A meta-analysis of resource pulse–consumer interactions

Louie H. Yang,[1,2,3,6] Kyle F. Edwards,[3] Jarrett E. Byrnes,[2,3] Justin L. Bastow,[3,4] Amber N. Wright,[3] and Kenneth O. Spence[5]

[1]*Department of Entomology, University of California, Davis, California 95616 USA*
[2]*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[3]*Section of Evolution and Ecology, University of California, Davis, California 95616 USA*
[4]*Biology Department, 258 SCI, Eastern Washington University, Cheney, Washington 99004 USA*
[5]*Department of Nematology and Department of Entomology, University of California, Davis, California 95616 USA*

Abstract. Resource pulses are infrequent, large-magnitude, and short-duration events of increased resource availability. They include a diverse set of extreme events in a wide range of ecosystems, but identifying general patterns among the diversity of pulsed resource phenomena in nature remains an important challenge. Here we present a meta-analysis of resource pulse–consumer interactions that addresses four key questions: (1) Which characteristics of pulsed resources best predict their effects on consumers? (2) Which characteristics of consumers best predict their responses to resource pulses? (3) How do the effects of resource pulses differ in different ecosystems? (4) What are the indirect effects of resource pulses in communities? To investigate these questions, we built a data set of diverse pulsed resource–consumer interactions from around the world, developed metrics to compare the effects of resource pulses across disparate systems, and conducted multilevel regression analyses to examine the manner in which variation in the characteristics of resource pulse–consumer interactions affects important aspects of consumer responses.

Resource pulse magnitude, resource trophic level, resource pulse duration, ecosystem type and subtype, consumer response mechanisms, and consumer body mass were found to be key explanatory factors predicting the magnitude, duration, and timing of consumer responses. Larger consumers showed more persistent responses to resource pulses, and reproductive responses were more persistent than aggregative responses. Aquatic systems showed shorter temporal lags between peaks of resource availability and consumer response compared to terrestrial systems, and temporal lags were also shorter for smaller consumers compared to larger consumers. The magnitude of consumer responses relative to their resource pulses was generally smaller for the direct consumers of primary resource pulses, compared to consumers at greater trophic distances from the initial resource pulse. In specific systems, this data set showed both attenuating and amplifying indirect effects. We consider the mechanistic processes behind these patterns and their implications for the ecology of resource pulses.

Key words: El Niño Southern Oscillation (ENSO); mast; multilevel (hierarchical) regression; numerical response; outbreak; predator–prey interactions; resource–consumer interactions; resource fluctuation; spatiotemporal variability; transient dynamics.

Introduction

In 1999, the National Science Foundation convened a panel to identify key research frontiers in ecology (Thompson et al. 2001:19). This group reported:

> *... we are only in the early stages of developing a general body of theory on how past periodic or pulsed productivity affects the dynamics of populations, interactions between resources and consumers, food webs, communities, and ecosystems. We need to continue to work toward a synthetic framework for explaining how temporally variable productivity influences food web processes, community dynamics, and ecosystem function.*

A decade later, while considerable progress has been made in the study of pulsed resources, the diversity and extraordinary nature of these events continues to challenge efforts to identify and understand general patterns among resource pulse–consumer interactions.

Resource pulses are events of increased resource availability that combine characteristics of low frequency, large magnitude, and short duration relative to the timescale of their consumers (Ostfeld and Keesing 2000, Yang et al. 2008). Some notable examples of resource pulses include El Niño rainfalls in arid systems (Polis et al. 1997, Grant et al. 2000, Meserve et al. 2003, Letnic et al. 2005), seed or fruit mast events (O'Donnell and Phillipson 1996, Wolff 1996, Jędrzejewska and Jędrzejewski 1998, Curran and Leighton 2000), rapid plant regrowth in flood-disturbed riparian zones (Nakamura et al. 2005), hurricane-driven litterfall events in tropical forests (Lodge et al. 1994, Woolbright 1996), insect outbreaks (Carlton

and Goldman 1984, Haney 1999, Yang 2004, Hogstad 2005), marine upwelling events (Bode et al. 1997), synchronous spawning life histories (Wipfli et al. 1998, Watt et al. 2000, Yanai and Kochi 2005), and major storm-driven nutrient runoffs (van Boekel et al. 1992, Gratton and Denno 2003). These examples point toward the great diversity of pulsed-resource phenomena in nature: resource pulses occur in a wide range of ecosystems, are caused by numerous biotic and abiotic drivers, and vary widely in their magnitude, duration, frequency, and material nature. These events affect communities at multiple trophic levels, representing resource–consumer interactions between nutrients and plants, plants and herbivores, prey and predators, and detritus and detritivores.

While it has become increasingly evident that resource pulses are widespread in nature (Ostfeld and Keesing 2000, Yang et al. 2008), they often appear to be exceptional or idiosyncratic deviations from the essential dynamics of a system. However, the shared defining characteristics of resource pulses suggest that fundamentally similar ecological processes may drive consumer responses to these events. Identifying general patterns among these responses would illustrate key dynamic similarities that unite diverse pulsed resource systems and allow a more predictive understanding of consumer responses to perturbation. Moreover, the study of resource pulses may also contribute insights into broader questions in ecology, including questions about the propagation of indirect effects in communities, differences between aquatic and terrestrial ecosystems, and the resilience of natural systems (Ostfeld and Keesing 2000, Yang et al. 2008). However, ecologists have only begun to consider resource pulses as a unified class of phenomena, and efforts to gain general insights into the ecology of resource pulses to date have lacked a common quantitative framework to compare the effects of resource pulses across different systems or events.

Here, we present a meta-analysis that attempts to identify and understand general patterns among resource pulse–consumer interactions. These investigations seek to understand the key mechanisms that influence community responses to resource pulses. In practice, our analysis focuses on four fundamental questions about resource pulse–consumer interactions: (1) Which characteristics of resource pulses best predict consumer responses to these events? (2) Which characteristics of consumers best predict their responses to resource pulses? (3) How do the effects of resource pulses differ in different ecosystems? (4) What are the indirect effects of resource pulses in communities?

This meta-analysis seeks to develop a robust analytical framework to compare resource pulse–consumer interactions across different systems and events. Our approach introduces several quantitative metrics and methods to evaluate how specific characteristics of the resource pulse–consumer interaction affect consumer

responses using available data in the literature. These analyses allowed us to investigate four existing hypotheses about resource pulse–consumer interactions: (1) We examine key assumptions and predictions suggested by simple population models about the effects of resource pulse magnitude and duration on consumer responses (e.g., Holt 2008). Assuming that the total resource input is held constant as the resource pulse duration varies, these models predict that the largest consumer responses will result from the most concentrated, shortest-duration resource pulse events if consumer responses are assumed to be unbounded, or at intermediate pulse durations if more realistic constraints on consumer responses are imposed (Holt 2008). (2) We evaluate the effects of consumer mobility and aggregative response mechanisms on the lag, magnitude, and persistence of consumer responses. Several previous studies have suggested that differences among consumers in mobility and the spatial scale of foraging may represent key explanatory factors for predicting consumer responses to resource pulses (Curran and Leighton 2000, Ostfeld and Keesing 2000, Lithner and Jonsson 2002, Yang 2004, Yang et al. 2008); (3) We consider predicted differences between aquatic and terrestrial systems in the speed and persistence of resource pulse effects (Strong 1992, Shurin et al. 2006, Nowlin et al. 2008). In general, these studies suggest that aquatic systems are likely to show more rapid and less persistent responses to resource pulses. (4) We examine the expectation of attenuating resource pulse effects with increasing trophic distance, as may be predicted under assumptions of thermodynamic constraints, diffuse interactions, stochastic environmental variation, and closed-system boundaries (Schoener 1993, Wootton 1994). Each of these phenomena might be expected to contribute to attenuating responses: thermodynamic constraints limit the efficiency of energy transfer during trophic interactions, diffuse interactions can dilute the impact of a resource pulse across multiple consumers, stochastic environmental variation results in the accumulation of uncorrelated effects that diminish the relative effects of pulsed perturbations with increasing trophic distance, and relatively closed system boundaries would limit the potential for aggregative consumer responses from surrounding communities. Finally, we explore new ideas that emerged from this analysis, expand upon existing hypotheses, and suggest hypotheses for future studies.

METHODS

Data collection

We built a data set of 189 pulsed resource–consumer interactions drawn from 68 peer-reviewed and published sources (see Table 1 and Supplement). These sources were gathered from extensive keyword and citation searches in several databases, including the ISI Web of Knowledge, JSTOR, and Google Scholar. Our literature search sought to identify published records that: (1) describe a naturally occurring resource pulse–consumer
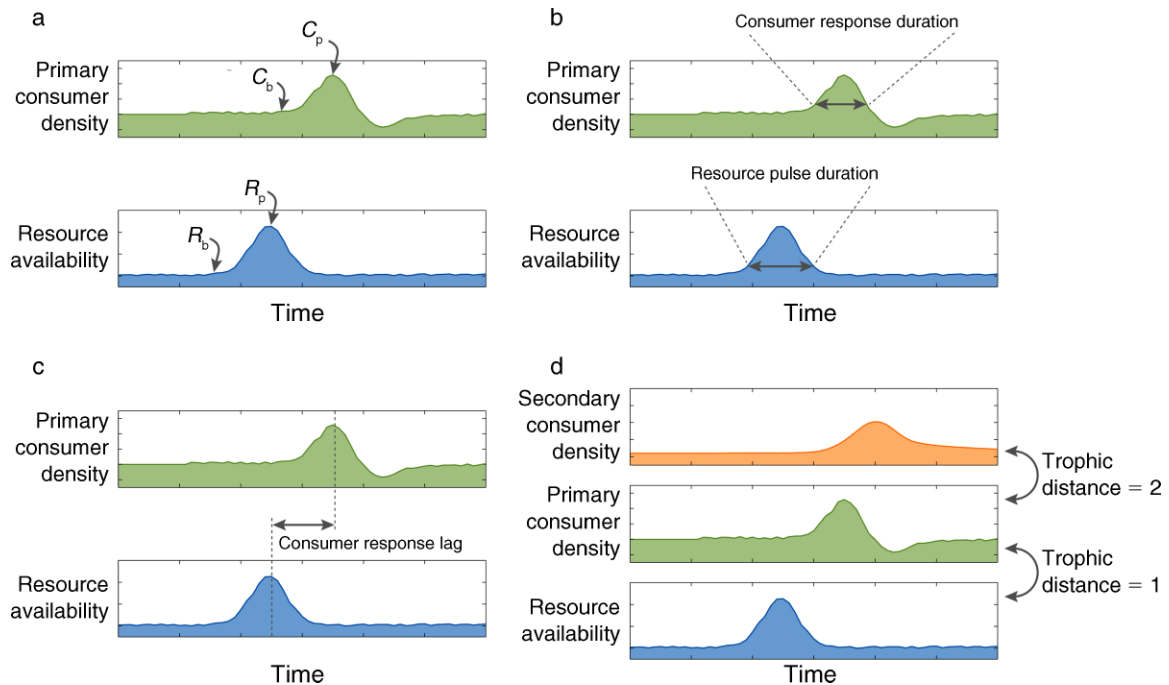
FIG. 1. A schematic diagram of extracted data used to investigate (a) resource pulse (R_p) and consumer response (C_p) magnitude relative to baselines (R_b and C_b), (b) resource pulse and consumer response duration, (c) the consumer response lag, and (d) indirect effects and trophic distance.

trophic interaction, (2) provide quantitative data describing the baseline resource availability during non-pulsed conditions (R_b) and the maximum resource availability during the resource pulse (R_p), and (3) provide corresponding quantitative data describing consumer densities or recruitment under non-pulsed baseline conditions (C_b) and the maximal consumer response following the resource pulse event (C_p). These quantitative data were gathered from published data tables, image analysis of published figures, and direct correspondence with authors. We included all sufficiently quantitative studies for which we could establish evidence of a resource pulse–consumer interaction, without regard to inherent characteristics of the resource, the consumer, the consumer response, or the ecosystem context. In multi-trophic food webs with primary, secondary, and tertiary resource pulses, quantitative data from each pairwise resource pulse–consumer interaction were recorded separately. We collected data from both observational time series ($N = 146$) and experimental ($N = 43$) studies of resource pulses. We excluded resource addition experiments without a naturally occurring analogue in order to focus our analysis within the range of natural variation. From time series data, baseline conditions were represented by the resource and consumer measurements in the time step immediately prior to the observation of a resource pulse event (Fig. 1a). The identification of the pre-pulse time step was generally unambiguous in our data set, due to the often low temporal resolution of these data

(often annual or seasonal measurements), the clearly defined pulsed dynamics, or both. These pre-pulse measurements were consistent with other measurements taken during non-pulsed conditions for those time series with sufficient documentation of inter-pulse intervals. A schematic diagram of these data is shown in Fig. 1a, and a table of variables is presented in Appendix A. For $N = 2$ interactions from one system, baseline resource availability was inferred from post-pulse time series data due to the lack of pre-pulse data (see Supplement). For experimental studies, control and resource addition groups were used to represent baseline and pulse conditions, respectively. The limiting criterion for inclusion in our data set was the quantitative measurement of key parameters that were necessary to build a minimal description of the resource pulse–consumer dynamics. A key benefit of these resource pulse metrics was the relatively low barrier to inclusion that they presented, which allowed us to include a wide range of observational and experimental data within a standardized, robust framework.

We used author descriptions to categorize consumer numerical responses as primarily reproductive, aggregative, or combined reproductive and aggregative (hereafter, "response mechanisms"). Reproductive responses are defined as mechanisms of numerical recruitment driven by locally increased reproduction, while aggregative responses are defined as mechanisms of numerical recruitment driven by the immigration of mobile consumers from surrounding populations. In $N = 43$

TABLE 1.   Qualitative summary of resource pulse systems in this analysis.

System	Ecosystem subtype	Summary
Agricultural landscape, Polana Mountains Biosphere Reserve, Slovakia	agricultural	A beetle outbreak was consumed by shrikes, which advanced laying date, increased clutch size, and produced heavier nestlings, but did not produce more fledglings.
Arid Gulf of California islands, Mexico	arid lands	Heavy rainfalls were followed by eruptive plant growth and increased densities of arthropod herbivores, rodent granivores, spiders, and spider parasitoids.
Arid rangeland, Australia	arid lands	Heavy rainfalls were followed by eruptive plant growth and increased densities of rodent granivores and vertebrate predators.
Fray Jorge National Park, semiarid Chile	arid lands	Heavy rainfalls increased plant growth and reproduction, followed by increased rodent densities and raptors.
Galapagos, Daphne Major, Ecuador	arid lands	Heavy rainfalls increased plant growth and seed production, followed by increased populations of caterpillars and finches.
Galapagos, Genovesa, Ecuador	arid lands	Heavy rainfalls increased plant growth.
Reserva Nacional Las Chinchillas, semiarid Chile	arid lands	Heavy rainfall events increased the cover of ephemeral and perennial plants.
Spruce–pine forest, Sweden	boreal forest	A beech mast event increased densities of rodents and owls.
Boreal forest, New Brunswick, Canada	boreal forest	Lepidopteran larvae outbreaks increased the abundance of two warblers.
Subalpine birch forest, Budal, Norway	boreal forest	Outbreaks of forest Lepidoptera increased brambling territory densities.
Subalpine lake, California, USA	freshwater	Massive mating swarms of alate ants were consumed by trout, increasing both ammonium concentrations and phytoplankton densities.
Experimental stream, Hokkaido, Japan	freshwater	Nutrients from decomposing salmon carcasses increased densities of epilithic algae.
Little Knife River, Minnesota, USA	freshwater	Nutrients from decomposing salmon carcasses increased biofilm mass.
Southeast Alaska streams, USA	freshwater	Nutrients from decomposing salmon carcasses increased biofilm mass, which was consumed by aquatic insects.
Ingazeira Reservoir, Brazil	freshwater	A bloom of cyanobactera was consumed by copepods, rotifers, and cladocerans.
West Florida shelf, USA	marine	Increased iron concentrations in seawater were followed by blooms of cyanobacteria.
Tatoosh Island, Washington, USA	marine	Increased nitrogen concentration in the seawater around kelp did not increase kelp growth.
Western Baltic Sea, Germany	marine	Increased nitrogen and phosphorus concentrations in seawater increased epiphyte and grazer densities.
Barnegat Inlet, Barnegat Bay, New Jersey, USA	marine	Extensive episodic settlement of blue mussels, followed by the immigration of predatory sea stars.
Coastal upwellings, Washington, USA	marine	Upwelling event increased nitrate concentrations, followed by a bloom of diatoms.
Coastal North Sea, Belgium	marine	Bloom of a colonial alga, followed by increased concentrations of bacterioplankton and ciliate consumers.
Coastal North Sea, Marsdiep, The Netherlands	marine	Bloom of a colonial alga, followed by increased concentrations of bacterioplankton and ciliate consumers.
Kaneohe Bay, Oahu, Hawaii	marine	A pulse of dissolved nutrients increased phytoplankton, followed by increases in herbivorous and carnivorous zooplankton.
Drift algae subsidies, California, USA	marine	Pulsed inputs of sunken drift macrophytes in submarine canyons are consumed by a variety of crustaceans and polychaetes.
Chesapeake Bay, Maryland, USA	marine	Increased ammonium concentrations in surface water, followed by a phytoplankton bloom.
Yasu River, Japan	riparian	Willow regrowth was followed by increased densities of herbivorous and predatory arthropods.
Beech forest, Denmark	temperate forest	A beech mast event was followed by increased densities of voles and mice.

Table 1. Extended.

Natural event driver(s)	Trophic levels	Selected references
outbreak population dynamics	1	Hoi et al. (2004)
heavy ENSO rainfall	4	Polis et al. (1997, 1998), Anderson and Polis (1999), Stapp and Polis (2003)
heavy ENSO rainfall	3	Letnic et al. (2005)
heavy ENSO rainfall	3	Meserve et al. (1995, 2003), Gutierrez et al. (2000)
heavy ENSO rainfall	3	Grant and Boag (1980), Grant and Grant (1980, 1987), Gibbs et al. (1984), Gibbs and Grant (1987), Grant et al. (2000)
heavy ENSO rainfall	1	Grant and Grant (1987)
heavy ENSO rainfall	1	Gutierrez et al. (2000)
beech mast life history	2	Lithner and Jonsson (2002)
insect outbreak	1	Morris et al. (1958)
insect outbreak	1	Hogstad (2000, 2005)
ant mating life history	2	Carlton and Goldman (1984)
salmon spawning life history	1	Yanai and Kochi (2005)
salmon spawning life history	1	Wold and Hershey (1999)
salmon spawning life history	2	Wipfli et al. (1998, 1999)
severe ENSO drought	1	Bouvy et al. (2001)
deposition of aerial Saharan dust	1	Lenes et al. (2001)
eutrophication and upwelling	1	Pfister and Van Alstyne (2003)
excretion, decomposition, upwelling, and wind-mixing	2	Worm and Sommer (2000)
mussel life history	1	Bologna et al. (2005)
post-ENSO coastal upwelling	1	Adams et al. (2000)
seasonal nutrient runoff	2	Lancelot and Mathot (1987), Billen and Fontigny (1987)
seasonal nutrient runoff	3	Van Boekel et al. (1992)
severe storm runoff event	3	Hoover et al. (2006)
storm disturbance	1	Okey (1997, 2003)
wind-driven mixing event	1	Yeager et al. (2005)
typhoon-driven flood disturbance	2	Nakamura et al. (2005, 2006)
beech mast life history	1	Jensen (1982)

Table 1. Continued.

System	Ecosystem subtype	Summary
Beech forest, Eglinton Valley, New Zealand	temperate forest	A beech mast event was followed by increased densities of mice, rats, parakeets, and stoats.
Beech forest, Hawdon, New Zealand	temperate forest	A beech mast event was followed by increased densities of mice and stoats.
Beech forest, Orongorongo, New Zealand	temperate forest	A beech mast event was followed by increased densities of mice and lepidopteran larvae.
Beech and dwarf bamboo forest, Akita, Japan	temperate forest	A beech mast event increased densities of mice.
Deciduous forests, Allee Memorial Woods, Indiana, USA	temperate forest	An emergence of periodical cicadas was followed by increased densities of shrews and decreased densities of mice.
Deciduous forests, Jefferson National Forest, Virginia, USA	temperate forest	Cicada carcasses increased densities of detritivore arthropods and soil microbes (bacteria and fungi); increased soil nitrogen was assimilated by plants.
Forest and pasture, Ozark Mountains, Arkansas, USA	temperate forest	An emergence of periodical cicadas was followed by increased densities of Red-winged Blackbirds.
Beech–maple forest, Pennsylvania, USA	temperate forest	An outbreak of lepidopteran larvae increased the abundance of several species of forest birds.
Kisatchie National Forest, Lousiana, USA	temperate forest	An outbreak of bark beetles was followed by increased densities of predatory beetles that appeared to reduce bark beetle densities.
Białowieża Primaeval Forest, Poland	temperate forest	A multispecies mast event increased densities of mice, voles, weasels, and pine marten.
Oak–beech forests, Great Mountain Forest, Connecticut, USA	temperate forest	A multispecies mast event increased densities of mice, voles, and chipmunks.
San Martin Experimental Forest, Chile	temperate forest	A multispecies mast event increased densities of mice.
Takakuma Experimental Forest, Kagoshima, Japan	temperate forest	A mast event increased densities of two species of mice.
Oak forest, Fermilab, Illinois, USA	temperate forest	An oak mast event was followed by increased densities of mice; similar events occurred following experimental food addition.
Oak-dominated forest, Millbrook, New York, USA	temperate forest	Oak mast events and experimental acorn additions were followed by increased mouse densities; tick densities appeared to increase in response to changes in deer distributions.
Oak–hickory forest, McDowell Nature Preserve, North Carolina, USA	temperate forest	An oak mast event was followed by increased densities of mice.
Oak–maple forest, Mountain Lake Biological Station, Virginia, USA	temperate forest	Multiple oak mast events were followed by increased densities of mice and chipmunks.
Pine–oak forest, Holt Research Forest, Maine, USA	temperate forest	Multiple oak mast events were followed by increased densities of mice.
Luquillo Experimental Forest, Puerto Rico	tropical forest	Hurricane disturbance increased the availability of structural retreat sites, resulting in higher frog densities; similar events occurred following experimental retreat site addition.
Tropical rain forest, Gunung Palung National Park, West Kalimantan, Indonesia	tropical forest	A multispecies dipterocarp mast event increased densities of several vertebrate seed predators, including pigs, birds, rodents, and primates.
Spartina salt marsh, New Jersey, USA	wetlands	One-time experimental nutrient additions to meadow and islet marshes was followed by increased densities of cordgrass, herbivores, and predators.

Notes: A complete table of the data used in this analysis is available in the Supplement. The abbreviation "ENSO" stands for El Niño Southern Oscillation.

interactions, we were able to determine the presence of one response mechanism, but were unable to confirm the presence or absence of the other. For these cases, we performed analyses that both included and excluded interactions with incomplete response mechanism data. These two analyses yielded qualitatively similar responses for all analyses, and we present results from the more inclusive data set here. When possible, we also recorded

the generation time ($N = 130$) and adult body mass ($N = 125$) of consumers estimated from additional published sources, the resource pulse and consumer response durations (Fig. 1b), and the time lag between the maximum resource pulse and the maximum observable consumer response ($N = 146$; Fig. 1c).

For each interaction, we recorded a short description of the study location (hereafter, "system"), the specific

TABLE 1. Continued. Extended.

Natural event driver(s)	Trophic levels	Selected references
beech mast life history	2	King (1983), Elliott et al. (1996), O'Donnell and Phillipson (1996)
beech mast life history	2	O'Donnell and Phillipson (1996)
beech mast life history	1	Alley et al. (2001)
beech mast life history	1	Abe et al. (2005)
cicada emergence life history	2	Hahus and Smith (1990), Krohne et al. (1991)
cicada emergence life history	3	Yang (2004, 2006)
cicada emergence life history	1	Strehl and White (1986), Steward et al. (1988)
insect outbreak	2	Haney (1999)
insect outbreak	1	Reeve (1997)
masting life histories	2	Pucek et al. (1993), Jędrzejewska and Jędrzejewski (1998), Zalewski and Jędrzejewski (2006)
masting life histories	1	Schnurr et al. (2002)
masting life histories	1	Murua and Briones (2005)
masting life histories	1	Sone et al. (2002)
oak mast life history	1	Yunger (2002)
oak mast life history	2	Jones et al. (1998), Schauber et al. (2005)
oak mast life history	1	Scarlett (2004)
oak mast life history	1	Wolff (1996)
oak mast life history	1	Elias et al. (2004)
hurricane disturbance	1	Stewart and Pough (1983), Woolbright (1991, 1996)
masting life histories	2	Curran and Leighton (2000)
storm-driven nutrient runoffs	3	Gratton and Denno (2003)

occurrence of each primary resource pulse in time (hereafter, "event"), latitude and longitude coordinates, the primary ecosystem type (i.e., aquatic or terrestrial; hereafter, "ecosystem type"), and the specific ecosystem subtype (i.e., marine, freshwater, agricultural, arid terrestrial, tropical forest, temperate forest, boreal forest, wetlands, and riparian; hereafter, "ecosystem subtype"). For the purposes of this analysis, we used the term "aquatic" to denote a variety of freshwater and marine ecosystems, including both pelagic and benthic zones.

The trophic level of the resource in each interaction was categorized into integer ranks using the following rules. First, the trophic level of nutrients, water, and detrital resources was defined to be 0. Second, the trophic level of plants and other autotrophs was defined to be 1. Third, the trophic level of heterotrophs was defined to be (1 + the trophic level of their principal

diet), based on available diet descriptions. The characteristic of autotrophy or heterotrophy was defined as trophic position.

Analysis overview

In these analyses, we sought to identify key biological traits that affected four aspects of the consumer response: magnitude, duration, lag, and the indirect effects of resource pulses in communities. Our analyses focused on explanatory factors that were shared and relevant across a wide range of resource pulses in nature, but also showed informative quantitative variation between resource pulses.

We used a multilevel random-effects modeling approach (Gelman and Hill 2007), also known as hierarchical regression (McMahon and Diez 2007), to investigate the magnitude, duration, and temporal lag of consumer responses. This approach allows the construction of models that incorporate the hierarchical structure of nonindependence in the data (Appendix B). In addition to explanatory factors, our data set was grouped by system, within which individual responses are nonindependent due to temporal, spatial, or experimental association. We accounted for this nonindependence by including system as a grouping factor in all analyses, analogous to blocking in ANOVA designs. The system factor is nested within ecosystem subtype, which is itself nested within ecosystem type. Throughout this analysis, we constructed multilevel models using the lme4 package (Bates 2007) in the R statistical software program (R Development Core Team 2008). Multilevel models have been used previously for similar analyses of compiled data (e.g., Gibson and Myers 2003, O'Connor et al. 2007).

We used information theoretic methods to compare models and quantify the explanatory importance of different variables. Models were compared using the small-sample Akaike Information Criterion (AIC) and the conditional Akaike Information Criterion (cAIC). Both information criteria are used to assess the goodness of fit of a specific model, balanced by penalties for increasing model complexity and corrected for sample size (Burnham and Anderson 2004). These criteria are relative metrics, and the model with the lowest value of the criterion is considered to have the greatest explanatory power. The AIC is appropriate for analyses without group structure or in cases in which groups in the analysis represent samples from a larger population of interest; conversely, cAIC is appropriate for analyses focused on differences between the specific groups themselves (Vaida and Blanchard 2005). We present model selection results based primarily on cAIC, but include the more traditional AIC criteria for comparison (Appendices E–G). Although both metrics provide qualitatively similar results, we believe that cAIC is more appropriate for these analyses due to its focus on groups as explanatory factors (Appendix C).

We used multi-model inference to assess the importance of each factor over a set of models. For each analysis, we constructed a set of models that included all possible combinations of each explanatory factor. This approach is appropriate when there are no a priori reasons to exclude any particular model (Burnham and Anderson 2002). We then compared these models by calculating the difference between each model's cAIC and the minimum cAIC in the model set to yield a ΔcAIC value. These ΔcAIC values were transformed to likelihood metrics and normalized to sum to 1 over the model set, yielding cAIC weights that represent the probability that a specific model provides the best explanation for the data when compared to all candidate models (Burnham and Anderson 2004). Finally, we used the cAIC weights to calculate variable weights, which sum the cAIC weights of all models that include a given explanatory factor (Burnham and Anderson 2002, 2004). These variable weights provide a relative metric of factor importance on a scale from 0 to 1, which allows the explanatory power of different factors to be compared. The combination of ΔcAIC, cAIC weights, and variable weights allows us to assess the importance of each factor. Models including system as the only factor serve as a comparative null.

In each model selection process, we constructed a 95% confidence set by summing the cAIC weights of each model in descending order until a cumulative weight of 0.95 was reached. The 95% confidence set accounts for uncertainty in assignment of the best model by including those models that could potentially have the lowest cAIC if the data were resampled (Burnham and Anderson 2002).

Response magnitude

We developed a metric based on log response ratios in order to compare the proportional effects of resources in a wide variety of systems (Hedges et al. 1999). For each resource pulse–consumer interaction, we calculated a resource pulse magnitude comparing pulse and baseline conditions, $\ln(R_p/R_b)$, and a corresponding metric of the consumer response magnitude, $\ln(C_p/C_b)$. These response ratios provide nondimensional measures of the maximal pulsed resource and consumer increases relative to observed baseline conditions, reflecting transient dynamics in a way that is similar to the "maximum amplification" concept described by Neubert and Caswell (1997). The difference between these two log ratios, $\ln[(C_p/C_b)/(R_p/R_b)]$, provides a single metric to quantify the magnitude of the consumer response standardized by the resource pulse magnitude (hereafter, "relative response magnitude"), and the slope of the relationship between $\ln(C_p/C_b)$ and $\ln(R_p/R_b)$ provides a regression-based measure of the normalized consumer response (hereafter, "response magnitude slope"). Both of these metrics provide essentially similar measurements of the consumer response magnitude relative to the resource pulse magnitude, and where they are

directly comparable, both yield identical conclusions. The key difference between them is that relative response magnitudes represent unmodeled "raw" data from the data set, whereas response magnitude slopes emerge from hierarchical regression analyses that incorporate specific model assumptions and structures, such as system groupings. In these analyses, relative response magnitudes were generally used to show patterns in the data that could not be meaningfully incorporated into hierarchical models (for example, due to constraints on the number of interaction effects that can be interpreted in analyses with several explanatory factors of interest). Importantly, both these metrics allowed for a robust and informative description of the essential resource pulse and consumer dynamics while imposing minimally restrictive criteria for inclusion in our quantitative analysis. In $N = 26$ and $N = 7$ interactions, quantitative data were not available to calculate $\ln(R_p/R_b)$ and $\ln(C_p/C_b)$, respectively. As a result, quantitative analyses requiring measures of relative response magnitude were based on the remaining $N = 161$ resource pulse–consumer interactions.

A fundamental and straightforward assumption of our analysis is that larger resource pulses are generally associated with larger consumer responses. Our analysis builds upon this expectation to investigate how factors other than resource pulse magnitude affect consumer response magnitude. We examined how characteristics of the resource pulse (resource trophic level and resource pulse duration), the focal consumer (consumer response mechanism, trophic position, generation time, and mass), and the ecosystem context (ecosystem type and subtype) affected response slopes in the regression between consumer response magnitude and resource pulse magnitude. In effect, these analyses seek to examine the manner in which key explanatory factors affect variation in the magnitude of consumer responses relative to their resource pulses. All regressions were constrained to pass through the origin, where both the resource pulse magnitude and the consumer response magnitude equal zero. The origin corresponds to the absence of a resource pulse, where the consumer response magnitude is assumed to be zero by necessity.

Due to the limited number of observations with complete data on consumer generation time, mass, and pulse duration, we conducted separate analyses of continuous and categorical factors. The analysis of categorical predictors included five factors: ecosystem type, ecosystem subtype, response mechanism, consumer trophic position, and resource trophic level. We used all combinations of these explanatory variables to construct a full set of 32 models for comparison (Appendix D). The analysis of continuous factors included consumer generation time, consumer body mass, and resource pulse duration as explanatory factors in a full set of eight models. In addition, because consumer generation times in our data set varied over three orders of magnitude, we also considered the quotient (pulse

duration/consumer generation time) as a measure of pulse duration standardized by consumer generation time (hereafter, "standardized pulse duration"). Standardized pulse duration was included as an explanatory factor in two additional models (as a single explanatory factor and in combination with consumer body mass; Appendix D). Standardized pulse duration was not included in models that included either consumer generation time or pulse duration factors due to their inherent correlation.

Response duration

Resource pulse duration and consumer response duration data were collected from time series data or author observations and translated into a common unit (days) for these analyses. For time series, the "resource pulse duration" was defined as the length of time that resource availability was >10% greater than the baseline condition (Fig. 1b, Appendix A). The "consumer response duration" was defined as the length of time that consumer density or recruitment was >10% greater than the baseline condition (Fig. 1b, Appendix A). Given the resolution of the available time series data, these criteria provided a generally unambiguous and consistent metric of resource pulse and consumer response durations. Although these definitions are based on arbitrary thresholds, we used them in order to obtain an objective assessment of resource pulse and response durations across systems (these criteria were not necessary to determine other resource or consumer metrics). We considered alternative metrics that used standard deviations from the baseline condition to define the pulse threshold, but these methods required interpulse time series data of considerable and consistent length and excluded many observational and experimental studies. When authors provided approximate estimates of duration, we rounded to the nearest number of days. As response durations ranged in magnitude from hours to years, we felt this approximation was justified for an analysis seeking general trends in the factors affecting response duration.

We conducted hierarchical regression analyses in order to evaluate how characteristics of the resource pulse affected the persistence of the consumer response. In this analysis, we assumed a positive underlying correlation between resource pulse duration and consumer response duration, then evaluated how resource pulse magnitude, consumer mass, consumer generation time, and consumer response mechanism explained residual variation in this regression. The slope of the relationship between resource pulse duration and consumer response duration provides a regression-based measure of the normalized consumer response (hereafter, "response duration slope"). Ecosystem type and subtype were also considered as potential explanatory factors, but were found to explain negligible variation and were subsequently excluded from this analysis. This approach allowed us to explain variation in the relative

duration of consumer responses with respect to these explanatory factors of interest. We evaluated all possible combinations of these factors in a complete set of multilevel models, including system as a grouping factor throughout (Appendix E). We used model selection criteria to evaluate which explanatory variables best predicted the observed variation in consumer response duration relative to resource pulse duration. In order to minimize the influence of outliers in body mass and generation time measurements, both variables were log-transformed.

We conducted a separate, subsequent analysis to examine the role of resource trophic level on the relative consumer response duration. For this analysis, we examined the regression of consumer trophic level against the log ratio of consumer response and resource pulse durations.

Response lag

The consumer response lag was defined as the interval of time between the peak resource availability and the peak consumer response (Fig. 1c). We evaluated ecosystem type and consumer response mechanism as potential categorical predictors of consumer response lag using a set of multilevel models that included system as a grouping factor in all analyses (Appendix E). We conducted a separate analysis including consumer body mass and generation time as potential continuous predictors of consumer response lag, using the available subset of data. As in previous analyses, we used cAIC and AIC metrics to evaluate and compare these predictive factors. Consumer body mass, generation time, and response lag were log-transformed to minimize the influence of outliers in the data set.

Indirect effects

In order to investigate the attenuation and amplification of resource pulse effects, we examined the manner in which response magnitude is affected by the trophic distance of a consumer from the initial (i.e., primary) resource pulse. Attenuating responses are interactions in which the consumer response magnitude is less than the resource pulse magnitude, while amplifying responses are interactions in which the consumer response magnitude is greater than the resource pulse magnitude. At the community level, a series of attenuating responses over successive interactions would result in the dissipation of bottom-up effects from the resource pulse, whereas a series of amplifying responses would indicate increasing consumer responses along a trophic chain. We defined trophic distance as the minimum number of resource–consumer interactions between each focal consumer and the initial pulsed resource for a specific resource pulse event (Fig. 1d).

To further investigate the attenuation of indirect effects along trophic chains, we focused on a subset of our data from 16 different resource pulse events in 10 different systems that provided complete quantitative descriptions of relative response magnitudes for food webs including at least three trophic levels. In order to compare consumer responses to these events, these data were combined into a series of graphical event summaries that present the magnitude of resource pulses and consumer responses separately for each of 16 resource pulse events that were documented in multi-trophic studies. This format allowed a large body of data to be organized and compared.

RESULTS AND DISCUSSION

Our data set included resource pulses in a wide range of terrestrial and aquatic ecosystems around the world, including temperate forests, arid lands, marine systems, wetlands, freshwater systems, boreal forests, riparian margins, tropical forests, and agroecosystems (Fig. 2a, b). These data represented resource pulses at several trophic levels, including pulses of abiotic resources, autotrophs, decomposers, herbivores, and predators (Fig. 2c).

Response magnitude

Consumers showing aggregative responses had greater response slopes than consumers showing reproductive responses, and consumers with combined aggregative and reproductive responses showed the greatest response slopes of all (Fig. 3a, b). Although this data set showed a wide range of attenuating and amplifying relative response magnitudes (Fig. 3c), consumer response mechanism explained a considerable amount of this variation. Consumer response mechanism was included in every model within the 95% confidence set of our analysis and had a variable weight near 1, indicating that this consumer trait was the most powerful explanatory factor in our categorical analysis of response magnitude (Appendix D). These results suggest that the immigration of consumers from outside the local community is likely to be an important part of large numerical responses to resource pulses in nature, and the combination of reproductive and aggregative consumer strategies may allow even larger numerical increases. These findings are consistent with previous observations about the role of consumer response mechanisms and mobility as predictors of response magnitude (Ostfeld and Keesing 2000, Yang et al. 2008). For example, a recent study described how strong aggregation responses among consumers led to dramatic changes in the structure and dynamics of a boreal forest community affected by eruptive outbreaks of spruce budworms, with particular increases in the representation of mobile higher-order predators and parasitoids (Eveleigh et al. 2007). The results of our analysis suggest that the important role of behavioral aggregation observed during this particular resource pulse may represent a general pattern in other pulsed resource systems.

In our data set, resource pulses at trophic level 1 (plants) showed larger consumer response magnitudes than pulses at other trophic levels (Fig. 4a), and our
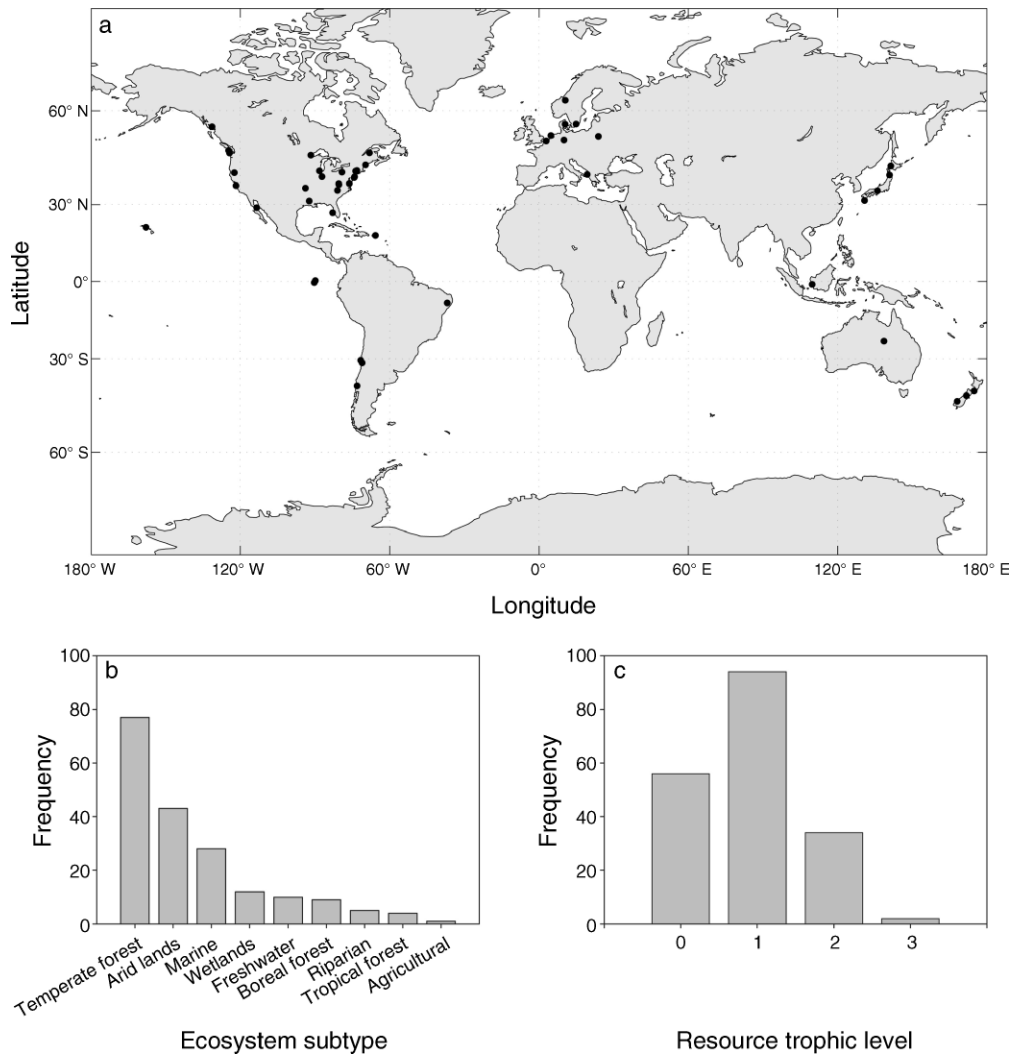
Fig. 2. The incidence of resource pulse–consumer interactions in our data set organized by (a) geographic coordinates (interactions are indicated by solid circles), (b) ecosystem subtype, and (c) resource trophic level.

multi-model analysis supported the role of resource trophic level as a predictor of consumer response magnitude: resource trophic level was included in the seven highest-weighted models, yielding a cumulative variable weight of 0.85 (Appendix D). An inspection of our data set suggests that this effect is driven by the larger magnitude of aggregative and combined responses to resource pulses at this trophic level (Fig. 4a). This observed pattern of response magnitudes was unexpected and may point toward some unique aspects of the plant–herbivore interaction. For example, these data suggest that strong aggregative responses may be more likely to occur when motile consumers aggregate to sessile resources.

Ecosystem subtype also emerged as a potential predictor of consumer response magnitude. Ecosystem subtype was included in the four most explanatory

models and had a variable weight of 0.81 (Appendix D). This result suggests that the magnitude of consumer responses to resource pulse varies with ecosystem subtype, perhaps reflecting common characteristics of the resource pulses and consumers in each. However, our ability to generalize the results associated with tropical forests, riparian systems, wetlands, and boreal forests is limited in light of the small number of systems and events representing these ecosystem subtypes (Fig. 4b). By comparison, temperate forests, arid ecosystems, and marine ecosystems were well-represented in our data set.

Temperate forests showed the smallest relative response magnitudes of all ecosystem subtypes (Fig. 4b). In part, this may reflect constraints on the abilities of consumers to respond to the large magnitude of mast events in many temperate forest systems. Mast reproduction strategies often satiate consumer demands with
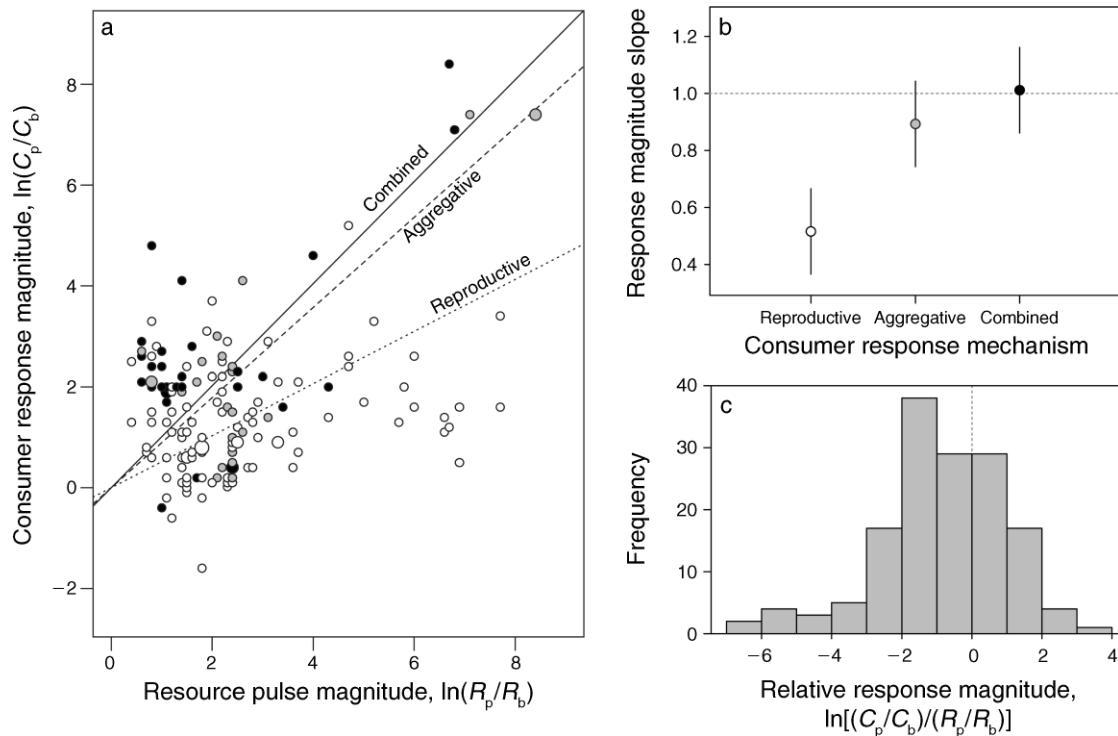
FIG. 3. (a) Effects of consumer response mechanism on the response magnitude slope, where open circles represent reproductive responses, gray circles represent aggregative responses, and black circles represent combined reproductive and aggregative responses. Circle size is proportional to the number of overlapping data points. The inclusion or exclusion of the five data points in the upper right-hand side of the figure had a negligible effect on the quantitative slope estimates and qualitative conclusions of this analysis. These data showed patterns consistent with the broader data set, and they represent interactions within a single system (the Yasu River in Japan). System effects were controlled in this multilevel regression, limiting the leverage of these data. (b) Response slopes associated with consumer response mechanism (mean ± SE). Response slopes greater than 1 represent amplifying responses. (c) Histogram of relative response magnitudes in this data set. Relative response magnitudes less than 0 represent attenuating responses.

a sudden superabundance of ephemeral resources (Silvertown 1980, Sork 1993, Kelly 1994, Kelly and Sork 2002). These dynamics provide an effective reproductive strategy for avoiding seed predation and allowing seed recruitment (Kelly and Sork 2002), contribute to the increased channeling of pulsed resources into detrital pathways (Zackrisson et al. 1999, Yang 2004, 2006, Yang et al. 2008), and reduce the relative response magnitudes of consumers in temperate forest systems.

Marine and arid terrestrial systems showed the largest relative response magnitudes in our analysis. These strong consumer responses may reflect the prevalence of rapidly recruiting consumers in these systems. For example, many of the marine consumers in our data set were microbes, phytoplankton, and zooplankton with especially short generation times; these consumers may be capable of effectively tracking even strongly pulsed resource perturbations. In many arid systems, small mammal consumers responded quickly to pulses of primary productivity driven by heavy El Niño rainfalls. These resource perturbations were often associated with longer and wetter rainy seasons, with

pulsed dynamics occurring on the timescale of multiple months or years. We suggest that the relatively long duration and sessile nature of these resource pulses may allow for particularly strong responses from mobile consumers. In general, it seems likely that ecosystem subtype emerges as a useful explanatory factor in these analyses because it represents a variety of other resource and consumer traits (such as pulse duration or consumer body size) that directly affect response magnitude and show systematic variation with habitat.

More persistent resource pulses were associated with larger consumer responses, especially when the duration of the resource pulse was standardized by the consumer generation time (Fig. 4c). Standardized pulse duration received strong support as a predictor (variable weight = 0.61), and a model including standardized pulse duration as the only continuous explanatory factor showed the minimum cAIC value in this model set, suggesting that this model provided the best combination of explanatory fit and model simplicity (Appendix D). By comparison, models including only consumer body mass (cAIC weight = 0.03), consumer generation time (cAIC weight = 0.04), and system (cAIC weight =
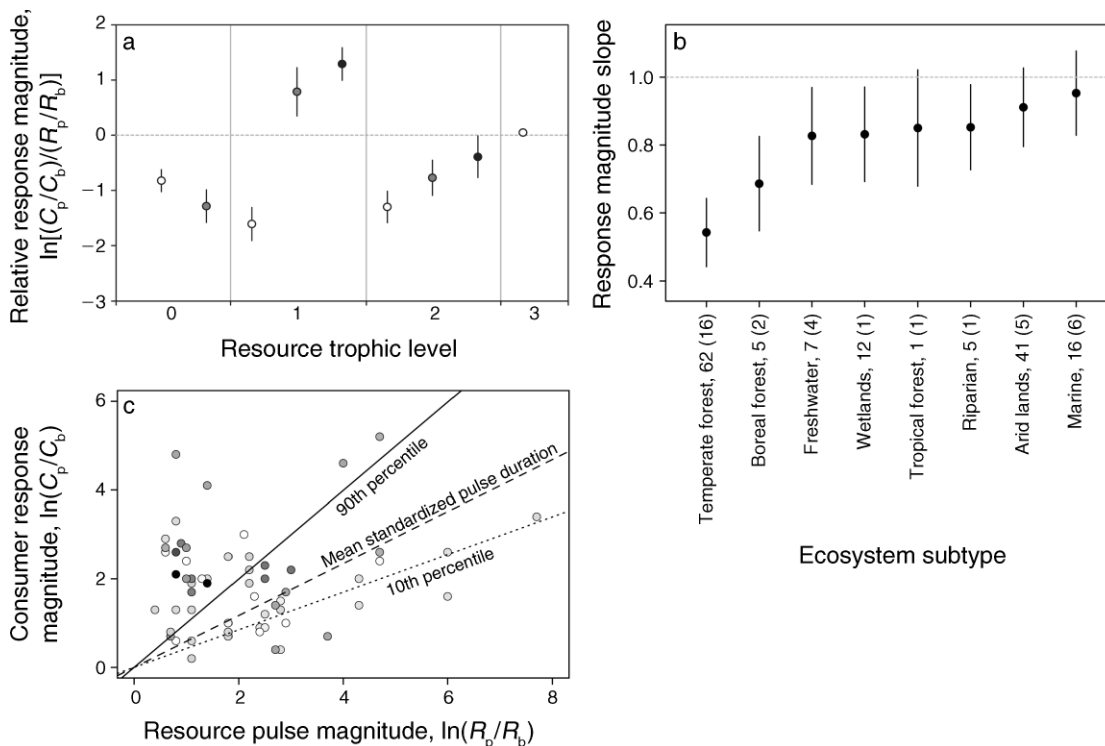
FIG. 4. (a) Effects of resource trophic level and consumer response mechanism on the relative response, where open circles represent reproductive responses, gray circles represent aggregative responses, and black circles represent combined reproductive and aggregative responses. Values are mean ± SE of relative response magnitudes for all response mechanisms and resource trophic levels. Relative response magnitudes are presented here instead of response magnitude slopes because our hierarchical model analysis was unable to meaningfully estimate or interpret all possible interaction effects among the five key explanatory variables. From left to right, the sample sizes are $N = 33$, $N = 8$, $N = 53$, $N = 7$, $N = 18$, $N = 9$, $N = 9$, $N = 11$, $N = 1$. Aggregative and combined responses are significantly larger for interactions in which the resource trophic level is 1. (b) Response magnitude slopes (mean slope ± SE) vary by ecosystem subtype, as estimated by best-fit models. The number of events and systems that comprise each ecosystem subtype in this analysis are noted along the x-axis as "number of events (number of systems)"; these counts represent a subset of the entire data set for which the required data for this analysis were available. (c) Longer duration resource pulses have larger responses. Solid, dashed, and dotted regressions represent groups based on the 90th, 50th, and 10th quantile of standardized resource pulse duration, respectively, based on the best-fit model. Darker points represent interactions with longer standardized resource pulse durations.

0.06) received substantially less support, and the additive combination of these three factors did not fit the data as well as standardized pulse duration (cAIC weight = 0.01).

These observations suggest that longer resource pulse durations generally allow for larger responses, especially in systems in which there is a strong reproductive component to the response. For example, particularly strong consumer responses have been observed in small-mammal populations responding to multiyear episodes of El Niño Southern Oscillation (ENSO) rainfall (Meserve et al. 2003) and mast seed superabundance (Wolff 1996). These large response magnitudes appear to occur because consumer populations show accelerating population growth that builds upon previous numerical gains during longer periods of continued resource superabundance. The effects of resource pulse duration on relative response magnitude may be particularly evident in systems in which aggregative

responses and emigration are limited and population increases are driven primarily by reproductive mechanisms. For example, multiple consecutive El Niño years in the arid Galapagos islands were often associated with particularly rapid population growth among finches, as greater primary productivity increased both reproductive success and survival (Grant et al. 2000).

Unlike the factors described above, ecosystem type (aquatic vs. terrestrial) and consumer trophic position (autotrophic vs. heterotrophic) were not well supported as explanatory factors for consumer response magnitude. These groupings may be too broad to effectively predict consumer responses to resource pulses.

Response duration

In our analysis, consumer body size was a good predictor of the relative response duration (Fig. 5a; Appendix E). Larger body sizes increased the slope of the relationship between resource pulse duration and
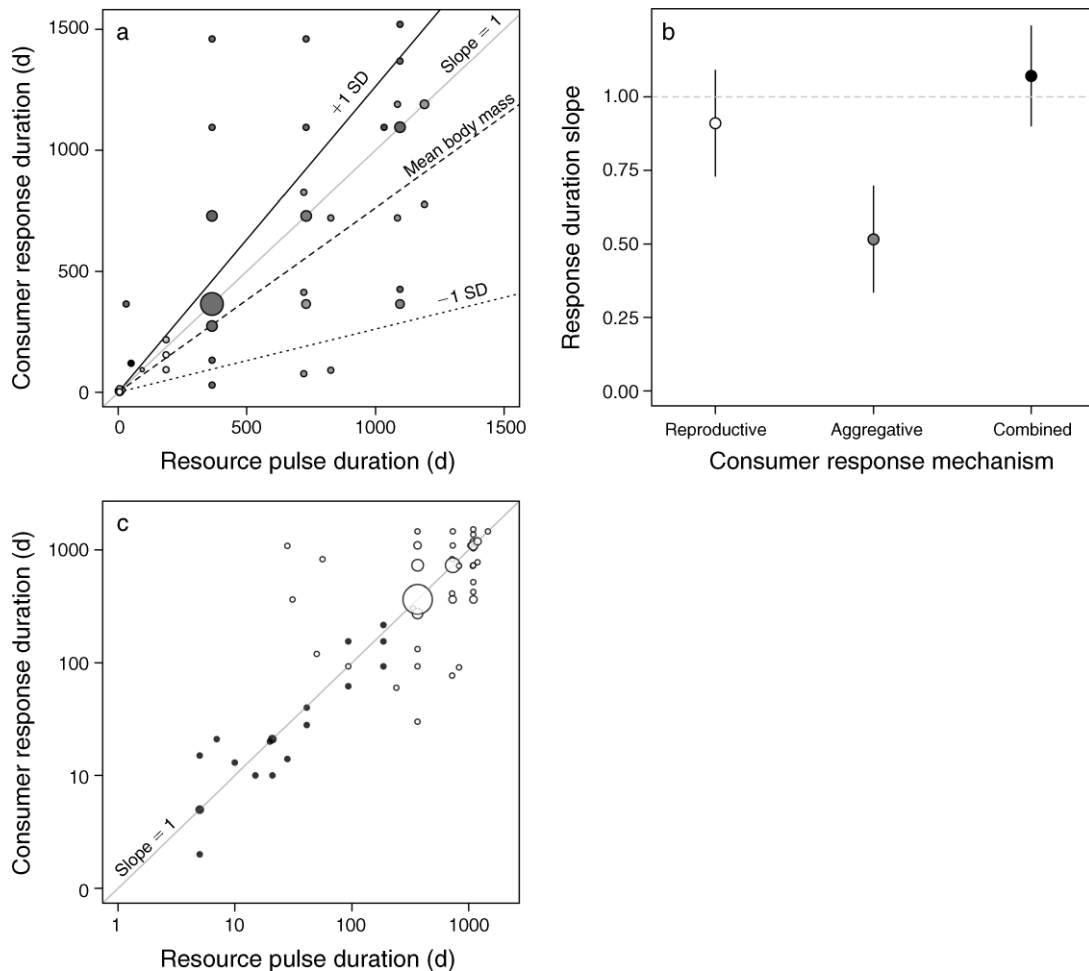
FIG. 5. (a) Regression of consumer response duration vs. resource pulse duration grouped by consumer body mass. The solid black line represents consumers one standard deviation greater than the mean body mass, the dashed line represents consumers of mean body mass, and the dotted line represents consumers with body mass one standard deviation less than the mean based on the best-fit model; the gray solid line represents the 1:1 line. Circle size is proportional to the number of overlapping data points. (b) Response duration slopes (means ± SE) associated with reproductive ($N = 38$, open circle), aggregative ($N = 6$, gray circle), and combined ($N = 18$, black circle) response mechanisms based on the best-fit model. (c) Aquatic systems had shorter pulse durations and consumer response durations than terrestrial systems in our data set, but ecosystem type did not affect the slope of the relationship between resource pulse duration and consumer response duration. The solid circles represent $N = 19$ aquatic systems, and the open circles represent $N = 101$ terrestrial systems. Circle size is proportional to the number of overlapping data points. Analyses comparing resource pulse duration and consumer response duration separately for the $N = 38$ and $N = 151$ terrestrial systems in our complete data set are consistent with this figure. Panel (c) shows slightly different data points than panel (a) because it is based on less restrictive criteria than the multilevel model analysis.

consumer response duration for all models in the 95% confidence set, suggesting that large-bodied consumers showed more persistent responses than small-bodied consumers when the response duration was considered relative to resource pulse duration. Consumers more than one standard deviation smaller than the mean body size showed responses that were shorter than the duration of their resource pulses, while consumers more than one standard deviation larger than the mean body size showed responses that were longer than the duration of the resource pulses (Fig. 5a). One potential explanation for this pattern is that smaller individuals

may be more likely to be consumed by predators at higher trophic levels. However, our analysis found no consistent effect of consumer trophic level on the log ratio of consumer response duration and resource pulse duration (slope ± SE = -0.0016 ± 0.174), suggesting little support for this mechanism. Alternatively, this pattern could reflect the higher specific metabolic rates or shorter life spans of smaller consumers (Peters 1983, Schmidt-Nielsen 1984, Enquist et al. 1998). Higher specific metabolic rates might allow these consumers to capitalize on temporary episodes of resource availability more rapidly, but might also contribute to more

precipitous declines as resources diminish, whereas long-lived consumers may allow the effects of resource pulses greater persistence over time.

Consumer response mechanism was also a strong predictor of the relative response duration; reproductive and combined consumer responses were more persistent than aggregative consumer responses (Fig. 5b). In this analysis, the model with the greatest support (cAIC weight = 0.58) included only consumer response mechanism and body mass, and both factors had variable weights greater than 0.99 over the entire model set (Appendix E). These results suggest that behaviorally aggregating consumers quickly emigrate away from areas of pulsed resource abundance during the phase of declining resource availability. Although intuition suggests that small-bodied and behaviorally aggregating consumers may be likely to show particularly rapid numerical increases following resource pulse events, these results indicate that these consumers may also show the least persistent responses.

In comparison, generation time and pulse magnitude were not well supported as explanatory factors (variable weight for generation time = 0.23, variable weight for pulse magnitude = 0.25), and their effects were within 1 SE of 0. However, because generation time and body mass were positively correlated in this data set (Pearson's $R = 0.79$), these analyses have limited abilities to separate and quantify their effects and may underestimate the explanatory role of generation time. As a result, the effects of consumer generation time on response duration remain uncertain.

The aquatic systems represented in our data set showed much shorter resource pulse durations and correspondingly shorter consumer response durations than terrestrial systems (Fig. 5c). However, ecosystem type did not explain significant variation in the slope of the relationship between resource pulse duration and consumer response duration. These two results suggest that the relative response durations of the two ecosystem types are fundamentally similar, but the absolute durations of resource pulses tend to be substantially shorter in aquatic vs. terrestrial systems. Whether our limited data set reflects broader patterns in nature remains unclear. There are certainly some notable examples of relatively persistent resource pulses in aquatic systems, including inputs of whale fall carcasses to marine benthic communities (Smith and Baco 2003). However, we found few similar examples and we were unable to obtain suitable quantitative data to incorporate these studies into our data set. Although certainly incomplete, it seems likely that our data set accurately reflects the preponderance of relatively short-duration aquatic resource pulses in the existing literature.

Response lag

The response lags of aquatic systems were shorter than those of terrestrial systems in our data set (Fig. 6a). In our multilevel analysis of categorical factors, ecosys-
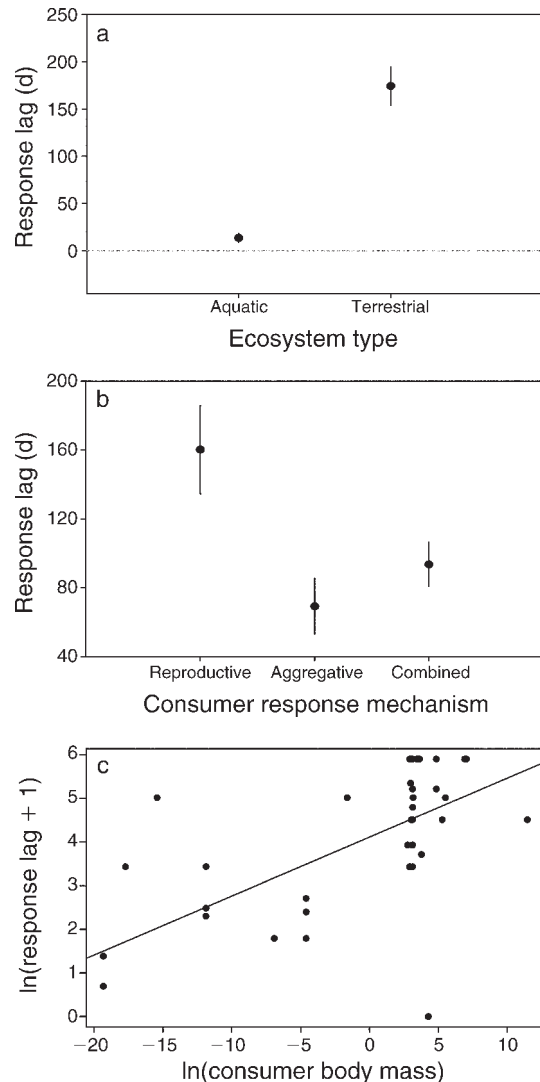

FIG. 6. (a) Consumer response lag (mean ± SE) for aquatic ($N = 33$) and terrestrial ($N = 113$) ecosystem types. (b) Consumer response lag (mean ± SE) for reproductive ($N = 89$), aggregative ($N = 33$), and combined ($N = 18$) response mechanisms. (c) Regression of consumer response lag (measured in days) by consumer body size (measured in grams).

tem type received moderate support using cAIC model selection criteria (variable weight = 0.73) and stronger support using AIC criteria (variable weight = 0.99; Appendix F). These results suggest that the time lag between the peak of pulsed resource availability and the peak consumer response is shorter in aquatic systems compared to terrestrial systems, consistent with existing ideas about fundamental differences in the structure of aquatic and terrestrial communities (Strong 1992, Shurin et al. 2006) and hypotheses about the manner in which these two broad ecosystem types should respond to pulsed resource perturbations (Nowlin et al. 2008).

Consumers with aggregative or combined responses also showed shorter response lags than consumers with
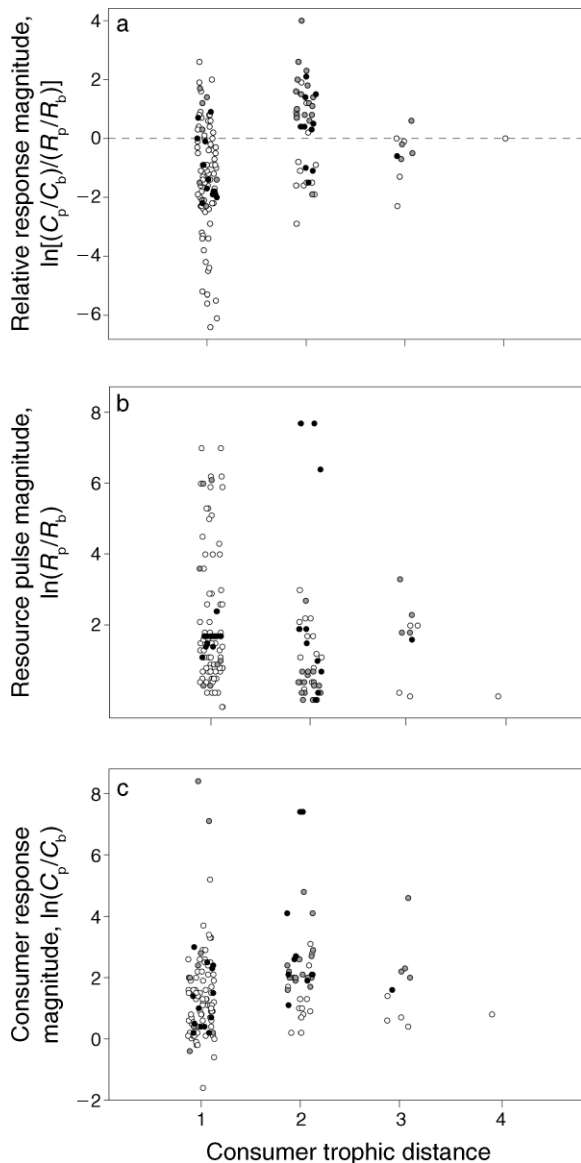
FIG. 7. (a) Relative response magnitude by consumer trophic distance. Points above the dashed line show directly amplifying consumer responses, while points below the dashed line show directly attenuating consumer responses. (b) Resource pulse magnitude and (c) consumer response magnitude by consumer trophic distance. In all panels, open, gray, and black circles represent reproductive, aggregative, and combined responses, respectively. Data points are randomly jittered along the x-axis for clarity.

response mechanism was often confounded with system and many systems showed limited within-system variation in response lag and response mechanism. As a result, the role of response mechanism remains equivocal, as the effects of response mechanism are difficult to separate from system-level variation.

Our data set suggested that response lag increased with increasing consumer body mass (Fig. 6c). In our analysis of continuous factors, models including consumer body mass as a factor consistently performed better than the null model including only system, and body mass was a better predictor of response lag than all of the other continuous explanatory factors in this analysis, such as consumer generation time or resource pulse duration (variable weight for body mass = 0.99; Appendix F). Given the observation of generally smaller consumers in aquatic systems, this pattern also supports the observation of shorter response lags in aquatic compared to terrestrial ecosystems.

Indirect effects

In our analysis of indirect effects, we considered relative response magnitude as a function of the trophic distance between the consumer and the initial resource pulse (Fig. 7a). Our analyses indicated an unexpected pattern of smaller relative response magnitudes for the primary consumers of initial resource pulses (i.e., consumers at trophic distances of 1), compared with consumers at greater trophic distances. This pattern suggested the possibility of a hump-shaped or saturating relationship between consumer trophic distance and the relative response magnitude. However, because consumer trophic distances greater than 2 are represented by relatively few data, our analyses focused on the observed differences between the well-represented interactions at trophic distances 1 and 2 (Fig. 7a). The difference in relative response magnitude between these two groups was significant in a mixed-model ANOVA that included trophic distance as a fixed effect and system as a random effect ($P = 0.001$, $F_{1, 102} = 11.52$). On average, the consumers at trophic distances of 1 showed attenuating responses to resource pulses, while consumers at trophic distances of 2 showed proportional or slightly amplifying responses (Fig. 7a). This pattern persisted whether we analyzed all the available data representing these two trophic distance groups or restricted the data to include only those events with trophic interactions extending over two trophic levels.

We suggest three nonexclusive ecological hypotheses to explain the observed patterns of relative response magnitude with increasing trophic distance. First, this pattern could result if the consumers of primary (i.e., initial) resource pulses are more likely to show consumer satiation, resulting in smaller relative response ratios than consumers at greater trophic distances (H_1, the "primary consumer satiation hypothesis"). This could occur if primary resource pulses tend to be larger than the subsequent (i.e., indirect) resource pulses that follow

primarily reproductive responses in a single-factor analysis of our data set (Fig. 6b). Although this pattern is consistent with intuitive expectations, response mechanism did not appear to be an important explanatory factor in our overall model selection analysis: with the inclusion of system as a factor, response mechanism explains relatively little additional variance in consumer response lags (Appendix F). In large part, these results likely reflect inadequate variation in our data set;

them (Fig. 1d). This hypothesis suggests that the relative response magnitudes (i.e., $\ln[(C_p/C_b)/(R_p/R_b)]$) of consumers at trophic distances of 1 are small because the ratio R_p/R_b tends to be particularly large for primary resource pulses. A key assumption of this hypothesis is that primary resource pulses are larger than indirect resource pulses, and Fig. 7b offers some limited support for this assumption, showing a suggestive but nonsignificant pattern of larger resource pulses at trophic distances of 1 (mixed-model ANOVA with trophic distance as a fixed effect and system as a random effect, $F_{1, 102} = 3.44$, $P = 0.066$). If this were generally true, it would suggest a fundamental and ecologically significant difference in the magnitude of initial resource pulses vs. indirect resource pulses. One explanation for this difference is that primary resource pulses often represent resource components that have been temporally or spatially stored over a large scale, while indirect resource pulses are generally limited by the immediate population responses of consumers in the community. For example, the largest resource pulses at trophic distances of 1 were often seed mast or climatic rainfall events that represent the rapid release of temporally or spatially stored resources. The consumers of these primary resource pulses often showed rapid satiation, potentially resulting in smaller proportional responses at trophic distances of 1.

Alternatively, the observed pattern could result if consumer responses to resource pulses are relatively larger for secondary and tertiary resource pulses due to correlations between trophic distance and response mechanism (H_2). This "response mechanism hypothesis" suggests that observed patterns of response magnitude may be explained by the increased likelihood of aggregative or combined response mechanisms with increasing trophic distance. Although trophic distance is not strictly correlated with either trophic level or response mechanism, aggregative and combined responses are more common at trophic distances greater than 1, and the largest of these consumer responses were usually associated with aggregative and combined response mechanisms (Figs. 4a and 7a). In part, this is because sessile plants are generally closer to the primary resource pulse, though even motile consumers appear more likely to show aggregative responses with increasing trophic distance. Because aggregative and combined responses tend to be substantially larger than non-aggregative responses, even an imperfect correlation between trophic distance and response mechanism could contribute to the observed pattern of relative response magnitudes.

Finally, this pattern could also result if top-down effects from higher-trophic-level consumers directly reduce the maximum numerical responses of lower-trophic-level consumers (H_3, the "rapid top-down control hypothesis"). For example, the observed pattern in Fig. 7a could result if predation from consumers at trophic distances of 2 reduced relative response magnitudes at trophic distances of 1. This hypothesis assumes some correspondence between trophic level and trophic distance; because initial resource pulses can occur at any trophic level, consumer trophic distance does not correspond perfectly with consumer trophic level. However, within each resource pulse event, increasing trophic distance is correlated with increasing trophic level. A key assumption of this hypothesis is that consumers are able to respond to resource pulses rapidly enough to reduce the maximum numerical responses of lower trophic levels. Conversely, inherent lags in consumer responses to resource pulses could lead to delayed top-down effects that occur during the declining phase of the resource pulse (Yang et al. 2008) without affecting the maximum response magnitude.

In order to further investigate H_2 and H_3, we conducted a hierarchical regression and model selection analysis using all eight combinations of three explanatory variables (consumer response mechanism, consumer trophic distance, and the resource trophic level) and one grouping factor (system). The data set for this analysis was limited to interactions at trophic distances 1 and 2. As in previous analyses, we used model selection methods to evaluate the explanatory power of each model and estimate the weight of each variable. These analyses indicate that the consumer response mechanism is a strong predictor of relative response magnitude (Appendix G), as this factor was included in all models within the 95% confidence set (variable weight = 0.99881). By comparison, trophic distance and trophic level variables did not contribute substantial additional explanatory power to models that also included consumer response mechanism as a factor. However, the model that included only system and trophic distance factors explained considerably more variation (ΔAIC = 12.1) than the null model including only the system grouping factor (ΔAIC = 21.1). The model including both system and trophic level as factors did not perform as well as the null model (ΔAIC = 21.8). These results support the hypothesis that relative response magnitude is greater at distances of 2 because those consumers are more likely to show aggregative responses in addition to reproductive responses (H_2). However, it is also possible that those same consumers show more rapid top-down control (H_3). Given the covariance between response mechanism and trophic distance, the results of this analysis cannot exclude the possibility that rapid top-down control contributes to the observed pattern. However, these results do suggest that if consumers at distances of 2 are directly suppressing the maximum numerical responses of consumers at distances of 1, it may be because they are more likely to show aggregative responses.

We also suggest one non-ecological hypothesis: this pattern could emerge from a particular version of the "file drawer problem." By definition, all studies in our data set included consumers at trophic distances of 1, but not all studies included consumers at higher trophic distances. If studies that investigated larger resource

pulses or showed larger proportional effects on consumers were also more likely to report the responses of multiple trophic levels, this reporting bias could potentially create a pattern of larger consumer responses at greater trophic distances. We investigated this possibility in two ways. First, we compared the relative response magnitudes of direct (i.e., trophic distance = 1) interactions that were documented as part of multi-trophic-level chains vs. direct interactions that were only documented in single-trophic-level studies. This analysis directly evaluates the assumption that studies of larger resource pulse events are more likely to report responses at multiple trophic distances: under the hypothesized pattern of reporting bias, relative response magnitudes at trophic distances of 1 would be expected to be larger in multi-trophic-level studies compared to single-trophic-level studies. This analysis showed a nonsignificant pattern of larger relative response ratios for direct interactions that were documented as part of multi-trophic chains compared to interactions documented as direct responses to resource pulses only (t test, $P = 0.22$, $t_{97} = 1.24$; Appendix H). Although there may be a weak trend in this direction, this analysis offers little support for a necessary assumption of the file drawer hypothesis. Second, we analyzed the effect of trophic distance on relative response magnitude in a restricted data set that included only those systems that reported multi-trophic responses extending to trophic distances of 2 or greater. This restricted analysis showed a similar and significant pattern of lower relative response magnitudes for initial resource pulses as the complete data set analysis (mixed-model ANOVA with trophic distance as a fixed effect and system as a random effect; $F_{1,55} = 6.98$, $P = 0.011$; Appendix H), suggesting that observed differences in the relative response magnitudes at trophic distances of 1 and 2 are unlikely to be driven entirely by reporting bias.

Taken together, our analyses suggest that the observed pattern of relative response magnitudes may be due to a combination of several mechanisms, including fundamental features of natural communities that result in larger resource pulse magnitudes at trophic distances of 1 (H_1) and more common aggregative consumer response mechanisms at trophic distances of 2 (H_2). Although it is difficult to assess the role of direct top-down effects (H_3) and reporting bias, neither of these hypotheses seems sufficient to explain the observed pattern entirely.

Our examination of resource pulse–consumer interactions in 16 multi-trophic systems suggested three key insights into the attenuation and amplification of resource pulse effects (Fig. 8). First, these quantitative case summaries provided evidence of both attenuating and amplifying response magnitudes with increasing trophic distance from the primary resource pulse and did not demonstrate a consistent pattern of attenuating consumer responses, as expected.

Second, several case summaries suggest the particular importance of aggregative responses across community

boundaries as a mechanism of amplifying consumer responses. For example, a single-pulse nutrient addition experiment conducted in a contiguous region of Spartina salt marsh meadow showed predictable differences when compared to a parallel experiment conducted on isolated islets of Spartina growth surrounded by open water (Gratton and Denno 2003): in the meadow habitat, all three consumers at the third trophic level showed aggregative responses to this indirect resource pulse, while only the most vagile of the three species was able to aggregate to the islet sites. Two species of less-mobile predators were apparently unable to aggregate to the islets, and these consumers showed attenuating responses, while the winged predator showed a strongly amplifying response to the same event. In the Daphne Major system (Galapagos Islands, Ecuador), the predominantly attenuating pattern of consumer responses to two ENSO events may reflect the relative isolation of these habitats and the limits of reproductive responses. In this island system, habitat boundaries and biogeographic isolation limit the potential for aggregative numerical responses and emphasize the role of reproductive constraints (Grant et al. 2000).

Third, these case summaries suggested the importance of initial resource pulse magnitude as a factor modulating the attenuation and amplification of consumer responses. For example, the observed differences between community responses to the 1976 and 1990 beech mast events in Eglinton Valley (Fiordland National Park, New Zealand) suggest that fundamental differences in the magnitude of the initial resource pulse may affect the incidence of attenuation and amplification responses in an intuitive way: larger resource pulses may lead to proportionately smaller consumer responses due to the effects of consumer satiation, while smaller resource pulses are used more completely by the non-detrital community, leading to proportionately larger consumer responses. In the Eglington Valley, the 1976 mast event was relatively small and resulted in a community-level amplification response, while the 1990 mast event was much larger and resulted in a community-level attenuation response. Although these patterns should be interpreted cautiously, these observations suggest that larger resource pulses may tend to be associated with attenuating consumer responses, while smaller resource pulses may tend to be associated with amplifying responses.

CONCLUSIONS AND FUTURE DIRECTIONS

Predicting consumer responses to resource pulses

Despite the broad range of ecosystems, taxa, and spatiotemporal scales from which our data were gathered, we found unexpectedly consistent patterns in resource pulse–consumer interactions, for which a surprisingly small number of explanatory factors explain significant variation (Fig. 9). These fundamental conclusions are encouraging. Although resource pulses are extreme, ephemeral, and unusual events, these findings
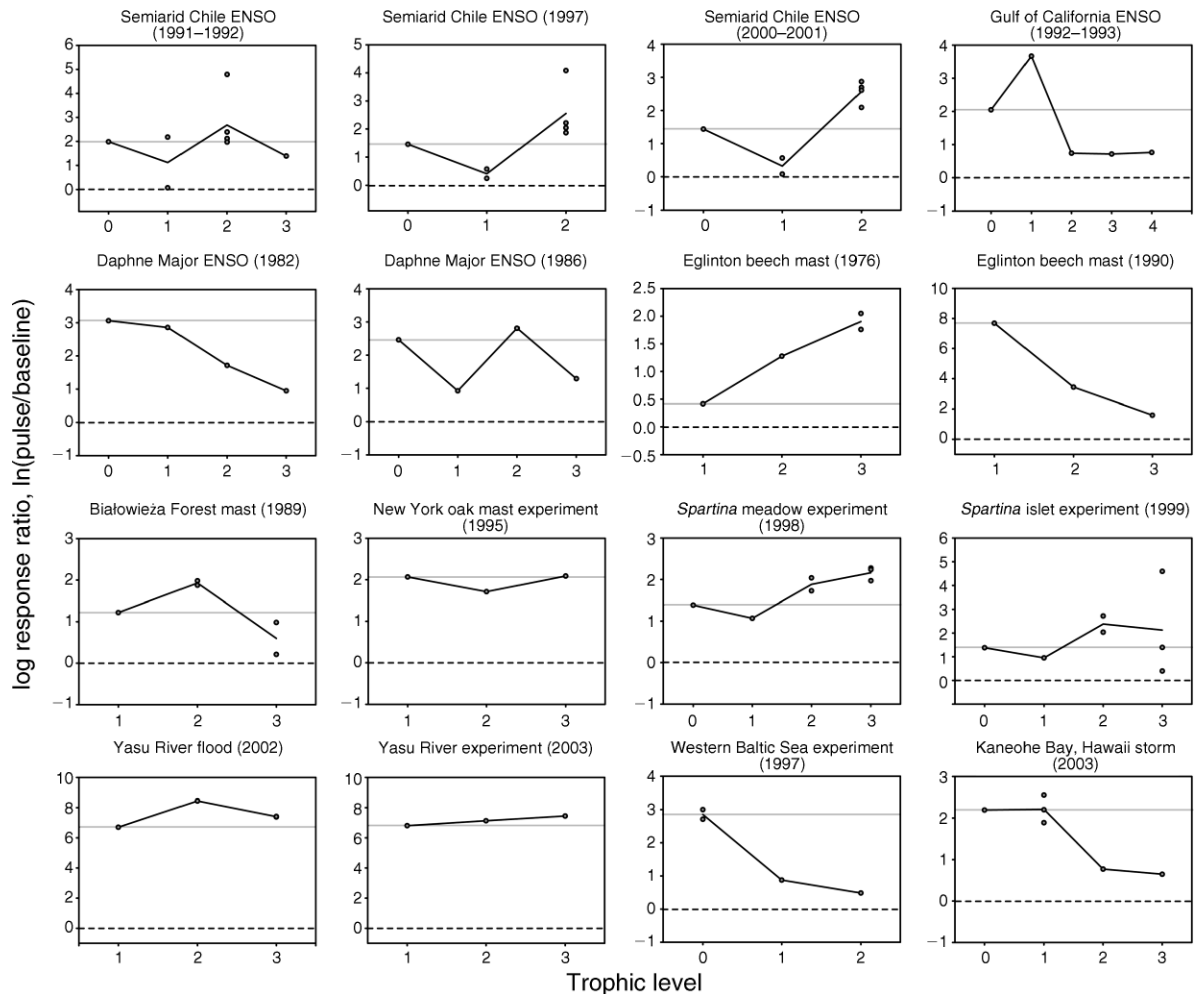
FIG. 8. The attenuation and amplification of indirect effects of 16 specific resource pulse events in 10 systems (see Table 1). Note that the y-axes represent log response ratios. The leftmost point in each panel represents the resource pulse magnitude for the primary resource pulse(s); all other points represent consumer response magnitudes. A solid line connects the mean response magnitude for each trophic level; a positive slope line leading to a trophic level indicates an amplifying response, while a negative slope line indicates an attenuating response. The solid gray line in each panel represents the magnitude of the primary resource pulse; response ratios above this line indicate consumer responses larger than the primary resource pulse, reflecting amplification relative to the initial resource pulse. By comparison, response ratios below this line represent response ratios smaller than the initial resource pulse, reflecting attenuation relative to the initial resource pulse. The dashed line in each panel represents the zero threshold; the height of response ratios above this line indicates the magnitude of positive responses relative to their baseline conditions. The abbreviation "ENSO" stands for El Niño Southern Oscillation.

suggest that they may be usefully examined as a general class of phenomena with a common dynamic process. Despite initial concerns, the wide diversity of resource pulses in nature did not preclude meaningful analyses; to the contrary, the broad range of resource pulse–consumer interactions in nature provided the essential variation necessary to examine multiple explanatory factors in a common framework. These analyses also demonstrate the importance of a quantitative approach for the examination of the characteristics of resource pulses, consumers, and ecosystems; while resource pulse–consumer interactions show general patterns, these patterns are clearly structured by identifiable and measurable characteristics. Quantifying variation

among resource pulses usefully places these events within the broader gamut of environmental variability.

The results of these analyses are generally consistent with model predictions emphasizing the importance of both resource pulse magnitude and duration on the dynamics of consumer responses to resource pulses (Holt 2008). However, our current analyses also differ from analyses of simulation models in important respects. First, while model analyses are able to modulate the duration of resource inputs while maintaining a constant total resource input, these two factors often appear to be correlated in natural systems. In our data set, longer duration resource pulses often represented repeated resource pulse events of large magnitude
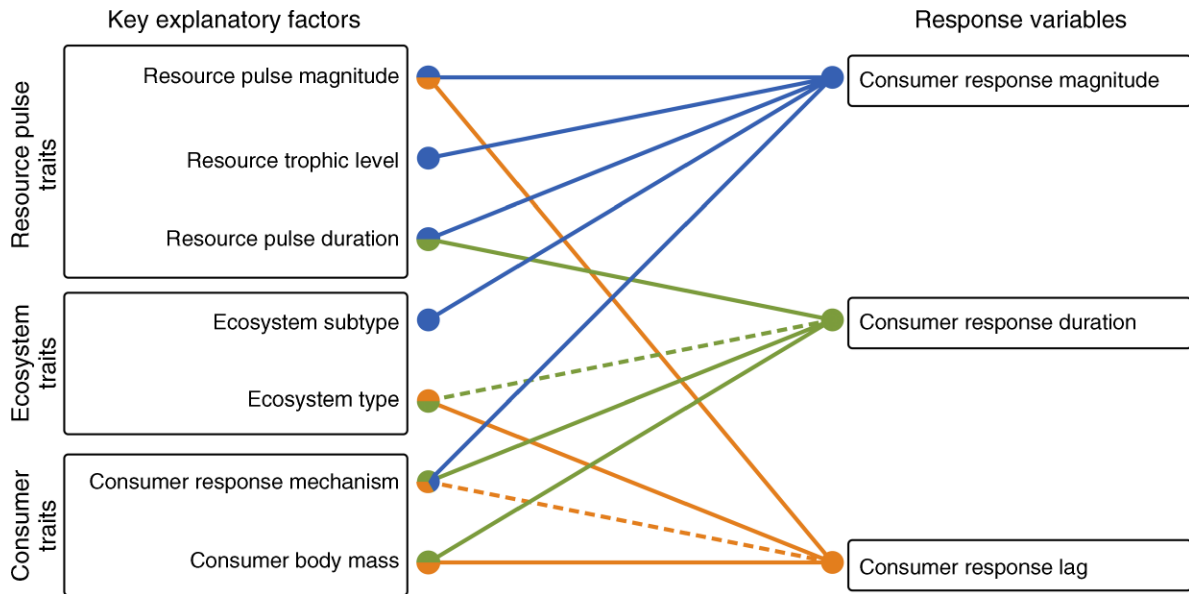
F̲ɪɢ̲. 9. A summary of key explanatory factors and their effects on three aspects of consumer responses to resource pulses. Solid lines connect well-supported explanatory factors and key consumer response traits. Dotted lines connect factors that were supported in single-factor analyses but not in multi-factor analyses.

or larger perturbations overall. Our metrics of resource pulse magnitude and resource pulse duration provide robust and relative measurements of distinct dynamic characteristics and do not assume constant total inputs. By comparison, Holt (2008) documented a pattern of decreasing consumer responses with increasing pulse duration in model simulations under the assumption of constant total input. Our analysis indicates that increasing pulse durations in nature are generally associated with significantly larger relative response magnitudes, with important implications for resource pulse–consumer dynamics. This difference does not result from fundamentally different dynamical processes, but rather distinctions between the assumptions associated with each analysis.

These analyses point toward the need for more targeted studies to better understand how specific characteristics of resource pulses are likely to affect consumer responses in natural systems. We suggest that future descriptive studies should provide quantitative measures of the magnitude and duration of both resource pulses and consumer responses relative to their baseline conditions and describe key characteristics of resource pulse–consumer interactions, such as the consumer response mechanism, body size, and generation time. Future experimental studies should aim to manipulate the key characteristics of resource pulses independently, within the realm of natural variation.

Differences between ecosystems

In a recent paper, Nowlin et al. (2008) considered the manner in which consumer responses to resource pulses would be expected to differ in aquatic systems compared

to terrestrial systems, given widespread differences in the structure and dynamics of these two ecosystem types (Strong 1992, Shurin et al. 2006). This paper suggested two key predictions: (1) consumers in aquatic systems should generally have more rapid responses to resource pulses than consumers in terrestrial systems because of fundamental differences in their growth rates, life history, and stoichiometry; and (2) the duration of consumer responses in aquatic systems should generally be shorter than the duration of consumer responses in terrestrial systems, due to the longer generation times of terrestrial consumers, the relative durability of many terrestrial resource pulses, and the reduced effects of top-down control in terrestrial systems compared to aquatic systems (Nowlin et al. 2008). Our analyses support several of these predictions, but remain equivocal about others.

Within our data set, aquatic systems showed shorter response durations and response lags than terrestrial systems. This result supports the hypothesis that responses to resource pulses are generally more rapid in aquatic systems when these two ecosystem types are compared on absolute timescales. In part, these patterns are likely to reflect prevailing differences between aquatic and terrestrial systems in the duration of underlying resource pulses, the body sizes of consumers, or resource–consumer body size ratios (Brose et al. 2006, Shurin et al. 2006, Nowlin et al. 2008). However, ecosystem type explains little variation in the slope of the relationship between resource pulse duration and consumer response duration, suggesting that the responses of aquatic and terrestrial consumers might be similar if resource pulses of similar duration were

compared. These findings suggest that aquatic and terrestrial systems may show both fundamental differences in the characteristics of their resource pulses and consumers and fundamental similarities in their essential resource pulse–consumer dynamics.

Response mechanisms and spatial scale

Consumer response mechanism proved to be a strong and robust explanatory factor in several analyses. This result is interesting because it indicates that a particularly simple categorical description of the consumer response mechanism, whether a consumer's numerical responses are reproductive, behaviorally aggregating, or both, can provide useful and predictive information about consumer dynamics following resource pulse events. The strong role of consumer response mechanisms in these analyses also suggests links between spatial and temporal variation. While behaviorally aggregating consumers search for resource-rich patches over larger spatial scales, consumers that respond to resource pulses with primarily reproductive mechanisms generally rely upon resource use flexibility and short generation times to capitalize on local pulses of resource availability. These two consumer response mechanisms reflect broad strategies for coping with resource variability (Ostfeld and Keesing 2000, Yang et al. 2008). By foraging over larger spatial scales, behaviorally aggregating species may be able to reduce temporal resource variability; in a sense, these consumers trade temporal variability for spatial variability, with implications for their population dynamics (Sears et al. 2004). Conversely, opportunistic resident consumers may be able to cope with local resource variability by using alternative resources or durable life stages. This result suggests a potential trade-off between aggregative and reproductive consumer responses to resource pulses. Whereas aggregative responses are associated with rapid and large magnitude responses, reproductive responses appear to be associated with more persistent responses in the local community. In part, this trade-off reflects fundamental differences between mobile consumers that recruit from surrounding areas and forage over larger spatial scales and opportunistic resident consumers that shift their diet to capitalize on local resource pulses.

The ecological implications of these two resource use strategies are manifold. At a fundamental level, behavioral aggregation responses demonstrate trophic links across habitat boundaries and emphasize the spatial scale of real interaction networks, but the transient nature of these consumer responses suggests that many trophic links between communities may not be apparent until a resource pulse occurs. Conversely, reproductive responses among opportunistic residents demonstrate the potential for rapid initial population growth following a pulsed perturbation (i.e., "reactivity" sensu Neubert and Caswell 1997) even in closed populations. In reality, most communities and many consumers combine aspects of both aggregative and reproductive responses, underscoring the need to quantify and integrate these two processes.

Persistence and resilience

Resource pulses have the potential to create persistent effects in communities through several mechanisms (Holmgren and Scheffer 2001, Holt 2008, Scheffer et al. 2008, Yang et al. 2008), but the extent to which natural systems are structured by resource pulses remains uncertain. Our analyses examined the persistence of resource pulse effects in order to identify factors that influence the resilience of ecosystems to strong perturbations and the limits of this resilience.

Our analysis suggests that naturally occurring resource pulses generally have strong but transient effects on their consumers. The relative duration of resource pulse effects varied widely in our data set, with many consumer responses persisting for multiple generations or long after resource availability declined to near-baseline levels. However, consumer responses were fundamentally transient, with durations generally within an order of magnitude of the resource pulse duration (Fig. 5a). Larger consumer body sizes, reproductive response mechanisms, and terrestrial ecosystems were generally associated with more persistent responses. Conversely, smaller consumers, aggregative response mechanisms, and aquatic ecosystems were generally associated with rapid and ephemeral consumer responses, suggesting that these interaction characteristics may contribute to more resilient communities with shorter timescale transient dynamics.

Resource pulses have been suggested as factors influencing transitions between alternative stable states in natural communities (Holmgren et al. 2001, Scheffer et al. 2008). Although transitions to alternative stable states have been documented or suggested in several studies (Scheffer 1990, Scheffer et al. 1993, 2001, 2003, Scheffer and Carpenter 2003), we were unable to identify examples of specific resource pulse events that showed permanent effects in the community and met the quantitative criteria for inclusion in our data set, suggesting that most resource pulses do not result in transitions to alternative stable states. However, the absence of such interactions in our data set should be interpreted cautiously. Although we attempted to build the broadest possible data set, these analyses focused on specific resource pulse–consumer interactions and did not attempt to systematically evaluate the incidence of broader community shifts, as the dynamic criteria for alternative stable states are notoriously difficult to demonstrate conclusively (Beisner et al. 2003, Scheffer and Carpenter 2003, Schroder et al. 2005). However, the ecological consequences of alternative stable states and long-term transient dynamics are likely to be similar in many systems; if the effects of pulsed perturbations are sufficiently persistent relative to the frequency of these events, the system will spend a large amount of time

away from equilibrium responding to the "ghosts of resource pulses past" (Yang et al. 2008).

These observations suggest that most natural systems are resilient to resource pulse perturbations within the range of natural variation. This is consistent with the idea that most populations in natural systems are dynamically stable despite considerable environmental variability (e.g., Sibly et al. 2007). However, this current analysis is unable to address the limits of ecological resilience and the likelihood of catastrophic shifts during periods of rapid environmental change. Several studies have suggested that the erosion of ecosystem resilience may be a necessary precursor for broader and more persistent community shifts (Scheffer and Carpenter 2003, Van Nes and Scheffer 2004). Future work will be necessary to investigate the manner in which anthropogenic changes in climatic regimes, land use, and biodiversity may affect community responses to resource pulses and the potential role of resource pulses as proximate drivers of catastrophic community shifts.

Attenuation and indirect effects

In an influential paper, Bender et al. (1984) suggested key differences between press and pulse perturbation studies in community ecology. Among these differences was the assertion that while pulse perturbations can provide information about direct effects, inference about indirect effects is limited to press perturbation studies. Our current analyses suggest two amendments to these conclusions. First, our analyses suggest that the useful conceptual distinction between press and pulse perturbations in experimental studies is likely to be less clear when considering the temporal variation that occurs in natural systems; the classical press vs. pulse dichotomy actually represents two extremes in a quantitative continuum reflecting both the duration of specific perturbations and the speed of community responses. Second, the study of resource pulses suggests that we can learn a great deal about the propagation of indirect effects in communities through the study of pulsed perturbations. While Bender et al. (1984) focused on understanding the indirect effects of press perturbations at equilibrium, the study of resource pulses explicitly investigates the propagation of indirect effects during transient periods away from equilibrium. This alternative approach offers a complementary perspective for the study of indirect effects. For example, while the indirect effects of press perturbations at equilibrium are often too complex to be predicted (Yodzis 1988, Abrams et al. 1996), the study of transient indirect effects following resource pulses helps to delineate the key pathways of interaction in a community's trophic network and highlight the mechanistic bases of observed effects.

Our analysis of indirect effects found evidence for both attenuating and amplifying responses, often within the same system. In general, factors that increased the magnitude of consumer responses relative to their resource input promoted amplifying responses, while factors that decreased consumer responses relative to resource availability promoted attenuation. For example, large resource inputs of short duration often promoted attenuating responses, possibly reflecting consumer satiation, while large-bodied consumers with long generation times may be more likely to show attenuating responses than smaller consumers with shorter generation times. Similarly, consumers with non-aggregative response mechanisms were more likely to show attenuation than consumers showing aggregative responses, suggesting that open boundaries may promote amplifying responses to resource pulses.

This investigation is related to persistent broader questions about the relative importance of direct and indirect effects in ecology (Schoener 1993, Wootton 1994, 2002, Abrams et al. 1996). Although numerous studies have illustrated the importance of indirect effects (Menge 1995, Fox and Olsen 2000, Wootton 2002), the conventional expectation that direct effects are generally stronger than indirect effects emerges from intuitive assumptions about the diffusion of indirect effects over complex networks, the increasing role of stochastic environmental variation, and the fundamental thermodynamic constraints involved in trophic interactions (Schoener 1993, Wootton 1994). However, the factors that influence the attenuation or amplification of consumer responses to resource pulses in natural communities are likely to be more complex, and this present analysis differs from past efforts in its particular focus on transient indirect effects. This analysis emphasizes the importance of three processes that appear to play a large role in community responses to resource pulses, but have not been well integrated into broader models of community dynamics. First, resource pulses of large magnitude often lead to consumer satiation, resulting in relatively small and attenuating responses among local consumers. Second, the pervasiveness of open system boundaries allows the aggregative responses of mobile consumers to exceed local thermodynamic constraints, contributing to amplification of effects. Third, many consumers demonstrate strategies of adaptive resource use such as diet switching and dormant life history stages, which allow populations to rapidly capitalize on infrequent pulses of high resource availability, maximizing the effects of pulsed resources in the community. The relative importance of these three processes seems to differ with increasing trophic distance and may contribute to the mixed pattern of attenuation and amplification responses observed in these analyses.

The study of resource pulses has contributed to longstanding questions about the balance of bottom-up and top-down factors in community dynamics (Ostfeld and Keesing 2000), but several of these questions were beyond the scope of our current data set and analysis. Whereas bottom-up and top-down processes are typically thought to act simultaneously in

communities, the inherent time lags of consumer responses to pulsed resource perturbations can often lead to more sequential bottom-up and top-down interactions (Ostfeld and Keesing 2000, Schmidt and Ostfeld 2003, Elias et al. 2004, Yang 2008, Yang et al. 2008). Recent investigations in this area have documented reduced resource availability following a resource pulse event due to consumer overcompensation (Ostfeld and Keesing 2000, Yang et al. 2008), delayed top-down effects of resource pulses on alternative prey due to diet shifts (Schmidt and Ostfeld 2003, Wilmers et al. 2003, Kitzberger et al. 2007, Schmidt and Ostfeld 2008), transient increases in the maximum food chain length of the systems in response to resource pulses (Eveleigh et al. 2007), and increases in the top-down effects of pathogens and parasites in response to resource pulses (Hjelle and Glass 2000, Walsh et al. 2007, Pedersen and Greives 2008). For example, consumer characteristics that increase the likelihood of diet switching during resource pulses (such as generalist diets and omnivory) might facilitate both positive and negative indirect effects on alternative resources: consumers that rapidly shift their diets to capitalize on a pulsed resource may create transient periods of apparent mutualism during the initial increase phase of a pulsed resource event, while diet shifting away from a pulsed resource during the phase of rapid resource decline could lead to transient periods of apparent competition with alternative resources. Similarly, ontogenetic niche shifts, intraguild predation, and cannibalism could have complex effects on the persistence of resource pulse effects. Future studies and additional data will be necessary to understand the potentially complex indirect effects of resource pulses in real-world communities.

Some remaining questions

This analysis demonstrates that several aspects of the resource pulse–consumer interaction can be predicted based on relatively simple characteristics. However, it also reveals the limits of these predictions. Anthropogenic changes in the environment may create perturbations beyond the range of existing variation or alter mechanisms of ecosystem resilience, while forecasts of an increasingly variable climatic future suggest increases in the frequency and intensity of climatically driven resource pulse events. The consequences of these changes remain uncertain.

Although this analysis attempted to address several fundamental questions about the ecology of resource pulses, several key questions remain, and many more have emerged. How do differences in the frequency of resource pulses affect community responses? How do different functional responses to resource pulses affect community dynamics? How do omnivory, intraguild predation, and ontogenetic niche shifts affect the persistence and attenuation of resource pulse effects? How do diet shifts and the indirect top-down effects of resource pulses affect communities via apparent competition or apparent mutualism? How do resource pulses affect competition, coexistence, and invasion? How will resource pulse–consumer interactions change with climate change?

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 future insights and the integration of specific observations into broader ecological ideas. Whereas many early studies of resource pulses were limited to opportunistic, qualitative descriptions of isolated incidents, we now call for a more focused and integrated approach to study the ecology of resource pulses. Developing a more predictive understanding of the mechanisms that govern the interactions between resource pulses and their consumers will likely require more detailed studies of specific systems as well as parallel efforts to integrate observations from multiple systems into a coherent synthesis.

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APPENDIX A

Definitions of variables (*Ecological Archives* M080-004-A1).

APPENDIX B

Multilevel regression example (*Ecological Archives* M080-004-A2).

APPENDIX C

A description of the conditional Akaike Information Criterion (cAIC) (*Ecological Archives* M080-004-A3).

APPENDIX D

Model selection tables for consumer response magnitude analyses (*Ecological Archives* M080-004-A4).

APPENDIX E

Model selection tables for consumer response duration analyses (*Ecological Archives* M080-004-A5).

APPENDIX F

Model selection tables for consumer response lag analyses (*Ecological Archives* M080-004-A6).

APPENDIX G

Model selection tables for trophic distance analyses (*Ecological Archives* M080-004-A7).

APPENDIX H

Analysis of single-trophic-level and multi-trophic-level studies at trophic distances of 1 (*Ecological Archives* M080-004-A8).

SUPPLEMENT

A table of raw data used in this meta-analysis (*Ecological Archives* M080-004-S1).