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Authors
Gilbert, Benjamin
Tunney, Tyler D
McCann, Kevin S
et al.

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IDEA AND PERSPECTIVE

A bioenergetic framework for the temperature dependence of trophic interactions

Benjamin Gilbert,[1]*
Tyler D. Tunney,[2] Kevin S. McCann,[2]
John P. DeLong,[3]
David A. Vasseur,[4] Van Savage,[5]
Jonathan B. Shurin,[6]
Anthony I. Dell,[7]
Brandon T. Barton,[8]
Christopher D.G. Harley,[9]
Heather M. Kharouba,[9]
Pavel Kratina,[10]
Julia L. Blanchard,[11]
Christopher Clements,[12]
Monika Winder,[13]
Hamish S. Greig[14†] and
Mary I. O'Connor[9]

Abstract

Changing temperature can substantially shift ecological communities by altering the strength and stability of trophic interactions. Because many ecological rates are constrained by temperature, new approaches are required to understand how simultaneous changes in multiple rates alter the relative performance of species and their trophic interactions. We develop an energetic approach to identify the relationship between biomass fluxes and standing biomass across trophic levels. Our approach links ecological rates and trophic dynamics to measure temperature-dependent changes to the strength of trophic interactions and determine how these changes alter food web stability. It accomplishes this by using biomass as a common energetic currency and isolating three temperature-dependent processes that are common to all consumer–resource interactions: biomass accumulation of the resource, resource consumption and consumer mortality. Using this framework, we clarify when and how temperature alters consumer to resource biomass ratios, equilibrium resilience, consumer variability, extinction risk and transient vs. equilibrium dynamics. Finally, we characterise key asymmetries in species responses to temperature that produce these distinct dynamic behaviours and identify when they are likely to emerge. Overall, our framework provides a mechanistic and more unified understanding of the temperature dependence of trophic dynamics in terms of ecological rates, biomass ratios and stability.

Keywords

Biomass pyramid, climate change, food web, interaction strength, predator prey, stability, temperature, transient dynamics, trophic dynamics.

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INTRODUCTION

Ecosystem responses to changing temperatures depend on a complex network of feedbacks among biological and physical processes (Walther *et al*. 2002; Harley *et al*. 2006; Traill *et al*. 2010). Although much of the research on biological responses to temperature focuses on individual species, interactions among species are being increasingly recognised (Dunson & Travis 1991; Davis *et al*. 1998). Species interactions mediate many ecosystem processes, and temperature has the potential to differentially influence the underlying traits of interacting organisms (Dell *et al*. 2011, 2013). As a result, even modest temperature shifts might generate a cascade of changing interactions in food webs (Barton & Schmitz 2009). These indirect effects of temperature may affect the structural and dynamic properties of ecosystems such as food web stability and biomass ratios (Yvon-Durocher *et al*. 2011; Nelson *et al*. 2013). The magnitude of these changes will depend not only on the types of interactions present within a food web, but also on how temperature regulates the strengths of those interactions (McCann *et al*. 1998).

The strength of trophic interactions often depends on temperature. The impacts of large mammalian herbivores (Post &

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[1] *Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord St, Toronto, ON, M5S 3G5, Canada*

[2] *Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada*

[3] *School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE, 68588, USA*

[4] *Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, 06511, USA*

[5] *Department of Ecology and Evolutionary Biology, UCLA, Los Angeles, CA, 90095, USA*

[6] *Division of Biological Sciences, University of California San Diego, San Diego, CA, USA*

[7] *Systemic Conservation Biology, Department of Biology, University of Göttingen, Göttingen, Germany*

[8] *Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, WI, 53706, USA*

[9] *Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada*

[10] *School of Biological and Chemical Sciences, Queen Mary University of London, London, E1 4NS, UK*

[11] *Department of Life Sciences, Imperial College London, Buckhurst Road, Silwood Park, Ascot SL5 7PY, UK*

[12] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK*

[13] *Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, 106 91, Sweden*

[14] *School of Biological Sciences, University of Canterbury, Christchurch, 8041, New Zealand*

[†] *Present address: School of Biology and Ecology, University of Maine, Orono, ME, 04469, USA*

**Correspondence: E-mail: benjamin.gilbert@utoronto.ca*

Pedersen 2008; Brodie *et al.* 2012) and the cascading effects of invertebrate (Barton & Schmitz 2009; Barton *et al.* 2009) and vertebrate predators (Post & Pedersen 2008) on plant communities can be magnified at elevated temperatures. Similarly, the direct impact of grazing zooplankton (Sommer *et al.* 2007; O'Connor *et al.* 2009) and indirect impact of fish predators (Kratina *et al.* 2012) on phytoplankton biomass have both been found to be more pronounced at increased temperature. These results suggest that top-down regulation of primary producers by herbivores and their predators may be enhanced by climate warming. In contrast, the response of producer biomass to nutrient fertilisation may be dampened (Kratina *et al.* 2012), and the direct effect of predators on herbivores may be reduced by elevated temperatures (Barton 2010). This diversity of empirical outcomes suggests that the response of trophic interactions is context-dependent, with some interactions magnified under warming while others are weakened.

Consumer–resource interactions form the most basic module of food webs, and can provide a foundation for understanding how temperature effects trophic dynamics (Vasseur & McCann 2005; O'Connor *et al.* 2011; Dell *et al.* 2013). In particular, they can be understood in terms of the vital rates of the component species (Rosenzweig & MacArthur 1963). Analysing empirical relationships between vital rates and temperature across taxa has led to the discovery of general temperature-dependencies across species and helped characterise systematic variation in those relationships. Data show how such relationships differ among distinct trophic levels such as herbivores and plants, as well as active predators and their prey (Gillooly *et al.* 2002; Dell *et al.* 2011; Amarasekare & Savage 2012). These results suggest that temperature effects on consumer–resource interactions may be predictable when details about taxa and habitats are known (Vasseur & McCann 2005; O'Connor *et al.* 2011; Dell *et al.* 2013). Such an approach could lead to a much needed theory for how food webs will respond to temperature change.

Apart from advancing theory, a framework that integrates temperature-dependent rates into trophic dynamics can guide the design and interpretation of experimental research. The broad array of responses that warming experiments have generated has been used to suggest there is not a single, shared response of trophic dynamics to warming (Moore & Townsend 1998; Post & Pedersen 2008; Post *et al.* 2009; Brodie *et al.* 2012; Kratina *et al.* 2012). Better theory could help quantify how big these deviations are and whether there are only a few or many types of responses. Currently, the wide variety of experimental designs and interaction strength metrics that exist make it difficult to determine which patterns arise from real differences in systems and which are simply methodological effects. For example, short- and long-term dynamics are often qualitatively different (Post & Pedersen 2008; O'Connor *et al.* 2011; Kratina *et al.* 2012), indicating that study duration may be one source of variation in responses. Predicting how and when a change in temperature will affect the outcome of trophic interactions requires tests and measures of trophic dynamics within a conceptual framework that allows translation across ecosystems and experimental designs.

Here, we use theory to identify how consumer–resource interactions depend on key ecological rates, which in turn often vary with temperature. We focus on the bioenergetic relationship between consumers and their resources to develop a simple metric that characterises biomass flows and predicts biomass distributions across trophic levels. Our metric also yields clear predictions about how temperature alters food web stability, whether stability is measured as extinction risk, variability in biomass following small perturbations or rates of recovery from perturbations. Although the theoretical framework that we develop is distinct from previous theoretical work on trophic interaction strength, we show that it is related to classic experimental measures of interaction strength. Our bioenergetic approach provides a single coherent framework to inform the design and interpretation of warming experiments and for predicting how temperature affects trophic dynamics in ecosystems.

BEYOND INTERACTION STRENGTH

Trophic interactions are often characterised by their interaction strength, which is broadly defined as *the change in the abundance of one species that results from the change in abundance of another* (MacArthur 1972; Paine 1980, 1992; Laska & Wootton 1998). Taking the example of a consumer's impact on a resource, experimental measures of interaction strength quantify the change in abundance of the resource when the consumer is removed, with the various measures differing in the duration of the treatment and how the results are standardised (Paine 1992; Berlow *et al.* 2004)(Appendix S1). Theoretical measures of interaction strength differ from experimental measures, and instead focus on interaction coefficients that measure the per capita effect of the consumer on the resource population or an individual of the resource species (i.e. they measure the effect of small changes in consumer density, not consumer removal; Laska & Wootton 1998; Abrams 2001; Novak & Wootton 2010).

Despite differences in experimental and theoretical measures of interaction strength, all may be understood as changes in fluxes of biomass that result from perturbations to the system. Indeed, an important insight for consumer–resource systems is that fluxes and standing stocks of biomass are not independent – the ecological rates that drive dynamics determine the standing stocks of the consumer and resource, which in turn alter the total magnitude of the fluxes between these pools (Rosenzweig & MacArthur 1963; Fig. 1). More concretely, this link between fluxes and standing stocks should allow the development of a measure that predicts both dynamical and equilibrium responses to changing temperature. Our approach links temperature to the ecological rates that structure consumer–resource interactions to determine how it affects these fluxes and standing stocks.

One method for understanding how ecological rates affect interactions is by experimentally modifying a key parameter, such as carrying capacity, and following changes in dynamics and standing stocks [e.g. (Rosenzweig & MacArthur 1963)]. A problem in predicting responses to temperature changes with this method is that many parameters are temperature dependent and thus are expected to change simultaneously. We modify this single-parameter approach by identifying aggregates of parameters that collectively govern the dynamic outcomes of

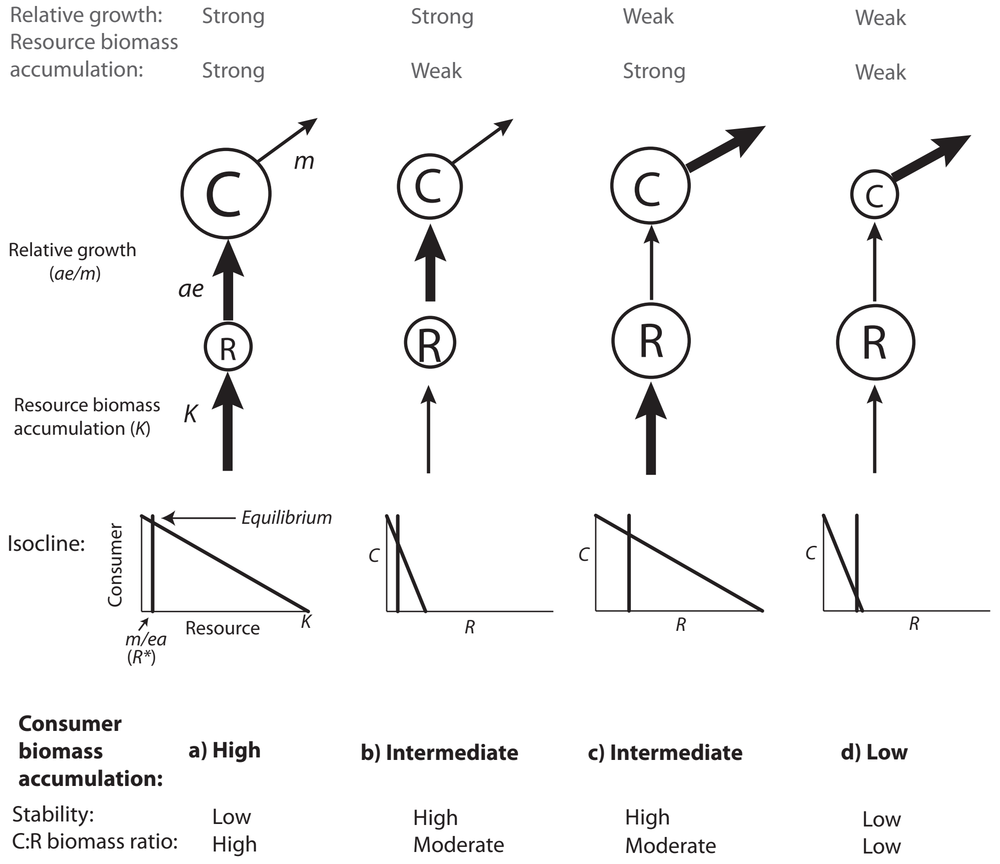

Figure 1 The effect of resource (R) biomass accumulation, measured as carrying capacity (*K*), and consumer (C) relative growth rate (*ae*/*m*) on the biomass pyramid and stability of consumer–resource interactions. Effects are shown as fluxes and standing stocks (top panels), with the size of the arrow or circle representing relative size. Zero-growth isoclines (bottom panels) give equilibrium conditions for a Type 1 functional response, with the consumer isocline equal to 1/relative growth and *K* setting the y-intercept of the resource isocline – the intersection of the isoclines marks the equilibrium. Strong resource biomass accumulation and relative growth lead to high consumer biomass relative to resource biomass and low stability (a). Weak resource biomass accumulation coupled with strong relative growth (b) or vice versa (c) leads to a moderate consumer–resource biomass ratio and high stability. When both resource biomass accumulation and relative growth are weak, the consumer–resource biomass ratio is low, as is stability (d).

interactions in response to temperature change (e.g. Yodzis & Innes 1992; Appendix S1).

To consider these components of consumer–resource dynamics more formally, we use the Rosenzweig–MacArthur equations (Rosenzweig & MacArthur 1963):

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

$$\frac{dC}{dt} = ef(R)RC - m(C)C \qquad (2)$$

Here, resource growth is logistic with *K* representing carrying capacity, or total biomass that the resource can accumulate in the absence of the consumer (see Table 1 for parameter definitions and units for a Type I functional response). Carrying capacity in conjunction with *r*, the maximum growth rate, determines the potential biomass accumulation of the resource when it is away from equilibrium. The consumer loss function, *m*(C), may depend on the consumer's own density but in most models is simply the fraction of biomass lost per unit time (*m*; Table 1). The functional response of the consumer (*f*(R)) may depend on the resource biomass (R), and in the case of a Type 1 functional response *f* (R) is equal to the attack rate (*a*). The consumption efficiency is given by *e f*(*R*) and measures the rate of consumption and conversion of the resource to the consumer per unit biomass of both; this can also be thought of as the biomass gain by the consumer for a given biomass of consumer and resource. In the simplest case of a Type I functional response, consumption efficiency is equal to the product of conversion efficiency (*e*) and attack rate (*a*; Table 1). Other functional responses (e.g. Types II or III) can also be straightforwardly expressed and measured within this framework (Table S1).

We define an aggregate approach for consumer–resource dynamics by introducing sets of parameters that govern the flux of biomass from resources to consumers through trophic interactions. Biomass flux is governed by parameters that determine three types of processes: (1) consumption efficiency of the consumer (*e* and *a* for a Type I functional response), (2) loss of the consumer (*m*) and (3) biomass accumulation of the resource (*r* and *K* in the case of logistic growth) (Fig. 1). We use *K* to represent biomass accumulation of the resource throughout this article, both because it represents the equilibrium biomass that the resource accumulates in the absence of the consumer and because it is commonly measured in experiments (below). A body of theory on consumer–resource interactions uses K as a surrogate for productivity (starting with Rosenzweig 1971), much as we do here because K implicitly scales the growth rate of the resource through the functional form of the logistic growth equation. However, we discuss how the effects of changes in *r* and *K* differ in the Appendix (S2 and S5).

Each of the three processes that govern biomass fluxes can be used to calculate population-level measures (i.e. the births and deaths of individuals), or biomass standing stocks (Yodzis & Innes 1992). For example, the consumer biomass that is maintained at equilibrium depends on these interrelated processes. First, increasing biomass accumulation of the resource increases the energy available for the consumer and the size of consumer standing stocks. Second, consumption efficiency measures how the consumer uses this resource biomass accumulation by incorporating its attack rate (*a*) and efficiency of converting the consumed resource into its own biomass (*e*). Finally, consumer biomass accumulation depends on how quickly converted biomass is lost (*m*) to metabolism or death (Fig. 1).

Two aggregates of ecological rates describe the dynamics of consumer–resource dynamics. The first is the ratio of the consumer rates (consumption efficiency/mortality: ae/m), which gives the consumer relative growth rate. The inverse of this aggregate rate defines the zero-growth isocline of the consumer (eqn 2 at $dC/dt = 0$); Fig. 1), which is termed R* (Tilman 1980). This isocline describes the equilibrium biomass of the resource when the consumer is present and is one of two quantities that need to be measured to calculate interaction strength experimentally. The second aggregate is the carrying capacity of the resource (*K*), which quantifies the equilibrium biomass of the resource when the consumer is absent. *K* is also the second quantity that is required to calculate interaction strength experimentally. Although *K* does not appear to be an aggregate, it is in fact the ratio of two rates in many mechanistic models of resource growth; *K* depends on the nutrient supply rate and resource loss rate (Rosenzweig 1971; Schoener 1973; Appendix S5). In other words, *K* represents an aggregate for the resource that is conceptually similar to the consumer's relative growth rate but also incorporates underlying supply rates of limiting nutrients.

The relationship between these aggregates suggests that inefficiencies in either one will prevent the accumulation of consumer biomass. Together, these aggregates describe the per biomass flow of energy between the consumer and resource (consumption efficiency) in the context of energy flow into the system (resource biomass accumulation) and energy loss from the system (consumer loss; Fig. 1). We express these aggregate parameters in a measure that defines the biomass potential of the resource that is captured by the consumer (B_{CR}):

$$B_{CR} \propto \frac{[\text{Consumption Efficiency}][\text{Resource biomass accumulation}]}{[\text{Loss}]} = \begin{matrix}\text{Consumer}\\ \text{RelativeGrowth}\end{matrix} \times \begin{matrix}\text{Resource biomass}\\ \text{accumulation}\end{matrix} = \frac{[ef(R)][K]}{[m(C)]} = \frac{K}{R^*} \tag{3}$$

Which is equally:

$$B_{CR} \propto \frac{\text{R without consumer}}{\text{R with consumer}} \tag{4}$$

Equation (3) unites three distinct approaches to understanding consumer–resource dynamics. First, it uses resource biomass accumulation and consumer relative growth to define B_{CR} in terms of biomass flow through the consumer–resource system. Second, it relates this flow to static measures of the resource biomass (K/R*); these two measures are used to quantify the interaction strength of the consumer on the resource experimentally and therefore link our theoretical approach to experimentally measured responses (eqn 4).

Finally, B_{CR} expresses biomass fluxes and standing stocks in terms of aggregates of parameters, which highlights how environmental conditions that modify the relative values of one or several ecological rates may influence the strength of interactions and biomass distributions. Much of the research on interaction strengths compares differences among species pairs, where species-level parameters are assumed to remain constant (Berlow *et al.* 2004; Novak & Wootton 2010). The rate-based approach we take here can also be used to track how interactions change when ecological rates are influenced by changes in other biotic or abiotic conditions, such as body size (Yodzis & Innes 1992; Brose *et al.* 2012; DeLong & Vasseur 2012). The B_{CR} framework is particularly important for temperature change, as it allows us to explore how temperature-sensitivities of multiple ecological rates scale up to influence consumer–resource dynamics.

The integrated approach used to generate B_{CR} also turns out to be important for unifying different empirical methods (Table 2). Several studies measure parameters directly (e.g. DeLong & Hanson 2011) or use model-fitting approaches on observational data to infer them (e.g. Laska & Wootton 1998; Novak & Wootton 2010). For these studies that calculate parameters, eqn (3 and 4) can be rewritten in terms of its component parameters and B_{CR} can then be calculated. For example, for a Type I functional response, eqn (3 and 4) becomes:

$$B_{CR\,Type1} = \frac{[ef(R)][K]}{[m(C)]} = \frac{eaK}{m} \tag{5}$$

For studies that measure standing stocks (densities or biomass), eqns (2 & 3 and 4) clarify that $ef(\mathrm{R})/m(\mathrm{C})$ is equal to the inverse of the resource equilibrium biomass with the consumer present (1/R*). This relationship facilitates measurement of B_{CR} for consumer–resource models with any functional response (Table S1); the ratio of the resource without vs. with the consumer present at equilibrium measures B_{CR} for all of these variations. Similarly, understanding the component rates that comprise B_{CR} for different consumer–resource models allows it to be tested when systems are not at equilibrium (Tables 1, 2, S1).

The definition of B_{CR} based on standing stocks (K/R*) can also be used in 3-level trophic chains so long as the appropriate measures of K and R* are incorporated (Appendix S5). Indeed, a closely related metric has been used in empirical studies of trophic cascades by examining resource abundance with and without a top predator (Borer

Table 1 Temperature dependency of ecological rates and model terms used in equation 5

Parameters and notation with units		Functional form of temperature dependence†	Eqn	Examples from previous studies
r: maximum repro. rate (biomass time^{-1} biomass^{-1})		$r(T) \propto e^{\frac{-E_B}{kT_R}}$	(7)	E_B = 0.53–0.85 (Savage *et al.* 2004; diverse ectotherms)
K: carrying capacity (biomass)	ΔK	$\Delta K \equiv \frac{K(T)}{K_0} = e^{E_B/kT_R - E_S/kT_S}$	(8)	$\Delta K \ll 1$ (Roemmich & McGowan 1995; marine) $\Delta K < 1$ (Kratina *et al.* 2012, aquatic mesocosms)
m: mortality (biomass loss) (biomass time^{-1} biomass^{-1})		$m(T) = m_0 e^{\frac{-E_m}{kT_C}}$	(9)	E_m = 0.65 (Dell *et al.* 2011 across diverse taxa) E_m = 0.45 (Savage *et al.* 2004 for fish)
a: attack rate* (biomass time^{-1} biomass^{-2})		$a(T) = a_0\sqrt{v_{0,C}^2 e^{-2E_{v,c}/kT_c} + v_{0,R}^2 e^{-2E_{v,R}/kT_R}}$	(10)	Dependent on type of foraging interaction (Dell *et al.* 2013)
e: conversion efficiency (biomass biomass^{-1}) (unitless)		e = constant		Independent of temperature (Peters 1983)
$\frac{ae}{m}$: relative growth (biomass^{-1})	ΔRG	$\Delta RG \equiv \frac{a(T)e}{m(T)}\frac{m_0}{ea_0}$ $= e^{E_m/kT_c}\sqrt{v_{0,C}^2 e^{-2E_{v,c}/kT_c} + v_{0,R}^2 e^{-2E_{v,R}/kT_R}}$	(11)	$\Delta RG < 1$ (Rall *et al.* 2010) $\Delta RG > 1$ (Kratina *et al.* 2012)

*Units are given in terms of resource biomass removal rate per consumer biomass as a function of resource biomass. The temperature-dependent function is expressed in terms of movement velocities, which determine the encounter rates of the consumer and resource and thus the potential attack rate. The constant a_0 scales encounter rates to attack rates. See text for more details.

†Temperature subscripts allow the consumer temperature (T_C), resource temperature (T_R) and nutrient temperature (T_S) to differ.

et al. 2005). B_{CR}, and its component aggregates, have also been used to theoretically explore simple and more speciose consumer–resource systems because of their important roles in determining relative abundances and stability (Rosenzweig 1971; Abrams 1998; Rip & McCann 2011). In what follows, we synthesise theoretical results for relative biomass and stability.

CONSUMER–RESOURCE BIOMASS RATIOS AND STABILITY

By defining B_{CR} in terms of its components we can generate predictions for how it influences dynamical outcomes of consumer–resource interactions. For example, when resource biomass accumulation and consumer relative growth rate are

Table 2 Interpreting experimental observations of consumer and resource densities, coefficient of variation (CV), and short- vs. long-term observations in terms of B_{CR}, stability and critical asymmetries. Effects are predicted from theory used to generate B_{CR}. All measures are relative to a control treatment of unmanipulated temperature

Densities					
Consumer	Resource	Correlation between density and CV of consumer	Consistency of transient and equilibrium dynamics*	Asymmetries ΔK; ΔRG	Stability
B_{CR} INCREASES					
Increase	Static	+	Different	ΔK > 1; ΔRG = 1	Destabilising
		–	Consistent		Stabilising
Increase	Decrease	+	Consistent†	ΔK = 1; ΔRG > 1	Destabilising
		–			Stabilising
Increase	Decrease	+	Different	ΔK × ΔRG > 1	Destabilising
		–	Consistent		Stabilising
B_{CR} DECREASES					
Decrease	Static	+	Different	ΔK< 1; RG = 1	Stabilising
		–	Consistent		Destabilising
Decrease	Increase	+	Consistent†	ΔK = 1; RG < 1	Stabilising
		–			Destabilising
Decrease	Increase	+	Different	ΔK × Δ; RG < 1	Stabilising
		–	Consistent		Destabilising

*Refers to whether the short-term direction of change in C and R densities is consistent with changes over the long-term (at equilibrium).

†Only ΔRG≠1, ΔK ≈ 1 can produce changes that are consistent over the short- and long-term at high B_{CR} (Appendix S4).

high, consumer biomass is maximised (Fig. 1a). Systems with low resource biomass accumulation (Fig. 1b) or low relative growth (Fig. 1c) dampen consumer biomass accumulation, which is lowest when both resource biomass accumulation and relative growth are weak (Fig. 1d). Recognising that resource biomass accumulation and relative growth also define B_{CR} allows us to generate a relationship between B_{CR} and consumer–resource biomass ratios (Fig. 2a). Together, these simple relationships enable us to better understand temperature effects on equilibrium population sizes, and also to elucidate how the temperature-sensitivity of any individual component rate is likely to alter $B_{CR.}$

The relationship between B_{CR} and stability is more complex, but nonetheless exhibits general properties whether stability is measured using time to extinction, resilience of equilibrium conditions or biomass variability (Fig. 2b). When B_{CR} is weak, stability is low because extinction risk increases when consumer densities are low and have slow return times following perturbations. At the other extreme, a strong B_{CR} also leads to low stability (Fig 2b). In this case, low stability is driven by intrinsic dynamics, with consumer–resource populations fluctuating widely following even small shifts away from equilibrium due to overconsumption by the consumer. These fluctuations can bring the consumer and resource to critically low densities, which increases extinction risk (Rosenzweig 1971; Rip & McCann 2011).

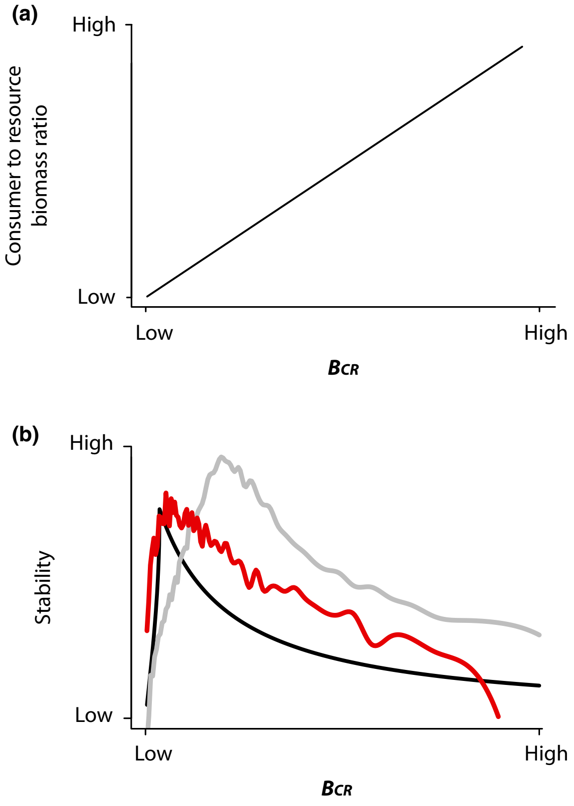

Figure 2 Relationship between B_{CR}, the consumer to resource biomass ratio (a) and three measures of stability (b). The C:R biomass ratio increases monotonically with B_{CR} (a), whereas stability shows a bi-directional response (b). Stability increases initially, but strengthening interactions beyond a critical point causes destabilisation. The rate of return (black line) measures how rapidly the interaction will return to equilibrium following a small perturbation, and is calculated here as -1*dominant eigenvalue. The red line is the inverse of the coefficient of variation of the consumer (1/CV). Time to extinction (grey line) is the logarithm of mean time to extinction of the consumer or resource, here divided by the maximum value (2.5) to present all stability measures on the same scale. Numerical solutions for (a) and (b) were obtained by varying the consumer mortality rate ($m = 0.25$–1.95) and holding other parameters constant ($e = 0.4$, $a = 0.05$, $r = 2$, $K = 100$).

The stability relationship can be explained more formally by exploring how B_{CR} influences the maximum eigenvalue of the Jacobian matrix; this eigenvalue quantifies the rate that the system returns to equilibrium following a perturbation. Importantly, the effect of B_{CR} on extinction rate and consumer coefficient of variation (CV) mirror trends in the eigenvalue, indicating that the analytic solution is a good proxy for common empirical measures of stability (Fig. 2b). For example, consumer consistency (1/CV) is lowest when B_{CR} is very weak or strong, and highest at weak to intermediate B_{CR} (Fig. 2b red line). Here, we have employed eqn 1 and 2 with a Type I functional response, but this equilibrium and stability relationship is common across consumer–resource models (Rip & McCann 2011; McCann 2012).

One benefit of B_{CR} (eqn 3) relative to measures of interaction strength lies in its use of aggregate parameters that have predictable effects on biomass ratios and stability. Other studies have provided in-depth critiques of interaction strength measures, a goal that is beyond the scope of this paper (Laska & Wootton 1998; Berlow *et al.* 1999, 2004; Abrams 2001; Novak & Wootton 2010). Nonetheless, we can compare the outputs from interaction strength measures by solving for the parameters that other measures quantify, as is done in Appendix S1 for a Type 1 functional response. For example, the Jacobian and Community Matrix measures of interaction strength provide information on elements of consumer relative growth (e/m and a, eqn S3, S4), but do not incorporate resource biomass accumulation. As a result, these interaction strength measures cannot predict how different responses in resource rates (driving K) and consumer rates (a, e and m) with temperature will alter consumer–resource dynamics, nor even if a change in one consumer rate (a, for example) will alter stability or biomass ratios. Paine's index (Paine 1992) measures a/r, or the consumer attack rate relative to the resource maximum growth rate. As with the Jacobian and Community Matrix, this measure predicts relative biomass distributions and stability only when other dynamics scale appropriately. In other words, although interaction strength measures provide information on specific parameters, none capture the scaling of biomass ratios and stability that are likely to occur when ecological rates have different thermal responses, as is explained below.

ASYMMETRIC THERMAL RESPONSES AND THE TEMPERATURE DEPENDENCE OF B_{CR}

Imbalances in temperature sensitivities between interacting species, such as between primary producers and herbivores (Allen *et al.* 2005; López-Urrutia *et al.* 2006; López-Urrutia 2008), and predators and their prey (Dell *et al.* 2011), or imbalances in energy ingested and metabolic costs of consumers (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011), may alter B_{CR} and therefore dynamic stability of a system (Binzer *et al.* 2012). Recent work has used empirical estimates from metabolic theory (Brown *et al.* 2004) to show that some combinations of resource and consumer vital rates ought to produce 'asymmetrical' temperature responses among interacting species (O'Connor *et al.* 2011; Dell *et al.* 2013).

Our metric allows us to determine when and how consumer–resource dynamics will change due to temperature-driven asymmetries in vital rates. For example, eqn 5 can be rearranged to predict that temperature will not change B_{CR} when

$$\Delta e(T)\Delta a(T)\Delta K(T) = \Delta m(T) \tag{6}$$

where delta (Δ) represents the relative change in each parameter with temperature (Table 1). Equation 6 can also be rewritten to show that B_{CR} changes whenever either relative growth (ea/m) or resource biomass accumulation (K) change with temperature. More generally, all consumer–resource models can be represented in a manner similar to eqn 6 (Table S1), illustrating that changes in vital rates with temperature must be symmetrical for relative biomass to be unaffected by temperature. Consumer–resource models with more complex functional forms require that even more vital rates be perfectly symmetric (e.g. Table S1: Type I vs. Type II functional response).

Biological rates frequently show an exponential increase with temperature up to a critical point. For a given body size, this increase is often well-described by a Boltzmann–Arrhenius factor ($ce^{-E/kT}$), where c is a species- and rate-specific constant, E is the activation energy of the biological rate, T is body temperature and k is Boltzmann's constant (Gillooly *et al.* 2002; Brown *et al.* 2004; Savage *et al.* 2004). This relationship is a central component of metabolic scaling theory, which provides a basis for understanding the environmental and biological control of key vital rates that underlie B_{CR} (Brown *et al.* 2004). There is a lack of sufficient data to model declines in biological rates that often occur at higher temperatures (Dell *et al.* 2011), so we provide quantitative estimates for the increasing phase here and discuss the declining phase qualitatively.

Growth of the resource is characterised by two parameters: carrying capacity (K) and maximum population growth rate (r). Maximum population growth rate is constrained by the temperature dependence of metabolic rate ($e^{-EB/kT}$, where E_B is the activation energy of the metabolic rate), and is therefore well approximated by a Boltzmann–Arrhenius factor (Table 1, eqn 7; Savage *et al.* 2004). The temperature dependence of carrying capacity is more difficult to quantify and requires an understanding of the relationship between temperature and limiting abiotic resources, such as nutrients (Brown *et al.* 2004; Savage *et al.* 2004; O'Connor *et al.* 2011). Conservation of energy requires that $K \propto S/e^{-EB/kT}$, where S is the rate of total nutrient supply entering the system (Schoener 1973; Savage *et al.* 2004). The nutrient supply (S) can also be represented by a Boltzmann–Arrhenius factor with activation energy Es. A general model of carrying capacity therefore depends on the difference in temperature responses of nutrient supply and resource metabolism, denoted ΔK, where $\Delta K = K(T_{new})/K(T_0)$ (Table 1, eqn 8). Equation 8 leads to two commonly considered cases, one where nutrient supply does not change with temperature so that carrying capacity decreases at $\Delta K = e^{EB/kT}$ (Allen *et al.* 2002; Savage *et al.* 2004; O'Connor *et al.* 2011), and the other where carrying capacity is independent of temperature ($\Delta K = 1$, $S \propto e^{-EB/kT}$; Vasseur & McCann 2005). However, eqn 8 is more general in that it also clarifies how asymmetrical temperature dependencies of nutrient supply and resource metabolic rate can cause carrying capacity to increase (DeLong & Hanson 2011) or decrease (Alto & Juliano 2001; Allen *et al.* 2005) with temperature.

The temperature dependencies of several consumer rates are well understood. Consumer mortality rate (m) is predicted to scale as a Boltzmann–Arrhenius factor (Table 1, eqn 9; (Gillooly *et al.* 2001; Savage *et al.* 2004). There is insufficient evidence to support a general relationship between conversion efficiency (e) and temperature so we assume that it is independent (Peters 1983). Finally, attack rate (a) depends on the searching behaviours and foraging modes of consumers and resources, so that attack rates can reflect how the movement of both species varies with temperature. Recent work formalising this approach (Pawar *et al.* 2012; Dell *et al.* 2013) predicts that the temperature dependence of a for randomly moving species depends on the body velocity (v) of the resource and consumer, both of which can be modelled with a Boltzmann–Arrhenius factor (Table 1, eqn 10).

Because the rate a depends on both the consumer and resource, its response to temperature is contingent on foraging strategy (Pawar *et al.* 2012; Dell *et al.* 2013). For active-capture interactions, where both consumer and resource are actively moving, attack rate depends on the temperature dependence of the body velocities of both species. In contrast, for interactions where one individual is moving and the other is stationary (i.e. sit-and-wait or grazing strategies), attack rate depends only on the temperature dependence of whichever individual is moving.

To identify the asymmetries that alter consumer–resource dynamics with warming, the temperature dependence of vital rates can be expressed in terms of the aggregate rates that drive B_{CR}. Both the change in relative growth (ΔRG; eqn 11) and carrying capacity (ΔK; eqn 8) have the potential to create asymmetries with changing temperature. Incorporating these into eqn 6 allows us to determine the thermal dependence of B_{CR}:

$$\Delta B_{CR} = \Delta K \times \Delta RG \tag{12}$$

Asymmetries determine the temperature dependence of B_{CR} by causing changes in carrying capacity or relative growth with warming. As a result, these asymmetries can predict how fluxes, biomass distributions and stability change with temperature (Figs. 1 and 2). A key finding is that asymmetries arise if the vital rates of interacting species, or the rates of biotic and abiotic processes, differ in their responses to temperature. Research indicates that responses to temperature will frequently differ among some of these rates (Melillo *et al.* 1993; Dell *et al.* 2011), causing shifts in trophic dynamics.

THE THERMAL DEPENDENCE OF B_{CR}: TESTABLE PREDICTIONS

The incorporation of temperature-dependent rates into B_{CR} allows ecologists to make predictions about the effects of temperature on consumer–resource dynamics. For example, warming is predicted to increase B_{CR} when consumer consumption efficiency increases at a faster rate than mortality (ΔRG> 1) or resource metabolism does not keep up with increased nutrient supply rate (ΔK> 1, black line in Fig. 3a). In this scenario, warming drives an increase in the consumer–resource biomass ratio and the system becomes more top heavy (Fig. 3b). This increase in the biomass ratio in turn stabilises the consumer–resource dynamic if both consumer and resource biomass are initially close to zero by decreasing the likelihood of extinction (Fig. 3c, solid arrow). However, if the consumer–resource biomass ratio is initially high, this further increase causes the interaction to become less stable (Fig. 3c, dashed arrow).

This simple example highlights three important factors that contribute to predicting when warming will change consumer–resource interactions, and when these changes will have a large impact. First, changes in consumer relative growth (ΔRG) will occur whenever a species' consumption efficiency (*ae*) and mortality change at different rates. Empiricists may expect this to occur in active-capture interactions when predator and prey movement rates respond differently to temperature (Dell *et al.* 2013) or when the temperature dependence of consumption efficiency and loss differ (Rall *et al.* 2010). Detailed knowledge on interacting species, or more general knowledge about the temperature sensitivities of different groups of organisms (Dell *et al.* 2011), are necessary for this level of prediction.

Second, ecosystems that are expected to quickly increase or decrease nutrient supply rates with warming are likely to show large changes in resource biomass accumulation (ΔK). For example, climate-driven changes in upwelling rates alter both water temperature and nutrient supply, and are considered responsible for large changes in zooplankton biomass in Southern California (Roemmich & McGowan 1995). In some regions, such changes in nutrient supply rates may be predicted from ecosystem models (e.g. Malmaeus *et al.* 2006). Although measuring *K* directly is difficult in observational studies, eqns (8 & S10a) suggest that ΔK can be coarsely estimated by calculating the difference in gross and net production with temperature change over short timeframes (Supplementary S.5).

The consumer–resource biomass ratio is the third factor that contributes to predicting when warming may have a large impact on a consumer–resource system. In particular, when the initial consumer–resource biomass ratio is at one extreme (extremely high or low), it tends to be very unstable (Fig. 2b). As a result, consumer–resource dynamics will show more dramatic shifts following changes in B_{CR}. For example, when the consumer–resource biomass ratio is very low at ambient conditions, any change in B_{CR} will cause a detectable shift in extinction rates by either increasing ($\Delta\ B_{CR} < 1$) or decreasing extinction ($\Delta\ B_{CR} > 1$, Fig. 2b). There is considerable variation in biomass ratios among communities (Cebrian *et al.* 2009; Rip & McCann 2011), suggesting that this metric could be used to identify ecosystems that may be particularly vulnerable to changes in temperature *a priori*.

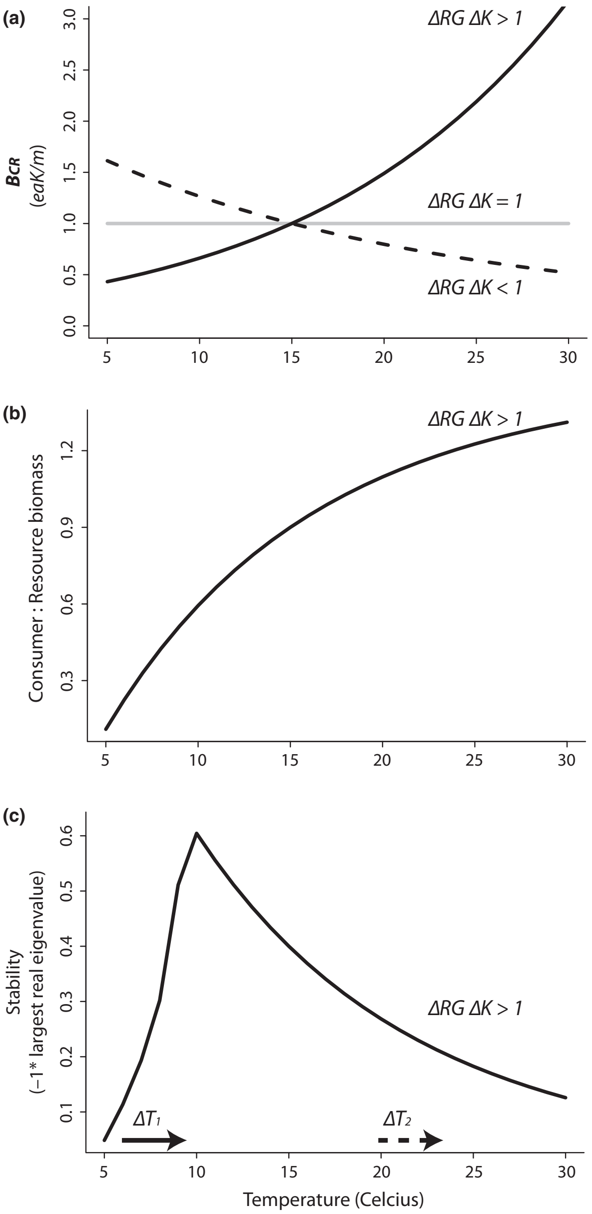

Figure 3 The effect of temperature on B_{CR}, equilibrium C:R biomass ratio, and stability. As temperature increases B_{CR} will increase if an asymmetry causes an increase in resource biomass accumulation or consumer growth (black line), and will decrease in the opposite scenario (dashed line; a). When raising temperature increases B_{CR}, consumers become more abundant relative to resources at higher temperatures (b). Increasing B_{CR} with temperature causes the interaction to become more stable when B_{CR} is initially low (solid arrow) but then destabilises over most of the temperature range (dashed arrow; c). Different stability responses depend on the starting conditions, as even identical changes in temperature produce different stability responses ($\Delta T_1 = \Delta T_2$; c). For the numerical solutions in panels b and c, *K* varied with temperature, with E_b=0.32, E_s=0.9 and *K* (15 Celcius) = 100. Other parameters were held constant (a = 0.1, e = 0.15, m = 0.6, r = 2).

Understanding how temperature-driven asymmetries influence B_{CR} also allows empiricists to interpret dynamical and equilibrium-based measures in terms of the underlying rates and vice versa (Table 2). For example, when the temperature sensitivities of interacting species are known, researchers can use these rates to predict how changes in temperature will alter biomass (Table 2, using asymmetries as predictor). Alternately, when experiments have shown temperature to alter biomass and stability, these joint responses can be used to predict whether temperature creates changes in resource biomass accumulation or relative growth (Table 2, using asymmetries as response), which can in turn be useful when trying to forecast the impacts of introducing new species, altering nutrient conditions, and so on.

Our testable predictions for B_{CR} imply that it may be used for retroactive tests of completed studies. Several studies report only some of the information needed to calculate B_{CR}, such as biomass or rate changes with temperature. When these studies have collected other, unreported data, they may be appropriate for testing changes to biomass ratios, stability or changes through time that are predicted by B_{CR} (Table 2).

PREDICTING SHORT-TERM (TRANSIENT) AND LONG-TERM (EQUILIBRIUM) RESPONSES

When warming alters B_{CR}, short-term responses are often qualitatively different from responses measured at the long-term equilibrium (Rall *et al.* 2010; O'Connor *et al.* 2011). These differences can cause experiment duration to alter inferences about the effect of warming on consumer–resource dynamics, even for otherwise identical experiments. Understanding the link between changing B_{CR}, transient and equilibrium dynamics is most easily understood by examining how changes to the aggregate rates that make up B_{CR} shift consumer–resource isoclines (Figs 1 and 4, S1).

Differences in transient and equilibrium responses can occur if populations cycle before reaching equilibrium. Cycling occurs over much of the B_{CR} range, whenever a slight increase in B_{CR} would destabilise the consumer–resource pair (Fig. 2, right side of peak on black line). This cycling causes consumer and resource populations to move in a counter-clockwise spiral towards the equilibrium (Fig. 4, all trajectories move from the open square to the black circle). If the pre-warmed densities of the consumer and resource are in the white region of Fig. 4, this clockwise movement causes the initial transient response to differ from the ultimate response in either the consumer or resource (Fig. 4a,c). For example, in Fig. 4a the abundance of the consumer initially decreases even though it increases in the long-term. Transient and long-term responses only coincide when starting conditions fall in a relatively narrow range of densities (grey region, Fig. 4b).

The aggregate rates that drive B_{CR} (resource biomass accumulation and relative growth) are useful for predicting when short- and long-term dynamics coincide under some circumstances. For example, when an experimental system is at the control (ambient temperature) equilibrium prior to warming, a change in B_{CR} that results from a change in resource biomass accumulation ($\Delta K \neq 1$) causes short-term dynamics to differ qualitatively from long-term dynamics – the point of 'origin' relative to the new equilibrium will always be in the white region of Fig. 4. Short- and long-term dynamics can only coincide when the change in B_{CR} results from a change in consumer relative growth ($\Delta RG \neq 1$), as this causes the equilibrium to shift along the resource isocline (Fig. 4). This link between different aggregate rates and the consistency of short- and long-term responses provides a tool for ecologists to reconcile apparent contradictions in outcomes of experiments that vary in duration (Table 2).

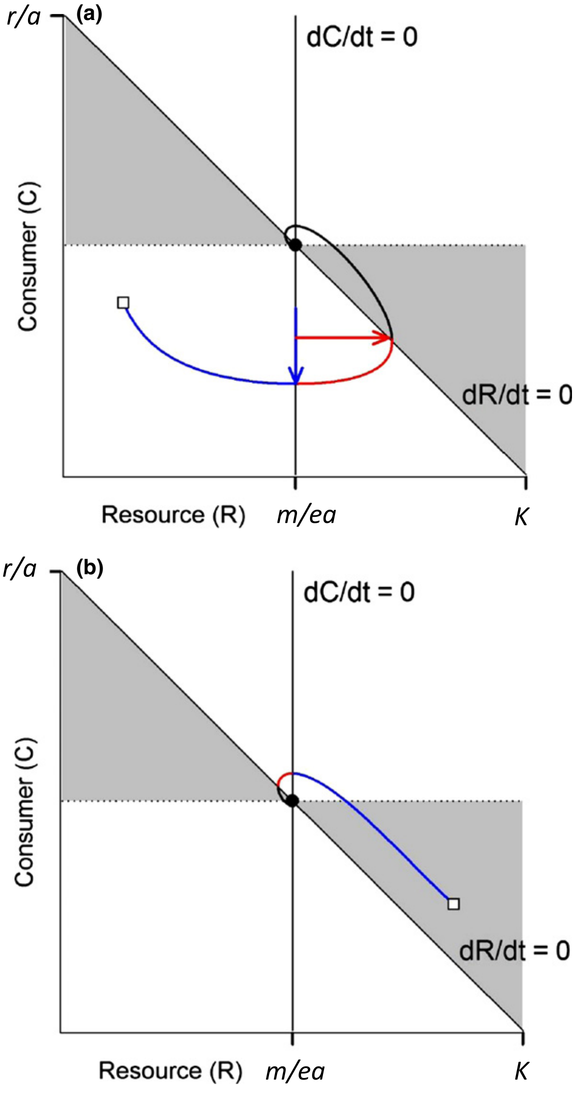

Figure 4 Transient changes in consumer and resource densities following temperature change. Open squares represent starting conditions and black circles indicate the equilibrium in each panel – long-term responses are the differences between these two points. Densities follow the spiral lines, with trajectories colour coded to show the early (blue), mid (red) and late stages (black) of the transient dynamics. An experiment starting in the white region has a transient response that is opposite to the long-term response. Arrows show a transient response that is opposite the ultimate response for the consumer (blue) or that overshoots the ultimate response for the resource (red, panel a). Experiments starting in the grey region have qualitatively similar transient and long-term responses (b).

When considering all possible starting conditions for consumer and resource abundance, it is likely that the initial transient responses will be different than the long-term responses. This white region, where short- and long-term responses differ (Fig. 4), tends to be larger than the grey (consistent) region and is even larger for other functional responses (Type II and III;

Appendix S4). Moreover, when warmed and control treatments are initiated with the same abundances, it is possible that transient dynamics will differ for the two treatments. The influence of starting conditions on transient responses highlights the need to measure ecological rates when experiments are too short to reach equilibrium conditions (Rall *et al.* 2010; O'Connor *et al.* 2011). These considerations motivate the collection of time series of consumer and resource abundance both before and after experimental manipulations are applied.

Demographic or environmental stochasticity can make it difficult to determine if equilibrium conditions are reached in an experiment, providing a further challenge for empiricists. A graphical approach can help resolve this issue by depicting changes in the size and periodicity of cycles and movement towards a new equilibrium (Rooney *et al.* 2006; Massie *et al.* 2010). Alternately, the rate of change of the consumer and resource biomass can be used to determine if the experiment is at or close to equilibrium. Rates of change decrease as equilibrium conditions are approached and the average directional change across replicates becomes indistinguishable from random (i.e. replicates may still change, but not in a unified direction). Once these conditions are met, the coefficient of variation, CV, becomes an important measure of the effect of temperature on B_{CR} (Table 2).

Finally, it is important to note that long-term responses may reflect changes in equilibrium conditions over time when species acclimatise, experience rapid evolution or exhibit multi-generational plastic responses to temperature. A notable example occurs when the mean body size of species change in response to temperature (Daufresne *et al.* 2009; Gardner *et al.* 2011). Body size has well-known effects on metabolic rates, and any directional change in body size could therefore alter consumer–resource dynamics (Yodzis & Innes 1992; Gillooly *et al.* 2002; Savage *et al.* 2004; Pawar *et al.* 2012). The diversity of body size responses to temperature within and among systems suggests that it will be necessary to account for this indirect influence of temperature in some ecosystems (Gardner *et al.* 2011; Forster *et al.* 2012; Shelomi 2012).

DISCUSSION

The B_{CR} framework we present offers new insights into how aggregate rates drive consumer–resource dynamics and how these rates are expected to vary with temperature. It does so by unifying two distinct approaches: experimental interaction strength measures that incorporate prey biomass in the presence and absence of the consumer, and flux-based measures that incorporate system inputs and outputs as well as biomass transfer from the resource to the consumer. The unification of these two conceptual approaches to food web ecology builds on previous ecosystem and food web research (Ulanowicz 1972; Halfon *et al.* 1996; Wootton 1997; Rip & McCann 2011, Tunney *et al.* 2012) and has the potential to lay the foundation for a broadly applicable theory of the temperature dependence of food web dynamics.

The first insight that emerges from this framework is that aggregating temperature-dependent rates allows us to identify when asymmetries will cause consumer–resource interactions to change with temperature. This provides a general scheme for quantifying changes in species interactions with temperature and relating them to asymmetries in resource biomass accumulation or consumer growth. For example, previous studies have found changes in consumer–resource interactions that resulted from asymmetries between consumer consumption and loss rates (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011), as well as from asymmetries in resource biomass accumulation (O'Connor *et al.* 2011). Identification of these asymmetries allows empiricists to focus measurements on a few key parameters, and should lead to generalisations about temperature-dependent asymmetries across ecosystems.

Recent research on the metabolic scaling of vital rates provides a powerful starting point for identifying when temperature-dependent asymmetries are likely to arise (Allen *et al.* 2005; López-Urrutia *et al.* 2006; Dell *et al.* 2011). For example, foraging effectiveness is often dependent on consumer and resource movement rates (Dell *et al.* 2013), which leads to asymmetries when consumer and resource metabolic responses to temperature differ. A number of consumer–resource pairings differ in mean responses, such as carnivore–herbivore and vertebrate–invertebrate pairings (Dell *et al.* 2011). These differences suggest that interactions involving these groups are more likely to show changes in B_{CR} with warming. Moreover, when the direction of the asymmetry is known, the direction of change in B_{CR}, and therefore abundance, can be predicted. As an example, carnivores are less sensitive to temperature on average than herbivores (Dell *et al.* 2011). This difference can cause an increased velocity of herbivores relative to carnivores with temperature, which in turn can generate increases in encounter rates that outstrip increases in carnivore mortality; the resulting asymmetry is predicted to increase B_{CR} with warming, causing a relative increase in carnivore density.

Applying metabolic theory to the B_{CR} framework also highlights gaps in current knowledge that are necessary for understanding and predicting impacts of temperature change. The carrying capacity of resources within ecosystems (K) is one such gap, as is the effect of declines in ecological rates that occur when temperature exceeds species thermal tolerances. Warming experiments that have manipulated nutrient supply rate, or used inferred measures, have illustrated its importance to trophic dynamics (O'Connor *et al.* 2009; Rall *et al.* 2010). Similarly, observational studies have shown that some of the strongest climate signals in marine zooplankton were not due to direct effects of warming, but rather resulted from decreases in nutrient supply rate at higher temperatures (Roemmich & McGowan 1995).

The B_{CR} framework clarifies that warming will alter trophic dynamics by altering K whenever resource metabolic rate and nutrient supply rates have different temperature sensitivities. Nutrient supply rates are often driven by both abiotic and biotic processes, such as temperature, water availability and microbial activity in terrestrial ecosystems (Melillo *et al.* 1993; Delgado-Baquerizo *et al.* 2013). Differences in the temperature-dependencies of these processes are likely in most ecosystems, and therefore determining how temperature affects carrying capacity in different habitats should be an important goal for ecologists. Ecosystem studies and predictive models can be used to make *a priori* predictions about the direction and magnitude of nutrient shifts with temperature, and thus to predict where changes in B_{CR} are likely to be driven by changes to resource carrying capacity. For example, a broad scale marine study showed that apparent temperature limitations of bacteria were actually due to limited resources (López-Urrutia & Morán 2007). Similarly, terrestrial models suggest that increases in soil nutrients will be prevalent following warming in northern ecosystems (Melillo *et al.* 1993), and fine scale models are available to understand differences in the temperature-dependency of phosphorus among lakes (Wang *et al.* 2003; Malmaeus *et al.* 2006).

The temperature-rate functions we have considered model increases in biological rates that occur with temperature, but do not capture declines in rates that occur at higher temperatures. The functional relationship between temperature and rates in this declining phase are only beginning to be understood and still lack empirical generality (Dell *et al.* 2011; Amarasekare & Savage 2012). Nonetheless, the B_{CR} framework allows scaling from vital rates to consumer–resource dynamics and vice versa, even when vital rates decline with temperature. For example, warming beyond a predator's temperature optimum will cause mortality rates to increase more quickly than attack rates, thus reducing relative growth (Fig. 3a, descending line). Direct measurement of these vital rates would lead to new insights in both physiological responses to temperature and how these responses scale up to affect community dynamics.

The second insight to emerge from the B_{CR} framework is that temperature changes that alter biomass ratios also have predictable effects on stability. This insight addresses two central goals for ecologists: predicting how biomass changes with temperature and when these changes cause trophic interactions to become unstable. Both measures have clear and broad implications for warming effects, ranging from changes in the stability and impact of insect herbivores (Frazier *et al.* 2006; Currano *et al.* 2008; Nelson *et al.* 2013) to increases or failures of fisheries (Rose 2004; Cheung *et al.* 2010). The novel insight we gain is that stability can change bi-directionally with B_{CR} whereas biomass ratios follow a consistent trend. Taking the carnivore–herbivore example from above, an increase in B_{CR} with temperature will cause a top-heavy system to become less stable following warming. In contrast, a system with initially low carnivore abundances that experiences a similar increase in B_{CR} would be less prone to extinction following warming (Fig. 2). This bi-directional relationship means that diagnostic measures, such as the correlation between consumer abundance and coefficient of variation, can be used to predict the long-term effects of warming on extinction (Table 2).

The relationship between stability and consumer to resource biomass ratios facilitates predictions about ecosystems that are most sensitive to shifts in B_{CR}. Recent studies have demonstrated that warming can have a large effect on stability (Rall *et al.* 2010; Binzer *et al.* 2012; Nelson *et al.* 2013), but ecologists have lacked general predictions about when these effects are likely to generate population fluctuations or extinctions. The link between B_{CR}, biomass ratios and stability may allow ecologists to identify vulnerable ecosystems *a priori* by quantifying biomass ratios across food webs. This quantification has been done to explore trophic structure and stability (Cebrian *et al.* 2009; Rip & McCann 2011), but has yet to be undertaken to generate predictions about sensitivity to climate change.

The explicit linking of dynamic outcomes (relative biomass and stability) with aggregate parameters (ΔK, ΔRG) also allows for greater synthesis across studies. Previous research has suggested that trophic dynamics can change through shifts in per capita interaction strengths or through changes in population sizes (Harley *et al.* 2006); B_{CR} clarifies how these two changes are linked through the role of per capita rates on aggregate parameters and biomass distributions (eqn 3 and 4; Appendix S1). Studies often measure either vital rates (Dell *et al.* 2011) or changes in abundance and stability (Barton 2010; Kratina *et al.* 2012), but rarely both. Translating parameters to B_{CR} and vice versa (Tables 2 & S1) creates a common currency for such studies. Moreover, because the B_{CR} framework clarifies the relationship between these measures in terms of temperature-dependent asymmetries, ecologists are now in a position to determine which asymmetries are shared by specific ecosystems. Effects that initially appeared idiosyncratic may actually be generalisable across systems as the numbers of studies that test relationships between temperature and food webs grow.

The third insight to emerge from the B_{CR} framework is that short-term, transient dynamics following warming will often differ from long-term trajectories. The question of the appropriate timescales for experiments is longstanding in ecology, as is the relevance of transient and equilibrium dynamics in different communities (Hastings 2004). Although our empirical measure of B_{CR} focuses on equilibrium conditions, our approach also allows ecologists to quantify B_{CR} by directly measuring ecological rates (Table 2). This relationship between equilibrium conditions and rates allows for a more complete scaling between transient and long-term trajectories, and therefore has the potential to clarify when different temperature responses among experiments are due to differences in timescales or the temperature sensitivities of organisms.

Finally, the B_{CR} framework provides the cornerstone for a modular theory of the temperature dependence of food webs. Just as our results highlight that a combination of high resource biomass accumulation and high consumer relative growth leads to unstable interactions (eqn 5, Fig. 2), previous research has shown that this combination can also decrease the stability and diversity of food webs (Rooney & McCann 2012). Although considerable work is required to develop a full food web model based on the consumer–resource interaction of two functional groups, the B_{CR} framework nonetheless highlights important future areas of research. For example, because temperature can increase or decrease B_{CR} in a single consumer–resource interaction (Fig. 3), food webs will contain numerous links that vary in the consistency of their temperature responses. If different consumer–resource interactions within food webs tend to behave similarly, we would expect the effects seen in single interactions to multiply through the food web. In contrast, modules within a food web that show opposite trends with temperature may dampen the overall effect of any single interaction.

In summary, our B_{CR} framework links the functioning of trophic dynamics to temperature changes using general, aggregated terms that translate across experimental systems and conditions. It clarifies that temperature is likely to change the outcomes of interactions in most communities because of asymmetries in temperature dependencies, such as an asymmetry in biotic and abiotic processes. It also highlights discrepancies between short- and long-term dynamics that likely arise in warming experiments. Finally, this general framework provides a foundation for understanding and predicting the effects of temperature on entire food webs, and provides clear directions for empirical and theoretical ecologists.

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AUTHORSHIP

BG led the article; JPD, BG, KSM, VS, TDT & DAV developed the modelling framework; JPD, BG, KSM, MIO, VS, JBS, TDT & DAV were the main writers; JLB, BTB, CC, AID, JPD, BG, HSG, CDGH, HMK, PK, KSM, MIO, VS, JBS, TDT, DAV & MW were involved in discussions and editing, and HSG & MIO initiated the NCEAS and CIEE working groups.

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