $K = 100$, $c_R = 1$, $c_H = 1$.

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 and Blasius 2004). Introducing variation in this manner could alter 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.

DISCUSSION

Bottom-up and top-down control interact to determine the pattern of attenuation and amplification of the variability caused by 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

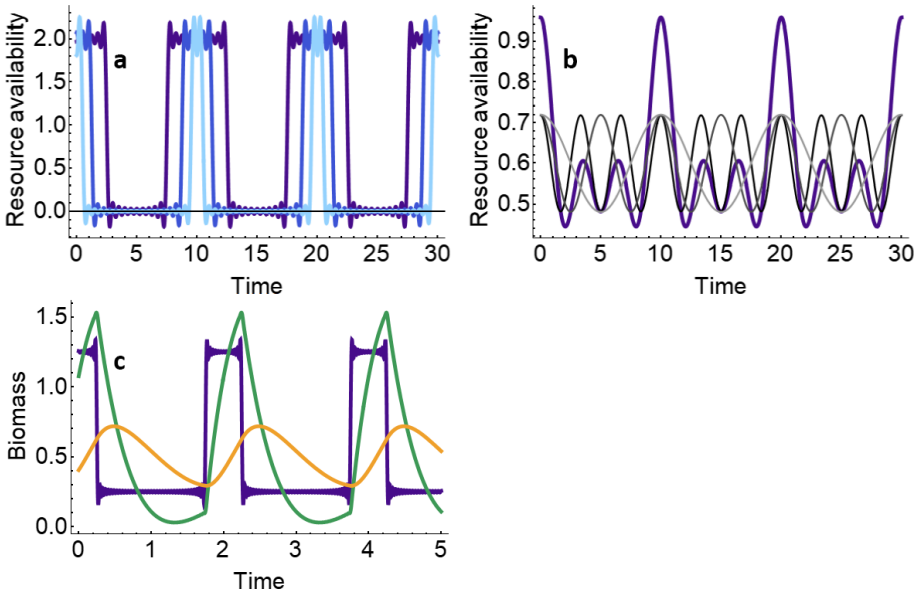

FIG. 8. Time series of episodic resource pulses and a community's response to complex dynamics. (a) Time series of three rectangular waves using their first 20 harmonics; $h = 2$, $L = 10$, purple ($\delta = 5$), blue ($\delta = 2.5$), and light blue ($\delta = 1$). (b) An approximation of a rectangular wave (using its first five harmonics) and the first five terms of its Fourier series (purple). The first five harmonics of the rectangular wave are shown. (c) The response of a producer and herbivore recreated using Fourier series and frequency response ($h = 1$, $\delta = 0.5$, $L = 2$, $d_H = 0.1$, $k = 10$, $c_H = 0.2$, $r = 0.5$, $a_{RH} = 0.1$). Biomass and time unit are in arbitrary units.

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 relative variability between a producer and consumer is a linear function of frequency (Ripa et al. 1998). By extending the Exploitation Ecosystem hypothesis (EEH) from an equilibrium-based theory, we have created a new general 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, variability in PPP will cause the primary consumer's biomass to fluctuate without generating variability in the producer's biomass. Therefore, the variability will be amplified up the food chain (Fig. 3b, 4b). Secondary consumers make the producer more variable, as the secondary consumer can suppress the variability in the primary consumer releasing the producer to increase during times of high PPP. Our theory reveals that EEH approximates the qualitative behavior of a community's response to low frequency resource pulses.

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. 5). The decreasing pattern is not caused by classical expectations such as energetic constraints (Lindeman 1942), nonlinear thresholds (Noy-Meir 1973), or stochastic averaging (Wooton 1994). Instead, the bottom-up dampening pattern is due to the dynamical averaging at each successive trophic level as each trophic level introduces an additional layer of averaging. At these high frequencies, only events of extreme magnitude will produce substantial ecosystem-wide effects. The vital rates of each member population are essential for determining the threshold at which communities will begin averaging across resource pulses. The bottom-up pattern of variability at high frequencies aligns with conceptual models of pulse-reserve theory and hierarchical theory by showing that top-down effects are limited at high frequencies (Noy-Meir 1973, Schwinning and Sala 2004).

At intermediate frequencies, the food chain experiences the broadest range of dynamics due to the interplay between top-down control and bottom-up forcing. For instance, when the intrinsic dynamics match the time scale of the fluctuations, resonance will amplify temporal variability at all trophic levels (Orland and Lawler 2004, McKane and Newman 2005, Benincà et al. 2011). We demonstrate that top-down effects can theoretically create the empirical pattern of amplification up food chains, seen in Yang et al. (2010). In some communities, resonance can be constrained to particular trophic levels (Fig. 6d). For example, large fluctuations can emerge between the primary and secondary consumers, while the producer's biomass remains static. Discovering the

time scales at which resonance phenomena occur in natural communities is an area deserving further research, potentially using allometric scaling following Yodzis and Innes (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.

Variation cascades clarify the role of top-down control in population responses to resource pulses across the frequency spectrum. Our theory demonstrates that a producer's response to resource pulses can only be understood in the context of the broader community (e.g., their primary and secondary consumers). Re-evaluating the patterns of amplification and dampening in natural communities in light of the time scale dependence of variation cascades could explain the ranging patterns seen in food chains (Yang et al. 2010) since amplification can be limited to particular frequency domains. The importance of variation cascades suggests that the high rate of loss of large carnivores from ecosystems will likely cause dramatic shifts in the expression of communities' variability.

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 1973); 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 nonlinear 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 exhibit 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 in developing a theory that predicts how temporal variability percolates through communities.

Establishing how variability percolates through communities opens up many future directions for research. Benincà et al. (2011) found that phytoplankton populations' resonant frequencies match the dominant frequency of variation in their environments, and this may extend or differ from those produced by interacting species. Communities near resonance frequencies appear to be more susceptible to invasion (Greenman and Norman 2007, Greenman and Pasour 2012), and thus fluctuations near resonant frequencies may support longer food chains. Our models rely upon a particular set of assumptions governing the flow of energy through the food chain; other assumptions (such as time lags and inducible defenses) are known to generate different forms of trophic cascades or eliminate them altogether (see Powers 1992). However, they also represent additional feedbacks that could introduce new resonant phenomena in the presence of productivity fluctuations or may be critical for allowing species to average across environmental disturbances. These and other mechanisms can be embedded in our current framework, enabling integrating feedback at different time scales within a general approach.

In summary, we have developed a novel theory that predicts how indirect effects control perturbations' impact across trophic levels and time scales. We find that variation cascades can amplify and attenuate temporal variability in surprising ways across 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 dynamics.

Acknowledgments

We would like to thank Oswald Schmitz, David Post, Charlotte de Vries, Anna Vinton, Luke Rogers, and two anonymous reviewers for their feedback on this manuscript. D. Vasseur was supported by NSF DEB #1050803 and #1754012. F. W. Simon was supported by the NSERC PGS D.

Literature Cited

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Benincà, E., V. Dakos, E. H. Van Nes, J. Huisman, M. Scheffer. 2011. Resonance of plankton communities with temperature fluctuations. American Naturalist 178:E85–E95.

Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. BioScience 38:764–769.

Chatfield, C. 1975. The analysis of time series: An introduction. Sixth edition. CRC Press, Boca Raton, Florida, USA.

Clodong, S., and B. Blasius. 2004. Chaos in a periodically forced Chemostat with algal mortality. Proceedings: Biological Sciences 271:1617–1624.

Cohen, J. E., C. M. Newman, A. E. Cohen, O. L. Petchey, and A. Gonzalez. 1999. Spectral mimicry: A method of synthesizing matching time series with different Fourier spectra. Circuits Systems and Signal Process 18:431–442.

Greenman, J. V., and R. A. Norman. 2007. Environmental forcing, invasion and control of ecological and epidemiological systems. Journal of Theoretical Biology 247:492–506.

Greenman, J. V., and V. B. Pasour. 2012. Threshold dynamics for periodically forced ecological systems: The control of population invasion and exclusion. Journal of Theoretical Biology 295:154–167.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Hastings, A. 2004. Transients: the key to long-term ecological understanding? Trends in Ecology & Evolution 19:39–45.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Ives, A. R. 1995. Measuring resilience in stochastic systems. Ecological Monographs 65:217–233.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1976. Theoretical ecology, principles and applications. Blackwell Scientific, Oxford, UK.

McKane, A. J., and T. J. Newman. 2005. Predator-prey cycles from resonant amplification of demographic stochasticity. Physical Review Letters 94:1–4.

Nisbet, R. M., and W. S. C. Gurney. 1976. Population dynamics in a periodically varying environment. Journal of Theoretical Biology 56:459–475.

Nisbet, R. M., and W. Gurney. 1982. Modeling fluctuating populations. First edition. Wiley, Chichester, New York, USA.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist 155:703–723.

Orland, M. C., and S. P. Lawler. 2004. Resonance inflates carrying capacity in protist populations with periodic resource pulses. Ecology 85:150–157.

Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and the Environment 2:13–20.

Pimm, S. L. 1982. Food webs: population and community biology. Chapman and Hall, London, UK.

Piovia-Scott, J., L. H. Yang, and A. N. Wright. 2017. Temporal variation in trophic cascades. Annual Review of Ecology, Evolution, and Systematics 48:281–300.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733–746.

Previtali, M. A., M. Lima, P. L. Meserve, D. A. Kelt, and J. R. Gutiérrez. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. Ecology 90:1996–2006.

Rinaldi, S., S. Muratori, and Y. Kuznetsov. 1993. Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities. Bulletin of Mathematical Biology 55:15–35.

Ripa, J., P. Lundberg, and V. Kaitala. 1998. A general theory of environmental noise in ecological food webs. American Naturalist 151:256–263.

Schmitz, O. J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.

Spagnolo, B., A. Fiasconaro, and D. Valenti. 2003. Noise induced phenomena in Lotka-Volterra systems. Fluctuation and Noise Letters 3:L177–L185.

Vasseur, D. A. 2007. Assessing the impact of environmental variability on trophic systems using an allometric frequency-resolved approach. Pages 41–60 *in* K. S. McCann and D. A. Vasseur, editors. The impact of environmental variability on ecological systems. Springer, Dordrecht, The Netherlands. https://doi.org/10.1007/978-1-4020-5851-6_3

Vasseur, D. A., and P. Yodzis. 2004. The color of environmental noise. Ecology 85:1146–1152.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–466.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. Ecological Monographs 80:125–151.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515.

Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. The American Naturalist 139:1151–1175.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3277/suppinfo