LETTER

ECOLOGY LETTERS cnrs WILEY

Interactions between temperature and nutrients determine the population dynamics of primary producers

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Funding information
Yale Center for Natural Carbon Capture; Natural Sciences and Engineering Research Council of Canada

Editor: Roberto Salguero-Gomez

Abstract

Global change is rapidly and fundamentally altering many of the processes regulating the flux of energy throughout ecosystems, and although researchers now understand the effect of temperature on key rates (such as aquatic primary productivity), the theoretical foundation needed to generate forecasts of biomass dynamics and extinction risk remains underdeveloped. We develop new theory that describes the interconnected effects of nutrients and temperature on phytoplankton populations and show that the thermal response of equilibrium biomass (i.e. carrying capacity) always peaks at a lower temperature than for productivity (i.e. growth rate). This mismatch is driven by differences in the thermal responses of growth, death, and per-capita impact on the nutrient pool, making our results highly general and applicable to widely used population models beyond phytoplankton. We further show that non-equilibrium dynamics depend on the pace of environmental change relative to underlying vital rates and that populations respond to variable environments differently at high versus low temperatures due to thermal asymmetries.

KEYWORDS
carrying capacity, Droop model, nutrient limitation, phytoplankton, population dynamics, theoretical ecology, thermal performance

INTRODUCTION

Within the ecological hierarchy, populations lie at the interface between abiotic environments and biotic community dynamics, integrating and coupling various responses to environmental change. Despite this, our current theoretical understanding of population resilience under multiple simultaneous environmental changes limits our ability to forecast population dynamics in today's changing, and increasingly variable, world. The multitude of rapidly changing environmental conditions is effectively altering multiple niche axes at once, creating novel environments and highlighting the importance of understanding the interaction between multiple 'stressors' (Doney et al., 2012; Steffen et al., 2015; van Moorsel et al., 2023).

Thermal responses of vital rates regulate population performance or fitness (i.e. growth rates), but researchers are beginning to understand the interactive nature of multiple stressors for population-level processes. For example, temperature and resource limitation have an interactive effect on population performance such that

a species' optimal temperatures for growth and the critical limits of its thermal niche are functions of resource availability—meaning populations are more sensitive to increasing temperature when resources are limited (Bestion et al., 2018; Huey & Kingsolver, 2019; Thomas et al., 2017; Vinton & Vasseur, 2022). While thermal performance curves relate directly to population rates of change under idealized (i.e. density-independent) conditions, it is less clear how this interaction translates to population-dynamic processes such as the thermal response of biomass and long-term population persistence. We therefore lack a mechanistic understanding of how processes regulating the density or resource dependence of populations are mediated by temperature. Similarly, it remains to be seen how environmental variability along multiple niche axes will alter these population responses. Indeed, environmental variability can have drastically different effects on population performance beyond those due to changes in the mean environment (Bernhardt, Sunday, Thompson, et al., 2018; Slein et al., 2023; Vasseur et al., 2014).

Understanding trends in population biomass is essential for population forecasting and management. For example, population decline is the key element used to determine a species' extinction risk (e.g. IUCN status), and biomass is central to dictating the flow of energy throughout food webs and whole ecosystems (i.e. energy flux and carbon or nutrient cycling via numerical responses). Empirically, the thermal dependence of population biomass (i.e. its equilibrium or carrying capacity) is somewhat ambiguous, with evidence ranging from invariant (Jarvis et al., 2016) to negative (Bernhardt, Sunday, & O'Connor, 2018; Fussmann et al., 2014) relationships, while theoretically a variety of nonlinear relationships have been suggested (Amarasekare, 2015; Lemoine, 2019; Savage et al., 2004; Uszko et al., 2017; Vasseur, 2020). One suggestion is that carrying capacity ought to follow a unimodal relationship with temperature, and be modified by resource availability given density- and temperature-dependent birth and death rates (Vasseur, 2020; Vinton & Vasseur, 2022); however, empirical evidence for this is still lacking. Despite the theoretical basis describing how a population's equilibrium (i.e. carrying capacity) ought to respond to multiple stressors (Vinton & Vasseur, 2022), population dynamics involve nonlinearities that make equilibrium behaviour just the starting point for forecasting responses to variable environments (Hastings et al., 2018). Under the rapid pace of global change, how populations will track changes in the mean and variance of the environment remains to be seen, as vital rates and underlying equilibria may be changing simultaneously.

Effective population forecasting in a time of global change requires an integration of mechanistic organismal research and efficient, generalizable theory. In this paper, we begin to do so by integrating recent empirical insights on the thermal dependence of various vital rates for phytoplankton growth within a generalizable framework for population dynamics under limiting nutrients. As the base of all aquatic food webs and a vital element of global carbon cycles, phytoplankton have critical functional importance and have become the hallmark for studying both metabolic/thermal ecology and for experimentally testing theoretical predictions, making them an excellent starting point for developing a mechanistically informed general theory. We use a nutrient- and temperature-dependent Droop model (Droop, 1974, 1977; Lemoine, 2019; Sauterey & Ward, 2022), to explore how temperature and nutrient limitation collectively impact populations in both constant and variable thermal environments. This model is well equipped to understand limiting factors for population growth and biomass accrual, as it separates the rates of nutrient uptake and assimilation via a dynamic cellular nutrient quota—both rates that are now known to be differentially regulated by temperature and can generate thermally dependent bottlenecks at different stages of population growth (Lemoine, 2019; Anderson et al., unpublished).

This framework allows for a mechanistic understanding of the interactive effects of temperature and nutrients on phytoplankton growth and complex population dynamics. Furthermore, exploring patterns in equilibrium biomass (e.g. population carrying capacity) as an emergent property of underlying processes provides mechanistic insight into the thermal dependence of carrying capacity in more general models.

This research provides insight into phytoplankton dynamics under global change, including non-equilibrium (e.g. transient, seasonal) dynamics in lakes and marine systems, with implications for whole ecosystem functioning and global carbon cycling. Simultaneously, our combination of analytical and numerical approaches allows us to make generalizable conclusions consistent with phenomenological modelling approaches. As such, our insights also motivate the inclusion of more realistic environmental context into general population models.

METHODS

Model description

To explore the interaction between nutrient availability and temperature on population growth, biomass, and dynamics, we incorporate the role of temperature (T) following recent adaptations to the Droop model framework (Droop, 1974, 1977; Lemoine, 2019) (Figure 1). We use a three-dimensional system of ordinary differential equations to describe the coupled dynamics of nutrient (N) availability, intracellular nutrient flux via a dynamic quota (Q) and population biomass (B) (Box 1). This model assumes a single limiting nutrient (e.g. phosphorus or nitrogen)—but we retain the use of 'nutrient' throughout since our model is general and does not incorporate parameters that are specific to a particular limiting nutrient. Nutrient uptake and assimilation are separated into two different processes, each temperature-dependent following empirical evidence (Lemoine, 2019), with the difference between the two determining dynamic intracellular nutrient accumulation in the quota (Figure 1). This more accurately accounts for nutrient effects on phytoplankton growth when not at a steady state (Droop, 1977), allowing us to explore non-equilibrium dynamics while retaining the analytical tractability of equilibrium solutions of more simple models (Cunningham & Nisbet, 1980; Grover, 1992; Smith & Waltman, 1994). In this model, nutrient drawdown and biomass accrual are largely regulated by nutrient accessibility: the availability and uptake of nutrients. Broadly, the quota regulates the total flux from resource (nutrients) to biomass and is determined by the balance between density- (and temperature-) dependent uptake and assimilation rates, as well as the available external nutrient pool (Box 1). Nutrient assimilation determines the rate at which stored nutrients (via Q) are converted
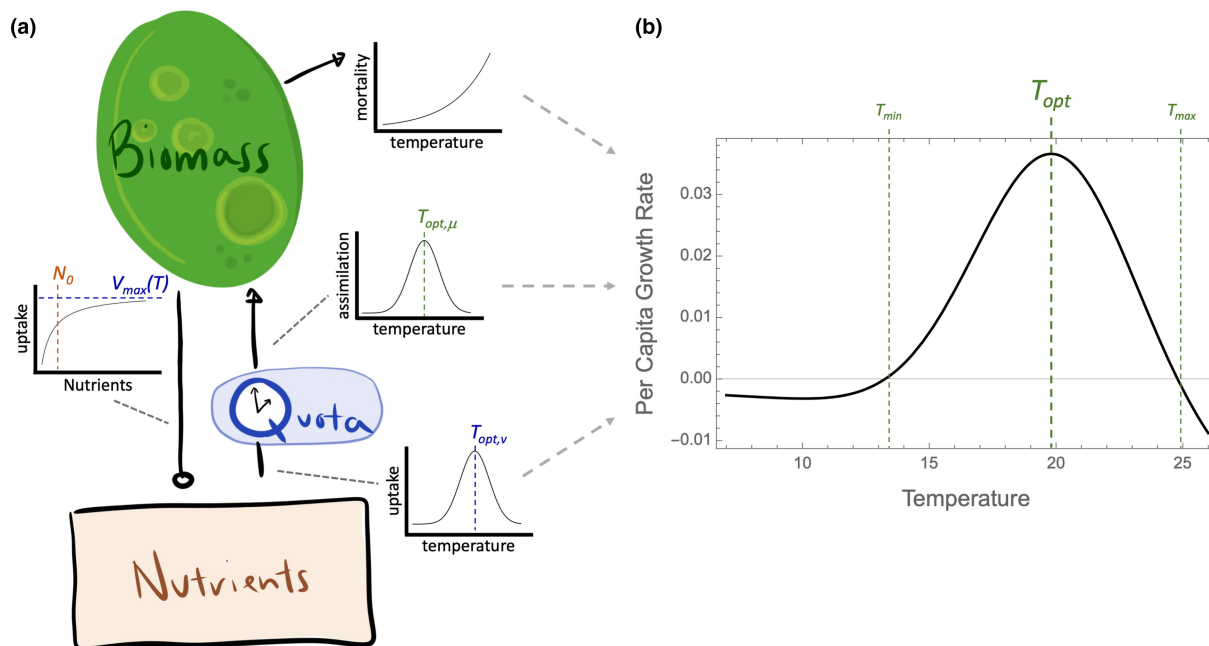
FIGURE 1 (a) Schematic showing model state variables and temperature dependence of various rates. Here, the inclusion of the nutrient quota splits uptake and assimilation into two separate temperature- (and density-) dependent processes and therefore acts to create a lag in the conversion of nutrients into biomass. The upward arrow indicates conversion of nutrients into biomass (via the intracellular nutrient quota). The rate of nutrient uptake (negative interaction, open circle) follows a saturating function of nutrient concentration. (b) Collectively, these temperature-dependent rates define a population's thermal performance curve (TPC), which is defined as the per-capita rate of growth at near-zero densities (i.e. non-limiting nutrients).

into biomass, such that growth is scaled relative to some minimum level required for positive assimilation. This can create a lag in population biomass responses to changing environmental conditions. Model equations and thermal responses are described in Box 1.

Model analyses

While the parameterization we use is loosely based on empirical measurements, the qualitative relationships between variables give us insight into phytoplankton growth and population dynamics in general, making our analytical approaches and resulting conclusions generalizable. When not explicitly stated or varied for analytical/simulation purposes, the following parameters were used: $T_{opt,v} = 20$, $T_{opt,\mu} = 20$, $\sigma_v = 3.25$, $\sigma_\mu = 3.25$, $v_0 = 0.0005$, $v_1 = 0.005$, $\mu_0 = 0.1$, $\mu_1 = 0.5$, $d_0 = 0.005$, $d_1 = 0.0012$, $d_2 = 0.1$, $Q_{min} = 0.1$, $N_0 = 0.5$, $N_{in} = 1$, and $D = 1$. This allows for population persistence across a reasonable thermal breadth, as shown in Figure 1b, and allows us to qualitatively explore the effects of varying multiple parameters on population persistence and dynamics relative to this baseline. Note that by setting D and N_{in} to 1, we normalize the inputs of the chemostat model and reduce its dimensionality. We then explore the role of nutrient limitation by varying the half-saturation constant, N_0 (uptake saturation), relative to the normalized parameters (as N_0 increases for a given nutrient concentration, N, growth is more limited by nutrients). Although some argue that N_0

and V_{max} may positively covary (Aksnes & Egge, 1991), we follow previous work that assumes they are independent (Thomas et al., 2017; Vasseur & McCann, 2005) to better isolate the effects of temperature-dependent uptake and so that we can independently vary uptake efficiency ($1/N_0$) as a tractable way of imposing nutrient limitation. Similarly, we follow other chemostat-based theory on biomass dynamics by assuming phytoplankton mortality is independent of the flow rate D, allowing us to better isolate the effects of temperature (León & Tumpson, 1975; Sauterey & Ward, 2022; Vinton & Vasseur, 2022). This approach will not alter general patterns in population dynamics relative to approaches that include D as a loss term since we retain an additional temperature-independent component of mortality (d_0).

While the individual rates used in this model are scaled by temperature and/or nutrient availability, we note that this format has not qualitatively changed the set of possible outcomes of the model (i.e. possibility of and qualitative stability properties of stable interior equilibrium). That is, since the model structure has not changed, the possible outcomes of our model are restricted to a set of well-understood phenomena (León & Tumpson, 1975; Sauterey & Ward, 2022; Vinton & Vasseur, 2022). Equilibrium solutions for all state variables are described in Appendix S1 (Equations A1–3), along with the isoclines depicting how temperature changes the general equilibrium structure (Figure A1). This model has two possible stable equilibrium states, depending on the availability of and ability to take up

BOX 1   Model equations and thermal performance curve

Model equations

Here, nutrient availability (N) is modelled as a chemostat, with nutrient uptake by phytoplankton (B) following a Type II functional response (Monod function), thus allowing for saturation in per-capita uptake:

$$\frac{dN}{dt} = D(N_{in} - N) - B\frac{V_{max}(T)N}{N + N_0}, \tag{1}$$

where N_0 is the half-saturation constant for nutrient uptake, D is the dilution rate, and N_{in} is the concentration of nutrients entering the system. $V_{max}(T)$ is the temperature-dependent maximum rate of nutrient uptake (moles of nutrient per unit of algal biomass per unit of time). Previous work has shown that V_{max} (or, more broadly, consumption when not distinguished from assimilation) is a unimodal function of temperature (Lemoine, 2019; Rhee & Gotham, 1981; also see Englund et al. (2011) for the meta-analysis) and following the work of (Amarasekare & Savage, 2012; Huey & Kingsolver, 2019; Thomas et al., 2017; Vinton & Vasseur, 2022), we define V_{max} as a normally distributed function of temperature around some optimal temperature for nutrient uptake, $T_{opt,v}$:

$$V_{max}(T) = v_0 + v_1 e^{-\left(\frac{(T - T_{opt,v})^2}{\beta_v}\right)}, \tag{2}$$

where β_v defines the breadth of the temperature response for uptake.

Within the cell, the intracellular nutrient quota, Q, is determined by the difference between temperature-dependent uptake and assimilation rates:

$$\frac{dQ}{dt} = \frac{V_{max}(T)N}{N + N_0} - \mu_\infty(T)(Q - Q_{min}), \tag{3}$$

where Q_{min} is the minimum nutrient quota (moles cell^{-1}) needed to maintain a positive assimilation rate and $\mu_\infty(T)$ is the temperature-dependent maximum rate of nutrient assimilation (time^{-1}), defined again as a normally distributed function of temperature around some optimal temperature for assimilation ($T_{opt,\mu}$), following Lemoine (2019):

$$\mu_\infty(T) = \mu_0 + \mu_1 e^{-\left(\frac{(T - T_{opt,\mu})^2}{\beta_\mu}\right)}, \tag{4}$$

where β_μ defines the breadth of the temperature response for assimilation. μ_∞ is so-named because it represents the rate of per-capita biomass growth that is achieved when the nutrient quota is infinitely large.

Biomass dynamics are thus described as:

$$\frac{dB}{dt} = B\left(\mu_\infty(T)\left(1 - \frac{Q_{min}}{Q}\right) - d(T)\right), \tag{5}$$

where B is the population biomass density (volume^{-1}; interchangeable with cell density since cell size is not considered in this model), and $d(T)$ is the temperature-dependent mortality rate (time^{-1}). Previous work has shown that mortality rates scale as Boltzmann–Arrhenius relationships (Brown et al., 2004; Gillooly et al., 2001; McCoy & Gillooly, 2008); however, similar to other theoretical work (Amarasekare, 2015; Vinton & Vasseur, 2022), we represent mortality as an exponential function of temperature to increase model tractability without losing much accuracy over biologically relevant temperature ranges:

$$d(T) = d_0 + d_1 e^{d_2 T}. \tag{6}$$

Together, these temperature-dependent rates define the population's thermal performance.

Integrating thermal responses into a thermal performance curve

We can derive the population's thermal performance curve (TPC), defining the per-capita growth rate (dB/Bdt) when nutrients are non-limiting. In this case, $N/(N + N_0) \rightarrow 1$ and the maximum equilibrium quota,

hereafter referred to as $Q_{\max}$, is reached. This maximum equilibrium value is obtained by simplifying Equation (3) and solving:

$$\frac{dQ}{dt} = 0 = V_{\max}(T) - \mu_\infty(T)\big(Q - Q_{\min}\big),\tag{7}$$

$$Q_{\max} = \frac{V_{max}(T)}{\mu_\infty(T)} + Q_{\min}.\tag{8}$$

Substituting this into Equation 5 yields the population's fundamental TPC:

$$\frac{dB}{Bdt} = \frac{V_{\max}(T)\,\mu_\infty(T)}{V_{\max}(T) + \mu_\infty(T)Q_{\min}} - d(T).\tag{9}$$

This curve represents a typical left-skewed unimodal function of temperature, with positive growth bounded by the lower and upper thermal limits, $T_{\min}$ and $T_{\max}$, defining the fundamental thermal niche and peaking at the temperature that maximizes growth (T_{opt}) (Figures 1 and 2). The first term of Equation 9 reflects the product of the two Gaussian functions $V_{\max}(T)$ and $\mu_\infty(T)$ and is therefore a symmetric, nearly Gaussian function of T (when $T_{opt,\mu} = T_{opt,v}$). Subsequently, subtracting $d(T)$ creates the classic skewed TPC shape (see Amarasekare & Savage, 2012; Vinton & Vasseur, 2022) and results in $T_{opt} < T_{opt,v}$ & $T_{opt,\mu}$ because of this differential.

Previous work has established that the optimum for thermal performance (here measured by the per-capita growth rate dB/Bdt) decreases under nutrient limitation due to the non-linearity of the two terms in Equation 9 (Thomas et al., 2017; Vinton & Vasseur, 2022). Under limiting nutrients, N cannot be factored out in the derivation of Equation (9) (though it retains the same general shape) and nutrient limitation therefore scales this curve. We demonstrate this result in Figure 2b by solving dB/Bdt (from Equation 5) for different levels of nutrient uptake half-saturation constant (N_0; indicating the efficiency of nutrient uptake, with the inverse being de-facto nutrient limitation), where N is held at the supply concentration ($N_{in}=1$) (i.e. the realized TPC). Eventually, nutrients become so limiting that the upper and lower limits of the thermal niche converge upon a single temperature; furthermore, nutrient limitation beyond this does not support population growth at any temperature.

nutrients, one with algae absent ($B=0$) and one with a positive biomass ($B>0$) (Figure 2) (Cunningham & Nisbet, 1980; Droop, 1977; Nisbet & Gurney, 1982). When $B>0$, the population always approaches the equilibrium monotonically and the model does not produce any complex (i.e. cyclic) dynamics. Given we know that if a positive equilibrium exists, it will be stable, changing parameters can (i) shift the boundaries of the thermal niche (i.e. $T_{\min}$ and $T_{\max}$ of the TPC), altering persistence at some temperatures; and (ii) if no change in persistence has occurred, cause quantitative changes in state variables but no change in qualitative stability. Therefore, certain parameters or assumptions about the thermal responses of various rates may modify specific outcomes (i.e. under changing temperature or nutrient conditions) within the set of possibilities defined by the underlying model structure. In this way, the qualitative nature of our results is general.

This equilibrium structure reflects the asymptotic behaviour of all simulations under static environmental conditions and simultaneously serves as a reference when environmental variability is incorporated. Therefore, we refer to all simulation results relative to underlying analytical solutions (i.e. the deterministic skeleton; Higgins

et al., 1997) to further emphasize the generality of our approach and results. Since the backbone of this model defining the range of possible outcomes has been previously well studied and remains unchanged in this iteration, we refrain from conducting a full-parameter sensitivity analysis and instead focus on the general nature of temperature and nutrient interactions within this overarching structure.

All analyses were done in Wolfram Mathematica v13.1. Numerical simulations were performed using Mathematica's NDSolve function with its automatic integration method. Simulations were run for sufficient time to reach an asymptotic state, which depended on the analysis being done (e.g. constant versus variable temperature and the time scale of temperature variation, if any).

To explore the effect of temperature variation, we modelled temperature using a sinusoidal function as follows:

$$T(t) = T_{\text{mean}} + A \times \sin(p2\pi\, t),\tag{10}$$

where T_{mean} is the average temperature, A represents the amplitude of temperature variation, and p is the frequency of forcing.

Equilibrium behaviour along a temperature gradient

We can determine the thermal and nutrient dependence of equilibrium biomass, which is akin to the carrying capacity in the logistic growth model—only here it is an emergent property of the model dynamics (rather than a parameter or input function). We find that temperature and nutrients have an interactive effect on equilibrium biomass that does not match the thermal performance curve (Figure 2). Although equilibrium biomass is a unimodal function of temperature with lower and upper bounds matching the TPC, it is maximized at temperatures below T_{opt}. The thermal response of equilibrium biomass, hereafter referred to as $K(T)$ or the *thermal biomass curve* (TBC), is skewed opposite to the TPC. The difference between these two temperature optima, which we denote T_r and T_K for optimal temperatures for growth (*r*) and biomass (*K*), respectively, is affected by the accessibility of nutrients.

Increasing the efficiency of nutrient uptake (i.e. decreasing N_0) effectively decreases nutrient limitation and alters both curves such that they become more dissimilar in shape and thermal optimum (Figure 2). When nutrients are replete, we see a linear relationship between temperature and biomass, aligned with predictions from the metabolic theory of ecology (Bernhardt, Sunday, & O'Connor, 2018; Brown et al., 2004). This upper limit sets a boundary for the maximum possible production given saturated nutrient uptake, with all dynamic possibilities contained within this region (a boundary that is interestingly similar to that derived by Loladze et al. (2000)). Here, as temperature increases, factors other than nutrient availability (e.g. mortality) contribute to a decline in potential production. Once nutrients become limiting, there becomes an interactive effect of nutrients and temperature that define the population's thermal niche and maximum production. As nutrients become more limiting, the TPC and TBC ultimately converge; at the very point where T_{min} and T_{max} intersect, T_r and T_K necessarily converge. Importantly, this result suggests that population productivity and biomass have different thermal responses that are mediated by nutrient limitation (Figure 2) and that equilibrium biomass is always optimized at seemingly sub-optimal temperatures, relative to the TPC. We will hereafter refer to this difference as *r–K* mismatch, or simply mismatch.

Although our model is specific to phytoplankton growth, it is interesting to note that mismatch between the TPC and TBC has been found in similar models where nutrient quotas were not included as a dynamic component (Vinton & Vasseur, 2022), suggesting that it is a general phenomenon generated by the interaction between temperature and nutrient (or, more broadly, resource) consumption and growth. In Appendix S1, we demonstrate the conditions under which our model can be simplified into a more general 2-equation system (analogous to Vinton and Vasseur's consumer-resource model) and show that biomass is always maximized at lower temperatures than productivity (i.e. $T_K < T_r$) because of relative differences in resource availability, per-capita consumption (i.e. density dependence), and mortality across the thermal niche, which together regulate the 'efficiency' of turning resources into biomass. Here, resource (nutrient) equilibrium densities follow a flat-bottomed U-shaped function of temperature, suggesting that while the resource equilibrium changes minimally over much of the thermal niche, the amount of consumers supported by it changes quite drastically (i.e. the B:N ratio in our model; Figure A2). In other words, each consumer requires less resources at lower temperatures because of lower metabolic requirements, meaning that for a given resource equilibrium, more consumers can be supported. The relationships identified here ought to be generally true in consumer-resource models that fit our two simplifying assumptions (e.g. the model used in Vinton & Vasseur, 2022; see Appendix S1).

While the thermally dependent nutrient quota in our full three-dimensional model adds some complexity, the general rules as identified in Appendix S1 remain. The quota indeed influences equilibrium biomass (see Appendix S1, Equation A8) by scaling the uptake/mortality ratios with temperature (Solution A9) and provides important mechanistic nuance for understanding growth dynamics specific to phytoplankton populations. Temperature and nutrients have an interactive effect on population biomass that is mediated by relative differences in uptake and mortality and regulated via the nutrient quota (Figures 1 and 2). This means that populations respond to changing temperatures (especially low temperatures) differently when nutrients are replete versus limiting. When nutrient uptake is saturated, growth occurs as soon as temperatures allow. This means that population biomass can be optimized at lower temperatures, where the equilibrium quota is larger (see Figure 2b for equilibria) and nutrients are efficiently turned into biomass without the large loss of biomass that would be caused by turnover at higher temperatures. Alternatively, when nutrients are limited, T_r and T_K begin to converge, the fundamental niche shrinks ($T_{max}–T_{min}$), and low-temperature rates of uptake and assimilation are not sufficient for high biomass. In this case, biomass is optimized at temperatures closer to where growth is optimized (i.e. T_r), yet at lower quantities due to increased turnover at these temperatures. Here, nutrients are rapidly converted into population biomass and then much of it lost to mortality.

Since biomass accrual directly depends on intracellular nutrient concentration, the quota represents the *potential* for biomass growth of a population and therefore ought to be important for non-equilibrium responses to variable environments. Population growth after any change in the environment will depend on (past) stored nutrients
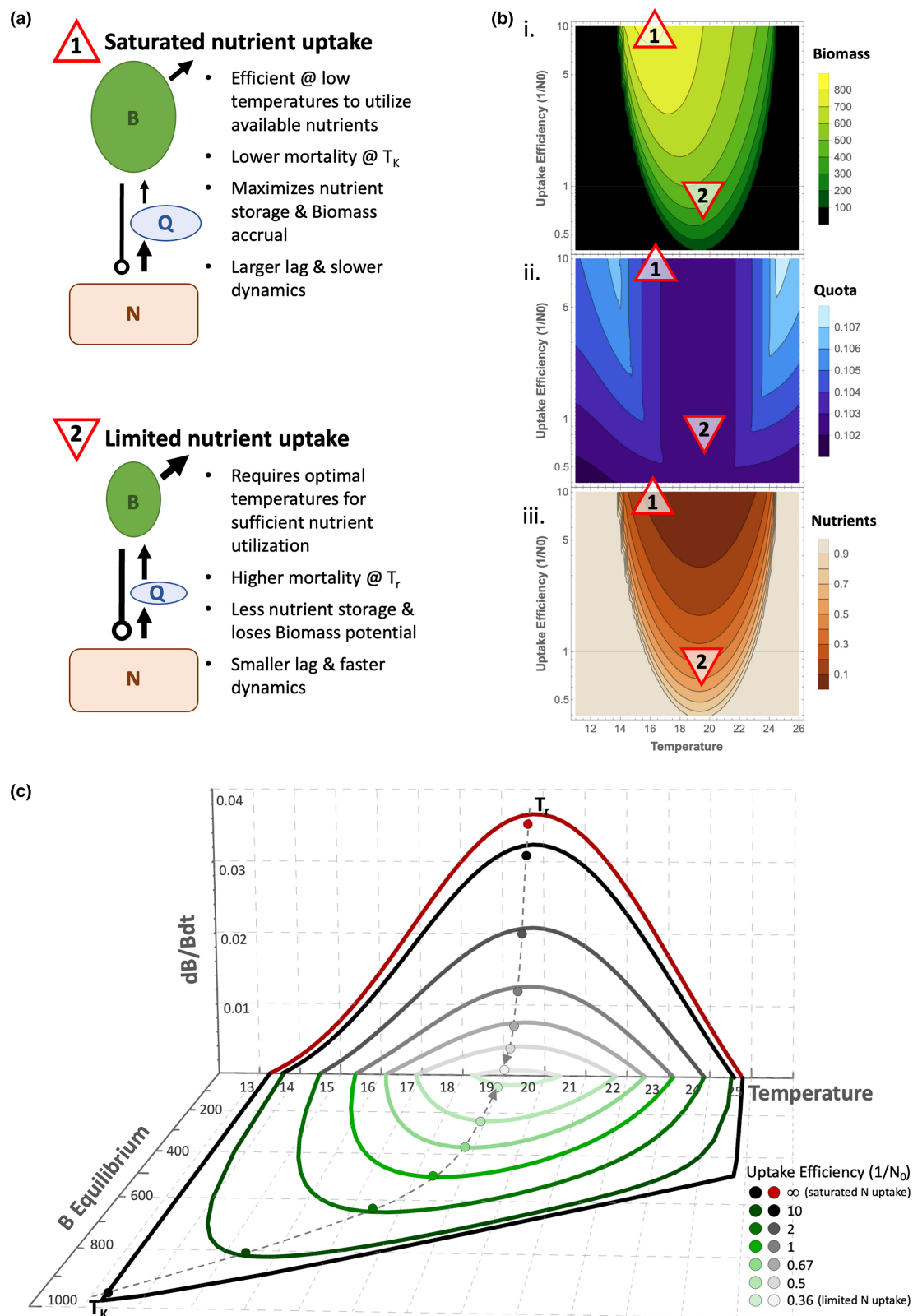
FIGURE 2 (a) Schematic showing the combined influence of nutrient uptake efficiency (defined as $1/N_0$, therefore describing the saturation of uptake) and temperature on various rates and thus the flux of converting nutrients to biomass under different environmental conditions; and (b) the corresponding nutrient, quota, and biomass equilibria across these two axes. (c) Thermal responses of productivity (i.e. the TPC; red line representing the fundamental TPC under infinite nutrients, and black-grey lines representing the realized TPC when $N = N_{in} = 1$) equilibrium biomass (green lines), at different levels of nutrient uptake efficiency ($1/N_0$). The temperature mismatch between the two temperature optima, T_r and T_K, for the TPC and equilibrium biomass (i.e. carrying capacity; K), respectively, decreases with nutrient limitation (see dashed arrows tracking optima). Here, N_0 is varied with line/point opacity reflecting limitation of nutrient uptake (higher uptake efficiency, $1/N_0$, effectively equates to saturating nutrients). From light to dark colouring: $N_0 = 0.1, 0.5, 1.0, 1.5, 2.0$.

and (current or future) ability to uptake new nutrients. The differential rates of growth and intracellular nutrient accumulation across the thermal niche thus become important in varying environments, such that both the nutrient storage ability (when assimilation rates are low) and implicit lag caused by the quota may act as buffering mechanisms for populations during stressful or harsh times. At low temperatures, for example, uptake and assimilation rates are lower, creating more lag through the quota and slower growth overall, whereas dynamics are faster (with less lag and stored nutrients through the quota) at higher temperatures. Collectively, the nutrient quota—or more accurately the lag associated with the quota—ought to drive differential dynamic responses to environmental change at high and low temperatures.
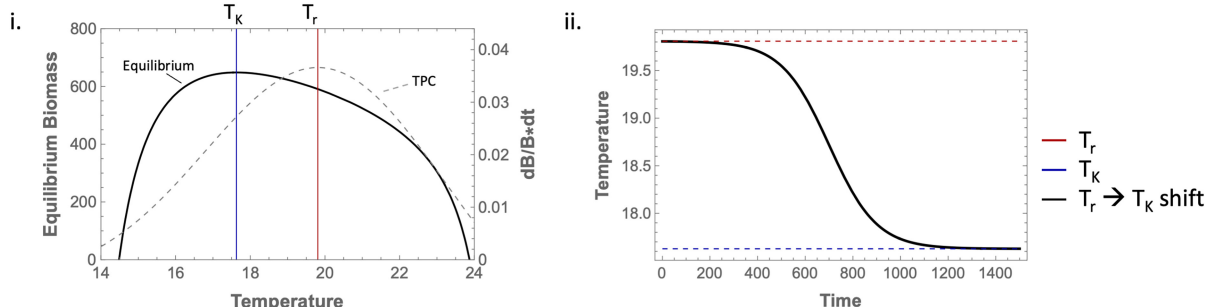
r–K mismatch and implications for transient dynamics

Together, vital rates and equilibrium biomass determine the eventual state of a population (i.e. the equilibrium) and how long it takes to get there (i.e. transient length or return time). Optimal temperatures for growth will result in short transients and therefore the fastest approach to equilibrium; however, this equilibrium is not the maximum possible across the thermal niche. Alternatively, lower temperatures near T_K will allow for higher biomass but take much longer to get there due to slower rates. The fact that temperature cannot optimize both performance (growth) and biomass (production) has implications for population trajectories under climate change and for effective management strategies.

This also suggests the possibility that certain forms of temperature change may facilitate both optimal growth and biomass. In classical population models (e.g. the logistic), r and K have an interesting relationship during dynamic population growth where the impact of r on dynamics is large when biomass is low, but weak when near K. Our model elucidates growth and biomass dynamics for phytoplankton populations more mechanistically than the logistic model, but follows the same principles. T_r maximizes population growth at near-0 biomass densities, but as biomass grows and resources become more depleted, it becomes more beneficial to be near T_K where the efficiency of conversion from nutrients to biomass is maximized and turnover is low. Indeed, we can see that T_r and T_K result in different equilibria and transient lengths, but when properly timed, a transition between the two temperatures ($T_r \rightarrow T_K$ shift) can maximize both the rate of population increase and eventual biomass obtained (Figure 3). These differential responses
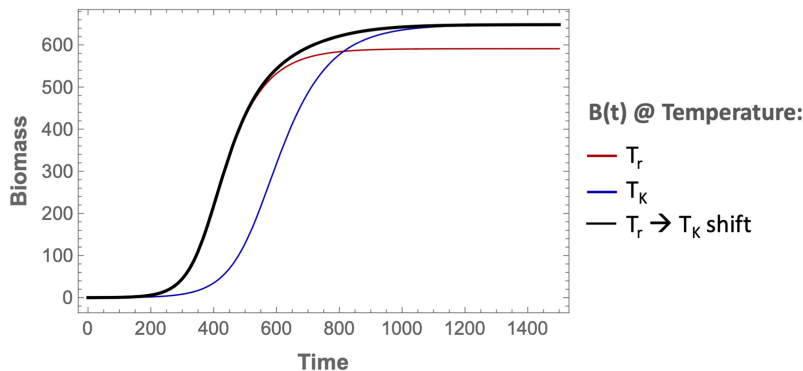

FIGURE 3 (a) i. Thermal optima for maximizing biomass (K) or growth rate (r) from equilibrium and growth thermal responses. ii. Temperatures are either static over time at T_r or T_K, or shift between the two optima to maximize the rate of growth from low densities and then biomass once densities are away from 0. (b) Corresponding biomass dynamics (transients approaching equilibrium) with these three temperature regimes. When temperature is varied such that temperature starts at T_r (maximum growth rates when biomass densities are low), then gradually decreases to T_K (maximum equilibrium biomass), the population is able to reach its maximum equilibrium faster. In this sense, temperature is optimized to facilitate rapid growth from low densities and keep this pace as it then approaches maximum biomass.

of population growth and size at different temperatures also suggest that there may be interesting dynamics when temperatures are continuously changing and the population is therefore in a perpetual transient state responding to an ever-changing equilibrium with simultaneously varying rates of change; we explore this below.

Non-equilibrium dynamics and population responses

Natural systems rarely exist in static environments, given the nature of temperature variation across temporal scales (e.g. diurnal to seasonal fluctuations). Figures 1–3 collectively show that population growth rate and quota-induced lags, transient lengths, and equilibrium biomass have different and interacting temperature dependencies. This means that the time scales that population dynamics operate on are temperature-dependent and that the relative time scale of environmental variation will be important in determining long-term population dynamics. Effective population forecasting requires us to identify time scales at which variation in temperature is going have to important effects beyond those predicted by equilibrium dynamics or average temperatures.

When temperature is varied sinusoidally between the boundaries of a population's thermal niche (T_{min} and T_{max}), the equilibrium (TBC) approaches (but does not pass) 0 at these extremes. Figure 4 shows the biomass dynamics over time under this form of temperature variation, relative to the changing equilibrium (also see Figure A9 for additional temporal scales and Figures A11 and A12 for N and Q dynamics). Note that when the forcing period is *very* long (e.g. here, >500,000 time steps but note this is relative to the rates of change defined by our model's parameters), biomass almost perfectly tracks the equilibrium (Figure A10) and population dynamics can therefore be accurately predicted using the TBC at all temperatures. At the other extreme, when forcing is very fast, the dynamics effectively cannot respond to the rapidly changing temperature and biomass becomes nearly invariant, approaching the mean equilibrium biomass over the thermal range (Figure 4c; Figure A10). These responses reflect two extremes of dynamical responses along a gradient of environmental forcing speed, relative to the population's rate of change (or ability to respond to environmental changes). At intermediate speeds of temperature variation, there is a dynamic interplay between a changing attractor, local stability, and thermally asymmetric vital rates, together causing the dynamics to lag unevenly behind the changing deterministic equilibrium (Figure 4).

Under relatively slow forcing (e.g. Figure 4a), population dynamics can track the equilibrium reasonably well at intermediate temperatures, but fail near the thermal extremes where population rates of change and local stability both approach zero (Figure A9). These extremes are also where thermal asymmetry in the quota-induced lag becomes apparent: the lag is highest at low temperatures (i.e. near T_{min}). This suggests the time scale that
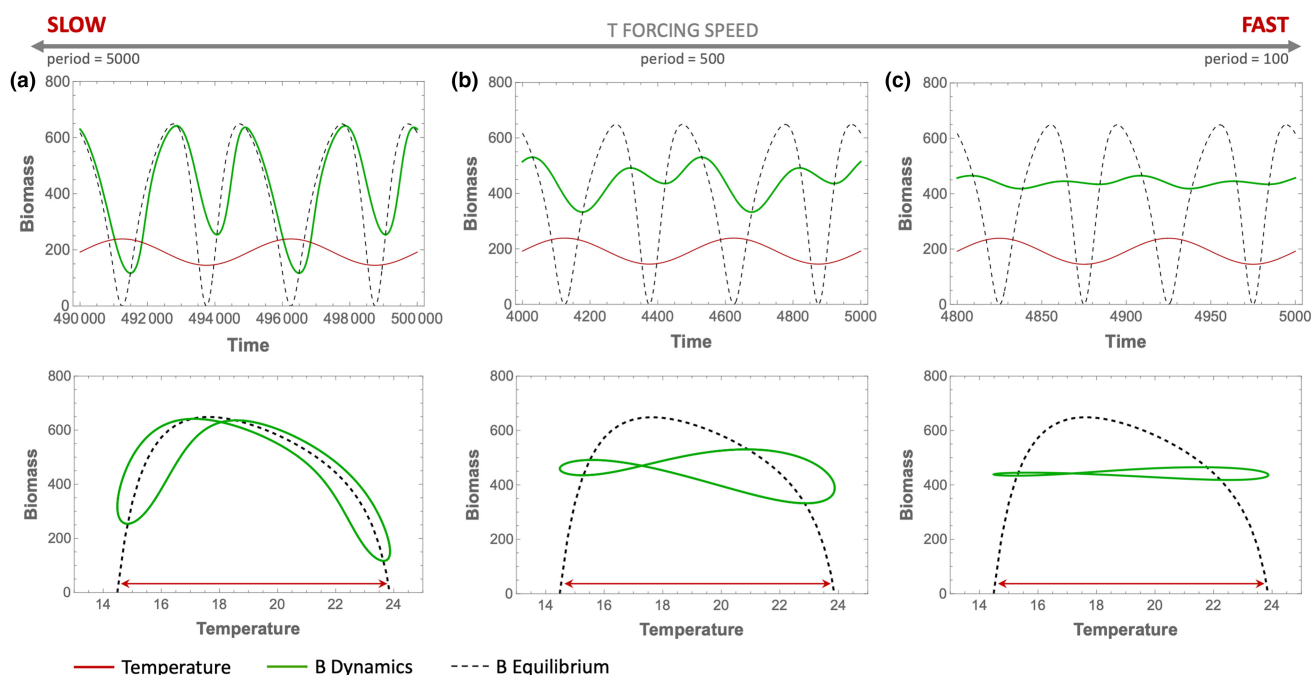

FIGURE 4 Population dynamics, relative to the temperature-dependent equilibrium, in response to sinusoidally varying temperatures between T_{min} and T_{max}. Here, dynamics have differential abilities to 'track' the changing equilibrium depending on the speed of forcing and temperature-dependent rates of population growth. Forcing periods shown here: (a) 5000, (b) 500, and (c) 100 time units. Temperature in top row is scaled for visualization purposes (multiplied by 10).

population dynamics operate on is different at high and low temperatures, influencing the responsiveness of biomass dynamics. Populations may be more likely to collapse when temperatures approach or surpass T_{max} versus T_{min} at these intermediate rates of environmental change (Figure 4; Figure A11). As temperature forcing becomes faster (Figure 4b,c), this same thermal asymmetry remains, making dynamics more 'reactive' (and therefore variable) at high temperatures (relative to low temperatures), even though the dynamics no longer closely follow the equilibrium. The magnitude of this variability is again dependent on the time scale of temperature variation, relative to the population, eventually approaching invariant population dynamics as forcing speeds further increase.

The mechanisms behind these dynamics are qualitatively general despite a modest interactive effect with nutrient limitation on the realized dynamics under variable temperature. When nutrients are limiting, the TPC and TBC are both altered and $r–K$ mismatch decreases (Figure 2), reducing the asymmetry in dynamics between high and low temperatures (i.e. via the quota) while also lowering the overall 'pace' of population growth. Here, the buffering effect of low temperatures seen above is lessened, and the population dynamics become more invariant than when nutrients are less limiting (Figure A14). Note, however, that this is in large part a result of *relative* time scales of population dynamics and temporal forcing, since a given frequency of forcing will 'seem' faster to a population with slower growth rates.

DISCUSSION

Here, we demonstrate that under a constant supply of (finite) resources, the thermal performance of a phytoplankton population (i.e. density-independent per-capita growth, *r*) is different than the thermal response of equilibrium biomass (i.e. carrying capacity, *K*), with biomass always optimized at cooler temperatures than performance. Hence, we refer to this thermal differential as *r–K* mismatch. Furthermore, we demonstrate that these thermal relationships are affected by resource availability; the optimal temperatures for the two traits converge as resources become more limiting, ultimately intersecting at the point where resources are so scarce that they can no longer support a viable population (Figure 2). We show that *r–K* mismatch is a result of relative differences in nutrient uptake and death across the thermal niche and that inclusion of a dynamic nutrient quota allows us to determine how both equilibrium and non-equilibrium dynamics depend on a combination of nutrients, temperature, and environmental fluctuations.

r–K mismatch ought to be a common phenomenon for more general populations with density-dependent growth and consumer-resource interactions (see Appendix S1). Specifically, these patterns likely always hold so long as mortality increases with temperature and differences

between the thermal responses of growth and mortality define an organism's thermal niche. Indeed, although we use unimodal functions of temperature for population growth, we note that the model behaves similarly when monotonically increasing functions are used (i.e. akin to 'double exponential' approaches) (e.g. Thomas et al., 2017; see Appendix S1, Figure A4), suggesting our results reveal a general representation of the thermal response of growth, turnover, and density dependence. Similarly, neither the assumption that both nutrient uptake and assimilation are temperature-dependent (Figures A7 and A8), nor that uptake and assimilation have and symmetric thermal responses (Figures A5 and A6), alter the qualitative nature of our results. While these qualitative results are highly general, it is worth noting that a more in-depth analysis of *all* vital rates in this model, by empirically parameterizing these rates and determining their importance relative to each other in a system-, species-, and nutrient-specific manner, may help elucidate whether population growth is more limited by uptake or assimilation and the true sensitivity to these assumptions.

One of the major challenges in predicting the dynamic response of populations to changing environments is the role of indirect effects; at the population level, various indirect effects manifest as changes in the strength of density dependence. An understanding of these changes is needed to improve general models of population responses. Here, we show that $r–K$ mismatch is generated by density-dependence strengthening as temperature increases, such that fewer individuals are supported per unit of resource at warmer temperatures (Appendix S1). Importantly, this change in density dependence will dictate population trajectories under global change; understanding the potential for thermal mismatches is necessary for predicting dynamics into the future. Our results suggest that the effects of global change on population densities may not match common forecasting approaches based on organisms' physiological thermal performance. With an $r–K$ mismatch, projections cannot be informed by the TPC of fitness ($r(T)$) alone. Clearly, TPCs are necessary for understanding rates of productivity for populations, material/energy flux within food webs, and nutrient cycling throughout ecosystems, but without a mechanistic understanding of biomass responses, we cannot accurately predict extinction risk of populations or numerical responses of important processes (e.g. inter- and intra-specific interactions).

Elucidating the thermal biomass curve for populations is a necessary first step towards understanding population dynamics—and therefore extinction risk—under global change. Where natural temperature variation occurs relative to a population's TPC *and* TBC will determine that population's dynamics, resilience, and extinction risk. The TBC provides a baseline for understanding patterns in non-equilibrium dynamics in variable environments, even when the dynamics do

not perfectly 'track' the equilibrium. Here, in contrast with 'classic' models where only r responds to the environment, there is an interplay the two simultaneously varying parameters (emergent properties in our model): K sets the target to which the population is attracted, and the strength of that attraction is determined by r. Furthermore, the nonlinear effects of nutrients on both the magnitude and shape of the TBC highlight another important layer of complexity. Population responses to naturally variable environments reflect a dynamic interaction between thermal responses in vital rates, density dependence, and resource limitation—all changing through time in response to abiotic and biotic conditions. For example, phytoplankton are known to have spring and fall blooms, a phenomenon generally thought to be driven by a combination of nutrient cycling and predation (Cebrian & Valiela, 1999; Martinez et al., 2011; Sigler et al., 2014), but which could in fact also be enhanced by annual temperature swings across the TBC.

Under varying temperatures, thermal asymmetries in population rates of change and resilience become apparent due to the implicit lag associated with our dynamic nutrient quota. While others have incorporated explicit lags into quota dynamics (e.g. Cunningham & Nisbet, 1980), thermal asymmetries within our model clearly still have implications for population dynamics. In Figure 4, we showed that the time scale of environmental variation is important for determining population dynamics as the relative influence of the thermally asymmetric lag wanes with increasing forcing period. This in turn changes the potential for collapse when temperatures approach an organism's thermal limits. Notably, these results suggest that (1) lagged dynamics mean that populations can likely withstand brief periods with temperatures outside the fundamental niche; and (2) brief periods with temperatures below T_{min} ought to be substantially less catastrophic for population persistence than brief periods above T_{max} (Figure 4; Figures A8 and A11). Furthermore, these patterns suggest that fluctuating environments (e.g. seasonal) could lead to increased variability in warmer (average) climates, and similarly that we may see more variability during warm (summer) versus cool (winter) times. Equilibrium estimates may, however, be insufficient for forecasting population dynamics under relatively high-frequency temperature variation. This has implications for population dynamics—and primary productivity for whole ecosystems—when seasons and weather patterns become less predictable.

Linking physiological processes to population-level responses allows us to more intentionally build generalizable population models that are better grounded in first principles. Developing fundamental ecological theory and forecasting predicted outcomes often require the simplification of more general models and contexts. One such example is the logistic model, which continues to be central to population theory despite the reliance of parameters on environmental attributes (e.g.

resource limitation and temperature) remaining open to interpretation. Here, we have developed mechanistic understanding of the dynamics of phytoplankton populations—the keystone to energy supply in all aquatic food webs, central to global carbon cycling, and a common study taxon for linking theoretical and empirical approaches in ecology. Simultaneously, our analytical insights apply to more generalizable model contexts with the goal of constructing fundamental theory in an intentional, informed way. Specifically, our r–K mismatch provides a framework for the nutrient and temperature dependence of population dynamics, and the next step ought to be developing a generalizable analytical form consistent with both our model and that used by Vinton and Vasseur (2022). Gaining a better understanding of the 'true' shape of the TBC will be important for understanding thermal responses of primary production for whole food webs and therefore general ecological functioning in changing environments.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14363.

DATA AVAILABILITY STATEMENT

No data were used in this study. Mathematical codes used for this study are available on GitHub at https://github.com/carlingbieg/TxN_DroopModel.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.