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RESEARCH ARTICLE

Temperature, resources and predation interact to shape phytoplankton size–abundance relationships at a continental scale

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Abstract

Aim: Communities contain more individuals of small species and fewer individuals of large species. According to the 'metabolic theory of ecology', the relationship of log mean abundance with log mean body size across communities should exhibit a slope of −3/4 that is invariant across environmental conditions. Here, we investigate whether this slope is indeed invariant or changes systematically across gradients in temperature, resource availability and predation pressure.

Location: 1048 lakes across the USA.

Time Period: 2012.

Major Taxa Studied: Phytoplankton.

Results: We found that the size–abundance relationship across all sampled phytoplankton communities was significantly lower than −3/4 and near −1 overall. More importantly, we found strong evidence that the environment affects the slope: it varies between −0.33 and −0.93 across interacting gradients of temperature, resource (phosphorus) supply and zooplankton predation pressure. Therefore, phytoplankton communities have orders of magnitude more small or large cells depending on environmental conditions across geographical locations.

Conclusion: Our results emphasise the importance of the environmental factors' effect on macroecological patterns that arise through physiological and ecological processes. An investigation of the mechanisms underlying the link between individual energetics constrain and macroecological patterns would allow to predict how global warming and changes in nutrients will alter large-scale ecological patterns in the future.

KEYWORDS
body size, phytoplankton, predation, resources, size–abundance relationship, temperature

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1 | INTRODUCTION

Climate warming and changes in resource supply are major drivers of global environmental change in freshwater ecosystems (Woodward et al., 2010). Changes in temperature and resources can modify physiological processes which, in turn, may affect ecological phenomena at population, community and ecosystem levels (White et al., 2007). Although the independent effects of temperature and resources on biological processes are relatively well studied (Cross et al., 2015), much less is known about how these factors interact with each other, with predation pressure and with body size to affect physiological and ecological processes.

Many physiological and ecological processes are strongly associated with organismal body mass (Brown et al., 2004). For example, population abundance (N) has been reported to be negatively related to body mass ($M^{-0.75}$) (Damuth, 1981), which has been explained as being inversely related to metabolic rate ($M^{0.75}$; metabolic theory of ecology – MTE), as specified by the Energetic Equivalence Rule (EER) (Nee et al., 1991), where the total energy used is unrelated to individual body mass (M^0). Consequently, larger individuals are fewer than smaller ones, because they use more metabolic energy. The EER has also been applied to the community level where total abundance is negatively related to the average M of individuals in a community, either through time or across space.

The size–abundance relationships across communities (i.e. Cross-Community Scaling Relationships, CCSR as defined by White et al., 2007) have received increasing attention in recent years and have been used to test EER predictions. Although the −0.75 slope of CCSR, expected by MTE, has been confirmed for marine phytoplankton communities (Li, 2002), desert rodent communities (White et al., 2004) and other communities (reviewed by White et al., 2007), considerable deviations have been reported for plant communities (Enquist et al., 1998), aquatic microbial communities (Long & Morin, 2005), land bird communities (Meehan et al., 2004) and lagoon macroinvertebrate communities (Gjoni et al., 2017).

This variation has been assumed to be idiosyncratic, with little investigation of whether it is systematically related to specific environmental factors or ecological processes. The MTE predicts that size–abundance relationship arises from metabolic demands (Brown et al., 2004), processes that alter metabolic demand, especially because metabolic scaling has been reported to be diverse (reviewed by Glazier, 2022), may, in turn, alter size–abundance relationships. Therefore, systematic variation in size–abundance relationship would provide evidence that MTE assumptions require further exploration, with important consequences for our understanding of nature (Enquist et al., 1998). Deviations can be measured as departures from quantitative MTE predictions and may allow to understand the mechanism that causes, which may result from the effects of environmental factors.

Temperature, in particular, affects the rates of physiological and ecological processes. MTE assumes that metabolic rates increase exponentially with temperature, independently of body size (Brown et al., 2004). This implies that the CCSR slope should not change across environmental temperature gradients (Figure 1a). However, temperature does cause the CCSR slope to deviate from the expected −3/4 slope and also the −1 slope often seen in natural planktonic communities (Gjoni & Glazier, 2020; Morán et al., 2010). Increasing temperature increases the proportion of small organisms, thereby decreasing the slope of the size–abundance relationship (Gjoni & Glazier, 2020; Morán et al., 2010; Pomeranz et al., 2022). This may arise derived from the size-dependent responses of the metabolism (Killen et al., 2010; Saito et al., 2021) or the direct effect on body size as described by several temperature 'rules' where temperature affects community size (Atkinson, 1994; Perkins, 2021). The plastic response of the individual-level body size may in turn decrease community-level body size in warmer conditions, thereby affecting the CCSR slope (Figure 1b).

Resource supply may also alter the slope of size–abundance relationships. The EER predicts that resources are equally partitioned between size classes in a community, causing no change to the scaling slope. Increased resource availability does increase population abundance, which should increase the intercept of size-metabolism and size–abundance relationships without changing their slopes (~0.75, Figure 1c). However, according to resource 'rules', changes in resource availability cause physiological changes that modify body size (McNab, 2010), which may change size–abundance relationships. This is true for plankton communities, where increasing nutrients increases the abundance of larger organisms (Irwin et al., 2006). Large species may be able to allocate more energy to growth under rich-resource conditions because of their higher resource uptake rates. Small species require fewer resources and therefore do relatively better when resources are limited (Litchman & Klausmeier, 2008). Poor-resource conditions may therefore decrease the CCSR slope (Figure 1d).

Predation may also cause changes in the size–abundance relationships of prey organisms. There is growing evidence that predation may be influential in two hypothetical ways. First, size-selective predation may interact with body size to affect the metabolic rate of prey (Glazier et al., 2011), which may, in turn, change the size–abundance slope. Second, size-selective predation may change prey-size distributions directly. In plankton communities, zooplankton (predator) grazing influences phytoplankton (prey) body-size distributions (Sommer & Sommer, 2006). Increasing size-selective predation may thus drive changes in the CCSR slope (Figure 1f,g).

Furthermore, temperature, resources and predation may interact to shape the size–abundance distribution, though presently we do not have clear expectations of how this should occur (see e.g. Sommer et al., 2017). Temperature effect on organismal body size (Agawin et al., 2000), growth rates (Thomas et al., 2017) and metabolism (O'Connor et al., 2009) is likely to be regulated by organisms in response to resource availability. Moreover, the prey body sizes and metabolic rates in response to predation pressure may also be temperature-dependent (Gjoni et al., 2020; Glazier et al., 2020). Therefore, any of those processes above could plausibly lead to temperature–resource–predation interactions shaping the CCSR slope. The mechanisms

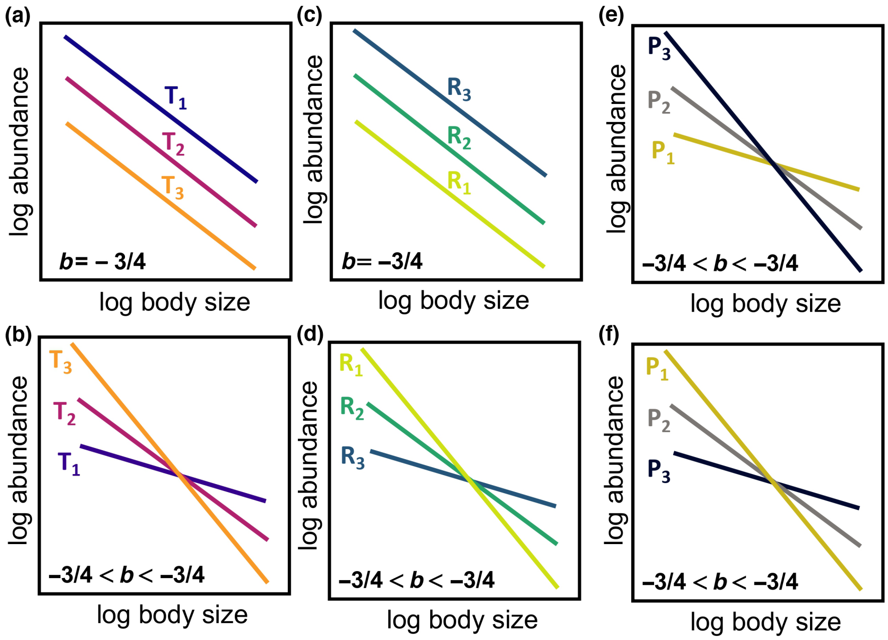

FIGURE 1 Effects of temperature (T) and resource supply (R) on log–log relationships of body size and abundance. (a) The Metabolic Theory of Ecology (MTE) predicts that increasing temperature (T_1 to T_3) should decrease population abundance, regardless of body size, thus without changing the size–abundance relationship slope ($b = -3/4$). (b) However, 'temperature-size rules' predict that increasing temperature (T_2 to T_3) should increase the proportion of small species present in the community ($b < -3/4$), whereas decreasing temperature (T_2 to T_1) should increase the proportion of the large species ($b > -3/4$). (c) The Energetic Equivalence Rule (EER) predicts that when resource availability increases (R_1 to R_3), abundance should increase in a similar – proportional – way for organisms of different body sizes, thus without changing the size–abundance relationship slope ($b = -3/4$). (d) However, 'resource rules' predict that when resource availability increases (R_2 to R_3) the proportion of large species should increase ($b > -3/4$), whereas when resource availability decreases (R_2 to R_1) the proportion of small species should increase ($b < -3/4$). Finally, size-selective predation pressure (P) may affect the size–abundance relationship in two different ways: (e) increasing size-selective predation pressure (P_1 to P_2 to P_3) may increase the proportion of small individuals relative to large ones, and (f) increasing predation pressure (P_1 to P_2 to P_3) may increase the proportion of large individuals relative to small ones.

underlying those interactions remain obscure, and future modelling work would be valuable in exploring these.

We investigated how temperature, resource availability and predation interact to affect the size–abundance relationships of phytoplankton communities across 1048 lakes in the USA. Our study takes advantage of large-scale observational data to evaluate whether systematic variations in temperature, resource availability and predation cause deviations from the quantitative predictions of EER and MTE. Therefore, our findings shed light on how important environmental drivers interact to influence community and ecosystem-level processes.

2 | MATERIALS AND METHODS

We used observational data from 1048 US lakes to model the effects of temperature, nutrients and zooplankton on the CCSR slope.

2.1 | NLA dataset

We used data from continental US lakes collected as part of the 2012 National Lakes Assessment (NLA) survey conducted by the US Environmental Protection Agency (Figure 2). NLA is a synoptic sampling programme of lakes, reservoirs and ponds implemented across the continental US. The lakes were sampled once in the summer (June–September) and were selected from the National Hydrography Database. At each lake, an extensive set of environmental variables was measured, but we provide sampling details only for variables used in our analysis. Field crews used standardised sampling methods across all sites, with collections made during the morning to early afternoon. All data are freely available online (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys).

2.2 | Variables examined in this study

To examine the size–abundance relationship (CCSR) slopes across lake phytoplankton communities of the NLA dataset, we used the following variables (biological, chemical and physical measurements, and samples were taken at a deep, open water location (i.e. <50 m) in each lake ecosystem). For each sample (corresponding to a different lake) all cell biovolumes of all identified taxa were quantified (μm^3/mL). Formulae for solid geometric shapes that most closely match

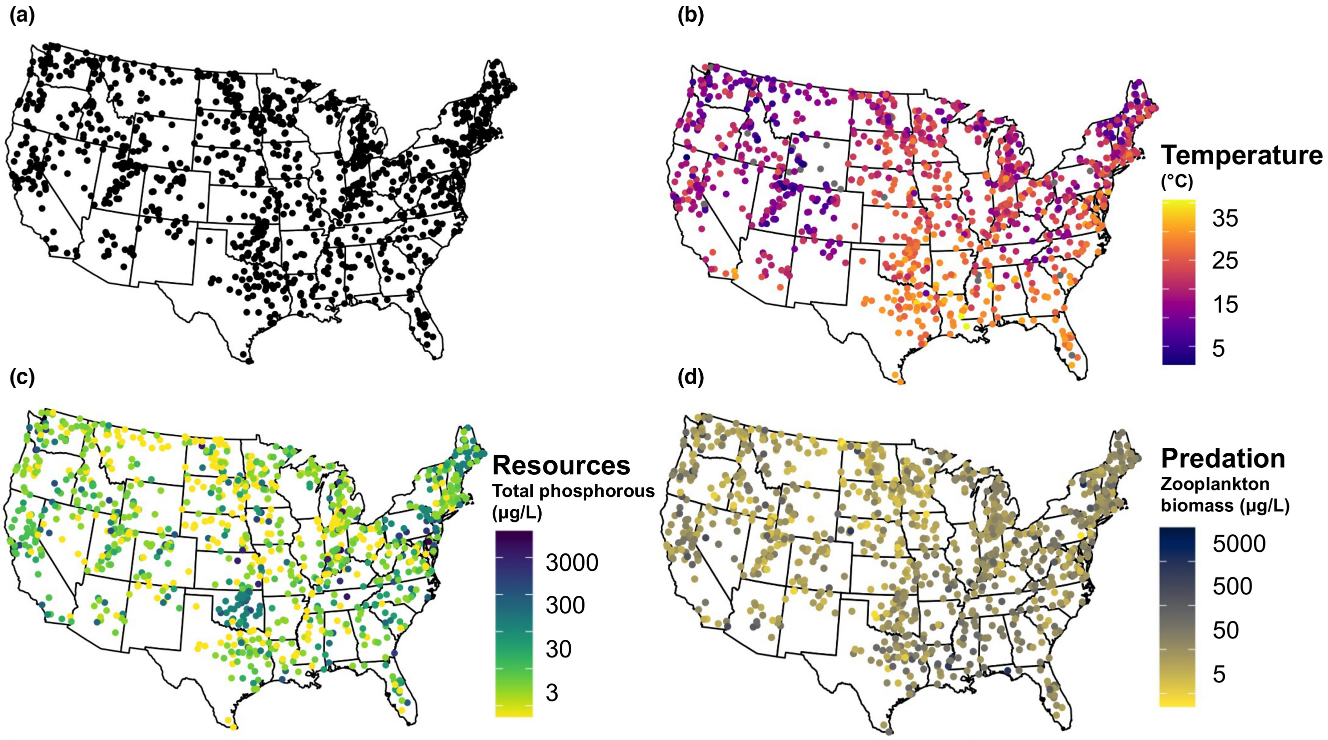

FIGURE 2 Map of the distribution of National Lakes Assessment sampling locations. Points are colour-coded based on: (a) sampling sites, (b) water temperature – T (°C), (c) total phosphorous – P (mg/L) and (d) zooplankton biomass – Z (µg/L).

the cell shape were used to estimate biovolume. Cell biovolumes of each taxon were then divided by the population density (cells/mL) to estimate the cell volume (*S*). For population density, phytoplankton population size per unit area (cells/mL) of all taxa was summed to estimate the total population density in each lake (*N*). Multi-parameter water quality metres (or sonde) were used to measure temperature (*T* – °C) at the open water location (i.e. <4 m) in each lake ecosystem (for each sample there was one temperature measurement taken). Moreover, water samples were then filtered (0.4 µm) and total phosphorous (*R* – µg/L) of each sample from each lake was measured by adding ultra-pure acid (e.g. H_2SO_4) to each water sample. For herbivorous zooplankton, the mean biomass of herbivorous zooplankton (µg/L) in each lake was used as a proxy for zooplankton predation pressure (*P*) on phytoplankton. The functional group (e.g. herbivore, predator and omnivore) for each zooplankton species was identified by an expert.

The NLA sampling of both biotic and abiotic components and sample processing procedures are described in detail and discussed elsewhere (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys).

2.3 | Data processing steps

For each lake, we calculated the following quantities:

- Total population density of phytoplankton cells in each lake.
- The mean volume of all cells in each lake.
- Mean zooplankton biomass in each lake.

2.4 | Hypotheses evaluated

We quantified the CCSR and its dependence on environmental variation using linear models. As a first step, we developed a priori hypotheses about how environmental variation should affect the CCSR. First, we tested whether the slope for the phytoplankton CCSR for all lakes sampled was −3/4, as predicted by the MTE, or closer to −1 as observed in previous studies. Second, we tested whether the CCSR scaling slope was invariant, regardless of variation in water temperature, total phosphorous availability and zooplankton biomass (as a proxy of predation pressure), again as predicted by the MTE (Figure 1). These environmental variables were selected because they are all known to affect physiological and ecological processes that are related to the body size and the abundance of the species present in the community (*see* Introduction).

2.5 | Model structure

We translated these hypotheses into the following linear model:

$$\log A \sim \text{Normal}(\mu, \sigma)$$

$$\mu = \alpha + \boldsymbol{\beta X}$$

where log abundance (*A*) (or rather log cell density) is normally distributed with an unknown mean μ and standard deviationσ, and μ is defined by a linear model with an intercept α, and 10 fixed predictors represented by $\boldsymbol{\beta X}$. These contain all main effects (mean cell size, temperature, nitrate concentration and zooplankton biomass) along with a few selected two, three and four-way interactions for which we had a priori expectations. Predictor and response data represent single measurements in each lake. We calculated means per lake when multiple measurements were taken during one sampling effort (no vertical structure in these variables was recorded and so this averaging does not bias measurements). All variables were $\log_{10}$-transformed before model fitting. After transformation, predictor variables (including temperature) were centred to improve model fitting and interpretation. More details about the model used evaluation are provided in Appendix S1.

2.6 | Statistical analysis

Models were assessed using Bayesian inference. Specifically, we generated joint posterior distributions for each model with the No-U-Turn sampler (NUTS) using *rstan* (Stan Development Team, 2022) via the *brms* (Buerkner, 2015) package in R (R Core Team, 2022). Priors were determined based on prior information and prior predictive modelling (Figure S1). We estimated the mean and 95% credible intervals (CrI) for each model parameter and each derived quantity, from the joint posterior distribution of each model. In addition, we assessed model fit using posterior predictive checking (Figure S2).

Finally, our method slices the data and fits their scaling slopes into groups where *T*, *R* and *P* are very similar (essentially constant). In this way, we can 'slice' the data so that *T*, *R* and *P* do not vary for each calculated slope (thus meeting the assumption of the MTE) and compare the slopes for groups of lakes with different environmental conditions and associated geographical locations.

3 | RESULTS

The slope of the size–abundance relationship for all phytoplankton communities in our dataset was substantially lower than the MTE expected value of −0.75. The slope averaged −0.97, with a >99% probability of being lower than −0.75 (Figure 3, Appendix S1, Table S1).

The inclusion of environmental predictors in the model revealed strong (and likely causal) relationships that altered the observed CCSR slope of −0.97, as presented in Figure 3. In particular, temperature (*T*), total phosphorous (a proxy for resource availability, *R*) and zooplankton biomass (a proxy for predation pressure, *P*) interacted strongly to alter the slope (Appendix S1, Table S1). In addition, following the MTE assumption, we 'sliced' the values of the continuous effects of *T*, *R* and *P* on the CCSR slope into conditionally grouped lakes where *T*, *R* and *P* do not vary simultaneously. For lakes with low *R* and *P*, no changes in the CCSR slope or intercept were observed with increasing *T* (Figure 4a). However, in lakes with high *R* and low *P*, the CCSR slope became increasingly more negative (i.e. the abundance of small phytoplankton increased relative to that of large phytoplankton) with increasing *T* (Figure 4b). Specifically, for lakes at 20°C (and *R* and low P), the slope was −0.75 as expected, whereas for lakes at 30°C the slope was steeper and at 40°C was shallower than −0.75. A similar pattern was observed for lakes with low *R* and high *P* (Figure 4c). However, in lakes with high *R* and *P*, neither the slope nor intercept changed with increasing *T*, where the CCSR slope was always steeper than −0.75 (Figure 4d).

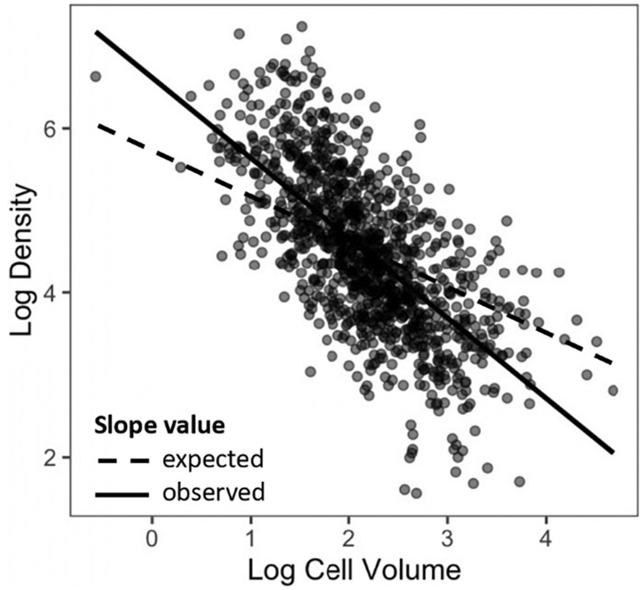

FIGURE 3 The relationship between total population density and mean individual cell size (volume μm^3) of each phytoplankton community in 1048 lakes of the continental United States of America (95% CrI: −1.03 to −0.91).

From a nutrient-supply perspective, in lakes with low *T* and *P*, the abundance of large phytoplankton increased more than that of small phytoplankton for lakes with higher *R*, thus making the CCSR slope less negative. Where for lakes with low total phosphorous (and low *T* and *P*) the slope was −0.75 as expected by MTE, whereas for lakes with higher total phosphorous, the slope was shallower (Figure 5a). However, for lakes with high *T* and low *P*, the CCSR slope did not change with increasing R (Figure 5b), being always steeper than −0.75. A similar pattern was observed for lakes with high *T* and *P* (Figure 5d). However, in lakes with low *T* and high *P*, the abundance of small phytoplankton increased relative to that of large phytoplankton with increasing *R*, in a similar way observed in Figure 4b,c and 5c.

From a predation-pressure prospective, in lakes with low *T* and high *R*, the abundance of small phytoplankton increased relative to that of large phytoplankton for lakes with higher *P*, thus making the slope more negative in a similar way observed in Figure 4b,c (Figure 6c). Where for lakes with medium predation pressure (and low *T* and high *R*) the slope was −0.75 as expected by MTE, whereas for lakes with low predation the slope was shallower and with high predation was steeper than −0.75 (Figure 5a). However, under the other conditions, there were no strong changes in the slope or intercept across lakes with increasing *P* (with shallow slopes ≈ −0.50 for lakes with low *T* and *R*, and steeper slopes ≈ −0.80 for lakes under other environmental conditions) (Figure 6a,b,d).

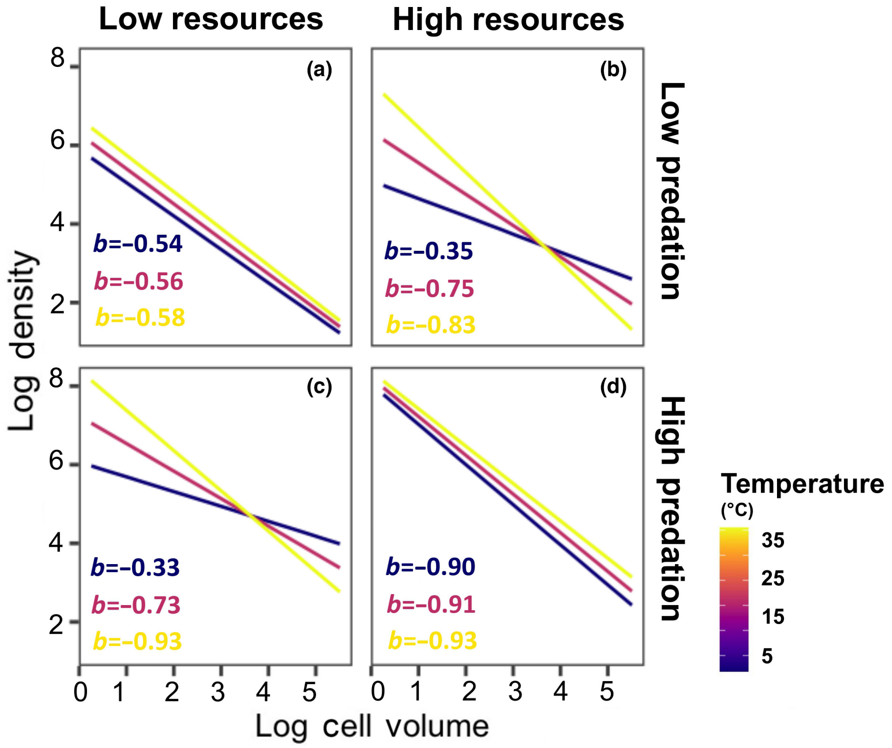

FIGURE 4 Temperature (T), resource availability (P; total phosphorous) and zooplankton predation (P) interact to alter size–abundance relationships across 1048 lake phytoplankton communities. This figure is a visualisation of a multiple regression model predicting total $\log_{10}$ population density (cells per mL) with mean $\log_{10}$ cell volume (μm^3), temperature (°C) and $\log_{10}$ nitrate concentration (mg/L), as well as interactions between those predictors. See methods for details of the fitted model. Although all predictors are treated as continuous in the model, we 'slice' the regression surface at three temperatures (10, 20 and 30°C), two total phosphorous concentrations (3 and 300 mg/L) and two zooplankton biomass levels (50 and 5000 μg/L) to show changes in slope driven by these predictors (thus meeting the assumption of the MTE).

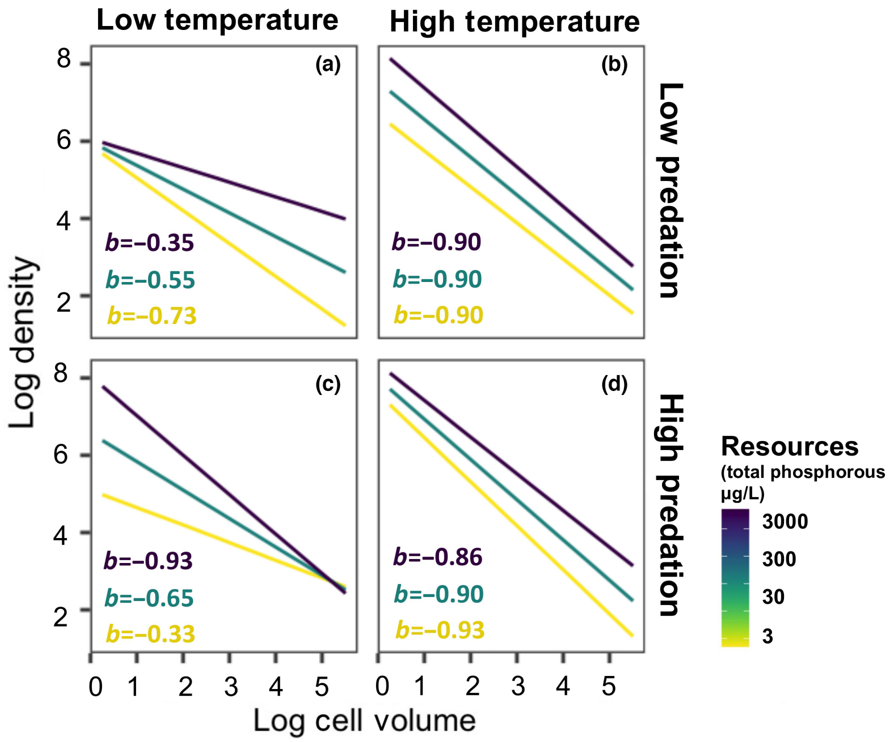

FIGURE 5 Temperature (T), total phosphorous (P) and zooplankton predation (Z) interact to alter size–abundance relationships across 1048 lake phytoplankton communities. This figure is another visualisation (see Figures 4 and 6) of a multiple regression model predicting total $\log_{10}$ population density (cells per mL) with mean $\log_{10}$ cell volume (μm^3), temperature (°C) and $\log_{10}$ nitrate concentration (mg/L), as well as interactions between those predictors. See methods for details of the fitted model. Although all predictors are treated as continuous in the model, we 'slice' the regression surface at three total phosphorous concentrations (3, 30 and 300 mg/L), two temperatures (10 and 30°C) and two zooplankton biomass levels (50 and 5000 μg/L) to visualise changes in slope driven by these predictors (thus meeting the assumption of the MTE).

The CCSR slope, in general, increases continuously and becomes less negative (i.e. with a value higher than ~−0.75 and closer to ~−0.25, yellow colour) with decreasing *T* and *P* and increasing *R* (Figure 7). By contrast, the CCSR slope decreases continuously and becomes steeper (i.e. with a value lower than of ~−0.75 and closer to ~−1, blue colour) with increasing *T* and *P* and decreasing *R* (Figure 7).

4 | DISCUSSION

The first major result of our study is that the CCSR slope for all phytoplankton communities analysed together is not −3/4, but is closer to −1 (Figure 3). This isometric size–abundance relationship has also been reported for phytoplankton assemblages by Huete-Ortega

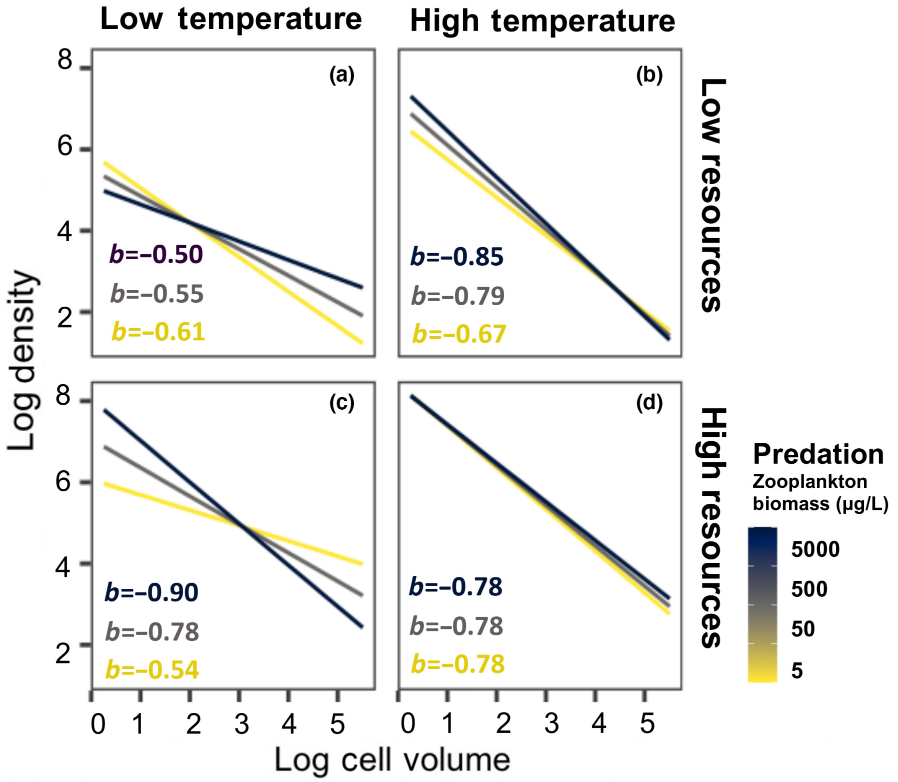

FIGURE 6 Temperature (T), total phosphorus (P) and zooplankton predation (Z) interact to alter size–abundance relationships across 1048 lake phytoplankton communities. This figure is another visualisation (see Figures 4 and 5) of a multiple regression model predicting total $\log_{10}$ population density (cells per mL) with mean $\log_{10}$ cell volume (µm3), temperature (°C) and $\log_{10}$ nitrate concentration (mg/L), as well as interactions between those predictors. See methods for details of the fitted model. Although all predictors are treated as continuous in the model, we 'slice' the regression surface at three zooplankton biomass levels (50, 500 and 5000 µg/L), two total phosphorus concentrations (3 and 300 mg/L), and two temperatures (10 and 30°C) to visualise changes in slope driven by these predictors (thus meeting the assumption of the MTE).

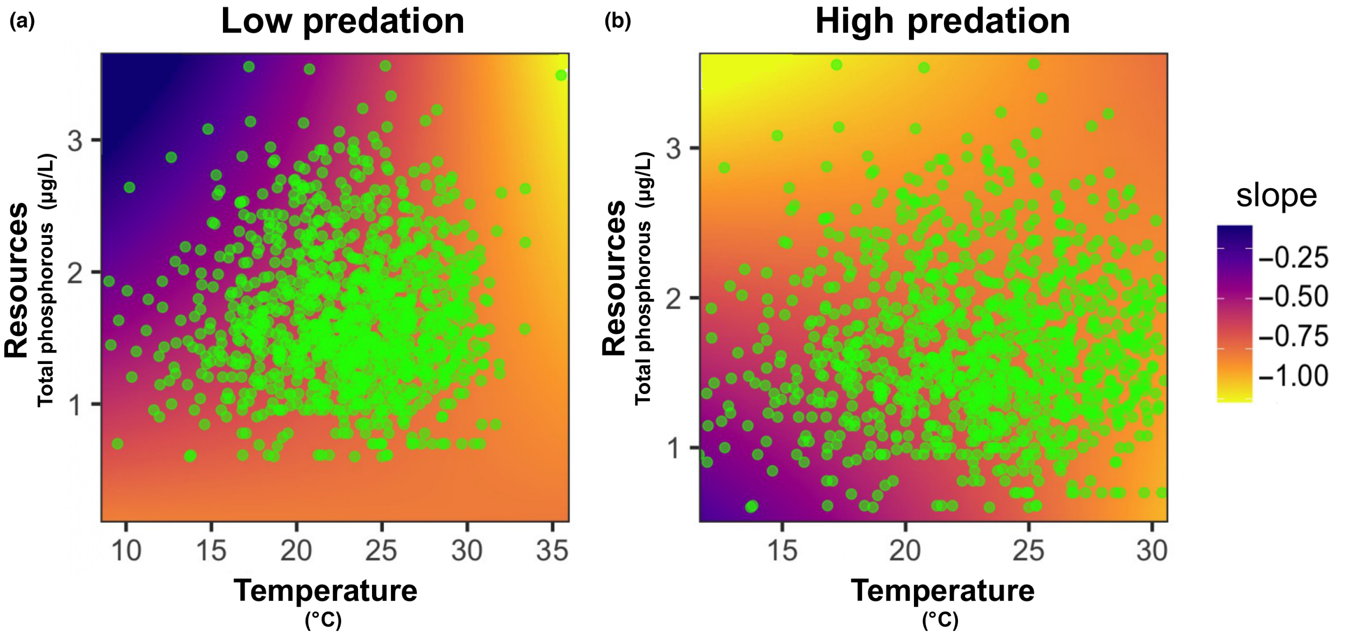

FIGURE 7 An alternate visualisation of the multiple regression results is presented in Figures 4–6. This figure shows the continuous change of CCSR slope across lakes with different temperatures and resources because of their geographical location under low and high predation. The colour variation indicates the slope of the size–abundance relationship across: temperature (°C) and resources (log-transformed phosphorous gradients – mg/L) under (a) low and (b) high predation (log-transformed zooplankton biomass – µg/L) pressure, estimated from the fitted regression. The green points represent all 1048 lakes and indicate the temperature and phosphorous conditions that characterise the lakes (note that the lowest phosphorus values represent measurements below the detection limit; see methods for more detail). Note that this entire range of values is not observed in nature.

et al. (2012) and Marañón (2015). However, in other empirical studies based on marine and freshwater phytoplankton communities, the slope is closer to −0.75 (Li, 2002; Perkins et al., 2019). Our finding yields the expectation that the metabolic scaling slope for phytoplankton should be 1, not 0.75, as predicted by the EER (Figure 3). This is consistent with experimental studies on phytoplankton communities that reported −1 for size–abundance slope and the inverse value for the metabolic scaling (Ghedini et al., 2020). In fact, two studies have reported that the metabolic scaling exponent for phytoplankton is >0.75 and near 1 (Huete-Ortega et al., 2012; Marañón, 2015), whereas Malerba et al. (2017) reported an exponent nearer to 0.75. Variation in the taxonomic composition of the phytoplankton studied may affect the mass-scaling exponents observed for both metabolic rate and abundance. For example, prokaryotes tend to show metabolic scaling exponents <1, whereas eukaryotic protists show exponents nearer to 1 (DeLong et al., 2010). The size–abundance relationship that we have observed (slope near −1) is based on samples that included both prokaryotic and eukaryotic lake phytoplankton species, whereas that of Perkins et al. (2019), where the scaling slope was near −0.75, was based on eukaryotic marine and freshwater phytoplankton species only. Given this variation in observed scaling, we cannot say for certain whether the phytoplankton communities in our study show energy equivalence.

The second major result of our study is that temperature, resources and zooplankton predation interact to affect the slope of the phytoplankton size–abundance relationships that we observed. This finding contradicts the MTE, which predicts that the CCSR slope should be invariant among groups of ecosystems with different environmental conditions. A key assumption of this prediction is that systems are in a steady state (i.e. that the systems are not changing drastically in response to disturbance, invasion or some other acute external pressure). We were unable to directly examine this assumption since our data represent single collections per lake. However, several aspects of the study make it likely that the steady state assumption is reasonable. First, communities had been exposed to consistent levels of temperature and resources for multiple years (because of their different geographical locations). Second, they were sampled during the summer when nutrient turnover occurring during the spring is most likely to have diminished (due to thermal stratification – Kraemer et al., 2015). Third, phytoplankton have relatively rapid responses to disturbance, making it unlikely that a large number of samples would occur in non-steady state conditions. Finally, while a few lakes may not be in a steady state, any effect of those lakes is likely small given the large sample size in this study ($n = 1048$). In other words, while the lack of replicated samples over time makes it impossible to directly test the steady state assumption, the large number of single samples helps to limit any large effects that might occur. Nevertheless, this represents a key caveat of our study and we cannot definitively rule out violations of the steady-state assumption, however unlikely they may be.

The environmental effects on the CCSR slope, and thus the relative abundance of small and large individuals, that we observed are quite complex and appear to require mechanisms that still need to be explored. To summarise our findings: in lakes with low predation risk (Figure 4a,b), small organisms are favoured (more abundant than expected based on −3/4 scaling) when temperature and nutrients are both high, whereas large organisms are favoured (more abundant than expected; Figure 4a,b) only when temperature is low and nutrient supply is high. However, in lakes with high predation risk (Figure 4c,d), small organisms are favoured when temperature is high and nutrient supply is low, whereas large organisms are favoured only when temperature and nutrients are both low. Finally, among groups of lakes with either low predation pressure and low-resource conditions, or high predation pressure and high-resource conditions, the CCSR slope showed negligible change with increasing temperature (Figure 4a,d).

The benefits of small size under low resource conditions are well understood in phytoplankton: small cells are more effective at assimilating resources (light and nutrients) and require fewer resources per cell, thus giving them a competitive advantage over larger cells under low-resource conditions (i.e. R* rule; Tilman, 1982). However, large individuals of terrestrial plants have been observed to have a competitive advantage in growing and competing for space under high light intensity (following the self-thinning rule – Westoby, 1977). Whether the self-thinning rule applies to phytoplankton communities is unclear. Small phytoplankton cells are favoured under high temperature and resource conditions (at low predation pressure), perhaps because the relative competitive advantage of small cells at high temperatures may be best expressed at high nutrient levels that allow them to manifest high rates of nutrient uptake, growth and reproduction. Prior theoretical work based on empirical measurements of phytoplankton physiology supports this claim (Reuman et al., 2014). If true, this would explain why large individuals are advantaged only in cold, resource-rich conditions (Figure 6c).

Two explanations for the patterns in our dataset that we can rule out are the intraspecific patterns of the TSR and RR, as strictly defined (Atkinson, 1994; McNab, 2010). The temperature 'rules' is a plastic response of individuals to being grown at colder temperatures. The resource 'rules' states that individuals tend to be larger in areas with high resource availability. These rules, as originally formulated, do not apply to our study because our size–abundance relationships included no intraspecific variation. Individual body sizes were not measured separately for each lake; instead, a single mean size for each species was estimated. Since intraspecific variation in body size was not measured, mechanisms based on intraspecific variation cannot explain variation in the size–abundance relationships that we observed.

However, patterns resembling the above 'rules' may be manifested at the community-level, despite the fact that the ecophysiological mechanisms underpinning these interspecific patterns may be considerably different and more complex than the physiological mechanisms governing intraspecific patterns. Setting aside these caveats about mechanisms for the moment, we see in our data that there is an increase in the relative abundance of small species at high temperatures (under some environmental conditions). There is growing evidence for this hypothesis where warming favours a disproportionate increase of small species in a community, which could be considered a community-level temperature 'rules' (Perkins, 2021). If resource 'rule' is extrapolated to the interspecific level, it would also be consistent with some of our findings: under some environmental conditions, the relative abundance of large species increases (causing a less negative CCSR slope) as resource availability increases. Size–abundance relationships in planktonic communities often show this pattern (Irwin et al., 2006; Marañón, 2015). Usually, a more negative CCSR slope (small organisms acquire more resources) is associated with limited resources, whereas a less negative CCSR slope (large organisms acquire more resources) is associated with high resource availability. However, despite this supporting evidence, the lack of precise, agreed-upon mechanisms for both 'rules' at various hierarchical scales means that presently we cannot clearly and conclusively link them mechanistically from the individual to community levels. Finally, it is also true that mixotrophy may affect the slope of phytoplankton communities under limited resource conditions (Ward & Follows, 2016). This is because mixotrophic phytoplankton may use alternative resources of energy, where the system may support larger individuals than expected by the resource 'rule' (McNab, 2010). This situation is not relevant to our study because removing mixotrophs from our analyses does not significantly alter our findings (Appendix S2, Figure S3).

In addition, the size-based community structure of lake phytoplankton appears to depend on zooplankton predation pressure. Size-selective predation by zooplankton can affect phytoplankton CCSRs and their relation to temperature and resource availability. Our findings showed that, under high predation, increasing temperature negatively affected the size–abundance relationship slope only at low nutrient availability, and increasing nutrients negatively affected the slope only at low temperatures. By contrast, decreasing temperature and resource supply positively affected the slope (Figure 7a). This implies that when predation pressure is high, increasing temperature under low resources, as well as increasing resource availability under cooler temperature favour small versus large individuals. Zooplankton may directly alter phytoplankton cell-size distributions by preferentially preying on relatively large phytoplankton cells (Sommer & Sommer, 2006). Indeed, under low predation, low temperature and high nutrients favour larger individuals whereas, under high predation, low temperature and high nutrients favour small individuals. The effect of size-selective predation on phytoplankton CCSRs seems to directly influence the proportion of large versus small individuals in a community. Whether interactions between predation and temperature affecting the metabolic scaling of prey organisms (Gjoni et al., 2020; Glazier et al., 2020) can alter size–abundance relationships is unknown. Another possibility is that size-selective predation may favour small individuals at low temperature and high resource levels. Phytoplankton species may accelerate physiological rates of metabolism, growth and reproduction to reproduce faster (i.e. before being eaten) where predation pressure is high, and smaller species may be better able to accomplish this. Therefore, different rates of population growth in small versus large species may help explain some of the variation in size–abundance relationships that we have observed in groups of lakes with high predation pressure. Finally, another response of the phytoplankton to predation pressure is colony formation by cell adhesion that can be induced by zooplankton grazing (Xiao et al., 2018). However, in our study, colony formation does not seem to mediate the effect of zooplankton grazing on CCSR of phytoplankton communities (Figure S3, Table S2).

Interestingly, Pomati et al. (2020) have also observed interactive effects of temperature, resource levels and zooplankton predation on phytoplankton CCSR slopes, as we have. However, they found that under high predation, increasing temperature and decreasing nutrients favoured large versus small phytoplankton individuals in a single lake ecosystem sampled at different times. They showed a seasonal effect of environmental factors on phytoplankton communities. By contrast, we explored a variation of the size–abundance relationship across lakes exposed to different environmental conditions in different geographical areas. Our study was to test whether key predictions of the MTE apply to size–abundance relationships slicing slopes for groups of lake ecosystems and explored variation among groups of lake ecosystems that differed systematically in temperature, resources and predation because of their geographical location. These contrasting results based on variation in time versus space, show that we still have much to learn about how and why temperature, nutrients and predation pressure affect size–abundance relationships.

Physiological mechanisms may be involved in causing the overall isometric size–abundance of lake phytoplankton communities, but are unlikely to explain completely the environmental effects on the CCSR slope that we have observed. Another possibility is that they are the result of environmental effects on body-size distributions acting via shifts in size-related mortality, growth or other biological processes. According to the MTE, increasing temperature should increase the metabolic rate and thus resource demand of phytoplankton cells, thus decreasing their abundance at a given resource level. The patterns that we observed may be the result of increased temperature causing increased population growth rates made possible by increased rates of protein synthesis, as found in phytoplankton communities by Toseland et al. (2013). Temperature may also affect the mortality rates of phytoplankton cells (Baker & Geider, 2021), and, in turn, population growth rates and possibly size–abundance relationships, a hypothesis requiring testing. In addition, although various hypotheses, including the metabolic-level boundaries hypothesis (Killen et al., 2010), and the size-dependent oxygen-uptake hypothesis (Verberk et al., 2021), predict that the slope for the rate of maintenance metabolism should decrease with increasing temperature, temperature effects on the size–abundance patterns that we observed across phytoplankton communities apparently cannot be explained simply in terms of these hypothetical physiological effects. It is also true, that some of the deviation of our results from that expected from energy-based models may be due to our focus on total abundance rather than maximum abundance, as used in some tests of the MTE (e.g. Belgrano et al., 2002).

Our findings show that resource availability may change the expression of a community-level temperature 'rules' and temperature may change the expression of a community-level resource 'rule' (Tabi et al., 2019). Furthermore, size-selective predation may change the expression of both community-level 'rules'. Nonetheless, although some aspects of our results still require further explanation, they demonstrate that predictions from major ecological rules or theories are contingent on environmental conditions. Therefore, our research provides important insights into the response of phytoplankton communities to climate change. To forecast changes in size-based community structure, we will need to account for the effects of not only temperature but also resource availability and predation pressure at large-scale monitoring. Understanding how and why size–abundance relationships respond to environmental changes may provide fundamental insights into the ecological dynamics and malleability of communities in nature. Our findings may be used to predict how climate change, nutrient enrichment and changes in predation intensity may affect phytoplankton communities in the future, which could be tested with NLA data that continue to be collected. Our research also shows that the effects of global change on ecological systems should be examined in realistic ecological contexts and at multiple scales.

AUTHOR CONTRIBUTIONS

Vojsava Gjoni, Mridul K. Thomas, Douglas S. Glazier and Bastiaan W. Ibelings conceived the ideas; Jeff S. Wesner, Vojsava Gjoni and Mridul K. Thomas performed the analyses; Vojsava Gjoni wrote the paper, with significant input of Mridul K. Thomas, Jeff S. Wesner and Douglas S. Glazier.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code are available at https://github.com/jswesner/NLA-lakes (to be archived at Zenodo upon acceptance).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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