Supplemental Material

S.1. Interaction strength measurements

In the main text, we develop an energetic measure that is closely aligned with consumer relative biomass (eqn. 3, Fig. 2a). This measure, close to Paine's 1980 definition, is given as the ratio of resource density without consumers to resource density with consumers: $R_{without}/R_{with}$ (eqn. 4). The resource equilibrium density with predators is commonly referred to as R*. We use the equilibria solutions of the consumer-resource model (eqns. 1, 2) with logistic growth and a Type 1 functional response to solve for this metric:

$$B_{CR} = \frac{R_{without}}{R_{with}} = \frac{K}{m/_{ea}} = \frac{Kea}{m} \qquad \text{(S1)}$$

Note that this measure increases (becomes more positive) as the consumer has larger effects on resource, whereas most measures of interaction strength become more negative (below). When comparing to measures of interaction strength, it is therefore most relevant to compare B_{CR} with the absolute value of the other measures.

There are several measures of interaction strength that are quantitatively and qualitatively different from our metric but that capture some measure of consumer resource flux. We outline these below by extracting aggregate parameters that result from applying these tests to the same consumer-resource model (eqns. (1 and 2) with a Type 1 functional response and logistic growth of the resource) when populations reach equilibrium.

Paine's (1992) per capita interaction strength is an empirical measure:

$$IS_{per.capita} = \frac{R_{with} - R_{without}}{C\,R_{without}} = -\frac{a}{r} \qquad \text{(S2)}$$

As evident from S2, this measure is the ratio of consumer attack rate (without considering uptake efficiency or loss, *e* or *m*) to one measure of resource biomass accumulation.

A simpler measure comes from the community matrix (Levins 1968 as summarized by Laska and Wooton 1998), which measures the per capita effect of the consumer on an individual of the resource. We consider the impact of consumers on resources, given by the partial derivative:

$$IS_{C\to R\ community} = \frac{\partial\left(r\left(1-\hat{R}/_{K}\right)-a\hat{C}\right)}{\partial\hat{C}} = -a \tag{S3}$$

Where the tilde indicates the equilibrium density of the consumer or resource. When considering the impact of the resource on the consumer, the community matrix would have an interaction strength of *ea*. In the latter case, the community matrix approach generates a measure that is equivalent to what we term consumption efficiency.

The Jacobian matrix differs from the community matrix in that it measures the per capita effect of the consumer on the resource population (May 1973, reviewed in Laska and Wooton 1998). Again, the element of this matrix that measures the effect of the consumer on the resource is given by:

$$IS_{C\to R\ Jacobian} = \frac{\partial\left(r\left(1-\hat{R}/_{K}\right)\hat{R}-a\hat{R}\hat{C}\right)}{\partial\hat{C}} = -\frac{m}{e} \tag{S4}$$

Here, the absolute value of the interaction strength is negatively correlated with B_{CR} (eqn. S1), all else being equal.

Finally, the negative inverse of the Jacobian measures the total direct and indirect effects of the consumer on the resource, and is given by:

$$IS_{C\rightarrow R\ inv.Jacobian} = \frac{-aK}{r(eaK-m)} \qquad \text{(S5)}$$

Although this measure appears quite complex, it can be rewritten as:

$$IS_{C\rightarrow R\ inv.Jacobian} = {-\hat{C}^{-1}}/{ea} \qquad \text{(S6)}$$

Which quantifies interaction strength as inversely proportional to the equilibrium density of the consumer and its consumption efficiency.

Finally, the log response ratio (Berlow et al 1999, 2004; Laska and Wooton 1998) is an empirical measure that is used over short time scales. Unlike many indices, it can be measured away from the equilibrium, and is given as:

$$IS_{LRR} = Log\left(\frac{R_{with}}{R_{without}}\right)\left(\frac{1}{C}\right)\frac{1}{\Delta t} = Log\left(\frac{rR\left(1-\frac{R}{K}\right)-f(R)RC}{rR\left(1-\frac{R}{K}\right)}\right)\left(\frac{1}{C}\right)\frac{1}{\Delta t} \qquad \text{(S7)}$$

Where Δt is the length of time. When a Type I functional response is an appropriate model, eqn. S7 provides an estimate of the consumer attack rate (a) if the timeline of the experiment is short enough to prevent large changes to population sizes (Laska & Wootton 1998; Novak & Wootton 2010). As can be seen from eqn. S7, anytime $f(R)$ is not linear (i.e. anything but a Type I functional response), the interaction strength will depend on the resource density. In other words, a different IS_{LRR} would result from an identical system that differs in the density of the resource at the outset of the experiment. Novak and Wooton have proposed an alternate approach to determining IS_{LRR} for a Type II functional response, noting that twice as many treatments are required to estimate both per capita attack rates and handling time (Novak & Wootton 2010). Over long timescales, any form of density dependent growth in the prey will cause this measure to deviate from the parameter(s) that it is designed to estimate (Berlow et al. 1999).

Note that each of these measures of interaction strength is relevant to different aspects of consumer-resource dynamics (Berlow et al 2004, Laska and Wooton 1998), as is discussed in the main text.

S.2. The Relationship between Consumer Relative Growth, Resource biomass accumulation and C-R Isoclines

The Lotka-Volterra with logistic growth produces increased C:R ratios with increases in the consumer relative growth rate (*ae/m*) or similarly, increased C:R ratios occur with increases in resource biomass accumulation (*K*; Fig. 1). Additionally, this increase in C:R ratio with increases in the flux parameters is accompanied by a decrease in stability over a large range of B_{CR} values (i.e., the real eigenvalues becomes less negative). In a stochastic setting, this reduced stability translates into increased variability in population dynamics (e.g., Rip and McCann 2011).

Collectively, within this framework and employing the simple model system (eqn. 1 and 2), we can make the following general predictions for relative growth and resource biomass accumulation from this C-R model:

Relative Growth

1) Increasing relative growth rate (*ae/m*) tends to increase C* and decreases R*;
2) Increasing relative growth rate (*ae/m*) tends to increase C*:R* ratio;
3) Increasing relative growth rate (*ae/m*) tends to increase stability if the C*:R* ratio is initially low, but has the opposite effect if the C*:R* ratio is initially high (Fig. 2b).

Resource biomass accumulation

1) Increasing resource biomass accumulation (*K*) tends to increases C* and not change R*;
2) Increasing resource biomass accumulation (*K*) tends to increase the biomass ratio C*:R*;
3) Increasing resource biomass accumulation (*K*) tends to increase stability if the C*:R* ratio is initially low, but has the opposite effect if the C*:R* ratio is initially high (Fig. 2b).

Mathematically, these results can be seen by looking at the response of the isoclines to change in the associated parameters (Fig. S1). Figure S1a identifies the general influence of the growth parameters and Fig. S1b identifies the influence of increasing the resource biomass accumulation term. Importantly, these general bioenergetic ideas can be extended to other plausible consumer-resource models and easily interpreted.

Having elucidated a way to bioenergetically understand the predicted dynamic outcomes of consumer-resource models, it is of use to take these results and interpret them in terms of common empirical removal experiments (i.e., remove the consumer). These experiments measure the change in equilibrium before the perturbation (i.e., the equilibrium C*, R*>0), and after the perturbation (i.e., removal of predator; C*=0, R*=*K*). Thus, a metric for this experimental B_{CR} can be defined by eqn. (S1). The relationship between the biomass accumulation and experimental outcome are depicted in the example of Fig. S1c,d. Figure S1c shows a strong net flux and the corresponding strong removal outcome (follow arrows); while Fig. S1d shows a weak net flux and a corresponding weak removal response. The important point here is that the vital rates governing the flux are the mechanisms behind the experimental outcomes. The above result is extended to the 3 species food chain case in Fig. S2.

S.3. Food Chains, Relative Growth Effects and Experimental Interaction Strengths

The above relationship can be extended to the simple food chain version of the Lotka-Volterra model. Figure S2a depicts a reduced nullcline for the three-dimensional food chain. A reduced nullcline is a simple trick for food chain models in which the consumer-resource phaseplane completely identifies the C and R equilibrium densities for both the entire food chain (rightmost dot in Fig. S2a) and the C and R equilibrium densities for the consumer-resource interaction alone. This is possible because the consumer and resource isoclines are invariant with P and so extend out into the predator dimension without changing their intersection point (see McCann and Yodzis 1993, for detailed discussion).

Given this, Fig. S2a shows the C and R equilibrium with predator (the right side, lower dark circle shows the density for C* and R* with the predator P*) and after the predator removal (the extreme upper left dot). Thus, in Fig. S2a, two strongly coupled relative growth effects mediate a large experimental B_{CR} result (the arrow shows the large shift in R).Similarly, Fig. S2b shows two weak relative growth effects and a weak B_{CR}.

Mathematically, this phenomenon can be seen by examining a 3-dimensional food chain in its general form (as in eqns. 1 and 2):

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - f(R)RC$$

$$\frac{dC}{dt} = e_C f(R)RC - m(C)C - g(C)CP$$

$$\frac{dP}{dt} = e_P g(C)CP - m(P)P \tag{S8}$$

In the absence of the top predator (P), eqn (S8) reduces to eqns (1 and 2). When the predator is present, the equilibrium abundance of the consumer is equal to $m(\mathrm{P})/e_p g(\mathrm{C})$, or 1/Predator Relative Growth, and the productivity of the consumer is the ratio of the consumer's consumption and conversion of available resources to its mortality rate:

$$K_{consumer} = \frac{e_c f(R)}{m} r R^* \left(1 - \frac{R^*}{K}\right) \qquad \text{(S9)}$$

This measure of productivity is identical to the ratio used to determine K for the resource, and turns out to be the equilibrium C when the predator is absent. Not surprisingly, B_{PR} measured between the resource and the predator (i.e. the ratio of resource abundance with the predator absent vs present), contains both the effect of the consumer on the resource (B_{CR}) and the effect of the predator on the consumer (B_{PC}). Indeed, it is bounded so that its inverse can never exceed B_{CR}, as is shown graphically in Fig. S2. Another way to consider this is that by preying on the consumer, the predator increases the abundance of the resource, but never beyond the abundance that the resource would achieve with the consumer absent.

As with B_{CR}, increasing the strength of B_{PC} (by having a strong effect of the consumer on the resource and the predator on the consumer) creates the familiar unimodal stability relationship seen in Fig. 2b (McCann 2012). Although measures of resource biomass accumulation (sensu eqn. 3) become less meaningful as impacts are measured across multiple trophic levels, the pool-based definition of the resource without vs. with the focal trophic level remains an appropriate measure (Fig. S2 and eqn. 4). Finally, it is important to note that B_{PR}, measured between the resource and the predator, is the inverse of that between any adjacent two levels because the presence of the predator increases the resource biomass. In this case, it can be measured on the logarithmic scale to compare the size of B_{PR} with B_{CR}.

S.4. Short- versus long-term dynamics

Consumer-resource models often have short-term dynamics that are qualitatively different from the long-term dynamics of the system. When consumer and resource abundance is plotted so that consumers are on the y-axis and the resource on the x-axis, the dynamics of the system when not at equilibrium often result in a counter-clockwise movement of abundances. In other words, as consumer densities fall, resource densities increase, which subsequently causes an increase in consumers, and so on. This cycling behaviour is exhibited whenever the leading eigenvalue of the Jacobian matrix is imaginary, which occurs over the range of conditions that leads to lower stability with an increase in B_{CR} (Fig. 2, black line to the right of its peak).

The plane that represents consumer-resource abundances has few zones where the direction of change of the consumer and resource are pointing towards the long term equilibrium (Fig. 4). These zones, shaded grey in figure 4, have one edge defined by the line where the consumer is at its equilibrium abundance and the other edge defined by the zero growth isocline of the resource (i.e. the density of the consumer where the resource growth is zero). The zone where short and long term dynamics coincide occurs where the zero growth isocline lies above the consumer equilibrium abundance when the resource abundance is low (i.e. to the left of the resource equilibrium) and above the consumer equilibrium when the resource is high (to the right of the resource equilibrium). These conditions for short and long term consistency in consumer-resource changes are most easily met with a Type 1 functional response, where the zero-growth isocline is a straight line. Consumer-resource interactions with Type 2 or Type 3 functional responses have smaller zones that can also be determined by examining the intersection of the equilibria and the resource zero growth isocline.

In experiments, short and long term changes will coincide most when the starting conditions fall along the resource zero growth isocline (Fig. 4). By examining the effects of changes in relative growth (ΔRG) or carrying capacity (ΔK) on the C-R isocline graphs, it is apparent that changes to relative growth shift the equilibria along the resource isocline (Fig. S1A), and these asymmetries are therefore most likely to cause similar short and long term dynamics. Changes in the carrying capacity shift the equilibria vertically (Fig. S1B), causing short and long term dynamics to differ.

S.5. The rate-dependence of K and effects of resource growth

We present *K* as a rate-dependent parameter that depends on nutrient input (S) and metabolic loss ($e^{-E_B/kT}$). This general dependency of *K* on the ratio of nutrient input and metabolic loss has been argued previously (Schoener 1973; Savage et al. 2004; O'Connor et al. 2011), and can be derived from simple models of resource dynamics when the upper limit of the resource population is described as:

$$\frac{dR}{dt} = R\left(\frac{ucS}{uR} - d\right) \qquad \text{(S10a)}$$

$$K \equiv \hat{R} = \frac{cS}{d} \qquad \text{(S10b)}$$

Equation S10, adapted from Schoener (1973), describes resource growth near *K* as a function of the nutrient supply (*S*), the per capita uptake rate or fraction of available nutrients accessed (*u*), the conversion of nutrients (*c*), and loss (or mortality) due to the metabolic rate of the resource (*d*). At this upper limit, *K* scales inversely with metabolic rate, giving eqn. 8. It should be noted that many forms of resource growth produce dynamics can be represented by eqn. (S10a) as the resource experiences negative density dependence (i.e. close to the equilibrium R), even when they have different inflection points than the logistic equation (Schoener 1973). In addition, eqn. (S10a) can be seen as the ratio of resource growth to loss near equilibrium. An estimate of changes in K with temperature (ΔK, eqn. (8)) may thus be possible by measuring short-term changes to gross and net production when r does not change. Gross primary production is equal to cS and the per biomass metabolic loss rate of the resource is d. This gives a net production equal to $cS\text{-}Rd$, and defines K =*gross production / (gross – net production)* when the resource is close to equilibrium.

The maximum rate of increase (r) also influences resource resource biomass accumulation. In the main text we focus on K, and show how changes to the carrying capacity of the resource influences B_{CR}. More generally, considering the consumer-resource interaction (Fig. 1), the change in total flux in resource biomass accumulation [r (1-R*/K)] with temperature must equal the change in flux in both consumption efficiency and consumer loss (ae and m respectively in Type 1 functional response). This requirement means that while K must stay constant, r must increase at the same rate as the consumer vital rates (Table S1).

This relationship can be seen graphically by examining the consumer-resource isocline graphs (Fig. S1). The effect of r on consumer biomass depends on resource uptake by the consumer (r/a). Importantly, the C:R ratio does not change if $r(\mathrm{T}) \propto a(\mathrm{T}) \propto m(\mathrm{T})$, so long as K and e are constant (Table S1).

The effect of r on stability is also different than that of K. In general, r decreases the return time of the resource, which dampens ‘overshooting’ by the consumer. This causes r to stabilize consumer-resource dynamics across all B_{CR} values.

Finally, there is considerable debate over the exact form of resource growth (Abrams 2009). The logistic growth model that we use derives from simple models where the resource is limited by nutrient competition at high densities, but unable to fully utilize resources at low densities (Schoener 1973). Other models, such as eqn. S10a but with nutrient uptake described by a Type 2 functional response $\left(\frac{dR}{dt} = R\left(\frac{aeS}{b+aR} - c\right)\right)$, generate logistic-type curves but with the maximum slope at a different location (i.e., not at $K/2$), which are often modeled with a more general theta-logistic model:

$$\frac{dR}{dt} = rR\left(1 - \left(\frac{R}{K}\right)^{\theta}\right).$$

The qualitative effects of B_{CR} that we present are consistent to the family of curves generated by the theta-logistic model, with the theta parameter regulating the rate of change in consumer to resource biomass ratio with B_{CR} as well as the rate of change in stability with B_{CR}.

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Table S1. Extending the B_{CR} framework to larger food webs and other consumer-resource models. In all cases, B_{CR} is equal to K/R*, where R* is the equilibrium abundance of the resource when the consumer is present.

Model	**Equilibria with both consumer and resource present**	**Temperature Independence Criteria†**
Logistic growth – Type I functional response		
$\frac{dR}{dt} = rR(1-\frac{R}{K}) - aRC$ $\frac{dC}{dt} = eaRC - mC$	$C = \frac{r}{a}\left(1-\frac{m}{eaK}\right)$ $R = \frac{m}{ea}$	$a(T) \propto m(T) \propto r(T), K(T) = K$
Logistic growth – Type II functional response		
$\frac{dR}{dt} = rR(1-\frac{R}{K}) - \frac{a}{1+ahR}RC$ $\frac{dC}{dt} = \frac{ea}{1+ahR}RC - mC$	$C = \frac{er(aeK - m - aKmh)}{a^2K(e-mh)^2}$ $R = \frac{m}{a(e-mh)}$	$a(T) \propto m(T) \propto \frac{1}{h(T)} \propto r(T), K(T) = K$
Logistic growth – Type III functional response		
$\frac{dR}{dt} = rR(1-\frac{R}{K}) - \frac{a}{1+ahR^2}R^2C$ $\frac{dC}{dt} = \frac{ea}{1+ahR^2}R^2C - mC$	$C = \frac{er\left(1-\left(K\sqrt{a(e-mh)}\right)/\sqrt{m}\right)}{aK(mh-e)}$ $R = \frac{\sqrt{m}}{\sqrt{ae-amh}}$	$a(T) \propto m(T) \propto \frac{1}{h(T)} \propto r(T), K(T) = K$

Logistic growth with density dependent consumer mortality – Type I functional response

$$\frac{dR}{dt} = rR(1-\frac{R}{K}) - aRC \qquad C = \frac{r(aeK-m)}{a^2eK+ir} \qquad a(T) \propto m(T) \propto i(T) \propto r(T), K(T) = K$$

$$\frac{dC}{dt} = eaRC - (m+iC)C \qquad R = \frac{K(am+ir)}{a^2eK+ir}$$

Logistic growth in 3-level food chain – Type I functional responses‡

$$\hat{R} = K\left(1-\frac{m_p a_c}{e_p a_p r}\right) \qquad a_c(T) \propto m_c(T), m_p(T)a_c(T) \propto a_p(T)r(T), K(T) = K$$

$$\frac{dR}{dt} = rR(1-\frac{R}{K}) - a_cRC$$

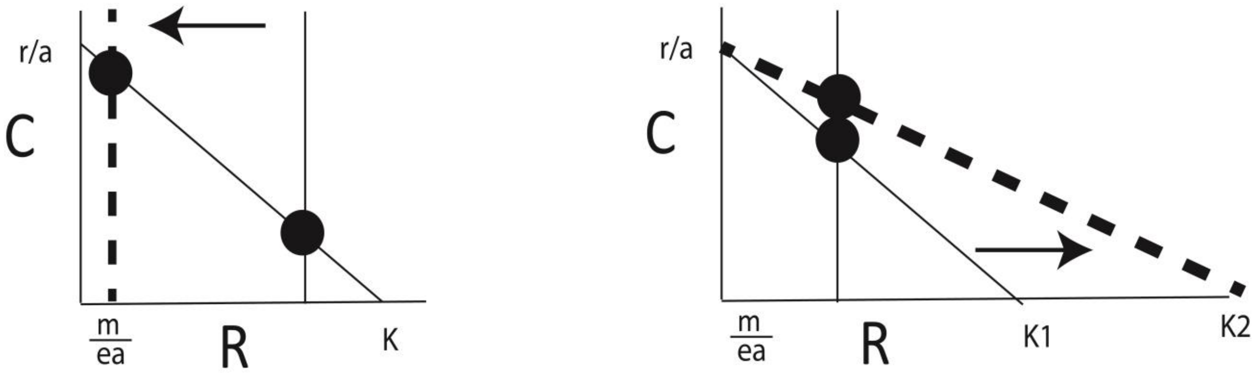
$$\frac{dC}{dt} = e_ca_cRC - a_pCP - m_cC \qquad \hat{C} = \frac{m_p}{e_pa_p}$$

$$\frac{dP}{dt} = e_pa_pCP - m_pP \qquad \hat{P} = \frac{a_ce_cK(ra_pe_p - a_cm_p)}{ra_p^2e_p} - \frac{m_c}{a_p}$$

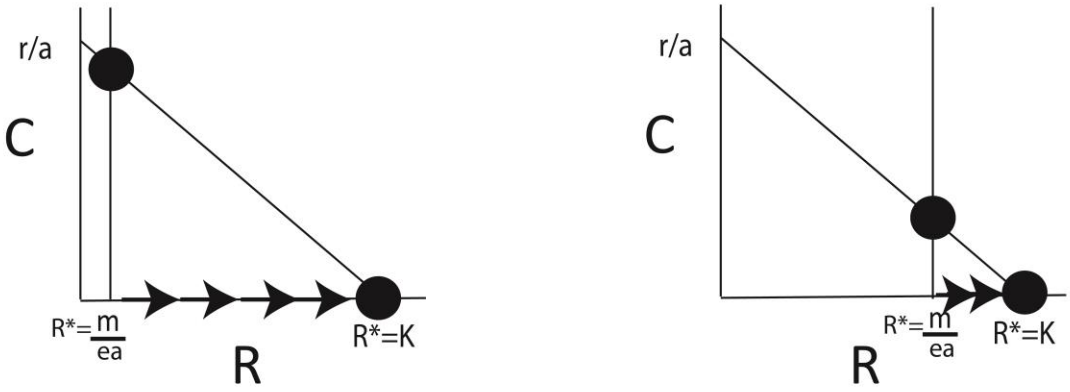
†The conditions necessary for B_{CR} to be independent of changes in temperature. Notations of $x(T)=x$ indicates that the parameter must not vary with temperature and the proportionality (∝) symbol indicates that variables can only vary by a scalar. Conditions are provided for both resource biomass accumulation parameters (*r* and *K*), with a description of the effects of *r* given in supplementary (S.5). All equations assume that conversion efficiency (*e*) does not vary with temperature.

‡For the 3-level food chain, the interaction between the predator and resource (B_{PR}) is defined as $R^*_{without\_top\_predator}/R^*_{with\_top\_predator}$

Figures


A) Relative Growth Effect

B) Production Effect

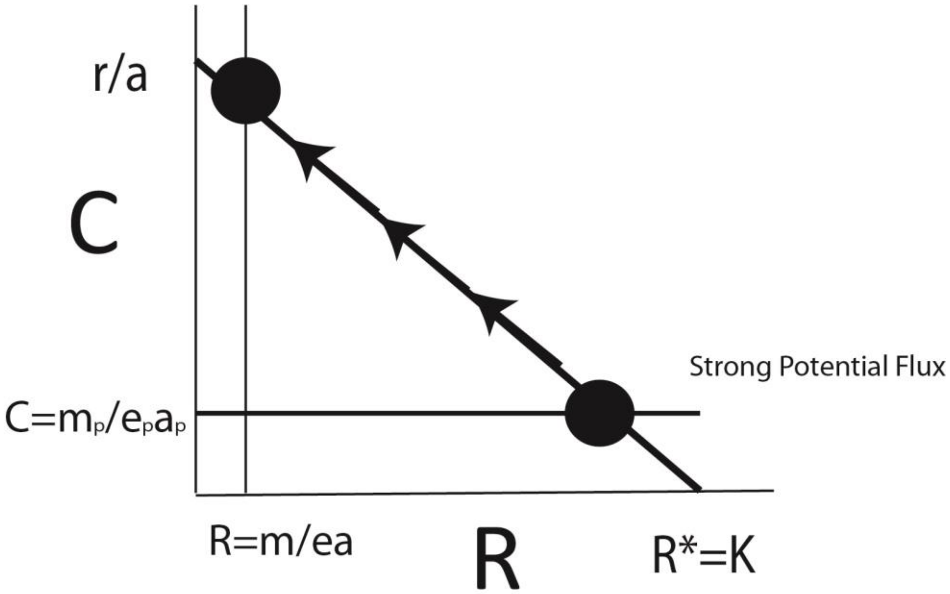

C) Strong B_{CR} (high K/R*)

D) Weak B_{CR} (low K/R*)

Figure S1: Understanding B_{CR} with C-R isoclines. An increases in B_{CR} can result from an increase in relative growth (*ea/m*), which decreases equilibrium of the resource (R*) when the consumer is present (R* = 1/relative growth). This shift in B_{CR} causes the C-R equilibrium to move along the resource isocline (A). An increase in B_{CR} can also result from an increase in carrying capacity (*K*), which shifts the C-R equilibrium vertically (B). A large difference between the R* with and without the consumer present (i.e. *m/ea* versus *K*) indicates a large B_{CR} (C), whereas a small difference indicates a weak B_{CR} (D).

Food Chain: Predator Removal

A) Strong B_{CR}



B) Weak B_{CR}

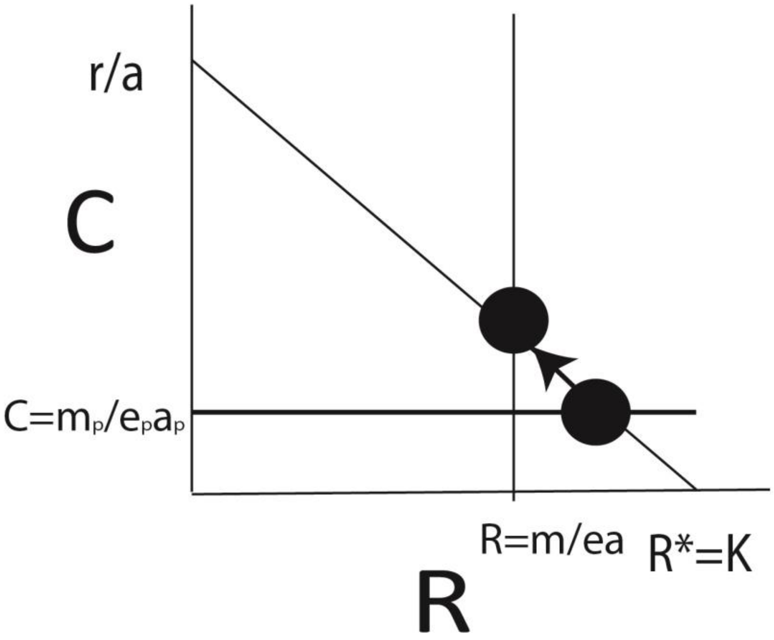


Figure S2: Reduced nullclines of a 3-level food chain with a resource (R), consumer (C) and a top predator. The effect of removing the top predator is shown by following the arrows from the bottom right circle to the top left circle in each graph. When the predator has a large effect on the consumer, which in turn has a large effect on the resource, the overall effect of removing the top predator is large (large B_{PR}, panel A). In the opposite case, where the consumer has only a small effect on the resource, the B_{PR} is small, as is seen when removal of the top predator has a small effect (B). Parameters with subscript p are for the top predator, with $m_p/e_p a_p$ giving the equilibrium abundance of the consumer when the top predator is present. Consumer and resource parameters do not have subscripts.