

Threshold levels of generalist predation determine consumer response to resource pulses

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Many ecological systems are characterized by brief periods of increased resource availability called resource pulses. Empirical studies suggest that some populations of primary consumers grow rapidly in response to resource pulses, but others instead remain at low abundance despite increases in resource availability. Previous theory suggests that the lack of increase in primary consumers might be due to predators, which can respond to increased prey density both numerically, by increasing their own population, and functionally, by killing prey at a faster rate. The complexity of potential population responses to resource pulses can be assessed with simulations, but analytical conditions determining when one observes qualitatively distinct dynamics have yet to be identified. Here we use a graphical method based on a bifurcation diagram to derive the conditions leading to qualitatively distinct steady state and transient prey population dynamics as levels of predation (abundance and diversity) vary. When predation thresholds are crossed, consumer populations respond numerically to increases in their resources and provide a secondary resource pulse to their predators and parasites. These community dynamics have broad implications for the impact of changing predator communities on insect and rodent population outbreaks, which are economically and epidemiologically important.

Many ecological systems are characterized by resource pulses – brief episodic events of high resource availability. Examples include the annual pulse of anadromous fish to and from terrestrial and marine systems (Willson and Halupka 1995), insect outbreaks (Yang 2004), mast seed and fruit production (Jones et al. 1998, Schmidt and Ostfeld 2008), and the pulse of productivity associated with desert rainfall (Polis et al. 1997). Some pulses are recurrent and predictable, whereas others are highly stochastic in the timing of their occurrence, amplitude, and duration. Although the influence of resource pulses on multiple trophic levels in ecological communities is now widely recognized (Yang et al. 2010), general insights and theory linking resource pulses to community level processes are largely lacking (Ostfeld and Keesing 2000). For example, seasonal or inter-annual resource pulses can cause the population of primary consumers to increase several orders of magnitude (Yang et al. 2010), but primary consumers can also remain at low abundance during resource pulses (Fig. 1; McShea 2000, Elias et al. 2004). One class of reasons for such constrained responses might be limitation and regulation by predators (Yunger 2002). For example, rodent and lagomorph populations frequently do not increase in food supplementation field experiments, or increase only inside predator exclosures

(Krebs et al. 2001, Korpimäki et al. 2002, 2004, Huitu et al. 2003). Given these observations, there is need for a general conceptual framework for understanding the conditions under which predation and resource pulses interact to produce prey-population outbreaks, versus when predation can dampen such outbreaks (Schmidt and Ostfeld 2008).

Resource pulses are by nature transient events. The transient dynamics (Hastings 2004) of the prey population response depend on many factors, including initial population density, the predator functional and numerical response, and the size and duration of the pulsed resource. The complexity of potential population responses to resource pulses can be assessed with simulations (Holt 2008b), but analytical conditions determining when one observes qualitatively distinct dynamics have yet to be identified. Here we use a graphical method based on a bifurcation diagram to derive the conditions leading to qualitatively distinct steady state and transient prey population dynamics as levels of predation vary.

Understanding the dynamic consequences of predation and resource pulses jointly acting on prey is important in many areas of ecology, such as in consumer front formation (Silliman et al. 2013) and shifts between alternative states (Scheffer 2009). One domain for which this understanding

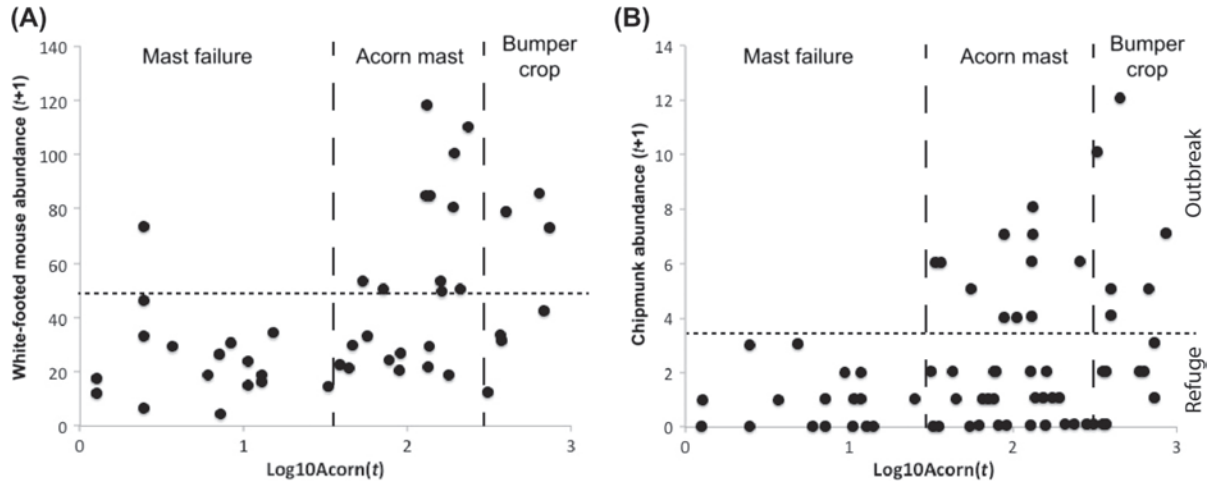


Figure 1. The response of small mammals to acorn masts (kg ha^{-1}) of variable sizes adapted from McShea 2000. (A) White-footed mice and (B) chipmunk abundances (number trapped) are low after a mast failure, but small mammals can either become very abundant (outbreak) or remain at low abundance (refuge) after an acorn mast, including after very large bumper crops.

may be particularly important is the ecology of infectious diseases. Many emerging infectious diseases, including Lyme disease, hantavirus diseases, plague, leishmaniasis, various hemorrhagic fevers and babesiosis, rely on reservoir hosts (particularly rodents) that occupy low trophic levels, where limitation and regulation by predators are likely (Daszak et al. 2000, Ostfeld and Holt 2004). The importance of predation in disease suppression has been suggested, but theoretical studies have largely emphasized equilibrium patterns rather than transient dynamics (Holt and Roy 2007, Holt 2008a). Empirical studies show that predators can either suppress (Ostfeld and Holt 2004) or enhance (Duffy et al. 2011) disease prevalence. A theoretical framework that encompasses both possibilities in how prey respond to resource pulses would provide pointers to a deeper empirical understanding of a poorly understood dimension of disease ecology.

Here we use models encompassing both top-down and bottom-up forces to explore how erosion of predation services impacts prey populations in a system driven by resource pulses. Our aim is to characterize how predation levels and pulse properties combine to determine the likelihood of a strong response by a prey species to a resource pulse.

Model and results

Predator-prey-resource model

We model changes in prey populations following the celebrated Ludwig et al. (1978) model of generalist predation and density-dependent prey population growth. This model elucidated a dramatic pattern observed in North American boreal ecosystems: episodic spruce budworm outbreaks and the resultant die-off and subsequent regeneration of spruce forests. In this model, a prey population of density N exhibits logistic population growth, and mortality due to predation following a Holling type III functional response (Holling 1959), which has a sigmoidal shape such as that

observed when generalist predators switch from the focal prey species to alternative food sources.

The differential equation for prey density in the Ludwig et al. (1978) model is

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \frac{aPN^2}{c^2 + N^2} \quad (1)$$

where r is the prey's intrinsic growth rate, K is its carrying capacity, a is the maximum predation rate, P is the density of predators (assumed fixed by factors other than the availability of the focal prey species), and c is the half-saturation prey density of the predator functional response. The resource supporting the prey population is not explicit in Eq. 1, but is potentially implicit in two parameters – r and K – either (or both) of which could increase with a surge in resource availability. In many species the maximal growth rate is set by aspects of basic organismal biology (e.g. litter size, inter-birth interval, age at first reproduction), so we will assume that an increase in resources is manifested as an increased carrying capacity.

As shown by Ludwig et al. (1978), the interaction between logistic growth and a type III functional response can produce alternative stable states. It should be noted that a comparable effect can arise for different assumptions about the predator functional and numerical responses, so long as the total predation imposed on the focal prey (i.e. the combined functional and numerical response) has a sigmoidal form (Hassell 1978). For example, a sigmoid shaped total response also occurs if mortality due to predation follows a type II functional response but there is a saturating numerical response of the predator (Supplementary material Appendix 1 Fig. A1) (see also Hassell 1978). Because the type III formulation above is more amenable to analysis, we focus on this formulation here.

Ludwig et al. (1978) introduced the dimensionless variables

$$X = \frac{N}{c}, \quad T = \frac{aPt}{c}, \quad R = \frac{cr}{aP}, \quad Q = \frac{K}{c}, \quad (2)$$

so that Eq. 1 could be rewritten with only two parameters (R and Q), both of which appear only in the growth term, as

$$\frac{dX}{dT} = RX \left(1 - \frac{X}{Q} \right) - \frac{X^2}{1+X^2} \quad (3)$$

Here we employ a different nondimensionalization that helps illuminate aspects of resource pulse effects on population dynamics. Let

$$x = \frac{N}{K}, \quad \tau = rt, \quad D = \frac{aP}{Kr}, \quad H = \frac{c}{K}, \quad (4)$$

where x is the dimensionless prey population density, τ is the dimensionless time, D is the dimensionless maximum death rate due to predation, and H is the dimensionless half-saturation parameter. Note that the carrying capacity term appears in the denominator of both D and H ; this helps illuminate aspects of resource pulse effects on prey population dynamics. With these dimensionless variables, the dynamics in Eq. 1 become

$$\frac{dx}{d\tau} = x(1-x) - \frac{Dx^2}{H^2 + x^2} \quad (5)$$

This formulation allows us to graphically explore distinct population dynamics in response to resource pulses in different regions of the two-dimensional D - H parameter space using a bifurcation diagram (Strogatz 1994, Scheffer 2009).

Equilibria of this system occur when prey recruitment matches predation, or

$$x(1-x) = \frac{Dx^2}{H^2 + x^2} \quad (6)$$

Equation 6 can have either a single non-zero stable equilibrium, or alternative (locally) stable states, separated by an intermediate unstable state. The ‘outbreak’ state refers to a stable equilibrium of abundant prey (intersection of red and blue lines in Fig. 2A), and the ‘refuge’ state to a stable equilibrium with rare prey (intersection of green and blue lines in Fig. 2A). The boundary between outbreak and refuge is roughly determined by whether the equilibrium prey density is on the left or right side of the maximum logistic population growth rate (which occurs at $N = K/2$, or $x = 1/2$). (If the prey had non-logistic growth, but with unimodal patterns of total growth rate versus population density, the maximal growth rate could occur for values either higher or lower than $K/2$; our essential points carry over to such prey as well, though the quantitative details would differ.) For some parameter sets (e.g. the yellow line in Fig. 2A), there are alternative stable states, one at high density, the other at low, separated by an unstable equilibrium (i.e. a separatrix between domains of attraction of the two stable steady states).

A bifurcation occurs when a parameter change causes a single stable equilibrium to transition into alternative stable states (Strogatz 1994). We construct a bifurcation diagram (Fig. 2B) by noting that the transition from single to multiple equilibria occurs when the two sides in Eq. 6 are both equal and tangent to each other (i.e. the point where the unstable state coalesces with either of the stable steady states), which is where

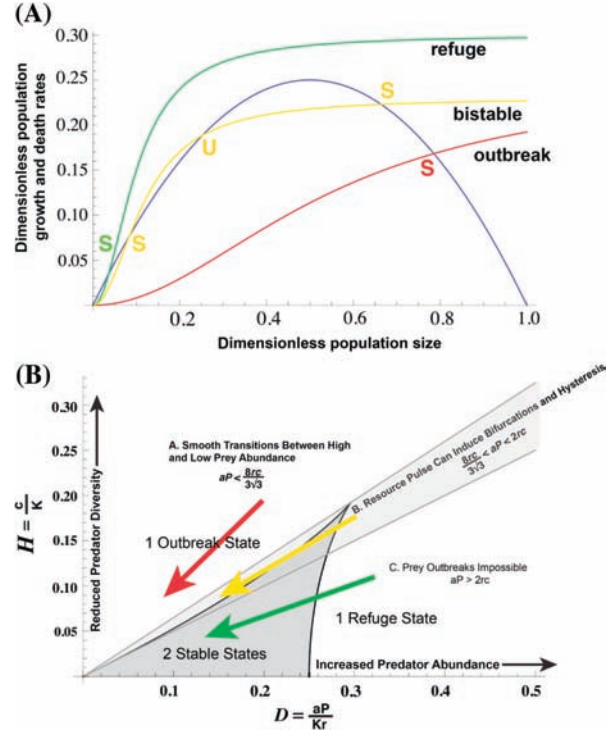


Figure 2. (A) The steady states of the small mammal population are determined by the intersection of the population growth (blue line) and predation rates (red, yellow, and green lines). It is possible to have a single stable steady state at low (refuge) or high (outbreak) small mammal abundance, or two stable steady states (bistable) with an unstable threshold in between. Stable and unstable states are labeled ‘S’ and ‘U’ respectively. (B) Bifurcation diagram for system of Eq. 5. As the dimensionless parameters (D and H) vary, the unstable state and either stable state of the bistable region can meet and annihilate in a saddle-node bifurcation, rapidly pushing the system to the other steady state. A resource pulse moves the system in parameter space toward the origin; lines through the origin naturally divide the bifurcation diagram into three qualitatively distinct regions (separated by light gray lines). In region A there is no bifurcation, but the resource pulse moves the steady state toward higher abundances of consumers (such as small mammals) in the outbreak region (red arrow). In region C, a resource pulse (green arrow) moves the system into the bistable region (shaded dark gray), but the system remains at the lower steady state keeping consumer populations low despite abundant resources. In region B (shaded light gray), the dynamics are partially buffered by the bistable region but it is possible for abrupt consumer pulses if the bistable region is fully crossed (yellow arrow).

$$x(1-x) = \frac{Dx^2}{H^2 + x^2} \quad \text{and} \quad \frac{d}{dx} [x(1-x)] = \frac{d}{dx} \left[\frac{Dx^2}{H^2 + x^2} \right] \quad (7)$$

Solving Eq. 7 for D and H as functions of the dimensionless population density x produces a parametric curve in the D - H plane given by

$$D = 2(x^3 - 2x^2 + x) \quad \text{and} \quad H = \sqrt{x^2 - 2x^3} \quad (8)$$

The boundary between regions in the bifurcation diagram (Fig. 2B) is then obtained by plotting $H(x)$ versus $D(x)$ for $0 < x < 0.5$ (above which H is not real), giving the black line, which has a cusp. Parameter combinations in the region between this curve and the D axis produce two stable states

(i.e. the bistable region, dark grey); to the right of this region there is only the refuge state; and above it, only the outbreak state (Fig. 2B, 3A).

The bifurcation diagram describes the stable states of the system. For example, changing the density of predators, P , moves the system parallel to the D axis in parameter space. If the value of H for the system is above the cusp in Fig. 2, then increasing the density of predators leads to a smooth transition from high to low prey densities (we assume that changes in P are slow enough so the system tracks the changing stable state). However, if H is below its value at the cusp, then varying the density of predators can lead to a bifurcation if the bistable region is entered from either the outbreak or refuge side of the bistable region and one stable steady state becomes two alternative stable states (Fig. 2B). If the bistable region is crossed, another bifurcation occurs, resulting again in a single stable state. If the bistable region is crossed from the refuge side (by decreasing P), then prey densities remain low until the bistable region is fully crossed into the outbreak region, at which point prey densities suddenly transition to the single steady state with high prey density. In contrast if the bistable region is crossed from the outbreak side (by increasing P), then the prey population remains high until the bistable region is fully crossed, at which point the population crashes. Thus whether prey populations are very

abundant or rare within the bistable region of parameter space depends on whether the bistable region was entered from an outbreak or refuge state (because both equilibria are stable, the system remains at the state it was in when the bistable region was entered). This dependence of the current state on the prior state is called ‘hysteresis’. Whether or not the system is above or below the cusp in Fig. 2B depends in part on the half saturation parameter of the functional response, c , which we posit is likely to be smaller for more diverse predator assemblages because multiple species of predators can better exploit different life history stages of their prey and can exploit their prey at different times of day (e.g. a mix of diurnal and nocturnal predators).

Changes in the the steady states with variation of other parameters (or combinations) can similarly be predicted from the bifurcation diagram. We are interested in resource pulses that vary the carrying capacity K , and the effect of the level of predators on prey response to the resources. Note that in contrast to P , varying K changes both D and H . Increasing K causes both D and H to decrease proportionally, and so moves the system along a line toward the origin in the bifurcation diagram (arrows in Fig. 2B). Increasing the level of predation shifts the line produced by varying K to the right (red to yellow to green arrows), which can cause prey to have qualitatively different responses to varying

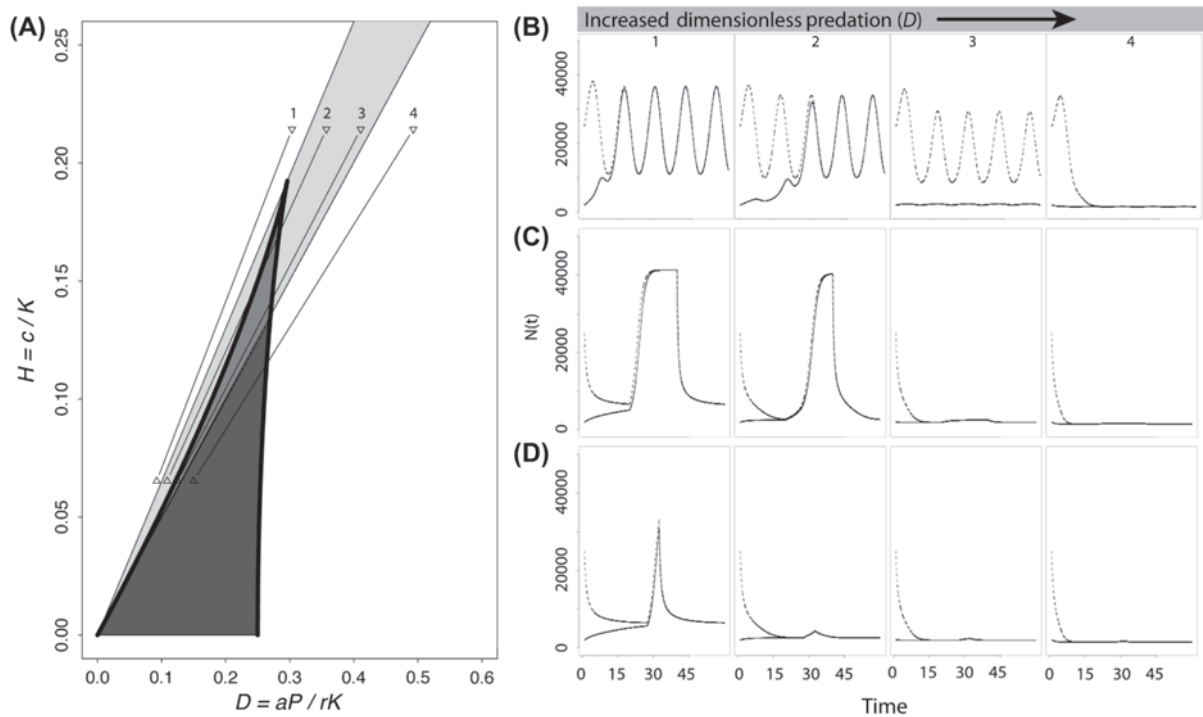


Figure 3. Four simulated resource pulses with maximum carrying capacity K_{max} (upward pointing triangles), and minimum carrying capacity K_{min} (downward pointing triangles). Note that D and H are closer to the origin for K_{max} than for K_{min} . Resource pulses move the system along trajectories in D - H space toward and away from the origin. (A) Moving from lower to higher predation, the four trajectories allow resource pulses to move within parameter space from 1) low to high steady state population density within the outbreak region (never entering the bistable region), 2) refuge to outbreak region by passing completely through the bistable region, 3) refuge into bistable region in response to a pulse that is not large enough to pass into the outbreak region, 4) refuge into bistable region, along a line that does not enter the outbreak region. These four trajectories are defined by $K_{min} = 14000$, $K_{max} = 46000$, $r = 1$, $c = 3000$ and $aP = 4250, 5000, 5750$ and 6900 for trajectories 1–4, respectively. Prey population dynamics across the four trajectories were simulated with initial population sizes of 2000 (solid line) and 20000 (dashed line) and (B) subject to a sinusoidally varying carrying capacity (between K_{min} and K_{max}) with angular frequency $\omega = 0.5$, (C) a long-duration single resource pulse with $K = K_{max}$ from time 20 to 40 (K_{min} at other times), and (D) a short-duration single resource pulse with $K = K_{max}$ from time 27.5 to 32.5.

K . If the system starts at a stable equilibrium and K is varied sufficiently slowly, the system will track the changing stable equilibrium (see Mangel 2006 for a simple example). As with changing P above, if changing K causes the system to enter the bistable region, then the system will remain at the stable state corresponding to the state (refuge or outbreak) from which it entered, and the other state will be approached only if the system moves completely through the bistable region. In a narrow region of parameter space, periodic variation in K can allow the system to pass through the bistable region and into both single stable state regions, which causes the prey density to show hysteresis such that the observed prey density in the bistable region depends on the recent direction of change in K .

Intersecting lines from the origin, one going through the cusp of the bistable region boundary (with slope $3\sqrt{3}/8$; upper line, Fig. 2B) and one tangent to this boundary at the origin (with slope 0.5; lower line, Fig. 2B), lead to three qualitatively distinct regions of the bifurcation diagram in terms of changes in K that can be written in terms of predator abundance, P , and the other system parameters. If the maximum predation rate, aP , is above a threshold set by the lower line, $aP > 2rc$, then a resource pulse can move the population from the refuge to the bistable region, but it cannot enter the outbreak region where there is only a single high-density steady state (Fig. 2B, region C). In region C, the system remains in the low-density steady state despite the presence of a high-density steady state in the bistable region (i.e. there can be sufficient top-down control to prevent population growth despite abundant resources, unless there is a perturbation large enough to shift the state in the bistable region). If the maximum predation rate is below another threshold set by the upper line, $aP < 8rc / (3\sqrt{3})$, a resource pulse moves prey populations from low to high abundance without passing through the bistable region (i.e. no alternative stable states are possible; Fig. 2B, region A). If a decrease in predation pressure causes this threshold to be crossed, the onset of a resource pulse can greatly increase prey populations (i.e. the prey are bottom-up limited). The only steady state in this region is an outbreak state, so x is always relatively high, but N will depend very much on K . Between these dynamically distinct regions is a smaller region of parameter space, $8rc / (3\sqrt{3}) < aP < 2rc$, where prey populations can move between outbreak and refuge states while passing through the bistable region (Fig. 2B; region B). In this region, the prey population response to resource pulses is highly dependent on the size and duration of the pulse, and the initial condition of the population. If the resource pulse is large enough, then the bistable region can be fully crossed, and the system will show hysteresis as discussed above, for slow variation in K . However, if the bistable region is fully crossed but the duration of the pulse is short, then there may be insufficient time for the population to move between steady states, and transient dynamics will dominate. Holt (2008b) discussed some aspects of varying pulse duration on populations. However, he assumed that the pulse is a conserved quantity, so that longer pulses go with shallower magnitudes of pulses, whereas in many empirical systems, longer pulses tend to be associated with larger-magnitude pulses (see meta-analysis in Yang et al. 2010). An approximate lower bound to the length of a resource pulse sufficient to permit a shift

between alternative states is as follows. Let the initial population size at the time of the pulse be N^* , and let N' denote the value of density at the separatrix where one observes a transition between alternative states. The maximal effect a resource pulse can have on K is to let it become indefinitely large, and the maximal growth rate a population can have (ignoring predation) is r , and so the maximal population size it will reach in T_p units is simply $N(T_p) = N^* \exp(rT_p)$. If the pulse ends at time T_p and the population has not yet reached N' (i.e. $N(T_p) < N'$) the population will decline to its original value of N^* . This will happen if the length of the pulse is $T_p < \ln(N'/N^*)/r$.

Whether pulses last long enough to observe a shift between alternative states depends upon the time-scale of response of the prey population (gauged by the quantity $1/r$), and the distance between the initial population size and the separatrix. This expression in general will underestimate the pulse duration required to flip between alternative states, because it 1) neglects direct density dependence in the prey, and 2) ignores mortality from predation. Removing each of these assumptions will make the prey population's response to a resource pulse more sluggish, which in turn means that a pulse longer in duration than T_p will be required to shift the system between its alternative states. To examine such effects in general requires numerical studies, as illustrated in the following paragraphs.

Simulating prey population dynamics with resource pulses

To illustrate potential scenarios for how predation can affect the response of consumers to resource pulses, we varied predator abundance and simulated resource pulses across four qualitatively distinct trajectories in parameter space (along lines through the origin) as determined by the bifurcation diagram and our previously identified thresholds (Fig. 3). Moving from lower to higher predator densities, the four trajectories in Fig. 3 allow resource pulses to move within parameter space from 1) low to high steady state population density within the outbreak region (without entering the bistable region), 2) refuge to outbreak region by passing completely through the bistable region, 3) refuge into the bistable region, in response to a pulse that is not large enough to pass into the outbreak region, 4) refuge into the bistable region along a line that cannot cross into the outbreak region no matter how large the pulse (Fig. 3). These lead to different prey responses.

We simulated prey populations subject to single rectangular resource pulses or a sinusoidal recurrent resource pulse (transient increases in carrying capacities) along these four trajectories (see Fig. 3 legend for parameters). We varied the duration of the single resource pulse to illustrate that both the size and duration of the pulse influence prey population dynamics. In all scenarios, we simulated the resource pulse with a low and high population density initial condition (Fig. 3).

Small changes in the level of predation sometimes led to qualitatively different prey population responses to resource pulses. Following trajectory 1, prey populations always fluctuate with resource availability irrespective of the initial population size or pulse shape (left panels in Fig. 3B–D)

(however, these fluctuations would not be observed if the pulse were so short that the prey population did not have time to numerically respond to any significant extent).

A small increase in predation results in trajectory 2. Both low and high initial populations eventually converged so that prey populations fluctuated in a stable limit cycle during the recurrent sinusoidal resource pulse (Fig. 3B), and also increased in response to the single rectangular resource pulse (Fig. 3C), unless the period of the pulse was not sufficiently long for the population to reach the outbreak state (Fig. 3D). To understand why fully crossing the bistable region leads to a prey population response with a recurrent or long pulse but not a short pulse, one must consider transient dynamics when inspecting Fig. 3A. During the recurrent pulse, the outbreak stage is reached and maintained if resources are abundant and the population remains large (relative to K) through the bistable region, but there is not enough time for the population to decline below the unstable equilibrium (Fig. 2A) once entering the refuge region of parameter space before resource availability increases again. The refuge region is only reached with the low initial population during the first two cycles; the variation in N after convergence occurs because the outbreak equilibrium changes with K .

Another small increase in predation gives trajectory 3, for which the prey population response to the sinusoidal resource pulse depended on the initial conditions, and reached either a high amplitude limit cycle with high population densities or a second low amplitude limit cycle with low population densities (Fig. 3B). Which limit cycle was reached depended on whether the initial conditions were in the domain of attraction for the low- or high-amplitude limit cycle. The initial resource level was at the mean carrying capacity $(K_{max} + K_{min}) / 2$, which for trajectory 3 (and 4) lies in the bistable region. When the prey population began at high population density, it was attracted to the upper steady state and initially increased. When K dropped to K_{min} , the only steady state was in the refuge state, so the prey level dropped, but because the period was short it did not have time to drop below the separatrix (unstable equilibrium) of the bistable region by the time the carrying capacity rose again. Therefore, the prey population was again attracted to the upper bistable steady state. If the period of the sinusoidal resource pulse following trajectory 3 were long enough, then the prey population would have time to decline to a refuge state when K was low. When K then increased and the system entered the bistable region, the prey population would be on the refuge steady state side of the separatrix and the prey population would remain attracted to the low- K refuge state despite plentiful resources. Therefore, high population densities could not be maintained. In contrast, when the population on trajectory 3 began at low population density, it was attracted to the lower bistable steady state at the start and never moved to high population density because the outbreak region of parameter space was never entered (which would be true for any period of the sinusoid). For the single resource pulses, K is initially at its low level for long enough for the prey level to be below the bistable separatrix when the pulse is initiated, and so there is little response to the resource pulse.

The shape of the resource pulse can also matter. In contrast to a sinusoidal wave, a square wave following trajectory 2 would cause the bistable region to be suddenly crossed.

Depending on the frequency of such a recurrent pulse, the population could either closely track the steady state (at lower frequencies) or vary between being attracted to a high and a low steady state but never reaching either. Thus transient dynamics are essential to the population response, because populations do not track their steady states unless the duration of the resource pulse is long relative to the time-scale of change in the prey population.

Trajectory 4 is similar to trajectory 3 in that the outbreak region is not entered, but in this case there is enough time spent in the refuge region for the prey level to drop below the bistable separatrix during the low- K phase with recurrent pulses starting with a large population. Therefore, after the first resource pulse (in the sinusoid), the prey level was never attracted to the high equilibrium and never recovered. Regardless of initial conditions, the population is regulated by predation to a low-density steady state and does not fluctuate in response to a resource pulse.

The above analyses are based on the assumption that resource pulses elevate prey carrying capacity, but not its intrinsic growth rate. If the intrinsic growth rate increases, but not K (for instance if prey are limited by direct interference at high numbers), then system changes would be described by horizontal line segments slicing through the parameter space of Fig. 2B or 3. Increases in r would shift states to the left, tending to move populations from stable low refuge levels to outbreak levels if the increase in r is large enough. In this case there are many more trajectories for which the bistable region is crossed, assuming H has a value less than that at the cusp. Increases in predation in this case would shift the horizontal line segment produced by variation in r to the right. For example, if the line segment describing a resource pulse in r is initially entirely in the outbreak state (region 1 of Fig. 2B), then increasing predation would first cause it to enter the bistable region, then possibly to fully cross the bistable region, then to span part of the bistable region and part of the refuge region, and finally to be fully in the refuge state. This would cause qualitative changes in the response of prey populations to pulses in r as predation levels vary.

Discussion

Seasonal and multi-annual prey population fluctuations are observed in many diverse systems in response to resource pulses, but prey populations can also remain low over a wide range of resource availability (Fig. 1; McShea 2000, Huitu et al. 2003, Korpimäki et al. 2004, Lubelczyk et al. 2004). By linking top-down and bottom-up forces, our results suggest that the presence or absence of fluctuations predictably depend on threshold levels of generalist predation and the properties of the resource pulse. These previously unidentified thresholds are cryptic in that crossing them produces little change in prey abundance until the onset of a resource pulse. This allows small changes in predation to alter the trajectory of a prey population generated by a resource pulse (Fig. 2–3). These theoretical results are supported by a large-scale field experiment demonstrating that vole abundance increases with food addition only when predators are excluded (Huitu et al. 2003). That is, these populations are regulated neither solely by top-down forcing nor solely

by bottom–up factors, but by both interacting in complex ways. But such complexity can be elucidated using models that include some of the nonlinear responses of predators to their prey.

Whether the predation–resource pulse interactions that we describe are common across different systems in nature is an open question. This depends on the ubiquity of density-dependent regulation of prey populations, and on whether these systems are near region B in parameter space of the bifurcation diagram (Fig. 2B), which dictates whether small changes in predation can produce large changes in the response of prey populations to resource pulses. Systems that are typically located within the bistable region (at the lower equilibrium) of parameter space will be susceptible to a bifurcation as the loss of predation services pushes the system closer to outbreak (D approaches 0), and may experience hysteresis if D increases again to reenter the bistable region. However, such systems will not be susceptible to the predation – resource pulse interaction that we describe, which relies on starting outside the bistable region and either entering it or not as resource availability increases. For systems in which adding resources increases r rather than K , the region of parameter space for which predation can qualitatively change prey response to resource pulses might be larger, as long as H is not so large that the system is above the cusp (Fig. 2B). If K and r both increase with nutrients, then the trajectories in Fig. 2B would have lower slope (D declines faster than H), again increasing the scope for the bistable region to be crossed.

The potential for the predation–resource pulse interactions that we describe can be qualitatively extended from generalist predation by a static predator population to any sigmoid total response, such as can be produced by considering the numerical response of predators (Supplementary material Appendix 1), or spatial aggregations of mobile predators in response to high prey density. Even if a predator is a specialist, often the numerical response of the predator takes much longer than the resource pulse and the prey’s response, so these results could apply within a year, with the resource pulse causing a change in the level of predation the following year. These results may also apply to both terrestrial and aquatic systems where tri-trophic interactions are of interest. In general, the existence of alternative stable states is difficult to diagnose without experimentation (Scheffer and Carpenter 2003), but our results are amenable to experimental tests that manipulate predator abundance and diversity while providing resource pulse treatments. Future experimental and theoretical work might also explore how spatial heterogeneity interacts with predation–resource pulse dynamics.

It is natural to explore the implications of these interactions in pulse driven terrestrial systems where predator communities are now significantly altered in many systems worldwide. For example, historic predator communities in many deciduous forests of North America featured top predators such as puma *Puma concolor* and wolves *Canis lupus*, had larger and widespread populations of fisher *Martes pennanti*, marten *Martes americana* and bobcat *Lynx rufus*, and contained few or no coyotes *Canis latrans*. Recent work has found that increases in Lyme disease are correlated with a decline of red foxes as a result of the coyote range expansion (Levi et al. 2012), which was likely facilitated by the absence

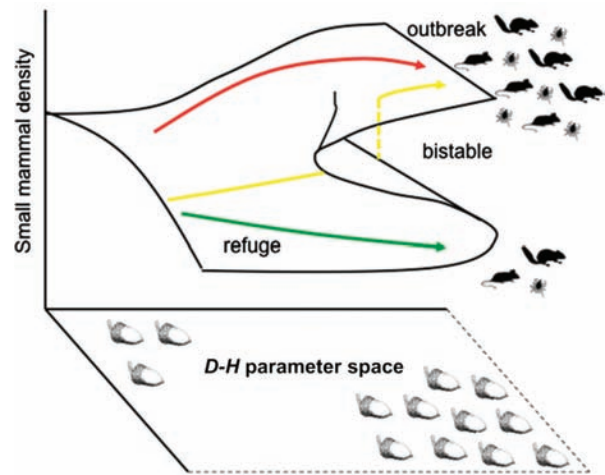


Figure 4. Conceptual diagram of the hypothesized relationship between resource pulses and small mammals, with plausible impacts on tick-borne disease, as a function of the location in D - H space. Small changes in predation can lead to qualitatively distinct trajectories when a resource is pulsed, leading to prey and associated disease outbreaks (red line), or continuing to suppress prey and disease (green line). An intermediate condition in which prey populations are partially buffered but can reach outbreaks depending on the size and duration of the resource pulse is also theoretically possible (yellow line).

of wolves (Levi and Wilmsers 2012). Suppression of foxes by coyotes is predicted to lead to lower predation rates on small mammals because red foxes are both more abundant than coyotes (Trehwella et al. 1988, Tremblay et al. 1998, Patterson and Messier 2001, Way et al. 2002), and consume more small mammals per capita (Major and Sherburne 1987).

Small mammals are believed to be important amplifiers of many emerging diseases. While the loss of predators could increase disease risk by simply increasing the abundance of these small mammals, our results suggest that more abrupt changes to population dynamics can occur due to the interaction between resource pulses and predation. For example, seed masts in eastern deciduous forests increase rodent density, which in turn increases the density of ticks and the proportion infected with *Borrelia burgdorferi*, a tick-borne bacterial pathogen that causes Lyme disease (Ostfeld et al. 2001, 2006). An unresolved question is whether historical predator communities were capable of suppressing prey outbreaks in response to seed masts (i.e. has predator decline moved the system from region C to region A in Fig. 2B?). What is known is that predators in other systems can maintain rodent prey at low abundance across a wide range of resource availability (Korpimäki et al. 2004). Our results provide a plausible and testable hypothesis for how changing predator communities and resource pulses interact to increase the risk of tick-borne disease (Fig. 4).

Top predators have been extirpated from diverse systems worldwide, which has caused the remaining predator populations to restructure (Talleklint and Jaenson 1997, Ritchie and Johnson 2009, Ripple et al. 2013), with a likely wide range of direct and indirect effects on prey communities. Here we show that changing predator communities can lead to critical transitions in the response of prey populations

to resource pulses. Other interactive effects might similarly lead to abrupt changes as thresholds are crossed, as in the classic spruce forest die-off due to budworm outbreaks (Ludwig et al. 1978).

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Supplementary material (available online as Appendix oik.01487 at <www.oikosjournal.org/readers/appendix>). Appendix 1.