

REVIEW

Interactions between temperature and nutrients across levels of ecological organization

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Abstract

Temperature and nutrient availability play key roles in controlling the pathways and rates at which energy and materials move through ecosystems. These factors have also changed dramatically on Earth over the past century as human activities have intensified. Although significant effort has been devoted to understanding the role of temperature and nutrients in isolation, less is known about how these two factors interact to influence ecological processes. Recent advances in ecological stoichiometry and metabolic ecology provide a useful framework for making progress in this area, but conceptual synthesis and review are needed to help catalyze additional research. Here, we examine known and potential interactions between temperature and nutrients from a variety of physiological, community, and ecosystem perspectives. We first review patterns at the level of the individual, focusing on four traits – growth, respiration, body size, and elemental content – that should theoretically govern how temperature and nutrients interact to influence higher levels of biological organization. We next explore the interactive effects of temperature and nutrients on populations, communities, and food webs by synthesizing information related to community size spectra, biomass distributions, and elemental composition. We use metabolic theory to make predictions about how population-level secondary production should respond to interactions between temperature and resource supply, setting up qualitative predictions about the flows of energy and materials through metazoan food webs. Last, we examine how temperature–nutrient interactions influence processes at the whole-ecosystem level, focusing on apparent vs. intrinsic activation energies of ecosystem processes, how to represent temperature–nutrient interactions in ecosystem models, and patterns with respect to nutrient uptake and organic matter decomposition. We conclude that a better understanding of interactions between temperature and nutrients will be critical for developing realistic predictions about ecological responses to multiple, simultaneous drivers of global change, including climate warming and elevated nutrient supply.

Keywords: activation energy, climate change, ecological stoichiometry, metabolic theory of ecology, nitrogen, nutrients, phosphorus, temperature, threshold elemental ratio

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Introduction

Nutrient availability and temperature play key roles in controlling the pathways and rates at which energy and materials move through ecosystems. The important role of nutrient availability is mediated by imbalances between the demand from organisms for growth, maintenance, and reproduction and the relative availability of required resources in the environment (Sturner & Elser, 2002). Temperature, on the other hand, is a master variable that controls biological activity through its fundamental effect on metabolic rate (Arrhenius, 1889; Gillooly *et al.*, 2001). Together, these two factors affect the acquisition, storage, and cycling of energy and

materials at organizational levels ranging from individuals to whole ecosystems (Kleiber, 1961; Reiners, 1986; Kaspari, 2012). Recent advances in ecological stoichiometry (ES; Elser *et al.*, 1996; Sturner & Elser, 2002) and metabolic ecology (ME; Brown *et al.*, 2004; Sibly *et al.*, 2012) have initiated a synthetic framework that enables quantitative predictions about how temperature and nutrients interact to control ecological dynamics (e.g. Kerkhoff *et al.*, 2005; Allen & Gillooly, 2009; Billings & Ballantyne, 2013). Although an increasing number of studies have begun to examine temperature–nutrient interactions (e.g. Woods *et al.*, 2003; Jeppesen *et al.*, 2010; Makino *et al.*, 2011), a conceptual synthesis is needed to help crystallize important concepts, identify emerging patterns, and highlight productive areas for future research.

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The frameworks of ES and ME provide a foundation for examining interactions between temperature and nutrients because they are based on first principles of mass balance and thermodynamics. Such an approach is not new. Lotka's classic 'Elements of Physical Biology' (1925) was one of the earliest attempts to use principles of physics and chemistry to examine how temperature (as solar energy flux) influences exchanges of chemical elements between organisms and the environment. Physiologists and limnologists have examined temperature–nutrient interactions, either through controlled laboratory and chemostat experiments (e.g. Goldman & Carpenter, 1974; Rhee & Gotham, 1981), mechanistic models (e.g. Shuter, 1979), or through correlative comparisons of populations across environmental gradients (e.g. Hutchinson, 1967 and references therein). Others have used bioenergetics/nutrient mass balance models (e.g. Kitchell *et al.*, 1977; Hanson *et al.*, 1997) to examine the fate of nutrients in organisms, populations, and ecosystems, implicitly incorporating thermal effects (e.g. Kraft, 1992; Schindler *et al.*, 1993). More recent developments, such as threshold elemental ratio (TER) models (Hessen, 1992; Sterner, 1997; Frost *et al.*, 2006), explicitly blend both metabolic and stoichiometric frameworks and have helped to further bridge the commonly disparate perspectives of energy and materials in ecology (Reiners, 1986; Allen & Gillooly, 2009). Together, these efforts show great promise for advancing our understanding of how temperature and nutrients interact to affect the structure and function of ecosystems.

An assessment of temperature–nutrient interactions is also critical for reducing uncertainty about the consequences of multiple global change drivers. Over the past century, mean air temperatures have risen ~ 0.8 °C, and most models predict an increase of ~ 2 – 4 °C during the next century (IPCC, 2013). Temperature regimes of freshwater and marine ecosystems have changed in parallel with air temperatures (e.g. Cane *et al.*, 1997; Pilgrim *et al.*, 1998; Kaushal *et al.*, 2010), suggesting continued warming of most ecosystems in the future, particularly at high latitudes. Humans have also modified global elemental cycles, leading to large shifts in availability of carbon (C), nitrogen (N), and phosphorus (P) in the biosphere (Falkowski *et al.*, 2000). Although changes in temperature and nutrient availability are occurring in parallel and are critical aspects of global change, we know relatively little about how these factors interact across levels of organization ranging from individuals to whole ecosystems (Jeppesen *et al.*, 2010; Sardans *et al.*, 2012). A research approach that leverages first principles and concepts rooted in ME may allow us to apply modern ecological theory toward solving important environmental issues. In addition, progress

in this area has great potential to improve our understanding of how environmental effects on individuals scale up to influence whole-ecosystem dynamics (Levin, 1992; Sibly *et al.*, 2012).

In this study, we examine known and potential interactions between temperature and nutrients from a variety of physiological, community, and ecosystem perspectives. We start at the level of individuals, exploring how temperature and nutrients interact to influence key organismal traits. We then use this framework to inform a discussion of potential temperature–nutrient interactions at higher levels of organization (i.e. populations, food webs, and ecosystems). Our treatment of these subjects is not restricted to any particular type of ecosystem or taxonomic group. However, most of our examples come from freshwater habitats and poikilothermic organisms because of our expertise and the large amount of relevant work in these areas. Although we recognize that other factors such as thermal windows and oxygen supply can play significant roles in shaping how organisms respond to warming (e.g. Pörtner & Farrell, 2008; Verberk *et al.*, 2011), we restrict our focus to basic temperature–nutrient interactions to make our synthesis more tractable. Our goal is to catalyze additional research on the important interactions and synergies between temperature and nutrient availability in ecological systems.

Interactive effects of temperature and nutrients at the individual level

We begin by considering how temperature and nutrients combine to influence rates and traits at the physiological or individual level. For simplicity, we focus on four fundamental traits that set the stage for scaling from the individual to the ecosystem: growth rate, respiration, body size, and body elemental content. Although additional traits, such as consumption and attack rates, are worthy of consideration (e.g. Petchey *et al.*, 2010; Englund *et al.*, 2011; Vucic-Pestic *et al.*, 2011; Lemoine & Burkepile, 2012; Rall *et al.*, 2012), too little work has been conducted on these traits in the specific context of temperature–nutrient interactions. We end this section by discussing the TER (Urabe & Watanabe, 1992; Sterner, 1997), a promising approach for integrating the multiple interactive effects of temperature and nutrients on individuals.

Growth rates

One-way effects of temperature or nutrients on individual growth rates have received considerable attention, but we know far less about their interactions.

Three hypotheses, clearly articulated by Rhee & Gotham (1981), describe multiple ways that temperature and nutrients may influence growth rates. For heuristic purposes, and to help clarify these hypotheses, we present models that use established temperature and resource dependences. Each of these models uses a generic resource term that could represent N, P, or another potentially limiting element (e.g. iron or potassium). However, a widely applicable predictive model should account for at least N and P, the two most frequently limiting elements (Sterner, 2004; Elser *et al.*, 2007).

The first hypothesis states that only temperature or nutrients can limit growth at any given time (Blackman, 1905). This hypothesis essentially extends Liebig's law of the minimum to temperature and acts as a null hypothesis:

$$\mu = \min[T, R], \quad (1)$$

where growth (μ) is some function of one limiting factor, either temperature (T) or resources (R). The temperature dependence of growth is commonly modeled using the Van't Hoff–Arrhenius equation:

$$\mu = b_0 e^{-E/kT}, \quad (2)$$

where b_0 is a normalization constant, k is the Boltzmann constant ($eV \text{ } ^\circ K^{-1}$), T is temperature ($^\circ K$), and E is the activation energy (eV). With respect to resources, the Monod equation (Monod, 1949) is often used to describe the relationship between growth and the availability of a single resource:

$$\mu = \mu_{\max} \frac{R}{(K_R + R)}, \quad (3)$$

where μ_{\max} is the maximum growth rate, R is the resource concentration (e.g. $\mu g \text{ NH}_4\text{-N L}^{-1}$ or %N of food), and K_R is the half-saturation constant, the R at which one-half the maximum growth rate is achieved. Although other formulations of temperature- and resource-dependent growth are possible (e.g. Droop, 1974; Clarke, 2006; Knies & Kinsolver, 2010), these equations are widely understood and thus represent a productive starting point for exploring how temperature and resources influence the growth and success of organisms.

The second hypothesis of Rhee & Gotham (1981) argues that temperature sets the maximum growth rate of an organism, while resource levels mediate the realized growth rate. This hypothesis can be expressed mathematically with a multiplicative model combining the Arrhenius and Monod equations:

$$\mu = b_0 e^{-E/kT} \frac{R}{(K_R + R)}. \quad (4)$$

While this model adds an explicit resource term to the metabolic framework (Brown *et al.*, 2004; Marquet *et al.*, 2004; Anderson-Teixeira *et al.*, 2008), it does not allow the form of the relationship between growth and resource concentration to vary with temperature (i.e. it does not allow a true temperature–resource interaction).

The third hypothesis states that temperature influences the maximum growth rate as well as the nature of the growth–resource relationship (Rhee & Gotham, 1981; Hall *et al.*, 2008; Davidson *et al.*, 2012). Here, the influence of resources on growth rate is dependent upon temperature, and hence, temperature and resources explicitly interact:

$$\mu = b_0 e^{-E/kT} \frac{R}{(K_{R,T} + R)}, \quad (5)$$

where $K_{R,T}$ is the half-saturation constant for growth, which varies as a function of temperature (this is one of many possible ways to represent a true temperature–resource interaction). Thus, this hypothesis allows temperature to influence how efficiently organisms capture and utilize resources.

Currently, hypothesis three has the most empirical support. The relative influence of nutrient availability on growth rate decreases with reduced temperature until extreme suboptimal temperatures eliminate nutrient limitation (Rhee & Gotham, 1981). Recent studies (e.g. Persson *et al.*, 2011; Wojewodzic *et al.*, 2011) generally show that the influence of phosphorus availability on growth rates of algae and zooplankton increases with temperature, such that growth is most sensitive to changes in nutrient supply in warm vs. cold environments (but see McFeeters & Frost, 2011). Alternatively, if hypothesis two had the most support, growth would show the same relative resource dependency at all temperatures. Taken together, these studies suggest that the influence of nutrient supply on growth rates should increase with temperature to some optimum, but additional research is needed to assess the generality of this pattern.

Respiration rates

Temperature and nutrient supply also interact to influence rates of respiration; however, the multiple roles that respiration plays in an organism's carbon economy make painting this picture somewhat complicated. When carbon and nutrient supply rates are near optimal, the relationship between temperature and

respiration is generally positive and well described by the Arrhenius equation (Eqn 2; Yurista, 1999; Gillooly *et al.*, 2001; Davidson *et al.*, 2012). As nutrients become limiting, respiration rates of plants and algae tend to decline along with growth rates (Theodorou *et al.*, 1991) and show a muted response to increased temperature (e.g. Staehr & Sand-Jensen, 2006). In contrast, respiration rates of heterotrophic invertebrates often increase when consuming a nutrient-poor or stoichiometrically imbalanced diet (Russell & Cook, 1995; Plath & Boersma, 2001; Jeyasingh, 2007). Invertebrates, unlike plants and algae, ingest carbon and nutrients in packages and must balance both elemental deficiencies and surpluses to maintain homeostasis. As such, respiration is often used as a pathway for eliminating excess carbon ('energy spilling', Russell & Cook, 1995; Hessen & Anderson, 2008; also see Darchambeau *et al.*, 2003; Jensen & Hessen, 2007). For example, *Daphnia* consuming high C : P diets in warm environments may 'burn off' excess carbon via respiration; at low temperatures, where high C : P diets are less likely to limit growth, diet C : P may have little effect on respiration (McFeeters & Frost, 2011). Recent work also suggests that temperature and resource availability may interact to influence bacterial respiration (e.g. Kritzberg *et al.*, 2010). Thus, the influence of temperature and resources on respiration will depend on the organism's mode of consumption, nutrient demands, and relative requirements for homeostasis.

Body size

Temperature and resource supply both have large independent effects on organism size, but less is known about how these factors interact. The weight of evidence suggests that warming leads to reduced body size in a broad range of taxa with diverse phylogenetic histories (Daufresne *et al.*, 2009; Finkel *et al.*, 2010; Sheridan & Bickford, 2011; also see Gardner *et al.*, 2011 and Adams *et al.*, 2013). We might expect such an effect to be even more pronounced under conditions of low nutrient availability, particularly among unicellular organisms (e.g. algae and bacteria) that obtain nutrients via transport across cell membranes. This is because taxa (and perhaps even individuals) with small cell volumes tend to have both lower nutrient requirements (i.e. minimum cell quotas) and a greater affinity for the acquisition of rare nutrients than large-celled taxa (Hein *et al.*, 1995; Litchman *et al.*, 2007; Reuman *et al.*, 2013). Thus, the negative effects of temperature on body size may be exacerbated under conditions of low nutrient supply. Among metazoans, resource limitation can lead to smaller body sizes via suboptimal growth and development rates (e.g. Sterner, 1993; Liess *et al.*,

2013), and such responses may also be influenced by ambient temperature (e.g. Sweeney & Vannote, 1984; Atkinson, 1994). Although few studies have examined the interactive effects of temperature and nutrients on body size, this represents an important area of future research considering the critical role of body size in ecological interactions (Peters, 1983; Hildrew *et al.*, 2007).

Body stoichiometry

A number of studies have shown that the N and P content (mg nutrient mg dry mass⁻¹) of whole organisms generally declines with increasing temperature (Rhee & Gotham, 1981; Woods *et al.*, 2003; Reich & Oleksyn, 2004; Cotner *et al.*, 2006; Brey *et al.*, 2010; Martiny *et al.*, 2013; Yvon-Durocher *et al.*, in press). A meta-analysis by Woods *et al.* (2003) showed that organismal P or RNA content (a primary determinant of body P for small invertebrates) was 49% higher in cold vs. warm environments when all taxonomic groups were considered together (including algae, plants, animals, bacteria, and yeast). Similarly, the N or protein content of all groups was 32% higher in cold environments. Although many factors could lead to these results (including body size, Woods *et al.*, 2003), one of the most likely explanations is that the efficiency of RNA and proteins in biochemical reactions increases with temperature (Sievers *et al.*, 2004; Toseland *et al.*, 2013); thus, as temperatures increase, the quantity of RNA needed to produce a given growth rate declines in conjunction with body P content (Rhee & Gotham, 1981; Woods *et al.*, 2003; but see Chrzanowski & Grover, 2008). Results from recent modeling efforts challenge this hypothesis (i.e. temperature invariance of P content; Gillooly *et al.*, 2005), suggesting that additional research is needed to fully assess these patterns.

It is of note that the rule of thumb described above, that is, that organismal nutrient content declines with temperature, is superficially inconsistent with the growth rate hypothesis (Elser *et al.*, 1996), one of the pillars of ES theory. This hypothesis predicts positive linkages among ribosomal RNA, P content, and growth rate based on the importance of rRNA in protein synthesis and the high P content (~9%) of RNA (Elser *et al.*, 2003). If rapid growth is associated with high P content, and animals grow more rapidly at high temperatures, why do most studies show a decline in P content with warming? Two simple calculations are informative. Over a temperature gradient ranging from 10 to 20 °C, the Arrhenius–Boltzmann equation ($E_A = 0.67$ eV) predicts that an organism's growth rate should increase approximately 250%. When temperature is held constant, a 250% increase in growth rate is associated with only a 15–17% increase in the P content of zooplankton

and bacteria (Elser *et al.*, 2003). This modest increase in P content is in sharp contrast to the observed 49% decrease in P content reported in Woods *et al.* (2003). Thus, these calculations suggest that any increase in P content associated with rapid growth in warm environments may be masked by a larger decrease in P content due to other factors (*but see* Simonds *et al.*, 2010). More research is needed in this area to examine the relative importance of these factors across diverse taxonomic groups.

Threshold elemental ratios: bridging metabolism and stoichiometry

Based on our discussion so far, it is clear that temperature and nutrients have strong interactive effects at multiple levels, that is, biochemical (e.g. RNA and protein activity), cellular (e.g. cell size and RNA content), and whole organism (e.g. body size, organismal stoichiometry, and metabolism). Yet, to understand how these interactions play out at higher levels of organization, we need quantitative tools that integrate the multiple responses of organism biochemistry and physiology to both temperature and nutrient supply. The TER (Urabe & Watanabe, 1992; Sterner, 1997), the diet stoichiometry (e.g. C : P) that separates C or energy-limited growth from nutrient-limited growth for a given taxon or life stage, offers a promising approach for integrating energetics and stoichiometry at the level of the individual. This approach has been used to predict interspecific patterns of nutrient demand (Frost *et al.*, 2006), population dynamics in the context of consumer–resource interactions (Andersen *et al.*, 2004), and fluxes of energy and materials (Allen & Gillooly, 2009). Nonetheless, there have been few attempts to explicitly incorporate temperature into the TER framework (Doi *et al.*, 2010), and doing so may enable a mechanistic understanding of how temperature influences the C and nutrient linkages mediated by consumers (Schmitz, 2013).

Frost *et al.* (2006) developed one common formulation of the C : nutrient (C : X) TER ($TER_{C:X}$):

$$TER_{C:X} = \left(\frac{A_X}{GGE_C} \right) \left(\frac{Q_C}{Q_X} \right), \quad (6)$$

where A_X is the assimilation efficiency of nutrient X, Q_C , and Q_X are the organismal C and nutrient contents (per unit dry mass), and GGE_C is the proportion of ingested C incorporated into growth. Here, GGE_C is a function of the mass-specific ingestion rate (I_C), the carbon assimilation efficiency (A_C), and the mass-specific respiration rate (R_C):

$$GGE_C = \frac{I_C A_C - R_C}{I_C}, \quad (7)$$

Each of the terms in the TER equation may be influenced by temperature, and this framework can thus provide a quantitative structure for making predictions. We now present two approaches for understanding how $TER_{C:X}$ may vary with temperature. Interestingly, predictions that emerge from these approaches do not agree.

To our knowledge, no one has taken the direct approach of simply measuring how TERs, that is, all of the interacting components, change with temperature. This may be a fruitful tactic for dominant taxa known to play important ecosystem roles, but prohibitive in the context of dealing with whole communities. A viable alternative is to empirically determine the combination of temperature and diet C : X ratios that maximizes growth (Fig. 1; e.g. Persson *et al.*, 2011). Unfortunately, such response surfaces are difficult to characterize under realistic conditions; instead, it is common to examine the proportional difference in growth between low and high C : X diets and to use this difference as a metric of sensitivity to nutrient limitation (Sterner & Elser, 2002; Hood & Sterner, 2014). As described above, many taxa (e.g. algae, bacteria, invertebrates) show greatest sensitivity to nutrient limitation when growing at high temperatures (Rhee & Gotham, 1981; Hall *et al.*, 2009; Persson *et al.*, 2011; Wojewodzic *et al.*, 2011). Because sensitivity to nutrient limitation is likely most prevalent for taxa with low $TER_{C:X}$ values, these patterns suggest that $TER_{C:X}$ should decline with temperature.

An alternative approach is to examine, in a general sense, the temperature dependence of key parameters in the basic TER equation (Eqn 6; Frost *et al.*, 2006). Multiple lines of evidence suggest that GGE_C generally declines with increasing temperature (Doi *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Lemoine & Burkepille, 2012; Iles 2014), and holding all other terms constant, this should lead to higher TER values by elevating the $\left(\frac{A_X}{GGE_C} \right)$ term. In addition, as discussed above, there is evidence that warming will lead to elevated $\left(\frac{Q_C}{Q_X} \right)$ values and hence higher TER values (Woods *et al.*, 2003). Unless the influence of warming on nutrient assimilation efficiencies (i.e. ' A_X ') overrides such effects, these patterns suggest that $TER_{C:X}$ should increase with temperature (Fig. 1c) – a result that is inconsistent with the previous prediction. Clearly, additional research is needed to predict how temperature will affect TERs, as well as how such changes will play out across multiple temporal scales (i.e. physiological adjustments vs. long-term adaptation; Woodward *et al.*, 2010a).

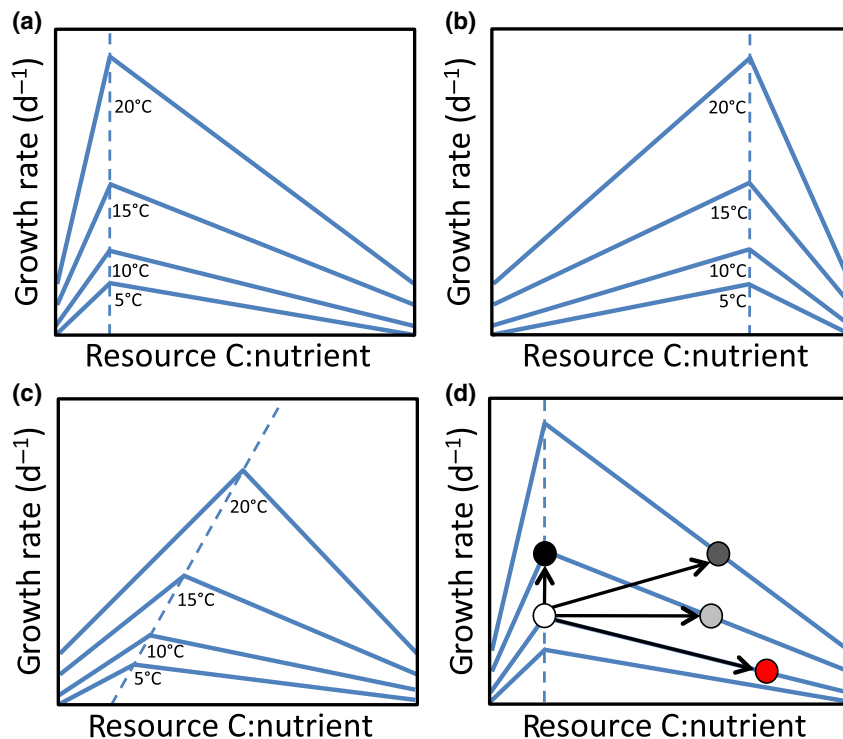


Fig. 1 Predicted effects of temperature and food quality (i.e. C : nutrient ratios) on consumer instantaneous growth rates. Resource C : nutrient ratio is depicted as having a linear effect on growth (i.e. straight lines in figure), while the effects of temperature are exponential (i.e. increased spacing between lines as temperatures increase). Note that relationships between temperature or resource quality and growth rate could be unimodal, but such effects are not described here. Panels (a) and (b) show predicted response surfaces for consumers with relatively low (a) and high (b) threshold elemental ratio (TER) values (dashed lines). In these panels, TER is assumed to be constant across temperatures (Doi *et al.*, 2010). Panel (c) depicts an alternative response surface in which the TER increases with temperature. Panel (d) shows predicted changes in growth for a consumer exposed to a change in temperature with no change in food quality (white circle to black circle), a change in food quality with no change in temperature (white circle to red circle), and simultaneous changes in both temperature and food quality (white circle to gray circles). In these scenarios, the initial condition (white circle) is at the consumer's TER at 10 °C, that is, the food quality that produces optimal growth at that temperature.

Interactive effects of temperature and nutrients on populations, communities, and food webs

How do patterns described above with respect to metabolism, body size, and stoichiometry manifest at higher levels of biological organization (i.e. populations, communities, and food webs)? This question is critical if we hope to use the principles developed above to make and test predictions about responses to global change (e.g. Elser *et al.*, 2010). However, dynamics at mid-range levels of biological hierarchy are perhaps the most difficult to understand, owing to the rich set of direct and indirect interactions that often elude simple predictive frameworks (Tilman *et al.*, 2004; Isaac *et al.*, 2012). In our effort to explore this area, we first consider empirical relationships between temperature and the structure of populations and communities, leveraging stoichiometric predictions from the previous section. We then turn to metabolic theory to examine how temperature alone is predicted to affect growth

and production of heterotrophic consumers, scaling from the individual to the population. Next, we examine how temperature and nutrients may interact to influence food webs by considering predictions about the quantity and quality of basal resources that fuel consumer populations. Together, these components provide a preliminary roadmap for understanding how changes at the consumer–resource interface might alter structure, productivity, and elemental flux through food webs.

Size spectra and biomass distributions

An increasing number of studies have examined how temperature alters community size spectra and biomass distributions (e.g. Petchey *et al.*, 1999; O'Connor *et al.*, 2009; Jennings & Brander, 2010; Morán *et al.*, 2010; O'Gorman *et al.*, 2012), yet few have investigated the stoichiometric consequences or potential interactions with nutrient supply. Yvon-Durocher *et al.* (2010b) was

among the first studies to experimentally quantify effects of warming on biomass size spectra, demonstrating a shift toward dominance of small taxa in warmed pond mesocosms (i.e. a steepening of the individual mass–abundance slope). In this case, size spectra were influenced by shifts in community structure (as seen in Winder *et al.*, 2009), rather than intraspecific reductions in body size (i.e. the ‘temperature–size rule; Atkinson, 1994; Atkinson *et al.*, 2003). This repeated pattern of declining average body size, in combination with a predicted net reduction in body nutrient content with warming (Woods *et al.*, 2003), suggests that increased temperatures should reduce total storage of nutrients in communities, with the potential for increased nutrient flux through smaller individuals. However, this prediction is likely to be contingent upon nutrient supply, as previous work has shown altered slopes of size spectra (i.e. typically increased average body size) in nutrient-rich ecosystems (e.g. Sprules & Munawar, 1986; Irwin *et al.*, 2006; Mulder & Elser, 2009; Ott *et al.*, 2014).

In addition to warming-induced shifts in size spectra, some investigators have reported changes in trophic structure, with important implications for nutrient storage and cycling. For instance, Petchey *et al.* (1999) showed that warming of experimental microcosms led to ‘bottom-heavy’ food webs favoring primary producers and bacterivores over top predators and herbivores. Because predators are often more nutrient-rich than their prey (Fagan *et al.*, 2002; Sterner & Elser, 2002), such a response could lead to either reorganization or reduction in storage of N and P in the food web. In contrast, more recent work by O’Connor *et al.* (2009) showed a shift toward dominance of herbivores (i.e. increased zooplankton to phytoplankton ratio) in response to warming, but this effect was only evident in nutrient-replete treatments and did not consider predators (also see Yvon-Durocher *et al.*, 2010b). In a series of geothermally heated streams in Iceland, Woodward *et al.* (2010b) showed that brown trout, the top predator, was apparently more abundant in warm vs. cold streams, with the potential to alter foodweb structure and nutrient dynamics in these streams (O’Gorman *et al.*, 2012). Clearly, these structural responses to warming and nutrient supply will affect the distribution and cycling of elements in food webs, but additional research is needed to assess whether general responses may be predicted.

Metabolic scaling predictions

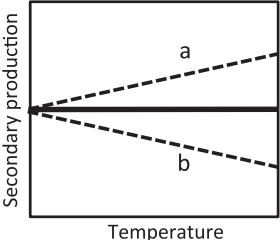
A complementary approach to understanding how higher levels of organization may respond to temperature and nutrients is to use metabolic scaling theory.

Savage *et al.* (2004) were among the first to develop theory linking individual traits (e.g. body size, metabolism, temperature) to population size and growth rate using a ME framework. This theory predicts increased maximum population growth rates (r_{\max}) and reduced carrying capacity (K) as temperatures warm. Thus, assuming no temperature-driven changes to resource availability, equilibrium population abundance should decline with temperature (also see Allen *et al.*, 2002; Vasseur & McCann, 2005). We can now leverage this theory to examine how temperature is predicted to affect secondary production of consumer populations. We focus on secondary production because it is a net ecosystem flux that incorporates a broad range of life-history characteristics (i.e. density, biomass, body size, individual growth rate, reproduction, survivorship, and lifespan; Benke, 1993, 2010; Benke & Huryn, 2010).

Box 1 presents basic metabolic scaling equations that, somewhat surprisingly, predict equivalence of secondary production across a broad range of temperatures (Brown *et al.*, 2004; Huryn & Benke, 2007). In brief, this theory predicts that increased temperatures should lead to reduced population abundance, biomass, and average body size, as well as higher individual mass-specific growth rates. Because secondary production can be derived as the product of mass-specific growth rate and population biomass (Benke, 1984), production should be equivalent across a wide range of temperatures (Box 1). In essence, reduced population biomass is compensated for by increased individual growth rates, leading to temperature invariance of secondary production. It is important to point out, however, that these predictions do not account for temperature-driven changes in the quantity or quality of resources at the base of the food web. How might this initial scenario differ when such changes to the resource base are incorporated?

First, we consider a scenario in which a single currency, such as energy or carbon, limits individual growth (Fig. 2, left column). This is analogous to including a linear resource term (R) in the basic metabolic theory equations (Brown *et al.*, 2004; Sterner, 2004; Kaspari, 2012). In this case, decreasing energy supply away from a theoretical optimum (i.e. moving from black lines to dashed lines in the left column of Fig. 2) leads to a change in the intercept, but not slope, of relationships between temperature and mass-corrected instantaneous growth rate (Fig. 2a) and population biomass (Fig. 2b). Thus, ecosystems with a greater supply of energy or carbon are predicted to support higher levels of population secondary production, but this production is still expected to be temperature-invariant (Fig. 2c).

Box 1 Metabolic scaling equations (Brown *et al.*, 2004) that predict effects of temperature on population abundance (N), population biomass (B), mass-specific growth rates (g), and population-level secondary production (P).

$N = M^{-0.75}e^{E/kT}$	Equilibrium population abundance (N) scales negatively with average body size (M) and temperature.
$B = M^{-0.75}e^{E/kT} \times M^1 = M^{0.25}e^{E/kT}$	Equilibrium population biomass (B) is equivalent to abundance times the average body size. B scales positively with M and negatively with temperature.
$g = M^{-0.25}e^{-E/kT}$	Mass-specific growth rate (g) scales negatively with body size and positively with temperature. This is equivalent to the scaling equation that describes biomass turnover rate of a population.
$P = M^{0.25}e^{E/kT} \times M^{-0.25}e^{-E/kT} = M^0$ 	<p>Secondary production is the product of biomass and mass-specific growth, or, similarly, the product of biomass and production:biomass ratio. This theory predicts temperature invariance of secondary production (solid line).</p> <p>'a' represents a predicted increase in secondary production of energy-limited consumers in response to a temperature-driven increase in resource quantity (see Figure 2d).</p> <p>'b' represents a predicted decrease in secondary production of nutrient limited consumers if resource quality declines (increased C:nutrient) as a function of temperature (see Figure 2h).</p>

In contrast, now consider an energy- or carbon-replete scenario in which the relative abundance of other resources (e.g. phosphorus) limits organism growth rates (Fig. 2, right column). This is analogous to habitats or ecosystems with resource C : nutrient ratios that exceed the TERs of most consumer taxa (i.e. to the right of dashed lines in Fig. 1). Here, we expect to find interactive effects of temperature and nutrient supply (as measured, e.g. in P content [or C : P ratios] of food resources) on mass-specific growth rates, population biomass, and secondary production. Specifically, a linear change in nutrient supply is predicted to have larger effects on individual growth rates and other population-level characteristics at warm vs. cold temperatures (Fig. 2e, f), consistent with recent empirical studies (e.g. Persson *et al.*, 2011; Kendrick & Benstead, 2013). As a consequence, secondary production is predicted to decline

with temperature in an energy-sufficient, but nutrient-poor, world (Fig. 2g).

While the above scenarios incorporate characteristics of resource supply, they do not yet deal with the possibility that resources may change *as a direct function of temperature*, as outlined in hypothesis three of the 'individual-level' section above. Thus, we need to consider how our predictions might be modified if we allow temperature to alter the quantity and quality of basal resources (Fig. 1d). If we incorporate evidence that net primary (or ecosystem) production increases with temperature (Yvon-Durocher *et al.*, 2010a; Demars *et al.*, 2011; *but see* Kerkhoff *et al.*, 2005), and assume that consumers are energy-limited, we predict a positive effect of temperature on secondary production (open circles in Fig. 2d). In contrast, if we assume that temperature leads to reduced nutrient content of basal resources

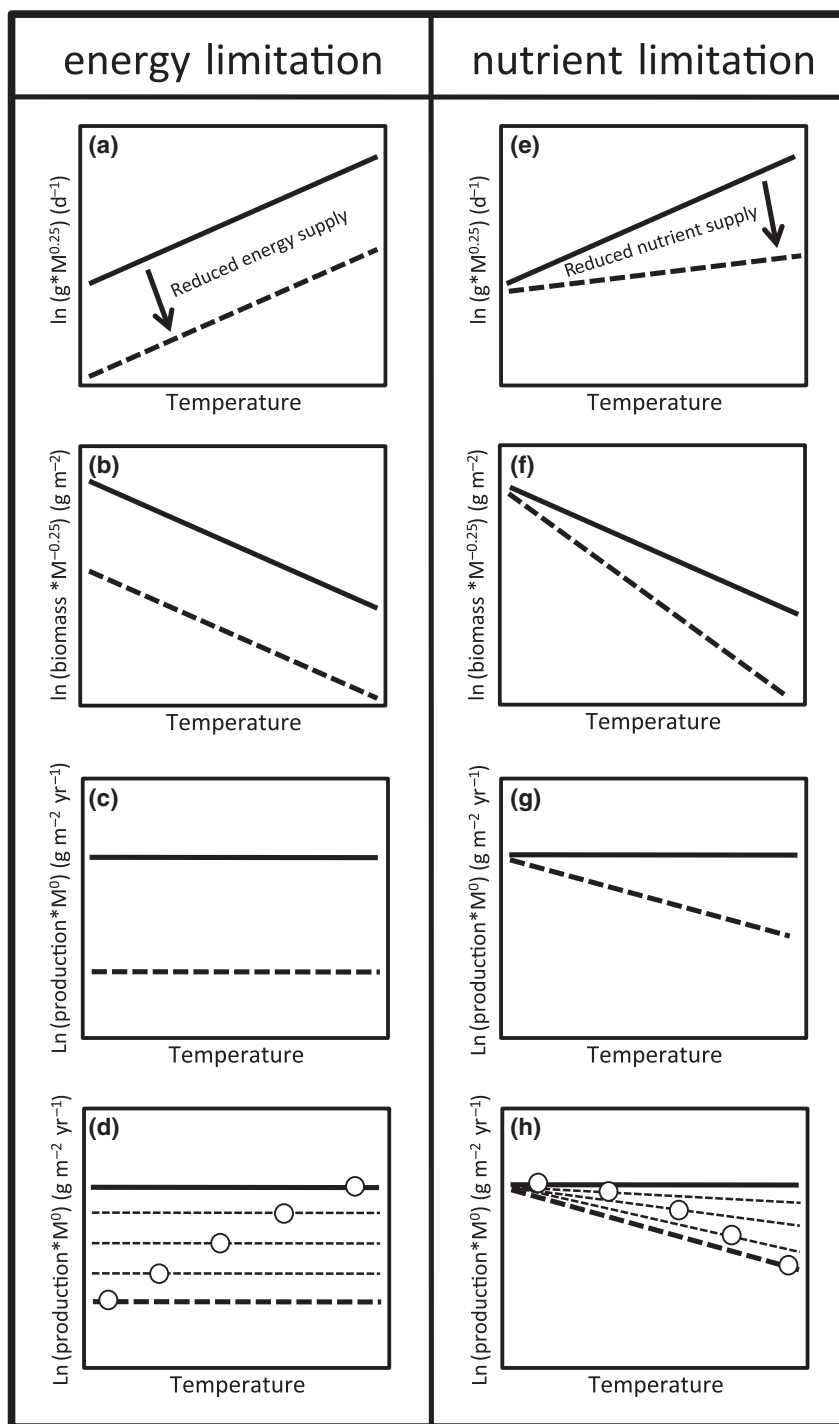


Fig. 2 Predicted interactive effects of temperature and food quantity (i.e. energy; left column) or food quality (i.e. N or P; right column) on consumer mass-specific growth rates (a, e), population biomass (b, f), and secondary production (c, g). Bottom panels depict predicted changes in secondary production (open circles) if resource quantity increases with temperature (d) and resource quality decreases with temperature (h).

(Woods *et al.*, 2003; De Senerpont Domis *et al.*, 2014), and consumers are nutrient-limited, we would predict a negative effect of temperature on secondary production (open circles in Fig. 2h). There are, of

course, many alternative scenarios for how temperature may alter resource quantity and quality, but this heuristic exercise provides a starting point for predicting how population-level secondary produc-

tion may respond to changes in both temperature and resource supply. This exercise also highlights a general need to assess the relative importance of energy vs. nutrient limitation among diverse consumers in nature (e.g. Frost *et al.*, 2006; Hessen *et al.*, 2013), a topic about which there is still considerable uncertainty.

Material flux through food webs

The conceptual predictions in the preceding section help lay the groundwork for understanding how temperature and nutrient supply might interact to affect material flux through food webs. Our focus on secondary production is germane to this effort because it is a flux (i.e. amount per area per time) and can be used to estimate the quantity and quality of resources needed to fuel this flux (Benke & Wallace, 1997; Cross *et al.*, 2007). Three factors are particularly important for estimating changes in material flux through food webs, including (i) secondary production, (ii) diet composition and elemental content, and (iii) gross and net growth efficiencies of ingested resources (Benke & Wallace, 1980; Sterner & Elser, 2002; Cross *et al.*, 2007). Based on our predictions above, warming should lead to increased production of energy-limited taxa and reduced production of nutrient-limited taxa, essentially favoring taxa with high TERs and low nutrient requirements (e.g. Fig. 1b). Because these taxa tend to have low body nutrient content and low carbon gross growth efficiencies (Frost *et al.*, 2006), elevated production of these taxa should lead to higher fluxes and turnover of carbon and energy relative to nutrients (i.e. N and P). In essence, we might expect the C : nutrient ratio of element flux through food webs to increase with warming, with the absolute amounts of material flux determined by the magnitude of warming and consequent effects on the resource base. These predictions provide a starting point for future investigations and would require some modification when dealing with differences in external nutrient supply (i.e. eutrophic vs. oligotrophic systems).

Ecosystem-level interactions between temperature and nutrients

Ecosystem-level processes are the sum of myriad biochemical reactions occurring in the trillions of cells embedded within biotic communities. From such a perspective, ecosystems can be perceived as 'meta-metabolomes' (Allen & Gillooly, 2009; Okie, 2012), the activity of which will be controlled, at least in part, by interactions between temperature and nutrient availability. In this section, we build on the theory laid out above for lower levels of ecological organization to

infer the consequences of potential interactions between temperature and resource stoichiometry at the level of entire ecosystems. We begin by considering how the activation energies of cellular processes scale up to higher levels, including how and why observed activation energies at the ecosystem level often diverge from their canonical values (Davidson & Janssens, 2006; Anderson-Teixeira & Vitousek, 2012).

Ecosystem-level activation energies

Just as the activation energy of organismal respiration reflects the average activation energies of the various reactions in the respiratory complex, so the activation energy of an ecosystem-level process should integrate the summed activity of all the contributing organisms (e.g. Allen *et al.*, 2005). Recent work has shown that intrinsic activation energies of cellular processes (e.g. photosynthesis and respiration) can predict the temperature dependences of ecosystem-level responses and hence their responses to warming (e.g. Yvon-Durocher *et al.*, 2010a, 2012). In addition, relative availability of resources (e.g. nutrients) can drive variation in the value of the intercept of the temperature dependence relationship, through effects on community biomass (Perkins

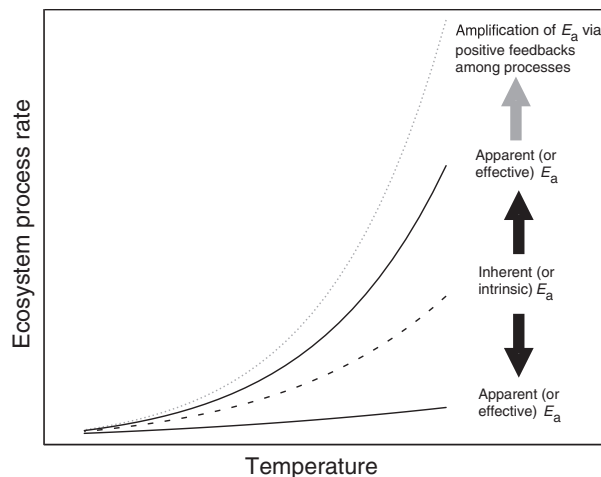


Fig. 3 Schematic plot showing how the activation energy (E_a) of an ecosystem-level process can deviate from its inherent or intrinsic value at the level of a cell or individual (dashed line). For example, the apparent or effective 'activation energy' (ε) of ecosystem respiration can be lower than 0.65 eV because of substrate or nutrient limitation, acclimation, changes in microbial abundance, or seasonal phenology (lower solid line). ε can also be higher than E_a if the abundance of resources or biological units covaries positively with temperature (upper solid line). Finally, the activation energy of a complex multiplicative process, such as ecological succession, can be greatly amplified via positive feedbacks among the various contributing processes (dotted line) (*also see* Anderson-Teixeira & Vitousek, 2012).

et al., 2012). However, true interactions between temperature and nutrients should result in changes in the slope of the temperature dependence relationship. While the sensitivity of respiration to seasonal changes in temperature displays the canonical activation energy of 0.65 eV across sites in all ecosystem types (Yvon-Durocher *et al.*, 2012), deviations from this value occur at individual sites. Such deviations may be observed if the supply of a limiting resource covaries with temperature, driving divergence between intrinsic activation energies and those that are actually observed (i.e. 'apparent' or 'effective' activation energies, ϵ ; Davidson & Janssens, 2006; Anderson-Teixeira & Vitousek, 2012; Fig. 3). Site-specific deviations in the temperature dependence of ecosystem-level processes from values expected from subcellular and individual rates occur for a number of reasons. Two recent examples from stream ecosystems include supply rates of detritus covarying inversely with temperature (Valett *et al.*, 2008) and extreme seasonality in light availability combining with relatively stable temperatures in an arctic spring-stream (Huryn *et al.*, 2014). In both cases, covariation in the supply of a limiting resource with temperature complicated predictions based on canonical temperature dependence. Further consideration of resource supply and quality in driving patterns of ecosystem-level activation energies should help explain such divergence from expected temperature dependences and so strengthen prediction of responses to variation in temperature.

Modeling temperature–nutrient interactions in ecosystem processes

Varying availability of limiting nutrients could also result in temperature dependences of ecosystem processes (e.g. gross primary production, respiration, denitrification) that deviate from canonical values (see Fig. 3). The current challenge is how to represent such interactions between temperature and relative resource supply in ecological theory, as it guides and is informed by empirical research.

There are at least two recent models that deal with this problem, but in slightly different ways. Both start by allowing temperature to set the maximum rate of an ecosystem process (V_{\max}) using the Arrhenius–Boltzmann factor:

$$V_{\max} = b_0 e^{-E_a/kT}, \quad (8)$$

an expression analogous to Eqn (2) that describes the temperature dependence of individual growth. These two recent models differ slightly in how they deal with the influence of resource availability (i.e. $f(R)$) on ecosystem processes (V). Anderson-Teixeira *et al.* (2008)

presented a model describing the influence of temperature and limiting 'reactants' on the rate of terrestrial primary succession:

$$V = V_{\max} [R_1]^{m_1} [R_2]^{m_2}, \quad (9)$$

where $[R_1]$ and $[R_2]$ are the concentration of potentially limiting reactants, while m_1 and m_2 define the relationship between V and $[R_1]$ and $[R_2]$, respectively. The strength of this approach is that it is a basic rate law expression borrowed from chemical kinetics theory that can be applied to a wide range of 'reactants' at the ecosystem level, including nitrogen and phosphorus, as well as structures that contribute to resource availability, such as leaf and soil biomass and concentrations of key enzymes. As the identity of these reactants varies widely, the relationships between $[R]$ and V can be modeled using a variety of forms: linear ($m = 1$), nonlinear increase ($m > 1$), and saturating ($m < 1$).

Others have developed similar models aimed at representing mechanisms that clearly relate substrate availability and enzyme kinetics to rates of ecosystem processes. For instance, Davidson *et al.* (2012) modeled the influence of temperature and multiple resources on soil respiration using a new Dual Arrhenius and Michaelis–Menten (DAMM) kinetics model. This model combines the Arrhenius expression (Eqn 8) with coupled Michaelis–Menten equations to link the effects of temperature with relative resource supply:

$$V = V_{\max} \times \frac{[S_1]}{kM_{S_1} + [S_1]} \times \frac{[S_2]}{kM_{S_2} + [S_2]}, \quad (10)$$

where S_1 and S_2 are concentrations of two potentially limiting resources (e.g. N and P), and kM_{S_1} and kM_{S_2} are their corresponding Michaelis–Menten half-saturation constants.

Although these models seem fairly different, they are actually quite similar in form. Both use an Arrhenius–Boltzmann factor and a multiplicative relationship between multiple resources and temperature. Importantly, the parameters in both models (e.g. m_1 and kM_{S_1}) cannot be predicted from the stoichiometry of the respective reaction and must be assumed (Anderson-Teixeira *et al.*, 2008), measured experimentally, or modeled (Davidson *et al.*, 2012). Note that the basic version of these models also assumes no true interaction effects, yet both can easily incorporate such interactions by relating the key parameters (i.e. m or kM_s) to temperature (see Davidson *et al.*, 2012; German *et al.*, 2012). Such work could advance theory by explicitly incorporating nutrient supply–temperature interactions into predictions based on metabolic theory. The potential for such interactions becomes particularly important when the supply rate of a limiting element may vary systematically with temperature, implying a true syn-

ergy between temperature and the balance of elements involved in ecosystem-level processes (Anderson-Teixeira *et al.*, 2008, Welter *et al.*, in press).

Temperature–stoichiometry interactions and ecosystem-level nutrient uptake

As described above, autotrophs can show considerable variation in C : nutrient ratios as a function of temperature, implying strong variation in their nutrient-use efficiency (NUE; Rhee & Gotham, 1981; Vitousek, 1982; Cross *et al.*, 2005). How might temperature-driven shifts in biomass composition and NUE affect ecosystem-level nutrient uptake? Both laboratory and field studies suggest that nutrient content of autotrophs may decline with increased temperature at fixed concentrations of limiting nutrients (Rhee & Gotham, 1981; Sardans *et al.*, 2012; De Senerpont Domis *et al.*, 2014). Thus, net primary production (NPP) rates can increase with temperature (within some range) independent of nutrient availability. Such responses should have important consequences for ecosystem-level nutrient uptake by autotrophs. In essence, autotrophs should use nutrients more efficiently as temperatures increase, and the magnitude of this change should depend on physiological effects of temperature on species-level nutrient demand, as well as the degree to which communities shift toward taxa with high NUE. Regardless of the mechanism, we might expect both total nutrient uptake and NUE to increase with temperature, so that the amount of limiting nutrient taken up per unit C biomass declines (i.e. nutrient uptake rates will not increase as steeply as NPP with increasing temperature). Such a pattern would be manifested as a lower activation energy for nutrient uptake than that observed for NPP, with the discrepancy between the two explained largely by changes in the C : nutrient stoichiometry (and demand) of autotroph biomass. Although suitable data likely exist, we are not aware of any explicit tests of this prediction.

Nutrient cycling by heterotrophic microbes often dominates at the ecosystem level (Wetzel, 2001; Chapin *et al.*, 2012). How might their responses to temperature differ from those of autotrophs outlined above? First, we might expect nutrient uptake by heterotrophic microbes to increase more rapidly with temperature (assuming no resource limitation), driven by the higher activation energy of heterotrophic metabolism relative to that of GPP (Allen *et al.*, 2005). The scaling of this increase in heterotrophic nutrient uptake depends on two factors: how microbial growth efficiency changes with temperature, and whether heterotrophic microbes are flexible with respect to nutrient content. If microbial growth

efficiency declines with temperature, as shown in some, but not all, studies (*see* Manzoni *et al.*, 2012), the temperature dependence of bacterial production should be less pronounced than that of respiration (i.e. <0.65 eV). Although relatively inflexible elemental content is common among metazoans (Sterner & Elser, 2002), the situation for microbes is still in question. Some studies suggest rigid cell quotas of N and P (Makino *et al.*, 2003; Cleveland & Liptzin, 2007), while others have found more variation (Cotner *et al.*, 2010; Scott *et al.*, 2012). Even fewer data are available for the responses of microbial cell quotas to temperature, although Woods *et al.* (2003) provide evidence that P (but not N) declines with temperature in several bacterial taxa. If heterotrophic microbes exhibit variable nutrient cell quotas, we can expect their nutrient uptake to show patterns of temperature dependence that deviate from production in a manner similar to that of autotrophs. Conversely, relatively fixed elemental content would drive the activation energy of heterotrophic uptake toward that of microbial production.

Temperature, stoichiometry, and mineralization

We now 'close the loop' by considering pathways along which temperature and nutrient availability may interact as organic matter is broken down and mineralized (e.g. Ferreira & Chauvet, 2011). In one such interaction, organic matter quality is known to affect the temperature sensitivity of microbial decomposition, with more refractory organic matter showing higher sensitivity to temperature (Bosatta & Ågren, 1999; Conant *et al.*, 2008; Wetterstedt *et al.*, 2010; Jankowski *et al.* 2014). Decomposition is mediated by enzyme kinetics and organic matter quality can therefore be defined as the number of enzymatic steps necessary to release carbon as CO₂ from organic substrates (Fierer *et al.*, 2005). This definition of organic matter quality is explicitly related to first principles of thermodynamics and explains the increase in decomposition rate with increasing quality (i.e. lower lignin concentrations, lower C : nutrient ratios, and a lower number of steps). Those compounds that require more steps to release carbon are typically of lower quality (i.e. higher lignin concentrations, higher C : nutrient ratios). Hence, the 'carbon quality–temperature hypothesis' (Fierer *et al.*, 2005; Craine *et al.*, 2010) states that the decomposition of recalcitrant organic matter is more sensitive to changes in temperature than that of labile organic matter due to differences in the activation energies of the enzymatic reactions required for its decomposition. The enzymatic reactions required to degrade more complex, recalcitrant substrates should have a higher activation energy than those reactions

that break down simpler, more labile substrates due to the increased number of steps required. The increased sensitivity of relatively stable organic matter stocks to temperature may have profound effects on the global carbon cycle, with possible feedbacks to climate change (Davidson & Janssens, 2006; Luo, 2007; Conant *et al.*, 2011).

The enzymatic foundation of decomposition has also formed the basis for explicit attempts to integrate the effects of temperature and nutrient supply : demand ratios. Ecoenzymes (i.e. extracellular enzymes) and their relative activity link metabolic theory and ES because their production is both derived from cellular metabolism and regulated by environmental nutrient supply relative to cellular demand. Robert Sinsabaugh *et al.* have developed an approach that uses ratios of different nutrient-yielding ecoenzymes and the temperature dependence of metabolic activity to link microbial demand for elements with environmental supply and so scale the use of different microbial resources across temperatures (e.g. Sinsabaugh & Follstad Shah, 2010, 2012). Ecoenzyme ratios also offer an empirical approach to calculating TERs for microbial consortia, as activity of enzymes that catalyze major environmental sources of C, N, and P can be measured relatively easily. The application of ecoenzyme kinetics is obviously limited to studying the activity of heterotrophic microbes and other osmotrophs. Nevertheless, this approach is capable of integrating microbial use of multiple resources across temperature gradients and therefore represents a bold attempt to unite the fields of metabolic theory and ES.

Consideration of acclimation and adaptation

Our synthesis has implicitly focused on organism and ecosystem responses that play out over relatively short time scales. However, it is well known that species may acclimate or adapt to shifting conditions of temperature and nutrient supply (e.g. Angilletta, 2009), and such changes may be critical for determining how individuals respond to various environmental constraints. For instance, Frisch *et al.* (2014) recently showed that the NUE of some freshwater *Daphnia* has evolved in response to cultural eutrophication (Frisch *et al.*, 2014). There has also been exciting recent discussion about whether thermal adaptation of bacteria may influence soil carbon cycling, with far-reaching consequences for carbon-cycle climate feedbacks (e.g. Bradford, 2013). Although these adaptive responses are outside the scope of our synthesis, consideration of such dynamics will be necessary if we hope to develop a comprehensive and predictive framework.

Concluding remarks

Climate warming and changes in nutrient supply are two of the most prominent anthropogenic drivers of global change. These factors also play fundamental roles in determining how, and at what rate, organisms acquire, store, and cycle key elements. It is thus imperative that we develop a strong basis for understanding how these factors combine to influence the structure and function of ecosystems globally. We have argued that ME (Sibly *et al.*, 2012) and ES (Stern & Elser, 2002) can provide a core foundation for making progress on this front, but there is clearly much work to be done. Our primary goal was to provide a conceptual basis for examining true interactions between temperature and nutrients at multiple levels of organization, recognizing that most of what we know is based on one-way analyses of either temperature or nutrients alone. It is our hope that the ideas presented herein will help to catalyze additional research and synthesis in the critical area of understanding how global change drivers interact to affect ecological processes.

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