

THEORETICAL PERSPECTIVES ON RESOURCE PULSES

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Abstract. Over the last several decades, there has been a growing appreciation of the importance of nonequilibrium phenomena and transient dynamics in explaining the structure of ecological communities. This paper provides an overview of theoretical themes related to resource pulses. Theoretical models suggest short-term responses to a single pulse can qualitatively differ from longer-term responses. Recurrent resource pulses can alter community structure, permitting coexistence that otherwise would not occur, or hamper coexistence mechanisms effective in stable environments. For a given resource input, system responses can be more dramatic with short pulses. Resource pulses can cause transitions between alternative states. Dispersal permits species to exploit locally sporadic resource pulses and persist in environments that on average are unsuitable. All these issues are ripe for further theoretical explorations.

Key words: reactivity; resource pulses; spatiotemporal variation; transient dynamics.

INTRODUCTION

Ecologists recognize that temporal variation in the environment is a fundamental feature of the natural world (e.g., Marion et al. 2000, Chesson 2003) and that such variation has profound consequences for population dynamics and community organization (e.g., Nisbet and Gurney 1982, Mysterud et al. 2001, Schmidt and Ostfeld 2003). “Resource pulses,” defined as “ephemeral events of resource superabundance” (Yang 2004) are dramatic examples of temporal variation. In response to large-scale fluctuations in resources, species that use these resources can respond markedly in birth, death, and movement rates (Ergon et al. 2001); in turn, any species utilizing these consumer populations as resources (either directly as prey, or indirectly as a source of dead organic matter, such as corpses or litter) will experience pulses in resource availability. This interlocking of species’ responses to a resource pulse can lead to ramifying shifts throughout a community (Yang et al. 2008). Witman et al. (2003), for instance, describe how a massive subtidal recruitment of larval mussel *Mytilus edulis* in the Gulf of Maine boosted the abundance of consumers such as sea stars: a year later, these elevated consumer abundances eliminated *Mytilus* over large regions, provoking cannibalism in consumer species. Emergences of periodical cicadas (Yang 2004) and masting by trees (Schmidt and Ostfeld 2008) provide other dramatic examples of impacts of resource pulses shifting interspecific interactions through entire guilds and communities. Resource pulses can have effects cutting across ecosystem boundaries (Sears et al. 2004,

Anderson et al. 2008). For instance, mobile predators can rapidly aggregate to localized prey increases, drawn from a much broader landscape (e.g., see Korpimäki and Norrdahl 1991 for an example of avian predators responding to rodent outbreaks in a boreal landscape); such aggregative responses logically imply in the short run a reduction in predator abundance and predation pressure elsewhere.

Analyzing the effect of resources on population dynamics and community interactions is a central theme in the ecological sciences (Sinclair and Krebs 2002). A rich body of resource–consumer theory exists (Grover 1997, Getz 1999, Murdoch et al. 2003), and in principle, any of the models in this literature could be fruitfully applied to the analysis of resource pulses. This has in practice rarely been done, so it is premature to attempt a comprehensive theoretical treatment of the effects of resource pulses. What I do instead is to identify key conceptual insights from the scattered theoretical literature that does exist. I contrast two broad theoretical approaches to resource pulses: treating them as singular events, or alternatively as recurrent environmental features. I use some simple models to illustrate some effects of resource pulses in closed systems, and then turn to the issue of the impact of pulses in spatially extended, open systems.

PULSES AS SINGULAR PERTURBATIONS

Imagine a system is in equilibrium where densities are constant and experiences a single resource pulse, outside “normal” resource levels. Because, by definition, resource pulses are large, relative to the “typical” resource levels, the pulse is experienced as a large perturbation. The theoretical task is to understand how the intrinsic structure of the system—nonlinear feedbacks, time lags, and in general the entire web of direct and indirect interactions—governs the time course and magnitude of

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responses to the pulse. If the pulse is a historically singular event, species will not necessarily have evolved adaptive responses to it, and some system responses may reflect nonadaptive behaviors and physiological effects. The problem of characterizing system responses to resource pulses is related to several larger problems in ecology, including transient dynamics, and transitions between alternative stable states. I consider these in turn.

Transient dynamics after a pulse

Ecologists increasingly recognize that understanding transient dynamics is central to understanding natural systems (Hastings 2004). Resource pulses can be a powerful initiator of transient dynamics. Some structural features of systems are likely to generate long transients. Theoretical studies in principle can provide guidelines as to which aspects of the interaction structure of local systems are key determinants of the time scale, magnitude, and pattern of transient behaviors. For instance, it has long been known that if direct density dependence is weak, even stable predator-prey interactions can show weakly damped, large-scale oscillations following perturbations (e.g., a resource pulse boosting prey numbers). But until recently, few theoretical studies specifically focused on such short-term responses.

Neubert and Caswell (1997) provided an insightful contribution to this question by focusing on transient responses to small perturbations for systems initially at equilibrium. In the short term, even in stable systems the immediate response to the perturbation may be to grow for a period, before finally decaying to the initial state. They started with a general community model (a generalization of Lotka-Volterra models for interactions among n species, including competition, predation, and direct density dependence), where an ordinary differential equation describes each species' dynamics as a function of the densities of itself and other community members. For moderate perturbations, community dynamics near equilibrium match the linearized community matrix model (Yodzis 1989, Ives et al. 2003). Much is known about how the structure of community matrices influences local stability (Yodzis 1989). For instance, some species must experience direct density dependence, and long feedback loops cannot be too strong (Puccia and Levins 1985). Given that a community is stable, what determines its potential for unstable transient dynamics?

Neubert and Caswell (1997) address this question by assuming a stable community is perturbed, for instance by a resource pulse boosting numbers in one species. They propose several measures of transient responses and provide formal results for the community matrix model. One measure is reactivity: the maximum rate at which the system responds just after the perturbation, examined over all perturbations (i.e., they allow each system component and combination to be perturbed). Using an elegant bit of linear algebra, these authors

show that reactivity can be found from the eigenvalues of a transformed community matrix (the symmetric part of the matrix). If the dominant eigenvalue of this transformed matrix is positive, but the community matrix has a negative dominant eigenvalue (i.e., the community is stable, so it eventually returns to equilibrium), the system will be reactive; some small perturbations are sure to initially grow, before damping out. This result provides a tool for assessing the capacity of particular systems to show transient unstable responses to resource pulses. Neubert and Caswell (1997) also propose a second index, maximal amplification, defined as the largest amplification in numbers emerging for any initial perturbation. Numerical analyses using standard protocols (e.g., in MATLAB) permit one to calculate maximal amplification.

In the final stages of return to equilibrium in a stable community, the trajectory of abundances will predominantly move along a particular vector of deviations in species abundances from their equilibrium values: the dominant eigenvector. The reason the trajectory may initially move away from equilibrium after a perturbation is that the initial community state after the pulse may be strongly displaced from this particular vector, and movement in other directions (e.g., along other eigenvectors) influences the overall pattern of movement.

These authors have specifically applied these techniques to food chain models (Neubert et al. 2004, Caswell and Neubert 2005). If one species in the food chain has a per capita growth rate that is independent of its own density (e.g., a food-limited predator [Holt 1977]), the equilibrium is reactive, so some perturbations grow before damping out. Adding direct density dependence to these species reduces system reactivity. This suggests that the presence of species in a community with weak density dependence makes it more likely that the community will show transient responses to perturbations, including resource pulses, moving away from equilibrium for a while before returning.

These innovative techniques have not yet been widely applied, so it unclear what generalities may emerge after examining a wider range of systems. As noted above, a number of structural features of communities are known to promote local stability. Only after techniques such as those proposed by Neubert and Caswell (1997) have been applied to a wider range of systems will we have a comparable set of rules-of-thumb for mapping structural features of communities onto their reactivities or maximal amplifications following perturbation. As Caswell and Neubert (2005) note, the effect of parameter changes on reactivity is often not intuitively obvious. In models examined to date, contrary to intuition, there is no tidy tendency for reactivity to increase as parameters approach instability thresholds. Analyzing small perturbations near thresholds may thus be a poor indicator of system responses to large perturbations, and so cannot fully characterize resilience (Holling 1973).

When considering resource additions that are relatively small in magnitude, these formal measures should gauge the potential initial response of the system. For much larger resource pulses, these measures will not fully capture system responses, because nonlinear effects loom large. Numerical studies in this case will usually be required, but the general concepts of reactivity (a measure of initial responses to the pulse) and maximal amplification (the largest excursion made by a system before returning to equilibrium) still provide useful ways to think about how systems react to pulses.

RESOURCE PULSES AND POPULATION PERSISTENCE

I will now use a few simple models to illustrate some basic conceptual points about the impacts of resource pulses. Almost by definition, the impact of a resource pulse upon a consumer is favorable, in that its birth rates should rise or death rates fall. However, over longer time scales a resource pulse could actually hamper persistence. To illustrate this effect, consider the simple Ricker model for a species with discrete generations:

$$N_{t+1} = N_t F_t e^{-dN_t}.$$

Here, N_t is abundance at the start of generation t , the exponential term describes density-dependent survival (d measures the strength of density dependence), and F_t is per capita reproductive output of the survivors. Assume for simplicity that reproductive output directly tracks resource availability R_t at the end of generation t , so $F_t = aR_t$, where a combines both attack rates and conversion of consumption into offspring. Further, assume the environment is usually stable with constant resource supply, R^* . The population equilibrates at its carrying capacity, $N^* = \ln(aR^*)/d$. In generation 0, a resource pulse pushes resources to δR^* ($\delta > 1$). This boosts density in the next generation to $N_1 = \delta N^*$, but the resource has by then returned to R^* , where it stays. The following generation, consumer numbers are $N_2 = N^* \delta e^{dN^*(1-\delta)}$.

Fig. 1 shows a numerical example of how consumer numbers in generation 2 depend upon the resource pulse in generation 0, with fairly weak density dependence. Because a resource pulse leads to an overshoot of the consumer's "normal" carrying capacity, numbers can decline very substantially in future generations, particularly for large pulses. After a sufficiently severe population crash, extinction may occur.

This simple model illustrates that one generic effect of a resource pulse for a consumer limited by resources is that in future generations there will be a resource trough, which may hamper local persistence. In this example, the resource pulse indirectly intensifies direct density-dependent interactions among consumers, leading to a time-lagged depression in consumer abundance. One could also splice resource pulses into the density-dependent term; this can likewise cause future declines in abundance to well below carrying capacity, risking extinction. If a resource pulse leads to a diminution in

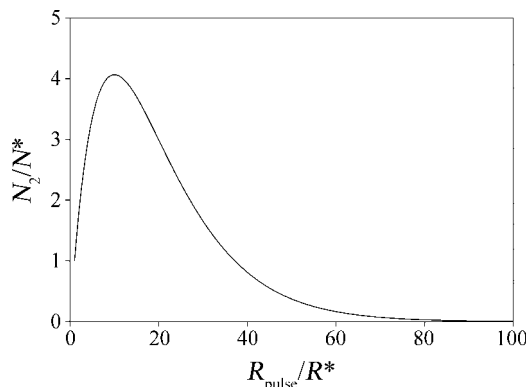


FIG. 1. Overshoots and undershoots in population size two generations following a resource pulse, for the Ricker model described in *Resource pulses and population persistence*, with $d = 0.1$ (d measures the strength of density dependence). Large pulses imply (with a time lag) low densities where extinction can occur. N_2 is population density in the second generation after the pulse, N^* is population carrying capacity, R^* is the constant resource supply at which the population is stable, and R_{pulse} is the pulsed resource supply level.

interference competition, for instance, the population will grow; following the pulse, if interference reemerges, the population may crash because of intense competition. Nicholson's famous blowfly experiments demonstrated exactly this effect; an increase in resources depressed total consumer abundance because of strong density-dependent feedbacks (Nicholson 1954). The essential point is that focusing on the immediate, short-term consequences of a pulse (e.g., relaxation of competition) needs to be balanced with a consideration of impacts over the intermediate to long-term, which may go strongly in the opposite direction.

RESOURCE PULSES IN PREDATOR-PREY INTERACTIONS

In generating Fig. 1, I assumed that resources are fixed independent of consumption (a "bottom-up" scenario). More typically, resource availability will be reduced by consumption (a "top-down" perspective). Responses to resource pulses and reciprocal impacts of consumption upon resource availability are built into all resource-consumer or predator-prey models. Consider a standard predator-prey model for species with continually overlapping generations, with additional terms describing different kinds of pulses, one mediated by changes in the prey population's intrinsic growth rate, the other by supplementing prey numbers directly (e.g., a pulsed spatial subsidy):

$$\begin{aligned} \frac{dN}{dt} &= N \left[r(t) - dN - \frac{aP}{1 + ahN} \right] + I(t) \\ \frac{dP}{dt} &= P \left(\frac{abN}{1 + ahN} - m \right). \end{aligned} \tag{1}$$

Here, N and P are, respectively, prey and predator densities; a is an attack rate, h is handling time, b is a conversion factor relating prey consumption to predator births, d is a measure of direct density dependence in the prey, and m is the predator's density-independent mortality. The prey grows logistically, and $r(t)$ is its intrinsic growth rate; the prey's instantaneous carrying capacity is thus $r(t)/d$. (This parameterization of the logistic in terms of r and d , vs. the usual r and K , often makes sense when one considers how individual traits in consumer–resource interactions map mechanistically onto population-level parameters [see MacArthur 1970, Schoener 1976, and Rueffler et al. 2006 for a recent discussion]; it means that resource supply influences both the intrinsic growth rate and the carrying capacity of the consumer.) Let $r(t)$ increase with resource availability, which can vary with time t ; for simplicity, I assume a linear relationship between $r(t)$ and resource abundance $R(t)$, so $r(t) = \alpha R(t)$. Finally, $I(t)$ is prey influx from an external source. Spatial subsidies into one population can reflect population fluctuations in the external environment, driven by resource pulses elsewhere but leading to local immigration surges.

Assume an initially stable system. Predator–prey interactions with a stable equilibrium often exhibit damped oscillations if perturbed; indeed, Neubert and Caswell (1997) show that models such as Eq. 1, in which the predator is strictly food limited, are always reactive, so the initial system's response to a perturbation is to move away from equilibrium. This can be true even if handling time is negligible; larger handling times lengthen the oscillatory phase, and when sufficiently great limit cycles occur.

Pulses can differ in terms of the total amount of resource entering a system, and the time course over which entry occurs. Fig. 1 provided an example of differences that arise when pulses differ in amount, but not their shape (all resources are available at whatever discrete point in the life cycle corresponds to reproduction). Here, I examine the effect of the length of the resource pulse on dynamics. For simplicity, in Eq. 1, I assume that usually $r(t) = r^*$, a constant, reflecting a steady resource supply. During a period of length T , resources increase sharply and uniformly, so $r(t)$ increases to a new level, and stays there through the pulse. Assume a fixed amount of resources enters the system; what varies is the amount of time over which this happens. For simplicity, I assume that the resource pulse can be represented as a single rectangular wave (see Fig. 2, dashed lines), with fixed area. The assumption of a fixed amount of resource that can be injected into the system in a single short burst, or instead spread over a longer period of time, should apply to many physical resources that obey a “conservation” principle (e.g., phosphorus), and can be a reasonable approximation for many others (e.g., a cohort of salmon maturing at sea and enjoying little mortality could in

principle return to their natal stream in a single day, or instead spread more gradually over a single summer, or be divided across several summers, with summed abundances being the same). For analytical purposes, it is also instructive to control for the amount of resources, and explore the impact of the length of the resource pulse; this complements insights that come from fixing pulse length and varying resource amount.

Consider what happens when the basal consumer (the prey) is present alone. Fig. 2A, B shows a typical example. With a temporally extended pulse, the population reaches a new carrying capacity, then later declines after the pulse ends. When the pulse is sharp, the increase is larger, as is the relative length of the period of population decline vs. growth. However, the qualitative effect of pulse length upon population response depends upon the particular range of pulse lengths considered. Fig. 3A shows how pulse width (for fixed total input) influences the maximal prey density (i.e., maximal amplification) reached during the pulse, for each of the two kinds of pulses (via r , and I). In both cases, a decrease in pulse width increases the maximum consumer numbers; but in this example, the magnitude of the effect is stronger for pulses that affect r than for an external input. The reason for this is the multiplicative power of local growth, vs. a simple additive subsidy from an external source. Note that an order of magnitude variation in pulse length may not be reflected in a marked change in the maximal population response (the left side of Fig. 3A). However, in general the response magnitude declines for sufficiently long resource pulses.

With a predator, the picture changes in some respects. Fig. 2C, D plots predator and prey dynamics following a single resource pulse, boosting prey r , as in Fig. 2A, B. In Fig. 2C, the pulse is tightly spiked. Prey numbers rapidly respond, with negligible predator growth. Because the pulse is very quick, prey density then declines more or less exponentially, undershooting before gradually converging on its original abundance. Because the predator satiates, it responds only to a small degree to dramatic shifts in prey abundance. In Fig. 2D, the same amount of resource is added, now spread over a longer time. This leads to more gradual and overall modest changes in prey numbers, with barely any response in the predator at all (note the differences in scale between Fig. 2C, D). The effect of the pulse is thus masked when one examines predator dynamics; the main impact of the predator in this example is to increase prey instability in response to the pulse. Again, the effect of the pulse is more dramatic when temporally concentrated than when spread through time. Fig. 3B, C shows how maximal and minimal magnitudes of the prey response (scaled against the long-term equilibrium) varies as a function of pulse width, for both pulsed r (Fig. 3C) and external inputs (Fig. 3B). The difference between maximal and minimal numbers in the oscillations induced by the pulse increases, as the pulse

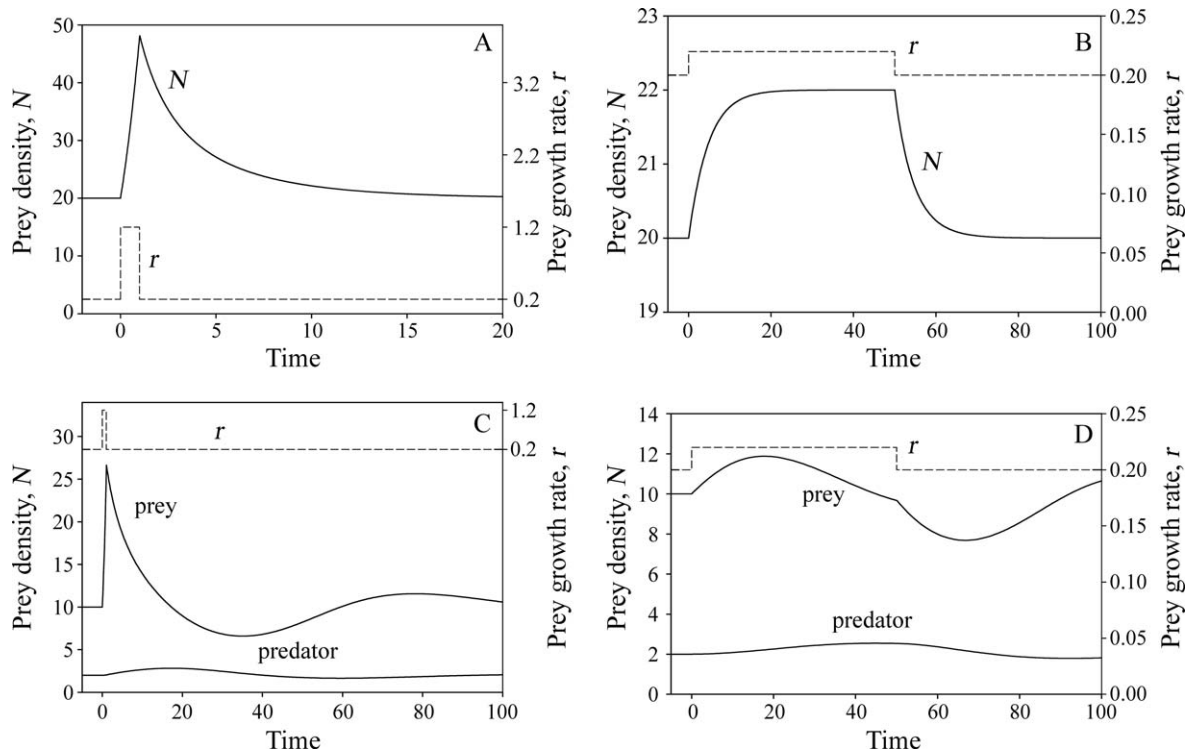


FIG. 2. Population response of a consumer with logistic growth to a resource pulse, with and without predation (Eq. 1). The consumer intrinsic growth rate is proportional to resource availability. For a given resource amount, shorter pulse width leads to a larger total population response. In all cases, the pulse is expressed via an increase in the prey's intrinsic growth rate r from a baseline value and is assumed for simplicity to be a square waveform. The "area" of the pulse is defined as the difference between the maximal value of r and the baseline value (the height or amplitude of the pulse), times the length of time this maximal value is maintained (the width or period of the pulse). The value of the baseline value is assumed in all cases to be $r = 0.2$; the other parameters are for all cases equal to the following: strength of density dependence $d = 0.01$, per capita attack rate by predator upon prey $a = 0.1$, benefit to the predator per prey consumed $b = 0.2$, handling time $h = 1$, and predator mortality $m = 0.1$. The area of the pulse in all cases = 1, so in the examples shown, there is a trade-off between pulse amplitude and pulse width. (A, B) No predator is present: (A) pulse width = 1, amplitude = 1; (B) pulse width = 50, amplitude = 0.02. (C, D) The predator is present: (C) pulse width = 1; (D) pulse width = 50. The predator has a negligible response to the resource pulse, but its presence induces oscillations in the prey response to the pulse, which is sharper during a pulse of shorter duration and higher amplitude (as the prey can escape predation more effectively).

becomes shorter in duration. The qualitative pattern is much the same for pulses via I as for those via r . Note that as in the single species example, order of magnitude changes in pulse length do not affect the maximal amplifications in abundances observed in predator-prey systems, when one compares moderately to very tightly focused pulses, but that widely spread pulses have a much more modest impact. Sears et al. (2004) conjectured that there should be similarities between spatial subsidies and temporal resource pulses; this figure suggests that fluctuations in subsidies via pulsed immigration do lead to consumer responses qualitatively resembling those produced by local resource pulses.

To gain analytical insight into these patterns, imagine a population at time zero has N_0 individuals, and a realized growth rate of zero (due to density dependence). A square-wave resource pulse of magnitude R occurs which increases the intrinsic growth rate by qR for a time T ; the total amount of the pulse is $RT = k$, a

constant. One can assume $q = 1$ (which defines how the resource is measured). Assume for simplicity that density dependence can be ignored during the pulse, so the population grows exponentially from $t = 0$ to T . The maximal population size, scaled against initial population size, is $N(T)/N(0) = e^k$. In Fig. 3A (which does have density dependence), I assumed a resource pulse of size unity ($k = 1$); on the left of the figure, it is clear that the asymptote for the pulsed resource affecting r approaches the value e ($\approx 2.71...$). In effect, when a resource pulse is tightly spiked, and the consumer response to the resource is elastic and proportional to resource abundance, the maximal consumer abundance reached during the spike is e , raised to a power equal to the pulse size. When pulses are broader, density dependence operates more effectively and reduces the magnitude of the response. When a predator is present, tight pulses permit much the same magnitude of response by the prey as without the predator, but the prey response is

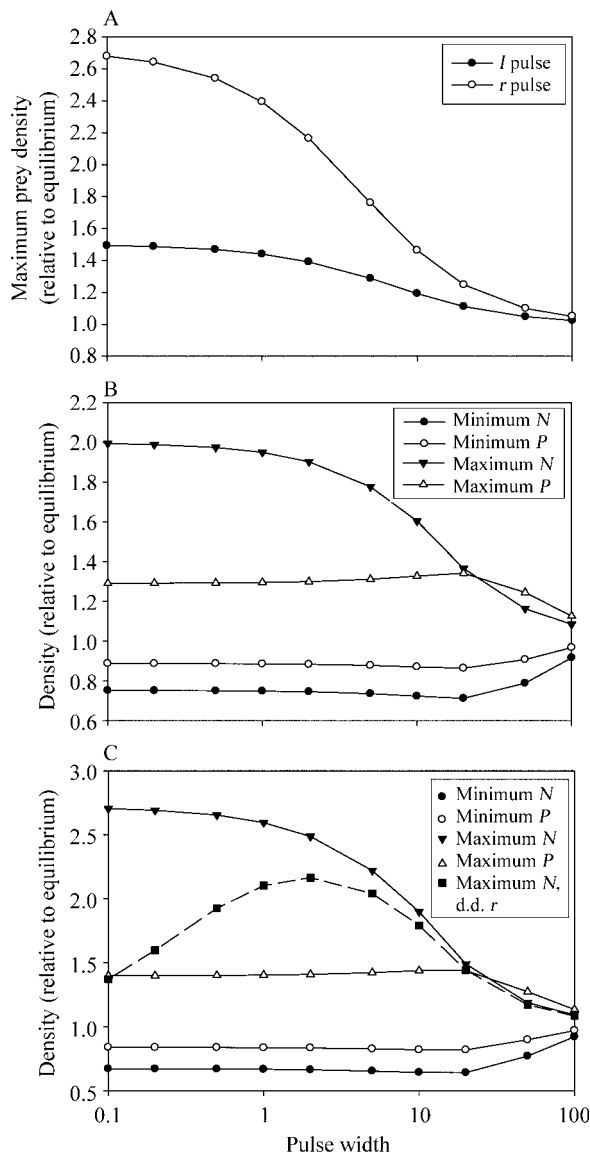


FIG. 3. Responses of maximum and minimum abundance after a pulse, as a function of pulse width (area of pulse = 1; see Fig. 2 legend for definition of "area"), for the model in Eq. 1. Open symbols indicate a pulse via intrinsic growth rate (r) of basal consumer species; solid symbols indicate a pulse via external subsidies (I). (A) Consumer without predation. Pulse area = 1 for r pulse; pulse area = 10 for I pulse. (B, C) Coupled predator-prey systems. The total amount of resource is fixed. The pulse effect increases with decreasing pulse width; the magnitude of the effect is typically larger for the prey than the predator. The overall pattern is similar for external subsidy and pulses via r . (B) Pulsed I , pulse area = 10. (C) Pulsed r ; dashed line, $r = R/(1 + cR)$, where $c = 0.2$ (in this case, R is pulsed with minimum $r = 0.2$; the quantity c is related to the maximal growth rate when resources are unlimited, by $r_{\max} = 1/c$). Saturating numerical responses imply that intermediate pulse widths have maximal impact on prey. Key: N , prey density; P , predator density; d.d., density dependent. Other parameters are as in Fig. 2. Note the x -axis log scale.

greater for wider pulses (compare Fig. 3B, C). The reason is that predation lowers prey abundance, reduces direct density dependence, and so increases the magnitude of the potential response by the prey to added resources. Moreover, with a tight pulse, the time lag in the predator response means its numbers will not have time to respond much during the phase of prey growth.

A biological limitation in the examples shown in Fig. 3A, B is that there is no upper bound to the numerical response of the prey to its resource. More realistically, one would expect a decelerating function to describe the relationship between consumer recruitment and resource levels. All organisms have an r_{\max} governed by basic organismal features such as body size, physiology, and generation length, as well as environmental factors (e.g., temperature) (Savage et al. 2004); such constraints bound the rate at which numbers can respond to resource pulses. This implies that the maximal transient effect of a resource pulse should occur at an intermediate pulse width (for fixed total resource input). The dashed line in Fig. 3C depicts this effect (assuming a saturation response of prey recruitment to resource availability, $r = R/[1 + cR]$; here, $r_{\max} = 1/c$). Saturation in recruitment can prevent population overshoots following a resource pulse of the sort shown in Fig. 1. Similar patterns emerge when one introduces the resource pulse via the prey's density dependence. One reason for this is that because the predator has a saturating functional response, decreasing the prey's density dependence makes it more likely the predator-prey interaction shows limit cycle behavior; this is more likely, the greater the handling time for the predator. Average abundances over a cycle often respond differently to changes in parameters than do equilibrium values. Understanding the interplay of resource pulses with intrinsically unstable dynamics is an important challenge for future work.

The model in Eq. 1 assumed continuously growing populations and just two species. Additional time lags (e.g., from developmental lags or additional species) could further exacerbate system responses to pulses. I conjecture that a pattern of maximal responses by consumers to intermediate pulse lengths will prove to be the norm, when a broader range of models are examined. The quantitative challenge will be to systematically relate the pulse width corresponding to the maximal amplification to structural features of the system, such as the degree of saturation in numerical and functional responses.

PULSES AND TRANSITIONS BETWEEN ALTERNATIVE STATES

Another general ecological issue where singular resource pulses could be of great importance is as a driver of shifts between alternative stable states. Some ecologists are skeptical of the existence of alternative stable states (Bertness et al. 2002), but there is increasing evidence that the phenomenon is important in many systems. Schroder et al. (2005) review experimental

examinations of alternative stable states and conclude that a reasonable number of good cases now exists (e.g., Cottenie et al. 2001). By definition, a system has alternative stable states if its dynamics tend toward any one of multiple stable configurations, depending upon initial conditions (Scheffer and Carpenter 2003). Around alternative states are domains of attraction defining the magnitude of perturbations needed “flip” the system between stable states. Transitions between stable states can require substantial perturbations; resource pulses could provide such perturbations. For instance, shallow lakes can have alternative states of clear water dominated by benthic macrophytes, or alternatively turbid waters dominated by phytoplankton (Scheffer 1997). Inputs of phosphorus can lead to phytoplankton blooms which shade out the macrophytes, increasing the resuspension of sediments and maintaining high phosphorus availability in the water column, even if the initial input is greatly reduced.

Theoretical studies suggest alternative stable states readily arise in multispecies (van Nes and Scheffer 2004) interaction webs or because of life history complexities. For instance, a classic model of insect population regulation (Holling 1973) portrays control by avian predators with type 3 functional responses, which is effective at regulating prey when prey recruitment rates are low. A sudden increase in resources can permit recruitment to outstrip predation, permitting the population to grow until it is limited by exploitative competition or direct density dependence. However, little theoretical work seems to have been done on characterizing quantitatively the magnitude of the perturbation (e.g., resource pulses) required to move among alternative stable states. In a general way, what matters is the rapidity and strength with which negative feedbacks act after a system is perturbed from equilibrium, and the operation of time lags (e.g., due to indirect interactions, or life history effects such as developmental lags). This is a challenging problem, as it involves examination of the entire nonlinear domain of system behaviors beyond the usual scope of linearized analyses.

PULSES AS RECURRENT EVENTS

It is useful to analyze population and community responses to singular pulses, but in nature many resource pulses recur over some time scale. In temperate forests, early each year on the forest floor spring ephemeral herbs enjoy seasonal resource flushes of light and nutrients (Anderson and Eickmeier 1998), and streams each fall experience a pulse of dead organic matter that sustains a rich community of detritus feeders. Over longer time scales, multi-annual geophysical forces such as El Niño events cause episodic pulses. Intrinsically unstable dynamics in any member of a community can drive recurrent resource pulses for other community members. Synchronized life histories such as periodical cicadas and masting trees provide dramatic examples of resource pulses that for short-lived con-

sumers recur at multigenerational scales. Such recurrent pulses are an intrinsic part of the spectrum of temporal variability that defines the environment for many species. Such species should be adapted to recurrent pulses, and may even evolve to utterly depend upon them. All species that persist in the face of recurrent resource pulses must have mechanisms for tolerating or avoiding negative aftereffects of resource pulses, (e.g., intensified density dependence or time-lagged increases in predation or competition during later resource troughs). The theoretical mission is to ascertain how the system as a whole exhibits unique features that would be absent, were resource pulses not reliably present in the palette of temporal environmental variability.

One widespread evolutionary response to recurrent resource pulses is the evolution of storage mechanisms such as internal fat bodies or external hoards (e.g., seed caches in desert rodents). Getz (1999) has argued that incorporating storage mechanisms into food web dynamics has important yet underappreciated implications for how ecological systems function. Abrams (2005) likewise suggests that adaptive behaviors can alter the qualitative responses of ecological systems to perturbations. There is a huge theoretical literature on temporal variability in population and community ecology relevant, at least indirectly, to analyzing the effects of recurrent resource pulses (e.g., Nisbet and Gurney 1982, Greenman and Benton 2005). I do not attempt a complete synthesis, but instead touch upon salient issues, all warranting more theoretical study.

Population-level responses to recurrent resource pulses

One ubiquitous pattern of temporal variation in resources is periodic variation. For instance, seasonal fluctuations lead to annual booms and busts in resource supply. Nisbet and Gurney (1976) showed that periodic forcing of intrinsic oscillations leads to resonance phenomena; several authors have since explored this idea, using models such as the predator-prey model (Eq. 1) above with periodic variation in the parameters (e.g., Rinaldi and Muratori 1993, Turchin and Hanski 1997). If the prey's intrinsic growth rate r is scaled by resource availability, periodic fluctuations in resources will drive periodic variation in r . King and Schaffer (1999) examine the rich dynamical behaviors emerging from the interplay of intrinsic predator-prey oscillations and periodic fluctuations in prey r , for the model in Eq. 1, and a three-species food chain. They show that subharmonic resonance generates cycles with a much longer period than the annual cycle, and chaos, with small parameter differences (e.g., in pulse magnitude) generating large differences in realized dynamics. Resonance phenomena do not require precisely periodic inputs, but can emerge with more approximate periodic drivers.

Recurrent pulses can strongly affect average population size, either to depress or increase it, depending on

how resources influence demography. Consider the classical discrete logistic growth equation, with temporal variation in either r or K :

$$N(t+1) = r(t)N(t) \left[1 - \frac{N(t)}{K_0 + \varepsilon(t)} \right].$$

Here $N(t)$ is population size in generation t , $r(t)$ is (time-varying) inherent growth rate, K_0 is average carrying capacity, and $\varepsilon(t)$ denotes deviations in K (with a mean deviation of zero). Resource pulses can drive variation in either r or K . Periodic variation in K depresses time-averaged mean abundance below K_0 (Nisbet and Gurney 1976). By contrast, periodic variation in r can increase average abundance (Cushing 1987).

An interesting series of papers extended the Ricker model for single-species density-dependent systems to include periodic fluctuations in resources (Henson and Cushing 1997, Henson et al. 1999, Henson 2000) so as to interpret laboratory experiments with *Tribolium* beetles sustained by fluctuating food resources (Jillson 1980). Jillson's experiments found that periodic fluctuations in the resource base (flour) increased average beetle numbers. Henson and Cushing (1997) show this effect occurs when inherent larval recruitment is high, and there are moderate resource oscillations. In part, this mechanism reflects the fact that cannibalism rates rise when resources are scarce, which then prevents the kind of overshoots shown in Fig. 1. Orland and Lawler (2004) carried out microcosm experiments with the ciliate protist *Colpidium striatum*, with periodic alternation of high and low nutrients. Resonance between this forced variation and intrinsic population processes increased average abundance. They argued that metabolic nonlinearities boosted average population size; resource storage during resource-rich times buffers population decline during resource-poor times. Another important population attribute is extinction risk. I argued above that a resource pulse can lead to a time-lagged crash in numbers during the resource trough that follows a resource pulse. If there is a nonzero probability of extinction during this crash, given recurrent pulses, a population faces a relentlessly recurring danger; in the absence of countervailing mechanisms for persistence through resource troughs, or dispersal among sites in a metapopulation, ultimate extinction is certain.

Community-level responses to recurrent resource pulses

The best-studied (from a theoretical perspective) community issue involving recurrent resource pulses is competitive coexistence in temporally variable environments. Theoretical studies of nonequilibrium coexistence have been thoroughly reviewed elsewhere (e.g., Chesson 2000). It has long been known that fluctuating resource supplies can permit competitive coexistence on a single resource (Stewart and Levin 1973). Such coexistence requires nonlinear responses to resources and can be facilitated by internal storage (Grover 1991) or life history stages that buffer population decline (the storage

effect [Chesson 2000]). Sommer (2002) reports interesting chemostat experiments where competing phytoplankton were disturbed by dilution of the medium, with different intervals separating dilution episodes. These experiments can be interpreted as providing resource pulses of varying lengths. In general, recurrent disturbance in resource levels facilitated competitive coexistence, with maximum diversity at intermediate dilution intervals.

Thus, resource pulses sometimes sustain species diversity. But pulses can also destroy classical mechanisms of coexistence for competitors, such as resource partitioning and keystone predation. In predator-prey interactions, given trade-offs between exposure to predation and resource consumption, a large increase in resources can relax top-down control, in turn leading to unstable dynamics (e.g., as in models for insect outbreaks [Holling 1973]). Competitive existence rests on the interplay of equalizing mechanisms preventing any species from ever having too large a fitness advantage, and stabilizing mechanisms permitting growth for species when rare (Chesson 2000). Large perturbations can destroy the efficacy of such mechanisms. In resource-ratio models, for instance, a surge in availability of one resource can lead to competitive exclusion (R. D. Holt, *unpublished data*). Noonburg and Abrams (2005) have shown that transient dynamics can hamper coexistence due to keystone predation; resource pulses generate transient dynamics that push a community out of a locally stable equilibrium, with extinctions ensuing. In apparent competition (Holt 1977), the conditions for coexistence between alternative prey species depend upon prey carrying capacities. An overall increase in resources, lifting all prey species' carrying capacities, indirectly boosts predator numbers, and can lead to the elimination of prey species with relatively low intrinsic growth or high attack rates. It is premature to craft general conclusions about whether or not resource pulses generically facilitate maintenance of species richness.

RESOURCE PULSES IN SPATIALLY EXTENDED SYSTEMS

In open systems, a key strategy for coping with large-scale temporal variation, including resource pulses, is dispersal. Recent theoretical studies reveal a rich array of phenomena that emerge from the interplay of temporal variation, dispersal and spatial subsidies. Given dispersal, resource pulses can alter the size of species' ranges, permit persistence in unfavorable environments, generate spatial cascades, and affect how spatial fluxes govern the outcome of interspecific interactions. Space precludes a full treatment of these issues, so here I briefly summarize some key effects.

Allee effects, resource pulses, and species' ranges

Allee effects are defined to be a decline in per capita growth rate with declining densities, at low densities. With strong Allee effects, isolated populations at low

density tend toward extinction, even in favorable environments with positive carrying capacities. Keitt et al. (2001) proposed that the interplay of Allee effects and resource pulses could lead to sudden expansions in a species' distribution. They considered a species in patchy environments that initially has a stable distributional limit, because at the range edge, too few dispersers cross unsuitable habitat into suitable patches outside the range to overcome strong Allee effects. A strong resource pulse in occupied patches within the range can lead to population increases, permitting a surge in emigration to patches beyond the range margin, which could then temporarily reach the abundances needed for marginal populations to surmount their Allee thresholds. A spatially widespread resource pulse could permit multiple populations to become established outside the prior range margin, setting up new sources of colonists for yet further colonization. This snowballing effect initiated by a resource pulse can foster a rapid increase in the size of the occupied range, which remains expanded even when resources settle back to their original levels.

Local pulses as a specialized resource

Communities contain a mix of species with radically different "spatial strategies" (adaptations for coping with spatiotemporal variation). If resource pulses are spatially asynchronous, some species can adapt via dormancy or dispersal to track those locally transient pulses, with many community-level consequences. Entire guilds (e.g., desert annual plants) may only exist because dispersal or resting stages allow persistence along with the exploitation of spatially and temporally localized resource pulses. Even random, undirected dispersal can permit the indefinite persistence of species in patchy environments, where on average all local patches are demographic sinks, if temporal variation in growth rates is positively autocorrelated (Roy et al. 2005; see Matthews and Gonzalez [2007] for an experimental confirmation). Ives et al. (2004) show in an experiment and in models that in persistent metapopulations not comprised of sinks, dispersal in temporally varying environments can enhance total population size. Local resource pulses creating temporary localized phases of positive population growth can provide the needed pattern of temporal variation for these metapopulation processes to work. Persistence is further enhanced when there are patchy, spatially uncorrelated resource pulses, if individuals can exhibit adaptive habitat selection by choosing to settle and remain in patches with transient high resource levels (Schmidt 2005).

Pulses, spatial cascades, and coexistence

If a consumer becomes dormant or migrates when resources are scarce, this can create a de facto refuge for the resource, which is less likely to be driven to low numbers. Such labile responses also permit specialist consumers to persist between pulses of their required

resources, in effect constructing a viable niche (Odling-Smee et al. 2003) by stitching together temporally spaced periods of resource abundance. But theoretical models suggest that sometimes adaptive habitat choice by consumers can be destabilizing when resource pulses are spatially localized; after a resource pulse occurs in one habitat, consumers should aggregate there, build up in numbers, and then disperse to adjacent patches when those resources are depleted (Abrams 2000). Dispersal by consumers, post-pulse, can create a much larger spatial footprint of the resource pulse than defined by just the site where it occurred. Local resource pulses can also end up as spatial subsidies elsewhere (Anderson et al. 2008). Localized pulses can thus generate waves of indirect effects rippling out over a large landscape (R. Holt, *unpublished results*). In open systems where a species is maintained by immigration, local resource pulses can reverse local competitive dominance in a given habitat patch or exclude locally superior prey species (Holt 2002, Holt and Barfield 2003, Holt et al. 2003). In exploitative or apparent competition, a locally superior species can be supplanted by an inferior species which immigrates at a sufficient rate; a resource pulse elsewhere in the landscape can lead to a surge in immigration of inferior species, knocking locally superior species to low densities where extinction is likely. Thus, resource pulses can magnify the impact of regional processes on local communities.

CONCLUSIONS

In the long run, the two perspectives on resource pulses sketched above—tracking a singular pulse through a system and examining the system properties that emerge in a regime of recurrent pulses—are complementary. By evaluating in detail how a single resource pulse reverberates through a community, one develops insights (e.g., into the time scales and magnitudes of transient responses) that inform one's understanding of systems where resource pulses recur over a characteristic time scale. In turn, focusing on the long-term structural consequences of recurrent resource pulses helps define what counts as the "normal" state of the system. At times, resource pulses endanger local persistence, since after every pulse is an inevitable trough. This is particularly true when the pulses exceed those experienced in the evolutionary history of the species. But in other systems resource pulses may be essential for persistence. Usually, this requires adaptations permitting the resource to be exploited, while avoiding the impact of periods of resource shortfalls and elevated predation, and often involves dispersal in open systems. The interplay of interspecific interactions and resource pulses reveals considerable dynamical complexity. Resource pulses may permit shifts between alternative stable states, with impacts on community structure much longer lasting than the pulse itself. More broadly, grappling with resource pulses suggests a reorientation of community ecology toward a concern with life history

variation, plastic responses, and transient dynamics as key dimensions of species coexistence and community stability (Sears et al. 2004).

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