

## WHAT CAN WE LEARN FROM RESOURCE PULSES?

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**Abstract.** An increasing number of studies in a wide range of natural systems have investigated how pulses of resource availability influence ecological processes at individual, population, and community levels. Taken together, these studies suggest that some common processes may underlie pulsed resource dynamics in a wide diversity of systems. Developing a common framework of terms and concepts for the study of resource pulses may facilitate greater synthesis among these apparently disparate systems. Here, we propose a general definition of the resource pulse concept, outline some common patterns in the causes and consequences of resource pulses, and suggest a few key questions for future investigations. We define resource pulses as episodes of increased resource availability in space and time that combine low frequency (rarity), large magnitude (intensity), and short duration (brevity), and emphasize the importance of considering resource pulses at spatial and temporal scales relevant to specific resource–consumer interactions. Although resource pulses are uncommon events for consumers in specific systems, our review of the existing literature suggests that pulsed resource dynamics are actually widespread phenomena in nature. Resource pulses often result from climatic and environmental factors, processes of spatiotemporal accumulation and release, outbreak population dynamics, or a combination of these factors. These events can affect life history traits and behavior at the level of individual consumers, numerical responses at the population level, and indirect effects at the community level. Consumers show strategies for utilizing ephemeral resources opportunistically, reducing resource variability by averaging over larger spatial scales, and tolerating extended interpulse periods of reduced resource availability. Resource pulses can also create persistent effects in communities through several mechanisms. We suggest that the study of resource pulses provides opportunities to understand the dynamics of many specific systems, and may also contribute to broader ecological questions at individual, population, and community levels.

**Key words:** accumulation and release; alternative stable states; delayed top-down effects; diet shifts; population outbreaks; pulsed resources; pulse–reserve; resource pulses; spatial and temporal variation; storage.

### INTRODUCTION

Although spatial and temporal variability are widely acknowledged to be important attributes of natural systems, ecologists are just beginning to integrate rare but large-magnitude events of resource availability into a general view of ecology. In recent years, the study of resource pulses has progressed from specific investigations in particular systems to a recognition that common characteristics and similar processes may underlie pulsed resource dynamics in a wide range of systems. The emerging ecology of resource pulses seeks to gather general insights into the causes and consequences of resource pulses from across the diversity of pulsed systems in nature.

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The study of resource pulses contributes to a broader understanding of natural systems for two reasons: first, because many natural systems are directly influenced by some pulsed resource component, and second, because resource pulses provide opportunities to investigate general questions in ecology. Resource pulses have been described in arid deserts and islands (Polis et al. 1997, Grant et al. 2000, Jaksic 2001, Meserve et al. 2003, Letnic et al. 2005), coral reefs (McCormick 2003), marine upwelling ecosystems (Vanboekel et al. 1992, Bode et al. 1997), lakes and rivers (Carlton and Goldman 1984, Wipfli et al. 1998, Vanni et al. 2001), coastal marshes (Gratton and Denno 2003), riparian floodplains (Nakamura et al. 2005) and boreal, temperate, and tropical forests (Lodge et al. 1994, Ostfeld et al. 1996, Wolff 1996, Jędrzejewska and Jędrzejewski 1998, Zackrisson et al. 1999, Curran and Leighton 2000, McShea 2000, Alley et al. 2001, Koenig and Knops 2001, Lithner and Jonsson 2002, Yang 2004). Brief events of resource availability account for a substantial proportion of all available resources in some systems, and it is increasingly evident that rare events can have

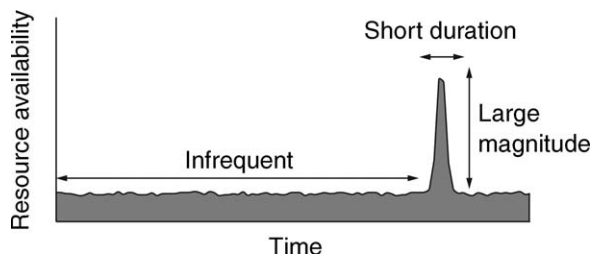


FIG. 1. Resource pulses are events of increased resource availability over time that combine low frequency, short duration, and large magnitude.

important and sometimes persistent effects on a wide range of communities (Ostfeld and Keesing 2000). A general understanding of how natural communities respond to these events would be directly relevant to a diversity of systems.

Studying the course of events leading up to, and arising from, resource pulses in natural communities may also provide valuable opportunities to investigate fundamental questions in ecology. In this overview, we explore how resource pulses can serve as natural experiments, allowing ecologists to track the indirect effects of strong perturbations in complex ecological networks. For example, the study of resource pulses can elucidate the structure of communities, clarify the roles of bottom-up and top-down effects in population dynamics, and document the attenuation of indirect effects over successive interactions. Resource pulses can also provide a natural context to investigate the stability, resilience, reactivity, and maximal amplification of ecological systems in response to perturbations (Neubert and Caswell 1997, Holt 2008). The study of resource pulses can show how ecological communities respond to temporal resource variability on multiple levels by suggesting patterns of physiological and behavioral responses to resource variability, revealing community links across habitat boundaries, and illustrating mechanisms of species coexistence.

We seek to contribute to a common framework for studying resource pulses by developing some general questions and conceptual syntheses in this emerging field. This paper does not seek to provide a comprehensive review. Instead, we have three specific goals: first, to propose a general definition of the resource pulse concept; second, to identify some common patterns in the causes and consequences of resource pulses; and third, to outline emerging directions, key questions and potential approaches for investigating the ecology of resource pulses in the future.

#### DEFINING RESOURCE PULSES

The concept of the resource pulse unifies a diverse class of events across a wide range of ecosystems that have in common the feature of being rare, brief, and intense episodes of increased resource availability in space and time. Because spatiotemporal variability in

resources is ubiquitous, however, a useful and general definition of resource pulses must be defined in relation to the background of natural variation.

#### *Building a definition*

Previously published descriptions of resource pulses suggest some common elements that could form the basis of a conceptual definition. Resource pulses have been variously described as “the temporary availability of dramatically higher than normal levels of resources, which then become depleted with time” (Ostfeld and Keesing 2000), the “intermittent production of abundant resources for consumers” (Schmidt 2003), “uncommon events of ephemeral resource superabundance” (Yang 2006), and “brief, infrequent event[s] of high resource availability” (Yang 2004). Using different words, these definitions all describe episodes of increased resource availability that combine low frequency (rarity), large magnitude (intensity), and short duration (brevity; Fig. 1).

Notable examples of resource pulses that fit this broad definition include periods of unusually heavy precipitation (Polis et al. 1997, Grant et al. 2000, Jaksic 2001); the mast production of flowers, fruits, or seeds (Kelly 1994, Wolff 1996, Ostfeld et al. 1996, Curran and Leighton 2000, McShea 2000); insect outbreaks or aggregations (Carlton and Goldman 1984, Haney 1999, Yang 2004); large inputs of animal carcasses, dung, or urine (Rose and Polis 1998, Peek and Forseth 2003, Wilmers et al. 2003, Yang 2006); eruptions of small mammal populations (Jaksic et al. 1997, Lithner and Jonsson 2002, Schmidt and Ostfeld 2003); synchronous coral spawning events (McCormick 2003); hurricane-triggered greenfalls in tropical forests (Lodge et al. 1994); storm-driven nutrient runoffs from terrestrial systems into aquatic or marine systems (Vanni et al. 2001, Gratton and Denno 2003); and episodic coastal upwellings of nutrient-rich deep water (Bode et al. 1997).

Observations from many natural systems suggest that resource pulses are often extreme events in a continuum, rather than a discrete and separate class of phenomena. In many (though perhaps not all) systems that we have examined, the frequency distribution of resource availabilities over units of time or space is more or less continuous and unimodal, often with a long tail of extreme values and no obvious separation between resource pulse events and background resource variability (Fig. 2). These observations suggest that clear distinctions between resource pulses and ongoing variability are not generally possible. Although system-specific definitions of resource pulses (establishing a threshold density of seeds to define a mast year or using quantile cutoffs to identify rainfall pulses, for example) can be objective, useful, and pragmatic, these methods belie the continuous nature of resource variability in many systems (Weatherhead 1986). Instead of asking whether an event *is* a resource pulse, it may be more

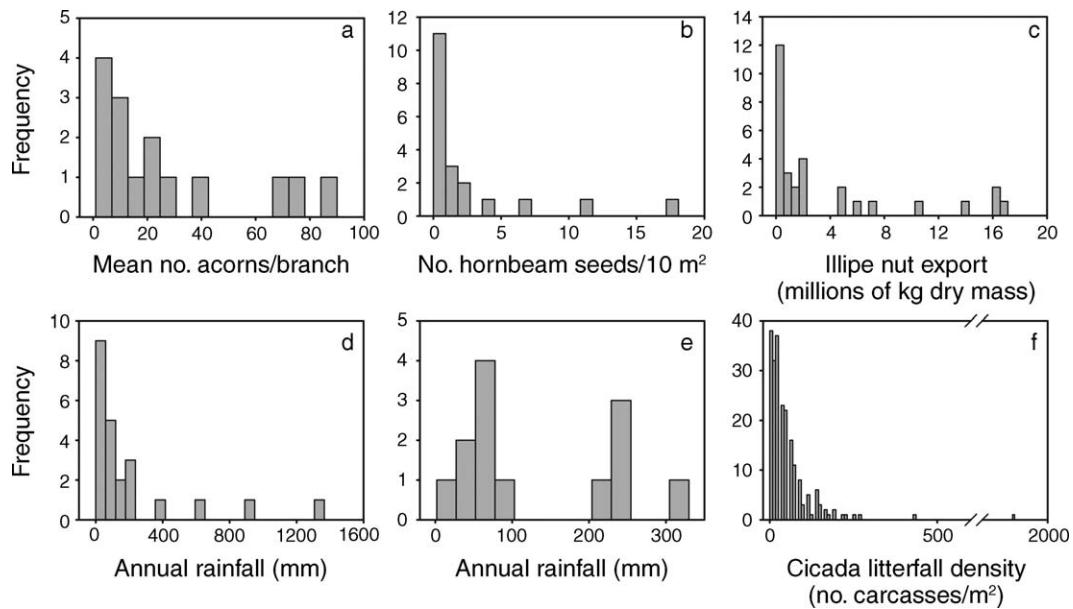


FIG. 2. Frequency distributions of variable resource availabilities in (a–e) time series and (f) space. (a) Mean number of acorns per branch at the Mountain Lake Biological Station, Virginia, USA between 1980 and 1993 (Wolff 1996), (b) density of hornbeam seeds at the Białowieża Primeval Forest, Poland, between 1972 and 1990 (Pucek et al. 1993), (c) illipe nut (*Shorea* spp.) exports from West Kalimantan province, Borneo between 1968 and 1997 (Curran and Leighton 2000), (d) annual rainfall totals on the Galápagos archipelago, Ecuador, between 1976 and 1998 (Grant et al. 2000), (e) annual rainfall totals at Fray Jorge, Chile between 1976 and 1998 (Meserve et al. 2003), (f) cicada carcass deposition in 216 traps at 18 locations over a range of 120 km during the 2004 emergence of Brood X periodical cicadas in the eastern United States (Yang 2004).

useful to ask how variation in the magnitude, duration and frequency of resource inputs influences their ecological consequences. This perspective shifts the focus to questions of degree: What are the characteristics of resource inputs in a system? Increasingly, studies have begun to investigate the variability of resource inputs explicitly (Schwinning and Sala 2004, Sher et al. 2004).

We suggest that resource pulses should be defined relative to the resource variability experienced by specific consumers, and at spatial and temporal scales relevant to these resource–consumer interactions. The essential elements that describe the pulsed nature of these events—low frequency, large magnitude, and short duration—are implicitly defined relative to the perspective of resource consumers. The key insight that emerges from the consideration of scale dependence is that a substantial resource pulse event for one consumer may recede into a noisy background of temporal variability from the perspective of a longer-lived consumer (Fig. 3), or represent minor local variation for a highly mobile consumer that integrates over a larger area. For example, mast seeding events are a substantial pulsed resource for short-lived mammalian granivores, but the decomposition of the many uneaten dead seeds is likely to be an inconsequential episode of nutrient variability for long-lived trees (Zackrisson et al. 1999). Similarly, animal carcasses may be resource pulses for local consumers but not for wide-ranging scavengers. Defining resource pulses in a consumer scale-dependent framework gives insight into why different consumers within a system may

respond differently to a particular increase in resource availability, and why some may not appear to respond at all. Considering the baseline resource availability experienced by consumers suggests that resource pulses which occur during periods of relative scarcity may have greater effects than similar pulses which occur during periods of greater availability. In addition, defining resource pulses relative to the scale of resource consumers may allow more general insights into the dynamics of resource pulses across different systems.

In this overview, we focus on resource pulses that are likely to represent a substantial perturbation for consumers. These events provide unique opportunities to observe community structure and dynamics in response to a perturbation, and provide a less ambiguous subset of pulsed systems for this overview. In contrast, consumer responses to consistent and recurring resource inputs such as deciduous litterfall may be strongly affected by the reliability of future resources. Though often important and sizable fluxes, consistently recurring resource inputs are likely to become part of a predictable pattern of background resource variability, and these inputs probably don't represent substantial perturbations to the community. However, systems with recurring resource inputs can also experience occasional events that are unpredictable in their timing, magnitude and location, and we consider these in the context of pulsed resources. For example, acorn (*Quercus* spp.) production varies widely from year to year (Koenig and Knops 2000) and many ant and termite nuptial flights are triggered by

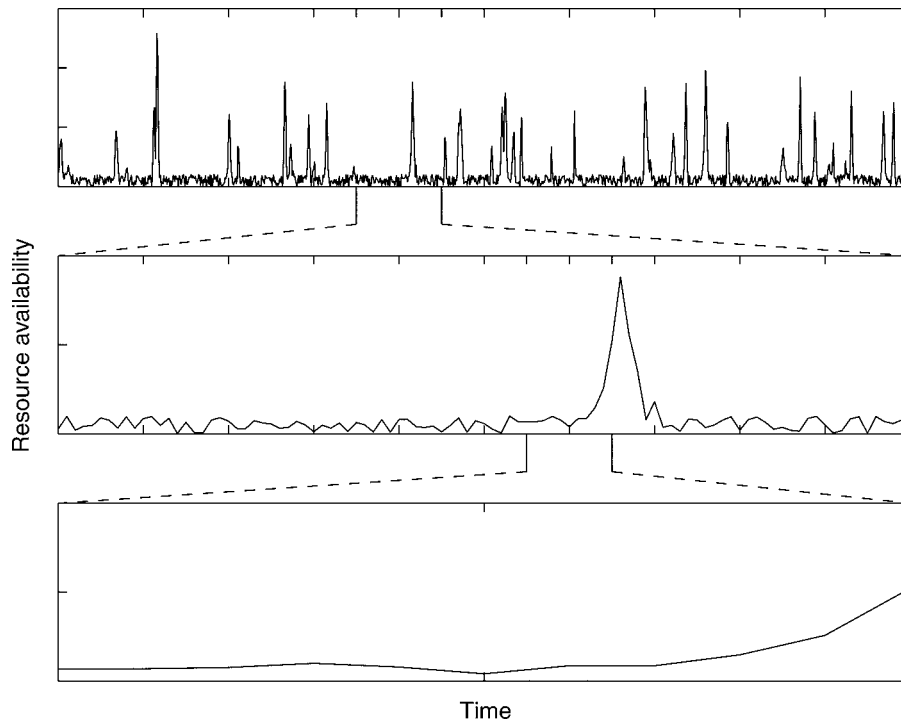


FIG. 3. A schematic illustration of simulated resource variability over three time scales that differ by an order of magnitude.

locally unpredictable rainfall cues (Cole and Wiernasz 2000). In these systems, the occurrence of some resource input is predictable, but the magnitude, timing, or location of the inputs is probably not (but see Boutin et al. 2006). In a few systems, events may be reliable in an absolute sense, but still remain unanticipated by consumer populations. For example, both El Niño episodes and 13- and 17-year periodical cicada (*Magicicada* spp.) emergences are predictable events, but are not anticipated by most potential resource consumers. We include such resource inputs in our investigation when they show the essential characteristics of a resource pulse (i.e., rarity, intensity, and brevity) combined with some important aspect unpredictability for their consumers. We hope that this general definition and the corollary consumer-scaled perspective may facilitate testable predictions about how differences in the characteristics of pulsed systems modulate their effects.

#### CAUSES OF RESOURCE PULSES

Although each resource pulse has specific ecological drivers, a broad view of the literature suggests a few recurring causal processes in multiple systems. Although these categories are neither entirely distinct nor mutually exclusive, we propose the following general mechanisms as a preliminary framework to examine the causes of resource pulses.

##### *Climatic and environmental causes*

Many resource pulses are caused by climatic or environmentally driven events. For example, El Niño

Southern Oscillation (ENSO) episodes create important pulses of soil moisture in many arid environments (Polis et al. 1997, Jaksic 2001, Schwinning et al. 2004, Letnic et al. 2005). Unusual precipitation events, sometimes in combination with postfire erosion, can also contribute to pulsed nutrient runoffs from terrestrial systems into aquatic systems (Benavides-Solorio and MacDonald 2001, Vanni et al. 2001, Gratton and Denno 2003). Although many floodplain systems are characterized by seasonally recurring disturbance and resource inputs, extreme flooding events could represent infrequent resource pulses of accumulated nutrients for outlying areas (Nakamura et al. 2005).

In many cases, climatically driven resource pulses co-occur as one component of a larger perturbation. Many combine multiple resource pulses, or include both pulsed resources and physical disturbance. For example, pulses of rainfall in arid environments often mobilize nutrients in the soil, creating simultaneous pulses of soil moisture and nutrients (Cui and Caldwell 1997, Polis et al. 1997, Anderson and Polis 1999). Similarly, hurricanes create windfalls of green litterfall in tropical forests, and these resource pulses often co-occur with tree falls and the creation of forest gaps (Brokaw and Walker 1991, Lodge and McDowell 1991, Lodge et al. 1991, Tanner et al. 1991, Whigham et al. 1991, Ostertag et al. 2003).

Climatically driven resource pulses are of particular interest to ecologists in light of global climate change. Many climate change models predict increasing climatic variability as a consequence of anthropogenic global warming, resulting in extreme weather events that are

more frequent, more intense, or both (Easterling et al. 2000, Meehl et al. 2000, Parmesan et al. 2000, Intergovernmental Panel on Climate Change and Working Group I 2001, Loik et al. 2004). This rapid environmental change may alter characteristics of extreme climatic events, with direct effects in pulse-driven ecosystems.

#### *Temporal accumulation and release*

Many resource pulses result from a process of temporal resource accumulation and release. This mechanism describes the gradual protected storage and sudden triggered availability of resources in some component of the ecosystem. In many systems, these resource pulses are associated with reproductive events. For example, nymphal periodical cicadas feed on plant roots for 13 or 17 years before emerging synchronously during their final reproductive year, providing a resource pulse for many consumers (Marlatt 1907, Yang 2004). Similarly, the synchronous release of propagules from sessile marine organisms (Clifton 1921, Babcock et al. 1992, McCormick 2003) and the mast production of flowers, seeds, and fruit in many species of trees and bamboo (Janzen 1974, 1976, Kelly 1994, Keeley and Bond 1999, Koenig and Knops 2000, Schaubert et al. 2002, Jaksic and Lima 2003) result from a process of resource accumulation and reproductive release. Not all temporally stored resource pulses are associated with reproductive events, however. For example, whale carcasses represent temporally stored resources for consumers in both terrestrial and marine systems (Polis and Hurd 1996, Rose and Polis 1998, Smith and Baco 2003). In all of these examples, resources are gradually accumulated over time and then suddenly released to consumers as a resource pulse.

#### *Spatial accumulation and release*

Resource pulses may also provide energy and nutrients that have been accumulated and transported over space, which are then released suddenly to consumers in a recipient community; these inputs could be described as pulsed subsidies (Fig. 4). From the perspective of local consumers in the recipient habitat, pulsed subsidies combine the dynamics of a resource pulse with the spatial transport of a subsidy (Sears et al. 2004, Anderson et al. 2008). For example, hurricanes and storms in the Atlantic Ocean can dislodge, aggregate, transport, and deposit pulsed subsidies of drifting seaweed into terrestrial systems (Blomquist and Pylon 1943). Similarly, storm-driven runoffs from agricultural or fire-influenced terrestrial systems represent nutrient pulses that have been accumulated and transported from a donor watershed to a recipient aquatic system (Novak et al. 2003, Caraco and Cole 2004, Ice et al. 2004, Kim et al. 2006). Whether resources are spatially stored, temporally stored, or both, these processes of accumulation and release can deliver ephemeral resource pulses that exceed rates of local productivity.

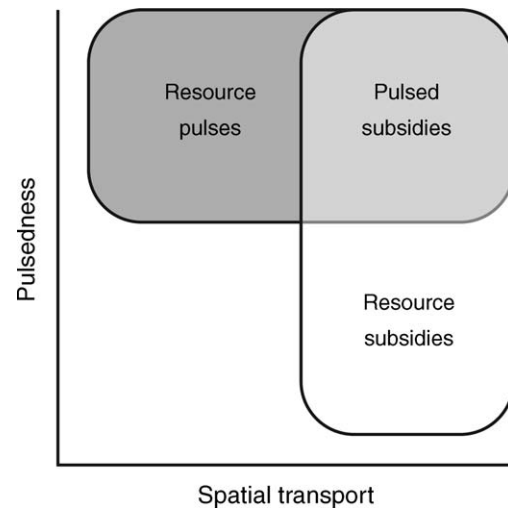


FIG. 4. A Venn diagram illustrating relationships among resource pulses, spatial subsidies, and pulsed subsidies.

#### *Outbreak population dynamics*

A tremendous amount of theoretical and empirical work has been invested in understanding the factors that cause population outbreaks (Harmsen et al. 1976, Rose and Harmsen 1981, Wallner 1987, Blarer and Doebeli 1999). However, relatively few studies have investigated how outbreak dynamics contribute to resource pulses. Population outbreaks can create resource pulses for consumers through direct trophic interactions, or indirectly via the non-trophic effects of outbreaking species. For example, predators consume outbreaking populations of small mammals in a wide range of communities (Jaksic et al. 1997, Schmidt and Ostfeld 2003, Letnic et al. 2005) and eruptive populations of forest insects are commonly consumed by birds (Fayt et al. 1915, Morris et al. 1958, Cooper and Smith 1995, Hoi et al. 2004, Hogstad 2005). The indirect non-trophic effects of outbreaking populations include the deposition of nutrient-rich frass and foliage greenfall resulting from forest herbivore outbreaks (Risley and Crossley 1988, 1993, Reynolds and Hunter 2001, Lovett et al. 2002, Frost and Hunter 2004).

#### EFFECTS OF RESOURCE PULSES

Resource pulses can affect consumer responses at the individual level, numerical responses at the population level, and create indirect effects at the community level. We suggest some general patterns of resource pulse effects that have emerged at each level of organization.

#### *Consumer responses at the individual level*

Several studies have suggested that mobile specialist and opportunistic resident consumers represent two common strategies among animal consumers that use pulsed resources (Curran and Leighton 2000, Ostfeld and Keesing 2000, Lithner and Jonsson 2002, Meserve et al. 2003). Mobile specialists often travel long distances

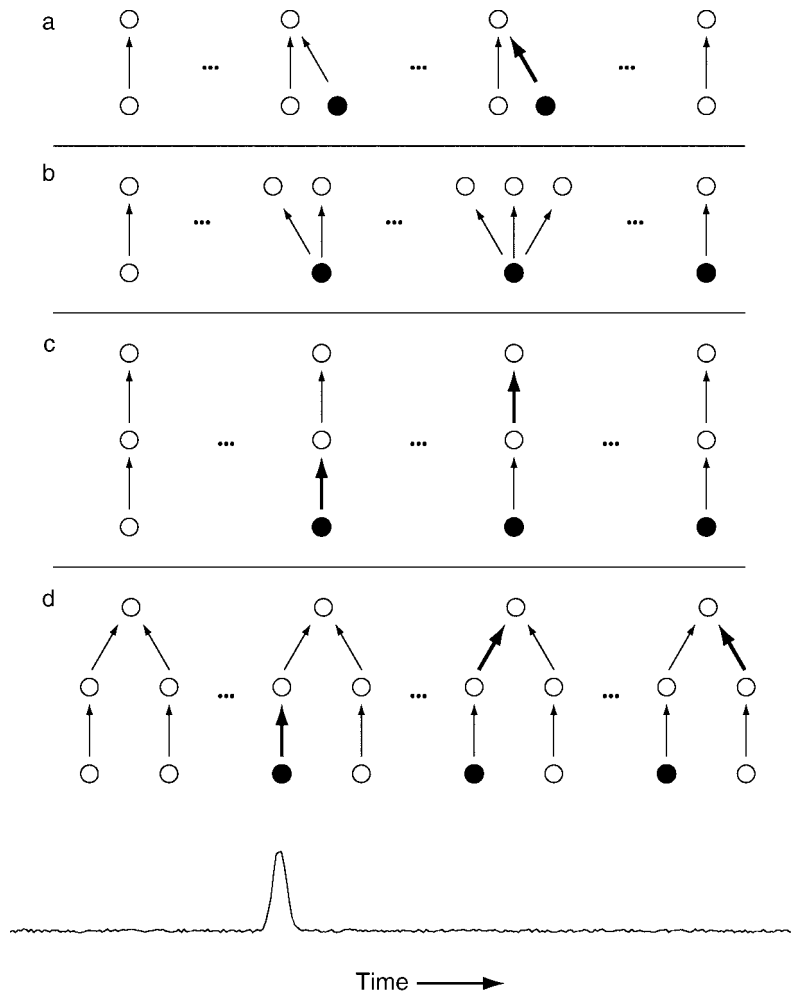


FIG. 5. Some community responses to resource pulses over time. Each row represents a dynamic community vignette at four time points, where the first vignette represents the pre-pulse condition. The timing of pulsed resource availability relative to these vignettes is indicated by the line at the bottom of the figure. Arrows represent the flow of resources between community components, where the width of arrows represents the magnitude of resource fluxes. Short dotted lines indicate separation in time, solid circles represent initial pulsed resource components, and open circles represent other members of the community vignette besides the resource pulse component. (a) Diet switching: a predator chooses to consume a newly available pulsed resource. (b) Behavioral aggregation: new consumers immigrate to a local area when resources are abundant and leave when resources diminish. (c) Direct bottom-up and delayed top-down effects along a trophic chain. (d) Bottom-up and top-down effects with apparent competition: a pulsed resource increases predation on a non-pulsed alternative prey.

to utilize patchy and asynchronously pulsed resources; in extreme cases, they may be able to reduce the apparent pulsedness of the resource inputs through spatial averaging. Examples of mobile and relatively specialized consumers include carrion beetles (Silphidae) feeding on periodical cicada carcasses (Yang 2006), the extinct Passenger Pigeon (*Ectopistes migratorius*) feeding on acorn mast events (Blockstein and Tordoff 1985, Blockstein 2002), and Long-tailed Parakeets (*Psittacula longicauda*) as consumers of dipterocarp mast in Bornean forests (Curran and Leighton 2000). In contrast, opportunistic residents are often widespread in their distribution and sufficiently generalist in their diet to recognize and use an infrequently available resource. Examples of opportunistic residents include

ground beetles (Carabidae) feeding on cicada carcasses (Yang 2006), white-footed mice (*Peromyscus leucopus*) feeding on acorn mast (Ostfeld et al. 1996), or brown spiny rats (*Maxomys rajah*) feeding on dipterocarp fruit mast (Curran and Leighton 2000).

Many generalist consumers opportunistically alter their diets in response to ephemeral pulses of resource availability (Fig. 5a). For example, the diets of American black bears (*Ursus americanus*) in Massachusetts, USA included a much greater proportion of acorns (*Quercus rubra*) in mast years than in non-mast years (McDonald and Fuller 2005). Similarly, damselfish (*Pomacentrus amboinensis*) focused on nutrient-rich coral propagules almost exclusively during a brief period of coral spawning in the Great Barrier Reef, Australia

(McCormick 2003). Opportunistic diet shifts in response to pulsed resources have been observed in many other systems, including passerine birds feeding on insect pulses (Anderson 1977, Steward et al. 1988, Hoi et al. 2004, Hogstad 2005); foxes, gulls, and owls consuming rodent outbreaks (Jaksic et al. 1997, Ruiz and Simeone 2001); sea otters feeding on spawning lump sucker fish (Watt et al. 2000); and rodents consuming pulses of insects (Hahus and Smith 1990). The diet-switching behavior of consumers is a general mechanism for the accelerating region of a sigmoidal (type III) functional response (Murdoch 1969), and may drive complex patterns of community dynamics in many pulsed systems (Oaten and Murdoch 1975a, b, Elliott et al. 1996, Schmidt and Ostfeld 2003, 2008, Turchin 2003).

The plants of arid environments show several strategies for utilizing pulses of soil moisture and mobilized nutrients, and tolerating dry interpulse intervals (Miao and Bazzaz 1990). According to the "pulse-reserve" paradigm, large inputs of rain initiate increased plant productivity in arid environments, some of which is diverted to reserve components (such as seeds or storage organs) that are better able to persist through the dry interpulse period (Noy-Meir 1973). Many plants also show plastic root growth (Hodge 2004) or rapidly increased uptake (BassiriRad et al. 1999, Ivans et al. 2003, James and Richards 2005, 2006) in order to capitalize on ephemeral and patchy resource pulses. For example, creosote bush (*Larrea tridentata*) was observed to assimilate soil nitrogen into leaves within 28 hours after a simulated summer rainfall event (BassiriRad et al. 1999). However, plants adapted to respond to ephemeral pulses with rapid growth or uptake may be less able to tolerate long interpulse intervals, reflecting trade-offs between adaptive responses to pulsed availability and long interpulse periods (Goldberg and Novoplansky 1997, Chesson et al. 2004, Sher et al. 2004). The range of strategies employed with plants in arid environments may be indicative of those employed by sessile resource consumers in other pulse-driven systems.

#### *Numerical responses at the population level*

The direct bottom-up effects of resource pulses are evident in many systems (Ostfeld and Keesing 2000). The numerical responses of consumer populations to these events may be driven by behavioral aggregative responses (Fig. 5b), increases in reproduction, or some combination of both processes. For example, nomadic owls aggregated rapidly in response to increased rodent densities following a beech (*Fagus* spp.) mast event, while populations of resident owls responded reproductively with a two-year delay (Lithner and Jonsson 2002). A similar pattern followed a masting event in a Bornean dipterocarp forest: although opportunistic residents were able to consume many fruits before the arrival of mobile specialists, the local density of nomadic consumers increased by behavioral aggregation well before the

reproductive increases of opportunistic residents (Curran and Leighton 2000).

Behavioral aggregation emphasizes links between local and surrounding communities, while reproductive responses illustrate the potential for local population growth. Behavioral aggregation is often a faster response to ephemeral periods of resource abundance, while delayed reproductive responses may have more persistent effects on local communities. Although the common assumption of faster behavioral responses and lagged reproductive responses appears to be broadly supported, a recent study demonstrated that two species of tree squirrels (*Tamiasciurus hudsonicus* and *Sciurus vulgaris*) anticipate the availability of seed mast with increased reproductive activity, suggesting that rapid reproductive increases can occur even in advance of pulsed resource availability (Boutin et al. 2006).

#### *Indirect effects at the community level*

Many resource pulses create indirect bottom-up effects that propagate across multiple trophic levels: as resource pulses increase the density of one consumer, these consumers themselves may become a secondary resource pulse for consumers at higher trophic levels. By tracking the direct and indirect effects that result from pulsed perturbations, ecologists can gain insight into both the structure and dynamics of community interactions. For example, the indirect effects of El Niño rainfalls in the Gulf of California, Mexico extended from increased primary productivity to affect insect herbivores, mammalian granivores, spiders and spider-eating parasitoid wasps, demonstrating the propagation of indirect effects over an interaction network (Polis et al. 1997, 1998, Anderson and Polis 1999, Stapp and Polis 2003).

Several studies suggest that resource pulses commonly initiate a predictable sequence of direct and indirect bottom-up effects, followed by strong delayed top-down effects (Ostfeld and Keesing 2000). Bottom-up and top-down processes are generally thought to operate simultaneously on populations in natural communities. In contrast, resource pulses often create substantial bottom-up and top-down effects that are somewhat more sequential, and less simultaneous (Fig. 5c). Following a resource pulse, top-down effects often lag behind the resumption of bottom-up control. For example, a phase portrait of small mammal prey densities and vertebrate predator densities during an El Niño-mediated population outbreak illustrates a counterclockwise path (Jaksic et al. 1997), indicating a pattern of prey-driven bottom-up dynamics followed by predator-driven top-down effects.

In some systems, predators may redirect their foraging efforts towards alternative prey in response to the declining phase of a resource pulse. This diet-switching behavior at higher trophic levels can result in a pattern of sequential apparent competition (Fig. 5d), rather than a directly over-compensatory top-down

effects along a trophic chain (Ostfeld and Keesing 2000, Sears et al. 2004). For example, acorn masts in central New York, USA have bottom-up effects on rodents and hawks, but both consumers increasingly feed on songbirds when pulsed resources become scarce (Schmidt 2003, Schmidt and Ostfeld 2003, 2008). A similar pattern occurs following beech (*Nothofagus* spp.) masts in some New Zealand forests, where beech mast increases populations of Yellow-crowned Parakeets (*Cyanoramphus auriceps*), mice (*Mus musculus*), and stoats (*Mustela erminea*), but stoats increasingly fed on bird populations following the depletion of beech seeds (King 1983, Murphy and Dowding 1995, Elliott et al. 1996, O'Donnell and Phillipson 1996, O'Donnell 1996a). Both of these systems indicate the importance of behavioral diet-switching mechanisms in community-level responses to resource pulses.

Parasites and pathogens could also play an important role in the top-down control of consumer populations responding to resource pulses, though relatively few studies have investigated these mechanisms specifically. Resource pulses commonly increase the density of consumer populations, potentially increasing the transmission of many parasites and diseases (Dobson and Meagher 1996, Jones et al. 1998, Miller et al. 2003, Altizer et al. 2006). For example, the incidence of vole tuberculosis (*Mycobacterium microti*) showed delayed dependence in cyclically fluctuating host populations (Cavanagh et al. 2004). While parasites and pathogens may plausibly exert substantial top-down effects following resource pulse-mediated population increases (Pedersen 2005), additional studies will be necessary to evaluate the generality of this pattern.

In a spatial context, patchily distributed pulses of resource availability may also create spillover effects in surrounding habitats. For example, some agricultural crops create patches of ephemeral resources that support high densities of predaceous insects, which exert top-down effects in adjacent habitats after harvest (Rand et al. 2006). A similar pattern of spillover top-down control results from the aggregated distribution of elk carcasses (*Cervus elaphus*) discarded by human hunters during a brief period of permitted hunting in the Greater Yellowstone ecosystem of Wyoming and Montana, USA (Wilmers et al. 2003). These elk carcasses attracted avian and mammalian scavengers, which exerted top-down effects on alternative prey in the surrounding area as carcass resources were depleted.

Resource pulses may also influence detrital consumers directly, as a result of consumer satiation. During periods of sudden and ephemeral resource superabundance, a substantial proportion of pulsed resource biomass can enter the detrital-based component of the ecosystem. During periodical cicada emergences, for example, most aboveground cicada consumers are rapidly satiated (Karban 1982, Williams et al. 1993, Williams and Simon 1995), and a large proportion of cicada biomass falls as detrital biomass (Yang 2004,

2006). A similar mechanism may contribute to the pulsed decomposition of spruce seeds following mast events (Zackrisson et al. 1999), and the deposition of alate ants in a subalpine lake (Carlton and Goldman 1984).

*Effects of resource pulses on competition, coexistence, and species diversity*

Considerable ecological thought has been focused on understanding how resource availability and temporal variability influence competition, coexistence, and species diversity (Wiens 1977, Chesson and Warner 1981, Keddy 1989, Chesson 1994, Caceres 1997, Chesson and Huntly 1997, Holt and Barfield 2003, Levine and Rees 2004, Chesson et al. 2004). A large body of work has examined how resource availability influences competition, but general insights have remained elusive (Wiens 1977, Keddy 1989, Craine 2005). Resource pulses may be readily integrated into this existing conceptual framework, especially building upon studies that have explicitly considered the temporal dynamics of resource availability (Goldberg and Novoplansky 1997), physiological responses to variable resource inputs (Schwinning and Sala 2004), increasing population size asymmetry in response to greater resource availability (Weiner 1990), and the effects of multiple shifting resource limitations (Weiner 1986, Wilson and Tilman 1993).

Resource pulses could contribute to coexistence if they create recruitment opportunities which allow reproductive potential to persist in populations (Chesson and Warner 1981, Warner and Chesson 1985). In particular, Chesson et al. (2004) emphasize that temporal variability in precipitation, including rainfall pulses, can create "temporal niche opportunities" (Chesson and Huntly 1997) that allow plant species coexistence in arid environments.

*Persistence of effects from resource pulses*

Although resource pulses are events of short duration by definition, the ecological effects of resource pulses can sometimes persist long after the pulse itself has diminished. If resource pulses are common phenomena, long-term effects from brief events could have broad implications in many systems: observations in the present may be affected by the "ghosts of resource pulses past." Whether resource pulses commonly have persistent effects in natural communities, what potential mechanisms could allow long-term effects to result from ephemeral pulses, and how important these legacy effects are in real communities remains largely unknown.

We suggest four general mechanisms that may contribute to the persistence of ecological effects from resource pulses: (1) resource or demographic storage in some community component; (2) the propagation of indirect effects over a community interaction network; (3) persistent changes in community structure, such as



extinction, invasion, alternative stable states or “slow” transients; and (4) changes in gene frequencies.

We use the term resource storage to describe the holding of pulsed resources in some durable component of the community, while demographic storage denotes persistent changes in the age-structure of a population resulting from an ephemeral resource pulse. In practice, these two storage mechanisms reflect similar underlying processes (Warner and Chesson 1985), and resource storage can be redirected to demographic storage, as in some seed bank systems (Pake and Venable 1996, Alvarez-Aquino and Williams-Linera 2002, Gutierrez and Meserve 2003). In arid environments, resource and demographic storage allow plants to persist through interpulse intervals (Noy-Meir 1973). Gratton and Denno (2003) observed a similar example of persistent effects from the storage of pulsed resources in a mid-Atlantic salt marsh following a simulated storm-driven terrestrial nutrient runoff event using a one-time experimental fertilization. These inputs increased the biomass and nitrogen uptake of the dominant cordgrass (*Spartina alterniflora*), causing indirect bottom-up effects on several herbivorous insects and predaceous spiders over the following three years. Despite the annual dieback of the cordgrass, effects persisted in this system due to the storage of nutrients in belowground plant parts and the remineralization of dead biomass at the plant–soil interface (Gratton and Denno 2003). In this case, resource storage provided a persistent source of nutrients, allowing community effects to persist for years after the initial pulsed input.

Resource pulses could have persistent effects via demographic storage if they create a brief window of opportunity for rare recruitment events. The signature of these events may be detectable in the population’s age structure long after the pulse has past. For example, the 1982–1983 El Niño episode in the Galapagos, Ecuador allowed an unusually large “baby boom” cohort of Darwin’s finches (*Geospiza* spp.), with demographic consequences evident in the population’s age structure at least three years after the El Niño episode had subsided (Grant and Grant 1987, Grant et al. 2000). A population of bank voles (*Myodes glareolus*) in Denmark showed a similarly persistent demographic response to a beech (*Fagus sylvatica*) mast (Jensen 1982). Rainy El Niño events have also had lasting demographic effects on the soil seed bank in semiarid Chile (Gutierrez et al. 2000, Gutierrez and Meserve 2003) and the Gulf of California, Mexico (Anderson and Polis 1999), and on the recruitment of woody plants in a wide range of arid environments (Holmgren et al. 2001, 2006, Holmgren and Scheffer 2001, Wiegand et al. 2004).

The effects of resource pulses may also persist simply as a result of lagged indirect effects. For example, populations of small mammals in a variety of ecosystems respond to pulsed resource inputs with increased population densities following time lags of several months to a year, and their predators commonly

respond to increased prey densities with additional time lags (Jaksic et al. 1997, Jędrzejewska and Jędrzejewski 1998, Ostfeld and Keesing 2000, Lithner and Jonsson 2002, Jaksic and Lima 2003, Schmidt 2003, Schmidt and Ostfeld 2003, Letnic et al. 2005). Similarly, the indirect effects of El Niño rainfalls persisted for several years on arid islands in the Gulf of California, Mexico (Polis et al. 1997, 1998, Anderson and Polis 1999).

Resource pulses may also create persistent effects through fundamental changes in community structure such as local extinction, invasion, alternative stable states, or long-lasting transient effects. In some cases, increasing temporal resource variability may increase the risk of local extinction (Wiens 1977, Pimm 1991). For example, threats to the viability of the native Mohua in New Zealand appear to be exacerbated by the bottom-up effects of beech pulses on stoats, an efficient predator of birds (O’Donnell and Phillipson 1996, O’Donnell et al. 1996, O’Donnell 1996b). Recent studies have also suggested that resource pulses may facilitate biological invasions by providing a window of opportunity during which resources are available to invading propagules (Davis et al. 2000, Davis and Pelsor 2001), though the general effects of resource pulses on invasibility may depend on the relative uptake abilities of both resident and invading individuals (Renne et al. 2006). Finally, an increasing number of theoretical and observational studies have investigated how strong pulsed perturbations may shift communities between alternative stable states (Scheffer 1990, Holmgren et al. 2001, Holmgren and Scheffer 2001, Scheffer et al. 2001, 2003, Scheffer and Carpenter 2003, Folke et al. 2004, Van Nes and Scheffer 2004, Schroder et al. 2005), or contribute to important nonequilibrium transient behaviors (Hastings 2001, 2004). Lakes and ponds provide a particularly well-studied set of systems in which pulsed nutrient inputs during storm-driven runoffs can have persistent effects by shifting communities over critical thresholds leading to a chronically eutrophied state (Scheffer et al. 1993, 2003, Carpenter et al. 1999). On the time-scales of most ecological observations, it may be difficult to distinguish between alternative stable states and long-term transients; in practice, both processes have similar implications for the persistence of resource pulse effects.

Although many consumers of pulsed resources show adaptive responses and strategies to utilize resource variability, few studies have investigated how specific resource pulse events might influence the evolution of consumers. Resource pulses and subsequent population crashes may create strong but ephemeral selective environments. For example, the substantial pulsed input of rainfall in the Galapagos, Ecuador during the 1982–1983 El Niño event reversed the prevailing direction of selection among Darwin’s finches, with increased resource availability favoring smaller birds with smaller beaks (Gibbs and Grant 1987). Population crashes following resource pulses may also decrease the effective

size and genetic variability of populations. More work will be necessary to evaluate the evolutionary effects of resource pulses in natural systems.

#### CONCLUSIONS

In 1927, Charles Elton described the complex and dynamic structure of communities this way: “The personnel of every community of animals is constantly changing with the ebb and flow of the seasons, with changing weather, and a number of other periodic rhythms in the outer environment. [At the same time,] the food relations of animals are extremely complicated and form a very closely and intricately woven fabric—so elaborate that it is usually quite impossible to predict the precise effects of twitching one thread in the fabric.” (Elton 1927).

The study of resource pulses may provide insights into both the structure and the dynamics of natural communities. In effect, the study of resource pulses allows one to observe how a community responds to the “twitching” of its components. Accumulating evidence suggests that pulsed resource dynamics are actually widespread phenomena across a diversity of ecosystems, and may be important processes in many natural communities. However, in order to learn general lessons from resource pulses, we must first learn specific things about resource pulses. As in many fields of ecology, a great many observations are already available, but currently remain well-hidden as specific observations of peculiar events spread over a wide range of concepts, systems, and approaches. These studies are often descriptive and focused, and ecologists have only begun to use common process-oriented terms to describe similar phenomena in diverse systems. Experimental pulse perturbations conducted at spatial and temporal scales that reflect natural events offer especially useful opportunities to examine how the characteristics of resource pulses influence their effects, and theoretical investigations of resource pulses provide a means to probe mechanistic models of rare events at multiple levels. The challenge ahead will be to collect all of these observations into a coherent whole. The study of resource pulses is still emerging, and developing a common framework of terms and concepts may be especially important in order to facilitate general insights and integrate specific observations into broader ecological ideas.

We define the resource pulse concept broadly, recognizing the variability of these phenomena in nature and suggesting some fundamental elements that unify this set of extreme events. This approach to investigating the diversity of resource pulses suggests several fundamental questions for future investigations: How does variation in the magnitude, frequency, duration, timing, material nature, and predictability of resource inputs influence their effects? How well does the generation time, behavior, and community context of consumers predict their individual, population and community

responses to pulsed resources? How do the effects of resource pulses differ in different ecosystems? What factors and what mechanisms influence the persistence of pulsed resource effects? How does pulsed resource availability affect the evolution of consumers? The range and depth of potential questions is varied, and the opportunities for contributing both specific observations and conceptual synthesis are extensive.

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