

Functional traits explain phytoplankton responses to environmental gradients across lakes of the United States

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Abstract. Ecological communities exhibit regular shifts in structure along environmental gradients, but it has proved difficult to dissect the mechanisms by which environmental conditions determine the relative success of species. Functional traits may provide a link between environmental drivers and mechanisms of community membership, but this has not been well tested for phytoplankton, which dominate primary production in many aquatic ecosystems. Here we test whether functional traits of phytoplankton can explain how species respond to gradients of light and phosphorus across U.S. lakes. We find that traits related to light utilization and maximum growth rate can predict species' differential responses to the relative availability of these resources. These results show that laboratory-measured traits are predictive of species' performance under natural conditions, that functional traits provide a mechanistic foundation for community ecology, and that variation in community structure is predictable in spite of the complexity of ecological communities.

Key words: *community assembly; freshwater ecology; microbial ecology; multilevel/hierarchical models; species sorting; trait-based ecology.*

INTRODUCTION

Ecological communities exhibit regular shifts in structure along environmental gradients, patterns that are typically quantified as correlation between species composition and environmental factors. The existence of such correlations is evidence for species sorting, whereby the local environment determines the relative success of species through a combination of abiotic factors and species interactions (Leibold et al. 2004, Cottenie 2005). Although there is abundant evidence for species sorting (Cottenie 2005), it is much more difficult to uncover the specific mechanisms that determine community structure as a function of environmental conditions. It is possible that a renewed focus on functional traits in a community context can help elucidate the mechanisms underlying the rise and fall of abundances (McGill et al. 2006, Litchman et al. 2007, Litchman and Klausmeier 2008). A growing body of work on terrestrial plants has shown that the distribution of functional traits within communities changes in regular ways across environmental gradients. For example, the community mean of specific leaf area increases with soil water content in coastal Californian plant communities (Cornwell and Ackerly 2009), and the relative abundance of better nitrogen competitors increases during succession in old-field grasslands in Minnesota (Harpole and Tilman 2006).

By linking shifts in community composition to shifts in trait distributions, these patterns help reveal how abiotic conditions modulate interactions such as resource competition to assemble communities across environmental gradients.

Although the trait-based community ecology of terrestrial plants is developing rapidly, these approaches are not as well developed for the phytoplankton that are the dominant primary producers of many aquatic ecosystems. Phytoplankton are a diverse, polyphyletic group of microscopic, photosynthetic eukaryotes and cyanobacteria (see Plate 1). In addition to being dominant primary producers, the community composition of phytoplankton affects the trophic dynamics of aquatic ecosystems (Sterner and Elser 2002) and water quality (Anderson et al. 1998). Species composition of phytoplankton can be controlled by a variety of factors, including nitrogen, phosphorus, silicon, iron, light, temperature, and grazers (Tilman et al. 1982, Berquist et al. 1985, Landry et al. 2000, Johnson et al. 2006, Reynolds 2006, Stomp et al. 2007). Phytoplankton are well suited for linking functional traits to community structure, because traits such as the rate and efficiency of resource use are commonly measured in the laboratory (Eppeley et al. 1969, Briand and Guillard 1981, Moore et al. 1995), and previous trait compilations have found evidence for trade-offs that should constrain species' performance across environmental gradients (Tilman et al. 1982, Edwards et al. 2011, Schwaderer et al. 2011). Traits are often used directly as parameters in population dynamic models, and these models can predict the

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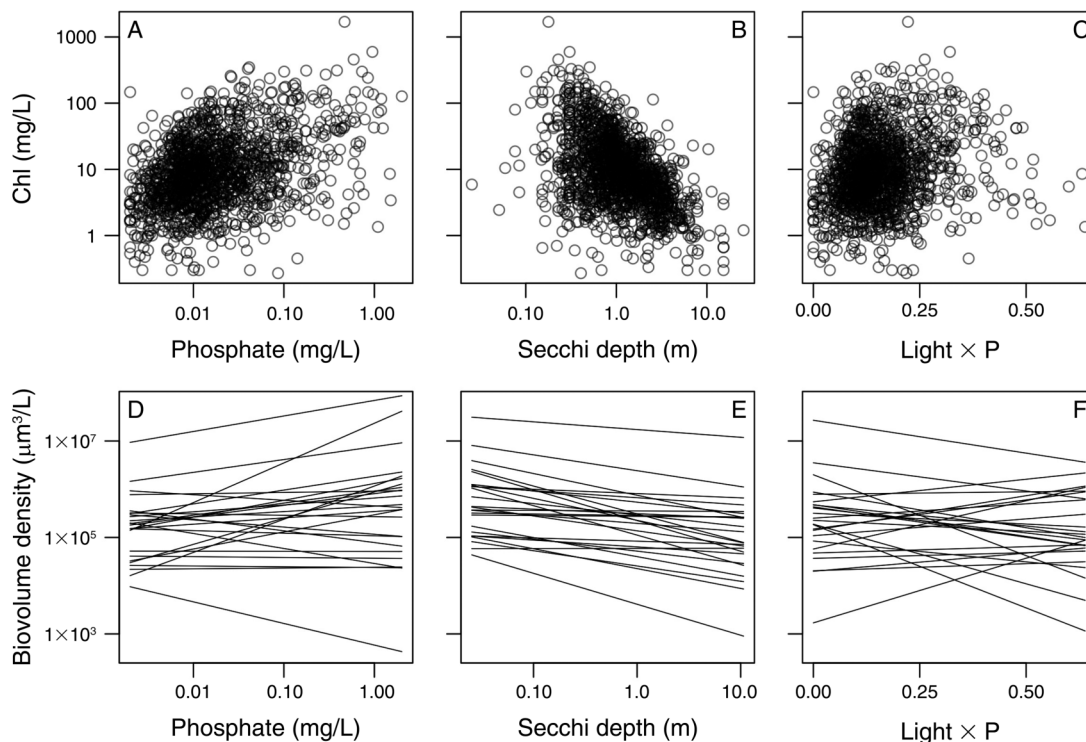


FIG. 1. Correlations of phytoplankton with phosphate, Secchi depth, and light \times P across lakes in the continental United States. (A–C) Chlorophyll concentration vs. phosphate, Secchi depth, and light \times P across all samples in the data set described in *Methods: EPA survey data* (note log–log scale). Light \times P quantifies simultaneous availability of light and phosphate, as defined in *Methods: Statistical methods*. (D–F) Interspecific variation in response to phosphate, Secchi depth, and light \times P. Each line is the model-fitted relationship between biovolume and the respective environmental predictor, for each of the 25 species in the analysis, using the abundance model defined in *Methods: Statistical methods*. Scatterplots of partial residuals illustrating species-specific fits are given in Appendix D: Figs. D2–D4.

outcome of interspecific competition as a function of environmental conditions in a laboratory setting (Tilman 1977, Grover 1991, Passarge et al. 2006), as well as under natural conditions (Tilman 1977, Huisman et al. 2004, Stomp et al. 2007). These results highlight the fact that the kinds of traits that are measurable for phytoplankton may have a particularly strong linkage to the mechanisms that determine the relative fitness of species across environmental gradients.

Here we test whether a set of functional traits can predict how species respond to gradients of light and phosphorus (P) across lakes in the continental United States. We will first introduce broad trends in the data and our predictions for the role of functional traits; we then describe the data set and analyses in detail. It is thought that much variation in lake ecosystems is driven by variation in the relative availability of phosphorus and light (Smith 1986, Reynolds 1998, Sterner and Elser 2002). Consistent with prior limnological analyses (Dillon and Rigler 1974, Watson et al. 1997), in the data set we use here, chlorophyll tends to increase with the supply of P (Fig. 1A; Appendix D: Fig. D1). In addition, an increase in P tends to be associated with a decrease in light availability (Appendix D: Fig. D1), presumably due to shading by the denser phytoplankton

community under high P supply. Consistent with this pattern, chlorophyll also covaries negatively with light (Fig. 1B). Finally, although the availability of light and P tend to covary negatively, there is substantial variation in this relationship. Light and P may be simultaneously high during transient periods when phytoplankton are growing rapidly but have not yet become dense enough to greatly reduce light, such as during the onset of stratification (Reynolds 2006). Alternatively, strong grazing pressure can reduce phytoplankton abundance and thereby alleviate both light and nutrient limitation (Sommer et al. 2012). Both light and P can be low in oligotrophic lakes where light is attenuated by dissolved organic carbon (Jones 1992). Consistent with these possibilities, there is no general trend between chlorophyll and the product of light and P availability (Fig. 1C).

These trends reveal how the aggregate phytoplankton community covaries with resource conditions, but individual species may vary in the sensitivity or even direction of their response to these conditions. In response to increasing P availability, most species increase at varying rates, while some species decline (Fig. 1D). As light availability increases, nearly all species decline, but they do so at varying rates and some

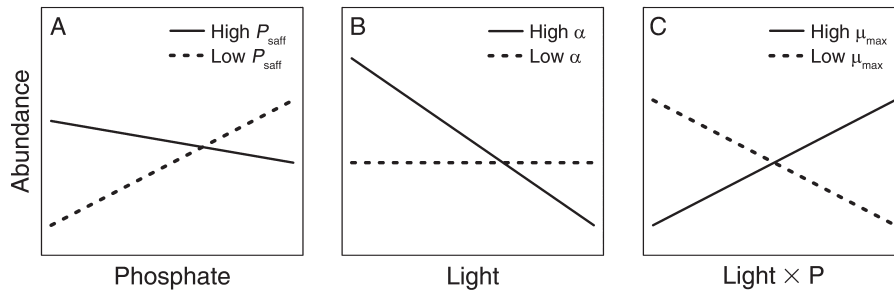


FIG. 2. Predictions for how functional traits should affect species' relative responses to phosphorus, light, and light \times P. The mean height of the lines is arbitrary, as the predictions concern the differences in slopes between species. Functional traits are defined in *Methods: Functional traits*. (A) Species with high competitive ability for P (high scaled uptake affinity for phosphate, P_{saff}) should have a relative advantage at low P availability. (B) Species with a high competitive ability for light, or a high tolerance of low light (high α), should have a relative advantage under low light. (C) Species with a high maximum growth rate (μ_{max}) should have a relative advantage when both light and P are available.

species show no trend (Fig. 1E). Finally, as both light and P become relatively high, individual species may increase or decrease (Fig. 1F).

The differential response of species to these gradients is presumably due to differential performance under conditions of P limitation, light limitation, and a lack of limitation by either of these factors. The goal of our analysis is to test whether laboratory-measured functional traits can explain interspecific variation in response to the environment, consistent with a priori predictions of how these traits should affect performance under different conditions. Specifically, we make the following predictions. As P decreases, species that are good competitors for P should have a relative advantage, and therefore should increase in abundance or decline less steeply when compared to other species (Fig. 2A). Conversely, species that are poor competitors for P should show a relative increase as P increases, because they likely possess other adaptations that allow them to prosper when P is less limiting (Fig. 2A). Likewise, as light decreases, species that are good competitors for light should have a relative advantage and increase more steeply (Fig. 2B). Finally, situations when both light and P are relatively available should favor species with a high maximum growth rate than can take advantage of reduced resource limitation (Fig. 2C). If the functional traits we use can predict these patterns, this will indicate that these traits are successful proxies of competitive ability for P, competitive ability for light, and maximum growth rate, while also supporting the hypothesis that shifting community structure is driven by these processes. We note that in this survey, oligotrophic lakes are relatively underrepresented relative to mesotrophic and eutrophic lakes (Appendix D: Fig. D1), resulting in a deficit of information on community response to extreme P limitation. Nonetheless, a wide range of phosphorus and light levels are represented, allowing us to test whether functional traits can predict interspecific variation in response to these factors.

It should be noted that the proposed trait differences will lead to differences between species in growth rate as a function of abiotic conditions. To test these predictions, we assume that differences in growth rate will translate into differences in abundance. This assumption is not ideal, because there will be a lag between enhanced (or reduced) growth and an increase (or decrease) in abundance (Allen et al. 1977, Klausmeier 2010). However, differences between lakes and between seasons should be persistent enough that abundance is a reasonable proxy. An advantage of our approach is that by focusing on differential responses to environmental factors, we can address shifting community structure without having trait information for all species in all communities, because differential responses to specific factors result in predictable shifts in the relative abundance of different trait values (Fig. 2). In other words, we expect that the outcome of species interactions depends on the environmental context (Agrawal et al. 2007), resulting in trait–abundance correlations that shift depending on environmental conditions (Harpole and Tilman 2006, Cornwell and Ackerly 2010).

METHODS

EPA survey data

We use data collected as part of the National Eutrophication Survey performed by the U.S. Environmental Protection Agency from 1973 to 1975. Full methods are described in Taylor et al. (1979); we summarize them here. Over 500 lakes and reservoirs were sampled on one to four occasions, with most sampled three times in the same year, during spring, summer, and fall. The number and spatial location of sampling stations at each waterbody were chosen to characterize the waterbody as a whole. Samples for chlorophyll and phytoplankton counts were depth-integrated, with water taken from the surface to 4.6 m depth, or from the surface to the lower limit of the photic zone (depth at which 1% of incident light remains), whichever depth was greater. If the depth of the sampling site was <4.6 m, the sample was taken

from just above the sediment to the surface. Chlorophyll concentrations were then averaged across stations, and phytoplankton samples were prepared by mixing equal volumes from each station. Temperature, turbidity, conductivity, pH, dissolved oxygen, total phosphorus, soluble reactive phosphorus (for simplicity, SRP is referred to as phosphate elsewhere in the text), nitrate + nitrite, ammonia, and total alkalinity were all measured at multiple depths chosen to characterize the water column. For the data used here, these parameters were first averaged at each station using only the depth range from which the chlorophyll and phytoplankton samples were taken, and then averaged across stations for each waterbody. Some sampling events were missing some environmental data, and these were dropped from the analysis, leaving a total of 511 waterbodies and 1046 sampling events. A total of 808 phytoplankton forms were counted over the entire data set, which includes varieties, species, and higher taxonomic groups for cells not identifiable to species level. Here we use data from 25 species for which appropriate functional trait data have been measured (Appendix B), including five cyanobacteria, six diatoms, 12 chlorophytes, and two cryptomonads.

Functional traits

Our analysis uses five functional traits, three related to phosphorus utilization, one related to light utilization, and finally maximum growth rate. Sources for trait data are listed in Appendix B. We note that the following description of these traits is nearly identical to the description given in Edwards et al. (2013), where similar traits were studied for marine phytoplankton. We characterize phosphorus utilization with scaled uptake affinity for phosphate (P_{saff}), which is a composite of three functional traits: maximum cell-specific phosphate uptake rate (V_{max}), the half-saturation constant for phosphate uptake (K), and the minimum phosphorus quota (Q_{min}). V_{max} and K are the parameters of the Michaelis-Menten curve typically fitted to measurements of uptake rate as a function of nutrient concentration in the medium. Uptake affinity (V_{max}/K) is the slope of the Michaelis-Menten curve at the origin, which quantifies the cell-specific clearance rate for a nutrient, as nutrient concentration nears zero (Healey 1980). Q_{min} is typically estimated when fitting the Droop model of phytoplankton growth (Droop 1973), which relates growth rate to internal nutrient content such that $\mu = \mu_{\infty} (1 - Q_{\text{min}}/Q)$, where μ is the specific growth rate, Q is cellular internal nutrient concentration or quota, Q_{min} is the minimum quota at which growth ceases, and μ_{∞} is asymptotic growth rate at infinite quota. Therefore, scaled uptake affinity ($V_{\text{max}}/KQ_{\text{min}} = P_{\text{saff}}$) combines these three traits in order to scale uptake ability (affinity) by the amount of phosphorus required for growth. Furthermore, in a model where Michaelis-Menten uptake is coupled to the Droop growth equation, P_{saff} predicts the winner of

nutrient competition at equilibrium, in the limit of zero mortality (Edwards et al. 2011). In a compilation of chemostat studies, we found that scaled uptake affinity is a good predictor of the winner in competition at equilibrium, even at relatively high mortality rates (dilution rates; Edwards et al. 2012). We therefore consider P_{saff} to be a good proxy of competitive ability for phosphate under limiting conditions. We compiled estimates of V_{max} , K , and Q_{min} from published studies in which cultures were maintained at or near 20°C and light was not severely limiting.

A species' light utilization is often characterized in the laboratory by measuring growth rate as a function of irradiance. This relationship is typically well fit by the following curve:

$$\mu(I) = \frac{\mu_{\text{max}} I}{\frac{\mu_{\text{max}}}{\alpha I_{\text{opt}}} + \left(1 - 2 \frac{\mu_{\text{max}}}{\alpha I_{\text{opt}}}\right) I + \frac{\mu_{\text{max}}}{\alpha}} \quad (1)$$

where μ is specific growth rate as a function of irradiance I , μ_{max} is maximum growth rate, α is the slope of the curve at the origin, and I_{opt} is the irradiance at which μ_{max} is achieved (Eilers and Peeters 1988). This curve is unimodal with a peak at I_{opt} , and as photoinhibition approaches zero ($I_{\text{opt}} \rightarrow \infty$), the curve becomes a hyperbola with an asymptote at μ_{max} . Our analysis focuses on α , because regardless of the strength of photoinhibition at high light, α quantifies the ability to grow under limiting light levels. We compiled data on growth vs. irradiance for each species from the literature, using studies in which cultures were maintained at or near 20°C and nutrients were not strongly limiting. For all cases in which original data were plotted, we extracted the data with ImageJ (Rasband 2011) and fit the curve (Eq. 1) to estimate α .

To quantify maximum growth rate (μ_{max}), we used estimates from studies in which growth rate was measured as a function of nutrient supply, irradiance, or temperature. In all cases, cultures were at or near 20°C and nutrients and light were not strongly limiting. If multiple estimates of μ_{max} were available for a species, they were averaged.

Trait \times environment predictions

Using the traits P_{saff} , α , and μ_{max} , we can test the predictions displayed in Fig. 2 for how differential abilities should affect species' responses to environmental variation. Because the predictions concern differences in slopes as a function of trait values, the predictions can be tested with interactions in a linear statistical model. Specifically, we predict a negative interaction between P_{saff} and a species' slope vs. P availability (higher P_{saff} leads to a more negative slope), a negative interaction between α and a species' slope vs. light availability (higher α leads to a more negative slope), and a positive interaction between μ_{max} and a species' slope vs. light \times P (higher μ_{max} leads to a more positive slope). The traits α and μ_{max} were available for 25

species, while P_{saff} was available for 13 of these species. Therefore, we ran the full models described in *Statistical methods* with the 13 species, and ran models removing the terms with P_{saff} using the larger group of 25 species.

Statistical methods

We used multilevel models (also known as mixed or hierarchical models) to test these interactions (Gelman and Hill 2006, Webb et al. 2010). Phytoplankton counts were recorded as algal unit densities (algal units/mL), where the algal unit is either a cell, a colony, or a filament, depending on the species. We converted all algal unit densities to biovolume densities ($\mu\text{m}^3/\text{mL}$), using mean cell volumes, colony sizes, and filament sizes collected from the literature. Our primary results are not sensitive to the method used to calculate biovolume for a given species because the hypothesized interactions concern slopes of log biovolume vs. environmental factors (Fig. 2), while the scaling factor used to calculate biovolume will only alter the intercept.

Because the phytoplankton count data are recorded as densities, the distribution of the data is semi-continuous (continuous on the positive reals with positive probability mass at zero). There are a large proportion of zeros (proportion of nonzeros ranges from 0.1% to 35% across species), presumably due to the large geographical extent of the survey and the lack of detection of very rare species in a sample. To account for this distribution we used a two-stage conditional approach (Cunningham and Lindenmayer 2005), in which presence/absence was modeled as a binary response vs. a set of predictors, and log biovolume conditional on presence, was modeled as gaussian-distributed using the same predictors. We refer to these as the occurrence and abundance models, respectively. In addition to properly modeling the distribution of the data, this approach allows for different predictors to influence occurrence vs. abundance when present. A variety of predictors were log-transformed, to linearize relationships with the response variables and ensure that rare large values of the predictors did not have excessive influence on parameter estimation: phosphate, Secchi depth, total alkalinity, nitrate, ammonia, conductivity, P_{saff} , α , and μ_{max} . All predictors were then standardized by centering around their median values and division by their standard deviation to aid model convergence and interpretation. In order to quantify a lack of limitation by light or P, we created a new variable $\text{light} \times \text{P} = ([\text{PO}_4 - \text{Min}(\text{PO}_4)] / [\text{Max}(\text{PO}_4) - \text{Min}(\text{PO}_4)]) \times ([\text{Secchi} - \text{Min}(\text{Secchi})] / [\text{Max}(\text{Secchi}) - \text{Min}(\text{Secchi})])$, where PO_4 and Secchi refer to the standardized versions of these predictors. Therefore, $\text{light} \times \text{P}$ has a minimum of 0 where either factor is at its minimum value in the data set, and a maximum of 1 when both factors are at their maximum value.

The predictions we test concern interspecific variation in slopes vs. environmental factors (Figs. 1 and 2). Multilevel models allow us to assume random interspecific

variation in slopes, while testing whether functional traits can explain that variation. In order to test relationships involving the focal environmental factors, it is important to account for interspecific variation in response to other important environmental factors. However, inclusion of all potential factors would result in a large number of parameters estimated from a moderate number of species. Therefore, we performed preliminary analyses to explore which additional factors showed the greatest interspecific variation in their effects; these were pH and total alkalinity. Other factors were modeled as having a common effect across species: nitrate, ammonia, conductivity, temperature, and chlorophyll. We also included random effects to account for variation in average conditions across waterbodies, variation due to the month of sampling, and species-specific responses to the month of sampling. Variation between years was modeled as a fixed effect. Detailed description of the statistical models is given in Appendix A.

RESULTS

Our analysis includes four models: the occurrence and abundance models for the 25 species with measurements of α and μ_{max} , and the occurrence and abundance models for the 13 species with measurements of α , μ_{max} , and P_{saff} . The abundance model with 25 species supports our predictions for α and μ_{max} . Biovolume of species with higher α tends to increase more steeply as light availability declines (Fig. 3A, Table 1; posterior mean $\gamma_{\text{L} \times \alpha} = -0.13$, 95% highest posterior density (HPD) credible interval = $[-0.25, -0.006]$). Biovolume of species with higher μ_{max} tends to increase more steeply when both light and P become relatively available (Fig. 3B, Table 1; posterior mean $\gamma_{\text{LP} \times \mu} = 0.33$, 95% HPD interval = $[0.04, 0.65]$). These patterns are not driven primarily by strong differences between taxonomic groups; although within-taxon replication is limited, the cyanobacteria, diatoms, and chlorophytes show broad and overlapping variation in traits and slopes (Appendix D: Fig. D5). Other important predictors of biovolume in this model include nitrate, ammonia, phosphate, pH, alkalinity, conductivity, chlorophyll, year, waterbody, and month (Table 1).

In contrast to the abundance model, the occurrence model with 25 species does not show evidence that interspecific variation in occurrence, driven by light or $\text{light} \times \text{P}$, is significantly explained by α or μ_{max} (Appendix C: Table C1). Important factors affecting presence/absence include phosphate, light, $\text{light} \times \text{P}$, pH, alkalinity, year, waterbody, and month (Appendix C: Table C1).

Our test of the effect of P_{saff} was restricted to the 13 species for which this trait has been measured. Neither the occurrence or abundance models showed evidence that species with greater P_{saff} gain a relative advantage as phosphate concentration declines (Appendix C: Tables C2, C3). In the abundance model with 13 species, the effects of α and μ_{max} are similar to their effects in the

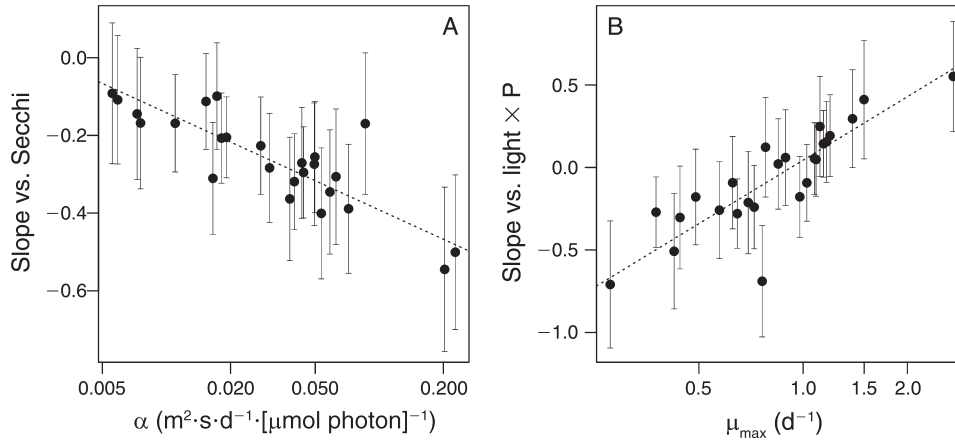


FIG. 3. Model-fitted slopes of biovolume vs. environmental predictors, compared to functional traits. (A) Slopes of biovolume vs. Secchi depth, compared to α , where α is the slope at the origin and quantifies the ability to grow under limiting light levels. Points are posterior means of model-fitted slopes vs. Secchi depth, i.e., $\beta_L^i = b_L^i + \gamma_{L \times \alpha} \alpha^i$ in the 25-species abundance model. Error bars are posterior standard deviations. These slopes remove the effect of μ_{\max} ($\gamma_{L \times \mu} \mu_{\max}^i$) in order to visualize the effect of α . Units for α are $\text{m}^2 \cdot \text{s} \cdot \text{d}^{-1} \cdot \mu\text{mol photons}^{-1}$ divided by irradiance ($\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). (B) Slopes of biovolume vs. light \times P, compared to μ_{\max} , maximum growth rate. Points are posterior means of model-fitted slopes vs. light \times P, i.e., $\beta_{LP}^i = b_{LP}^i + \gamma_{LP \times \mu} \mu_{\max}^i$ in the 25-species abundance model. Error bars are posterior standard deviations. Scatterplots of partial residuals illustrating species-specific fits are given in Appendix D: Figs. D2–D4.

25 species model, but only the effect of α is clearly different from 0 (Appendix C: Table C2).

DISCUSSION

Two of our predictions for how functional traits should relate to community structure were supported by our analysis of the EPA data set. Species with greater α , indicative of superior performance under low light, increase in biovolume more steeply as light in the water column decreases (Fig. 3A). Species with greater μ_{\max} , indicative of faster growth when resources are not limiting, increase in biovolume more steeply when both light and phosphate increase (Fig. 3B). These results were found when the response variable was biovolume conditional on presence in the community. When the response variable was presence/absence, α and μ_{\max} did not predict interspecific variation in occurrence. This difference between response variables may be due to the fact that a measure of abundance is more informative than presence/absence; because different processes affect presence vs. abundance, such as some species being absent from suitable locations due to dispersal limitation; or because species may remain present during unfavorable times due to carryover from previous favorable times.

We did not find evidence that species with greater P_{saff} , indicative of greater competitive ability for phosphate, had a relative advantage as phosphate decreases. The lack of evidence for this relationship may be due to the small number of species in the P_{saff} analysis, or it may be due to the fact that the lakes in this data set are mostly eutrophic (Taylor et al. 1979), resulting in less information about community structure under P limitation. In principle, the effect of P_{saff} on

responses to phosphate could be masked by the effect of α on responses to light; if P_{saff} and α are strongly negatively correlated (e.g., due to a functional trade-off), then these two traits would be nearly collinear in

TABLE 1. Coefficient estimates for the 25-species model of abundance vs. lake environmental conditions.

Coefficient	Estimate
\bar{b}_0	12.1 (11.2, 12.9)
\bar{b}_L	-0.29 (-0.48, -0.12)
\bar{b}_P	0.11 (-0.27, 0.39)
\bar{b}_{LP}	-0.28 (-3.68, 3.00)
\bar{b}_{pH}	0.31 (0.16, 0.44)
\bar{b}_{alk}	-0.11 (-0.18, -0.03)
β_{nit}	-0.10 (-0.14, -0.07)
β_{amm}	0.04 (0.003, 0.07)
β_{cond}	0.08 (0.02, 0.14)
β_{temp}	0.05 (-0.06, 0.17)
β_{chl}	0.002 (0.001, 0.003)
σ_0	1.78 (1.14, 2.32)
σ_L	0.14 (3×10^{-6} , 0.27)
σ_P	0.36 (0.03, 0.61)
σ_{LP}	0.27 (2×10^{-5} , 0.49)
γ_α	-0.15 (-0.97, 0.71)
γ_μ	-0.76 (-1.6, 0.15)
$\gamma_{L \times \alpha}$	-0.13 (-0.25, -0.006)
$\gamma_{L \times \mu}$	-0.16 (-0.33, 0.002)
$\gamma_{P \times \mu}$	-0.37 (-0.67, -0.05)
$\gamma_{LP \times \mu}$	0.32 (0.02, 0.60)
σ_{pH}	0.24 (0.12, 0.34)
σ_{alk}	0.064 (2×10^{-4} , 0.11)
σ_{lake}	0.58 (0.49, 0.64)
σ_{monsp}	0.25 (0.15, 0.35)
σ_{mon}	0.32 (0.09, 0.49)
σ_{res}	1.10 (1.06, 1.13)

Notes: Values reported are posterior means, with 95% highest posterior density credible intervals in parentheses. Residual standard deviation is σ_{res} ; see Appendix A for an explanation of the other subscripts.

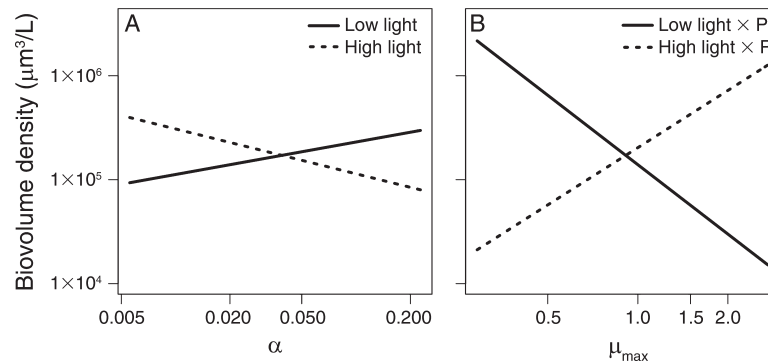


FIG. 4. Model predictions for how the relationship between traits and abundance changes across environmental gradients. Note that, in contrast to Fig. 2, these plots show abundance vs. trait relationships under particular environmental conditions, as opposed to abundance vs. environment relationships for particular trait values. (A) Predicted relationship between biovolume and α , under the lowest ("low light") and highest ("high light") values of Secchi depth in the data set. These lines are calculated as $b_0 + \gamma_\alpha + \gamma_{L \times \alpha} \alpha \times \log(\text{Secchi})$, using the posterior means for all parameters. (B) Predicted relationship between biovolume and μ_{\max} , under the lowest ("low light \times P") and highest ("high light \times P") values of light \times P in the data set. These lines are calculated as, $b_0 + \gamma_\mu \mu_{\max} + \gamma_{LP \times \mu \times P} \times \text{light} \times P$ using the posterior means for all parameters.

the statistical analysis. However, these traits are not correlated (data not shown), suggesting that any trade-off between them would likely only be detectable when additional important traits are accounted for (Edwards et al. 2011). These considerations are related to a more general quandary, that a trait effect quantified using observational data could be due not to the focal trait, but to unmeasured correlated traits. We think this is one advantage of using traits to test a priori mechanistic hypotheses, because unstructured trait–abundance–environment correlations could yield patterns that are more difficult to interpret. Finally, it is possible that P_{saft} is not a significant predictor in this analysis because it is a poor proxy for competitive ability for phosphate, but we consider this unlikely because a separate analysis using scaled uptake affinity for nitrate in a marine system found that this trait was strongly predictive of species' responses to nitrate limitation (Edwards et al. 2013).

Due to the labor-intensive methods necessary to measure ecophysiological phytoplankton traits, our analysis took advantage of published trait data. Nonetheless, our statistical approach allows us to use a subset of the community to infer how community structure changes along environmental gradients. The species in our data set possess a broad range of values for α and μ_{\max} (Fig. 3), and this is predicted to cause large changes in relative abundance across gradients. At the lowest observed values of Secchi depth, our model predicts the species with the highest α to be approximately fivefold more abundant than the species with the lowest α , while the converse is true at the highest observed values of Secchi depth (Fig. 4). Likewise, at the lowest observed values of light \times P, the species with the highest μ_{\max} is predicted to be ~100-fold more abundant than the species with the lowest μ_{\max} , and the converse is true at the highest observed values of light \times P. The values of these predictions have low

confidence, due to the many other factors that influence abundance within lakes (95% HPD credible intervals for the slopes for "low light," "high light," "low light \times P," and "high light \times P" are [−0.58, 1.3], [−1.4, 0.4], [−2.3, −0.33], and [−0.88, 2.9], respectively). However, these predictions illustrate how a sample of species that represent the breadth of trait variation can be used to quantify variation in community trait structure across divergent communities.

For the lakes in this data set, sampled from spring–fall, much of the variation in light availability is correlated with variation in nutrient loading (Appendix D: Fig. D1), with low light associated with high P and high chlorophyll. Therefore, the species with high α that perform relatively better under light limitation are likely the species that are more dominant at high phytoplankton biomass. These results are consistent with prior limnological work arguing that lake productivity is organized primarily along an axis of nutrient loading, and that variation in community and ecosystem structure is driven by the relative availability of light vs. P (Smith 1986, Watson et al. 1997, Reynolds 1998, Sterner and Elser 2002). However, not all variation in Secchi depth is correlated with chlorophyll concentration, implying that high α species may also dominate under other light-limited conditions such as deep mixing depths or high allochthonous dissolved organic matter. Likewise, low α species benefit from high grazing pressure in addition to low nutrient supply, because grazing will tend to reduce shading by phytoplankton.

Variation in community structure associated with μ_{\max} occurs along an axis of lake variation distinct from the light vs. P axis; in some samples both light and phosphate are relatively limiting or non-limiting, and there are multiple temporal and spatial processes that may lead to this variation. Phytoplankton blooms are often associated with seasonal variation in mixed layer depth; increased stratification during the spring or

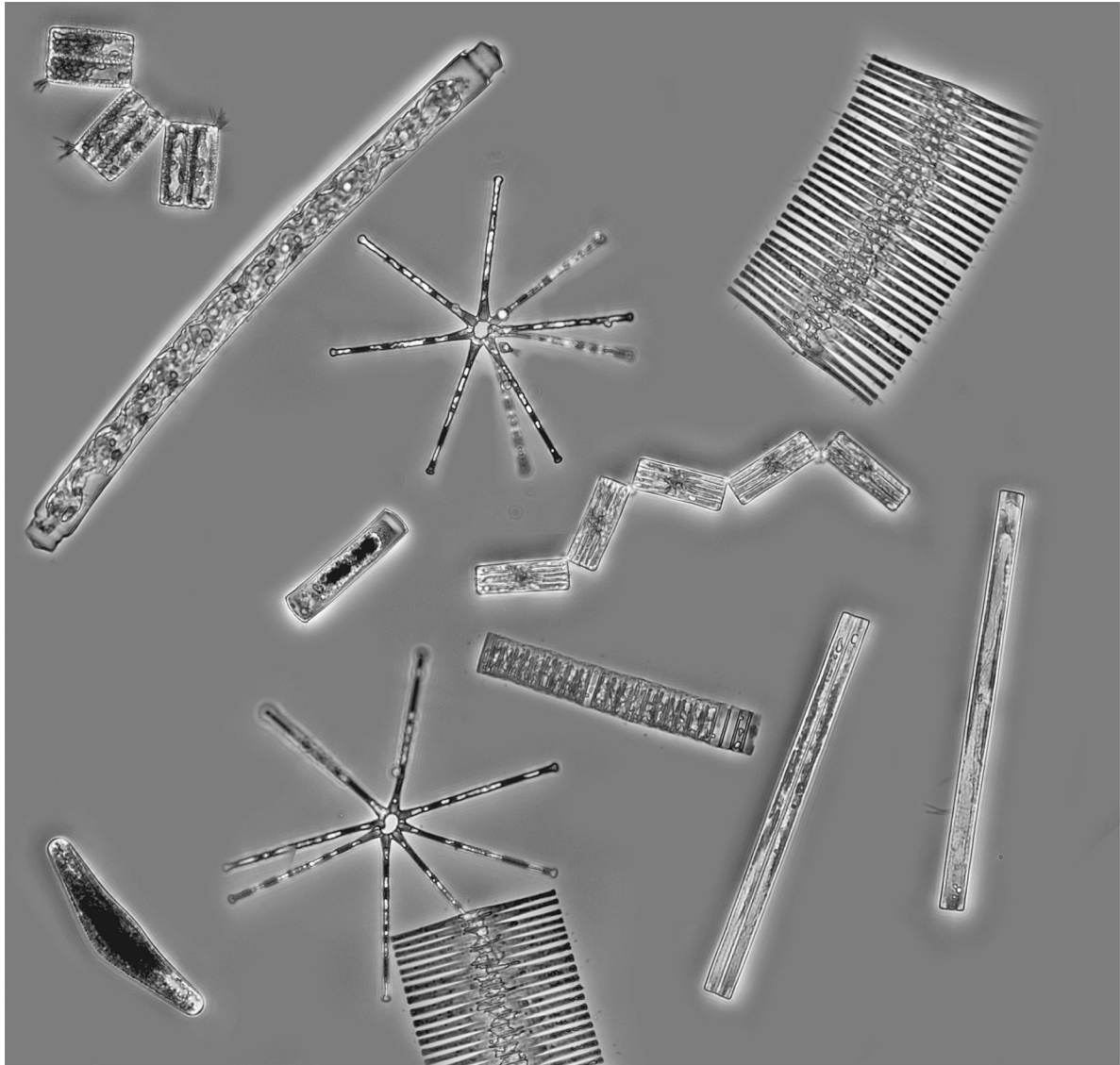


PLATE 1. Diatom diversity. Diatoms are one of the dominant groups of phytoplankton. Photo credit: Anne Schwaderer.

entrainment of nutrient-rich water during the fall often leads to both light and nutrients being transiently abundant (Reynolds 2006). Rapid increase in mixed layer depth due to storms, followed by a return of stratification, can also lead to transient rapid growth (Robarts et al. 1998). During periods of strong stratification, nutrient limitation may be alleviated by strong grazing pressure, e.g., during “clear-water” periods (Sommer et al. 2012). In this case, resource abundance by itself can select for fast-growing species, while theory shows that high grazing pressure may also select for rapid growth via apparent competition (Holt et al. 1994). However, strong grazing pressure is known to cause shifts in phytoplankton composition toward taxa that resist consumption but grow slowly (Agrawal 1998). Finally, conditions of relatively high light and

phosphate could be associated with limitation by another resource such as nitrogen, which may benefit nitrogen-fixing cyanobacteria. The relationship between μ_{\max} and $\text{light} \times \text{P}$ in this data set suggests that high $\text{light} \times \text{P}$ often indicates a lack of resource limitation, rather than strong grazing or limitation by a different resource. However, it is likely that additional variation in species’ responses to these conditions could be explained by traits related to grazer resistance and other nutrients.

Our results demonstrate that laboratory-measured microbial traits can be predictive of the success of species under natural conditions. We think this is noteworthy, because there are many reasons why laboratory-measured traits might not be representative of natural processes. The many studies from which we have compiled trait data do not use identical experi-

mental methods; laboratory culture conditions differ from the natural environment in ways that are often difficult to account for; the cultured strains for which trait data were available will not capture potential intraspecific trait variation across the continental United States; trait data for individual species were typically compiled from multiple studies by different researchers. Nevertheless, the patterns we have found indicate that the traits typically measured by phytoplankton ecologists can be robust indicators of interspecific variation, and the measurement of a greater number of traits on a broader range of species will be an important contribution to understanding the ecology of these organisms.

Substantial variation in community structure associated with light and P can be explained by α and μ_{\max} , but other factors are important for variation in community structure, such as pH, nitrogen, alkalinity, and grazers. If traits related to these factors are quantified for a moderate number of representative species, it may be possible to create a statistical foundation for predicting the composition of phytoplankton communities using a moderate number of environmental variables. The implication of this approach is that although ecological communities are extremely complex, involving nonlinear interactions among a large number of species in a high-dimensional environmental setting, nonetheless shifts in the distribution of functional traits across environmental conditions may be predictable. Ultimately, a statistical approach to quantifying community trait structure can be used as a foundation for building mechanistic dynamic models of trait distributions that predict shifts in trait structure across lakes as well as the maintenance of trait diversity within lakes.

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SUPPLEMENTAL MATERIAL

Appendix A

Supplementary statistical methods ([Ecological Archives E094-146-A1](#)).

Appendix B

Species in the analysis, trait data, and sources ([Ecological Archives E094-146-A2](#)).

Appendix C

Coefficient estimates for the 25-species occurrence model, the 13-species abundance model, and the 13-species occurrence model ([Ecological Archives E094-146-A3](#)).

Appendix D

Supplemental figures showing environmental covariation and species-specific responses to environmental predictors ([Ecological Archives E094-146-A4](#)).