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Niche expansion via acquired metabolism facilitates competitive dominance in planktonic communities

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Abstract

Acquired phototrophs, organisms that obtain their photosynthetic abilities by hosting endosymbionts or stealing plastids from their prey, are omnipresent in aquatic ecosystems. This acquisition of photosynthetic metabolism allows for niche expansion, and can therefore influence competition outcomes by alleviating competition for shared resources. Here, we test how acquired metabolism alters competitive outcomes by manipulating light availability to control the energetic contribution of photosynthesis to acquired phototrophs. Using freshwater protists that compete for bacterial prey, we demonstrate light-dependent competition outcomes of acquired phototrophs (*Paramecium bursaria*) and strict heterotrophs (*Colpidium* sp.) in laboratory model experiments. We then synthesize these findings using a series of mathematical models, and show that explicitly accounting for resource competition improves model fits. Both empirical and mathematical models predict that the acquired phototroph should increase in competitive dominance with increasing light availability. Our results highlight the importance of acquired metabolism to community dynamics, highlighting the need for more empirical and theoretical studies of this mechanism for niche expansion.

KEYWORDS
Colpidium, direct competition, mathematical modeling, niche partitioning, *Paramecium bursaria*

INTRODUCTION

Outcomes of competition between species have long captivated ecological research, and niche theory offers a quantitative approach to predict these outcomes (Vandermeer, 1972). The fundamental niche is governed by the match between an organism's traits—for example metabolic rate, stoichiometry, and physical attributes such as body mass and shape (McGill et al., 2006)—and environmental conditions, while the realized niche includes performance shaped by biotic interactions (Grinnell, 1928; Hirzel & Le Lay, 2008; McGill et al., 2006; Vandermeer, 1972). Niche overlap occurs between organisms that share space, food, or other resources, and often leads to competition (Hurlbert, 1978). Classical niche theory predicts an upper limit to the degree of niche overlap that allows two competing species to coexist (MacArthur & Levins, 1967; May & MacArthur, 1972). If this limit is exceeded, direct competition will lead to competitive exclusion (Hardin, 1960).

While the traits that determine an organism's niche may seem predetermined by an organism's genome, some organisms are capable of expanding their fundamental niche through acquired metabolism. Organisms can acquire metabolism by incorporating genetic material (Falkowski et al., 2008; Ochman et al., 2000), retaining cellular machinery (Johnson, 2011; Park et al., 2014;

Stoecker et al., 2009), and/or exchanging metabolites with other lineages (González & Gonzalez-López, 2013; Zientz et al., 2004). For example, planktonic ciliates can acquire phototrophy by retaining chloroplasts from cryptophyte algae (Moeller et al., 2016; Stoecker et al., 1987), and giant hydrothermal vent clams house endosymbiotic bacteria that metabolize inorganic materials (Scott & Fisher, 1995).

By accessing a new set of resources, organisms with acquired metabolism can persist alongside and even competitively exclude direct competitors for other resources, as predicted by niche partitioning (Moeller et al., 2016). Niche partitioning refers to a differentiation in ecological niches, which promotes coexistence between competing organisms (Chesson, 2000; Levine & HilleRisLambers, 2009; Vacher et al., 2016). While niche expansion can enhance the competitive dominance of the acquiring organism, the impact of acquired metabolism, specifically acquired phototrophy, on competitive outcomes remain relatively unknown. In acquired phototrophy, planktonic ciliates incorporate photosynthetic machinery to access a new resource, light, thereby transforming organisms from heterotrophic taxa to mixotrophs. Here, we test the hypothesis that the acquisition of photosynthetic machinery allows acquired phototrophs to persist alongside their competitors and alleviate competition for food by using light for energy.

We worked with a classic model system for competition: freshwater bacterivorous protists. Since Gause's foundational work in 1935, laboratory experiments with protists have played an important role in developing population ecology by bringing together theory, observation, and experiments (Gause & Witt, 1935; Holyoak & Lawler, 2005; Müller et al., 2012). Specifically, experimentation with protist model systems have been important to study interspecific competition by manipulating environmental conditions (Fox & Morin, 2001; Jiang & Morin, 2004; Müller et al., 2012) and to understand competition outcomes in natural populations (Gill & Hairston, 1972).

We used two ciliate species: *Colpidium* sp., which in our system is a strict heterotroph, and a competitor, *Paramecium bursaria*, which can become mixotrophic by hosting a photosynthetic endosymbiont, the algae *Chlorella vulgaris*. *Paramecium bursaria* is thought to have a mutually beneficial relationship with *C. vulgaris* (M. W. Karakashian, 1975; S. J. Karakashian, 1963; Reisser, 1980; Reisser & Häder, 1984; Siegel, 1960; Weis, 1974), and is rarely found without its endosymbiont in the wild (Tonooka & Watanabe, 2002). However, the benefits of this acquired metabolism to *P. bursaria* can be context dependent: the growth rate of *P. bursaria* with the symbiotic algae varies by temperature (Salsbery & DeLong, 2018) and light level (Lowe et al., 2016; Pado, 1965; Weis, 1974). Therefore, this

system provides an opportunity to isolate and test the role of acquired metabolism in shaping species coexistence.

To test the effects of acquired metabolism on competitive outcomes, we manipulated light to control the contribution of acquired phototrophy to the growth of *P. bursaria*. We hypothesized that the competitive dominance of *P. bursaria* would increase with light availability, and that this competitive dominance would be mediated by increasing access to photosynthate as a resource pool. First, we performed laboratory experiments in which we quantified the population dynamics of *P. bursaria* and *Colpidium* in isolation and in competition. Second, we developed new mathematical models that recapitulated our results. Although we began with a Lotka–Volterra model for competition, this model did not fit our data well. Therefore, we developed a new mathematical model that captured our empirical findings because it explicitly accounted for resource availability. Overall, our findings suggest the importance of acquired metabolism as a means to promote coexistence among competitors by alleviating niche overlap through access to new resource space.

METHODS AND RESULTS

Competition experiments

Laboratory experimental methods

Cultures of *Colpidium*, *P. bursaria*, and all bacterial species used as protist resource were obtained from Carolina Biological Supply Company. Laboratory stock cultures of both species were maintained at 50, 100, or 200 µmol quanta $m^{-2} s^{-1}$ in an incubator at 24°C under controlled 12 h to 12 h, light:dark conditions for at least 2 weeks prior to the start of the experiments, allowing the stock cultures of both *Colpidium* and *P. bursaria* to adjust to the light environments corresponding to the experimental conditions.

To control the bacterial prey community available to the ciliates in our experiments, we inoculated the initially sterile protozoan pellet media (Carolina Biological Supply Company, Burlington, NC, USA) with a uniform set of bacteria 2 days prior to the start of the experiment. For inoculation, we used a set of three bacteria: (1) *Serratia marcescens*, and the dominant bacterial species from purchased protist cultures of (2) *Colpidium* and (3) *P. bursaria*. The dominant bacterial morphospecies of each ciliate culture was determined by plating the protist culture onto Nutrient Agar (Research Products International), isolating the most abundant morphotype, and growing the species in liquid media. The purpose of using

Increasing light intensity, µmol quanta m^{-2} s^{-1}
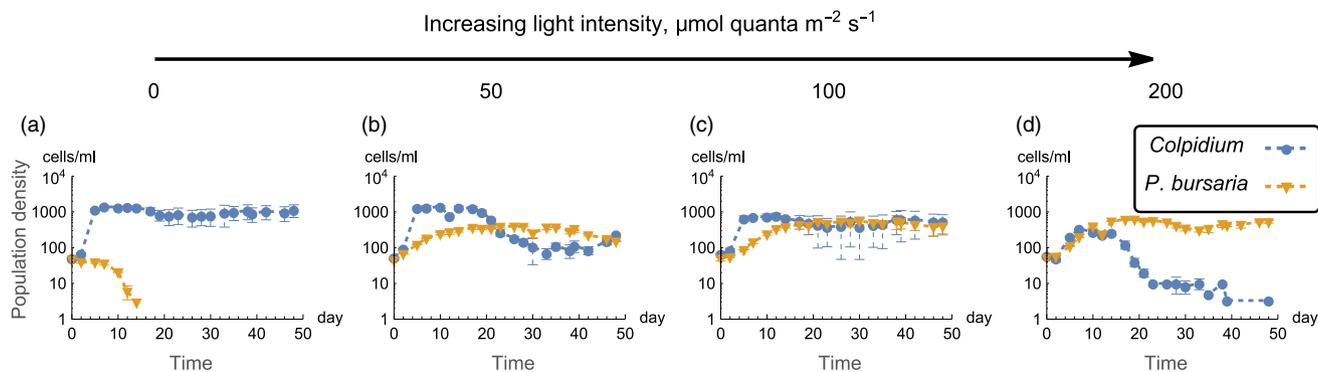
FIGURE 1 Population dynamics of *Colpidium* and *Paramecium bursaria* in competition when simultaneously inoculated on Day 0 at varying light levels at (a) 0 µmol quanta m^{-2} s^{-1}, (b) 50 µmol quanta m^{-2} s^{-1}, (c) 100 µmol quanta m^{-2} s^{-1}, and (d) 200 µmol quanta m^{-2} s^{-1}. As light level increases, *P. bursaria* becomes more numerically dominant, whereas *Colpidium* decreases in abundance and eventually becomes competitively excluded at 200 µmol quanta m^{-2} s^{-1}. Note that population densities were recorded on a logarithmic scale, and error bars represent ± one standard error for replicates.

these dominant morphospecies was to ensure that experimental competition cultures and single-species ("monoculture") flasks contained the same key community members.

To experimentally investigate the role of acquired metabolism in direct competition, we simultaneously inoculated *Colpidium* and *P. bursaria* into experimental microcosms at four light levels: 0, 50, 100, and 200 µmol quanta m^{-2} s^{-1}. On experimental Day 0, triplicate microcosms were established in 50 ml cell tissue culture flasks containing bacterized pellet media and one wheat seed (which provided a long-term carbon source). The target initial concentration for both *Colpidium* and *P. bursaria* was 50 cells/ml. Each microcosm was sampled three times per week to determine ciliate population densities. During sampling, experimental flasks were well mixed, and an aliquot of known volume (50, 100, 200, or 1000 µl) was withdrawn from each microcosm, and the number of individuals of each ciliate was counted using a dissecting microscope. The sample volumes spanned from 50 to 1000 µl because density estimates of the ciliates varied greatly, often up to two orders of magnitude, across experimental treatments and species (Appendix S1: Figure S1). Therefore, we withdrew sufficient sample volume to count at least 50 individuals per experimental flask.

To differentiate between the effects of competition and environmental filtering (e.g., to differentiate between the realized and fundamental niches), we also ran single-species ("monoculture") trials, in which either *Colpidium* or *P. bursaria* were inoculated at an initial concentration of ~50 cells/ml. All other culture conditions and enumeration techniques were as described above. Therefore, our experiment spanned 36 microcosms: 4 light levels × 3 treatments (*Colpidium* only, *P. bursaria* only, competition) × 3 replicates.

All empirical data analysis and plotting were performed using the open-source software package R (R Core Team, 2018) and Wolfram Mathematica 12.1 (Wolfram Research, Inc., 2020).

Light availability determined competitive outcomes

In our experimental system, the competitive dominance of *P. bursaria* increased with increasing light availability (Figure 1). In darkness, *P. bursaria* disappeared from cultures, at intermediate light levels it coexisted with *Colpidium*, and at the highest light level it competitively excluded *Colpidium* (Figure 1). These results were likely to be a function of increased photosynthetic performance by *P. bursaria* with increasing light. In monoculture, we noted that, while *P. bursaria* could not persist in darkness, its growth rate and maximum population size increased with increasing light levels (Figure 2). In our study, we calculated growth rates from linear regression of log-transformed densities versus exponential growth periods of each treatment (Rothhaupt, 1996).

We found evidence for light-dependent competition between the two protists. Although long-term population sizes for *Colpidium* declined more sharply under higher light intensities in monoculture (Appendix S1: Figure S1), when *Colpidium* was in competition with *P. bursaria*, its maximum abundance and growth rate were significantly lower at every light level when compared with monocultures (Tukey's honestly significant difference [HSD] test, $p < 0.05$; Figure 2). *Colpidium* limited the growth of *P. bursaria* by decreasing maximum abundances, but not growth rate (Figure 2). In high-light environments, *P. bursaria* reached higher population
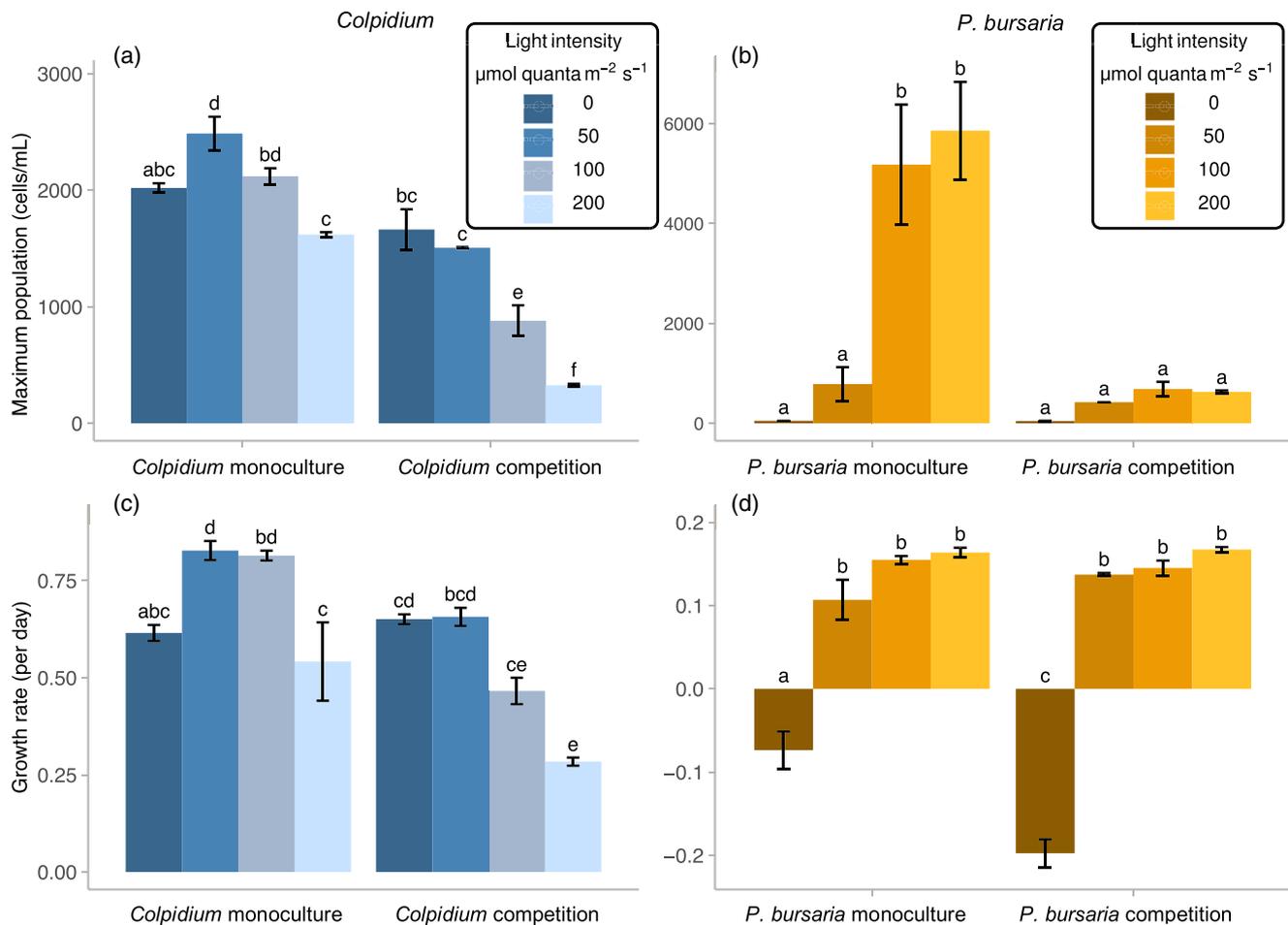
FIGURE 2 Maximum abundances and growth rates calculated over the range of light levels for monoculture and competition treatments, using the species' observed light level response curves shown in Figure 1. Specifically, growth rates calculated from linear regressions of log-transformed densities versus exponential growth periods of each treatment (Rothhaupt, 1996). Different letters represent statistically significant differences at the $p < 0.05$ level (Tukey's honestly significant difference), and error bars represent ± one standard error. (a) Monoculture treatments for *Colpidium* at 200 µmol quanta m^{-2} s^{-1} are significantly lower than at 50 µmol quanta m^{-2} s^{-1}. When comparing *Colpidium* monocultures to direct competition with *Paramecium bursaria*, *Colpidium* has lower maximum abundances at 50, 100 and 200 µmol quanta m^{-2} s^{-1}. (b) *P. bursaria* in the monoculture treatments reach significantly higher maximum population sizes than competition treatments at 100 and 200 µmol quanta m^{-2} s^{-1}, while there was no difference at 0 and 50 µmol quanta m^{-2} s^{-1}. (c, d) *Colpidium* in competition has significantly lower growth rates at 100 and 200 µmol quanta m^{-2} s^{-1} than in monoculture, while for *P. bursaria*, only the growth rate at 0 µmol quanta m^{-2} s^{-1} in competition is lower than in monoculture.

abundances while maintaining similar growth rates as monoculture treatments. These results indicated a negative effect of *Colpidium* on the sustained growth of *P. bursaria* in competition (Appendix S1: Figure S1), which also meant that *P. bursaria* reached maximum population sizes at an earlier time point in competition, compared with monoculture at all light levels, especially at 200 µmol quanta m^{-2} s^{-1} (Appendix S1: Figure S2). Although *Colpidium* had sustained growth across light levels (Appendix S1: Figure S2), Figure 2 demonstrates its suppressed growth rates and maximum population abundances in the competition treatments (Figure 2), especially in high light. As light level increases, *P. bursaria* became capable of competitively excluding its competitor *Colpidium*.

Modeling competitive outcomes

A Lotka–Volterra model for competition between *P. bursaria* and *Colpidium*

To generalize our results to other systems, we sought to use a mathematical model to synthesize our findings into a predictive framework. First, we used a classic Lotka–Volterra representation of competition to fit model dynamics, because this model is widely used to quantify the strength of competition and to predict coexistence and competitive exclusion outcomes. The Lotka–Volterra model accounts for three mechanistic processes: (1) population growth, which incorporates both density-independent birth and

death processes; (2) density dependence, in which increases in the abundance of conspecifics reduce birth rates and increase death rates, causing the population to equilibrate at a "carrying capacity;" and (3) competition, in which the presence of individuals of other species exacerbates density dependence (Lotka, 1932; Volterra, 1926). Competition in this model is implicit: each species can be thought to occupy a portion of the other's carrying capacity. The Lotka–Volterra competition model is commonly written as:

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \alpha_{ij} N_j}{K_i} \right) \tag{1}$$

where N_i is the number (or density) of individuals of species i, r_i is the per capita growth rate when population sizes are small, K_i is the carrying capacity, and a_{ij} is the competition coefficient that scales the effect of species j on species i.

However, the carrying capacity K in the Lotka–Volterra competition model is actually the ratio of density-independent and density-dependent vital rates. To see this relationship, we can decompose the model into these components, with $b_{i,0}$ and $d_{i,0}$ representing density-independent birth and death rates, and $b_{i,1}$ and $d_{i,1}$ representing density-dependent decreases in birth rates or increases in death rates, respectively:

$$\frac{dN_i}{dt} = N_i \left[b_{i,0} - d_{i,0} - (b_{i,1} + d_{i,1})(N_i + \alpha_{ij} N_j) \right] \tag{2}$$

Note that we have incorporated density dependence into both birth and death rates. This is mathematically equivalent after rearrangement (shown below), but represents different biological processes (i.e., inhibition of reproduction in the former case; increased mortality in the latter). The difference between the density-independent birth and death rates $(b_{i,0} - d_{i,0})$ is equal to the per capita growth rate r_i. We use ℓ_i as the density-dependent effect representing the sum of $b_{i,1}$ and $d_{i,1}$. Using the notation P to represent *P. bursaria*, C to represent *Colpidium*, and P and C subscripts to represent species-specific parameters, the equations that describe our two-species system are:

$$\frac{dP}{dt} = P[r_P - \ell_P(P + \alpha_{PC}C)] \tag{3}$$

$$\frac{dC}{dt} = C[r_C - \ell_C(C + \alpha_{CP}P)] \tag{4}$$

Because *P. bursaria* grows both heterotrophically and photosynthetically, we assumed that its growth rate r_P was a function of light. Most phototrophs have a growth

rate that is a saturating function of light, that is, above a certain light intensity, growth rates asymptotically approach a maximum set by other limiting factors (Falkowski & Raven, 2013). We represented *P. bursaria* growth as the sum of a baseline heterotrophic growth rate r_0 and a light-dependent growth acceleration, which approaches a maximum level of r_{max} depending upon the light intensity I and the half-saturation of photosynthesis k:

$$r_P = r_0 + r_{max} \frac{I}{k + I}. \tag{5}$$

Lotka–Volterra model fitting

We used a model-fitting approach to estimate the values of the model's parameters (please refer to Table 1 for a list of parameters, their units and meanings, and their estimated values from our model fits). The parameters were optimized by minimizing the squared differences between the experimental data and the model trajectories. For the optimization, we transformed the population densities X with $Log(X + 1)$ to balance the weighting of early, low abundance data (to accurately estimate growth rate) and late, high abundance data (to accurately estimate density dependence). We estimated confidence intervals for each fit parameter using the likelihood approach described by Jager and Ashauer (2018). The fitting was implemented using Wolfram Mathematica 12.1 (Wolfram Research, Inc., 2020), and code is freely available at DOI: 10.5281/zenodo.5908706.

The Lotka–Volterra model is useful because it captures numerous outcomes of competition: competitive exclusion, coexistence, and alternate states. Given our experimental results, we were especially interested in model transitions from competitive exclusion by *Colpidium*, to coexistence, to competitive exclusion by *P. bursaria* with increasing light. When we simultaneously estimated all parameters in the Lotka–Volterra model using all available data ("One-Stage Fit"; Table 1), we were able to reproduce these dynamics (Appendix S1: Figures S3 and S4). However, the model fit was poor (Akaike information criterion (AIC): 2946, R^2: 0.28), and model estimates of single-species dynamics (i.e., the carrying capacities of *Colpidium* and *P. bursaria*) diverged substantially from the empirical data (Appendix S1: Figure S3).

Therefore, we performed a "Two-Stage Fit" in which we separately estimated parameters obtained from single-species ("monoculture") and two-species ("competition") data. In the first stage, we used monoculture data to estimate the growth rates (r_C and r_P, the latter of which required estimation of r_0, r_{max}, and k) and density-dependent mortality rates

TABLE 1 Model symbols, their meanings, and their estimated values from model fitting for the Lotka–Volterra model (one-stage and two-stage fits, Equations 1–5)

Symbol	Units	Meaning	One-stage estimate (95% CI[a])	Two-stage estimate (95% CI[a])
State variables				
C	$\text{cells}_C\ \text{ml}^{-1}$	*Colpidium* population density	...	...
P	$\text{cells}_P\ \text{ml}^{-1}$	*Paramecium bursaria* population density	...	...
Parameters				
I	$\mu\text{mol quanta m}^{-2}\ \text{s}^{-1}$	Light availability	0, 50, 100, 200	0, 50, 100, 200
r_0	day^{-1}	Light-independent growth rate of *P. bursaria*	−0.12 (−0.14, −0.10)	−0.11 (−0.12, −0.10)
r_{max}	day^{-1}	Maximum photosynthetic growth rate of *P. bursaria*	0.56 (0.50, 0.64)	0.36 (0.33, 0.40)
k	$\mu\text{mol quanta m}^{-2}\ \text{s}^{-1}$	Light level at which *P. bursaria* achieves half its maximum photosynthetic growth rate	54 (45, 72)	49 (40, 60)
r_C	day^{-1}	Growth rate of *Colpidium*	0.92 (0.74, 1.21)	1.1 (0.3, ∞)
l_C	$\text{day}^{-1}\ \text{cells}_C^{-1}\ \text{ml}$	Density-dependent increase in mortality rate of *Colpidium*	1.8×10^{-3} $(1.4 \times 10^{-3}, 2.5 \times 10^{-3})$	2.3×10^{-3} $(1.3 \times 10^{-3}, ∞)$
l_P	$\text{day}^{-1}\ \text{cells}_P^{-1}\ \text{ml}$	Density-dependent increase in mortality rate of *P. bursaria*	3.0×10^{-4} $(2.4 \times 10^{-4}, 3.9 \times 10^{-4})$	3.8×10^{-5} $(2.8 \times 10^{-5}, 5.0 \times 10^{-5})$
α_{CP}	$\text{cells}_C\ \text{cells}_P^{-1}$	Competitive effect of *P. bursaria* on *Colpidium*	0.62 (0.50, 0.80)	0.36 (0.27, 0.48)
α_{PC}	$\text{cells}_P\ \text{cells}_C^{-1}$	Competitive effect of *Colpidium* on *P. bursaria*	0.36 (0.14, 0.60)	3.1 (2.1, 4.1)
Initial conditions				
$C(0)$	$\text{cells}_C\ \text{ml}^{-1}$	Initial *Colpidium* population density	0 or 50	0 or 50
$P(0)$	$\text{cells}_P\ \text{ml}^{-1}$	Initial *P. bursaria* population density	0 or 50	0 or 50

[a]Confidence intervals (CIs) calculated from likelihood profiles as described in Jager and Ashauer (2018).

(ℓ_C and ℓ_P) for both species. In the second stage, we used competition data to estimate the competition coefficients (α_{CP} and α_{PC}). However, our two-stage fit was slightly worse (AIC: 2977, R^2: 0.26), and these simulations failed to predict the coexistence observed at intermediate light levels (Table 1; Appendix S1: Figures S5 and S6). This is confirmed by the model's estimates of the competition parameters α_{CP} and α_{PC}: The most likely product of these competition coefficients is 1.116 (>1), indicating competitive exclusion (aka priority effects; Appendix S1: Figure S6), although we note that the 95% confidence interval for the product of the competition coefficients overlaps with 1 (Appendix S1: Figure S7), indicating equivocal support for competitive exclusion. Neither approach to fitting the Lotka–Volterra model captured the system's initial dynamics (e.g., overshooting and then decline of *Colpidium* in monoculture).

A simplified mechanistic model

In search of improved model fits, we turned to a modeling approach in which we explicitly accounted for two types of resources: bacteria and light (please refer to Table 2 for a list of parameters, their units and meanings, and their estimated values from our model fits. A full derivation of the model's formulation, which accounts for the contributions of carbon (from bacteria and photosynthesis) and nitrogen (from bacteria) to the growth of *Colpidium* and *P. bursaria*, can be found in Appendix S2). In brief, we modeled the change in density of *Colpidium* (C) as the balance between growth due to the consumption of bacteria (f_C) and turnover (m_C):

$$\frac{dC}{dt} = (f_C - m_C)C \qquad (6)$$

TABLE 2 Model symbols, their meanings, and their estimated values from model fitting for the simplified mechanistic model (Equations 6–16)

Symbol	Units	Meaning	Estimate (95% CI[a])	Equations
State variables				
C	cells$_C$ ml^{-1}	*Colpidium* population density	...	6, 15, 16
P	cells$_P$ ml^{-1}	*Paramecium bursaria* population density	...	10, 15, 16
B_1	cells$_B$ ml^{-1}	Bacteria 1 population density	...	8, 9, 12, 13, 15
B_2	cells$_B$ ml^{-1}	Bacteria 2 population density	...	8, 9, 12, 13, 16
Functions				
f_C	cells$_C$ (cells$_C$ day)$^{-1}$	*Colpidium* growth rate	...	6, 7
u_{C,B_1}	cells$_B$ (cells$_C$ day)$^{-1}$	*Colpidium* uptake of bacteria 1	...	7, 8, 15
u_{C,B_2}	cells$_B$ (cells$_C$ day)$^{-1}$	*Colpidium* uptake of bacteria 2	...	7, 9, 16
f_P	cells$_P$ (cells$_P$ day)$^{-1}$	*P. bursaria* growth rate	...	10, 11
u_{P,B_1}	cells$_B$ (cells$_P$ day)$^{-1}$	*P. bursaria* uptake of bacteria 1	...	11, 12
u_{P,B_2}	cells$_B$ (cells$_P$ day)$^{-1}$	*P. bursaria* uptake of bacteria 2	...	11, 13
g	cells$_P$ (cells$_P$ day)$^{-1}$	*P. bursaria* photosynthesis contribution to growth	...	10, 14
Parameters				
I	μmol quanta m^{-2} s^{-1}	Light availability	0, 50, 100, 200	14
y_C	cells$_C$ cells$_B$$^{-1}$	Conversion efficiency of bacteria to *Colpidium*[b]	10^{-7}	7
y_P	cells$_P$ cells$_B$$^{-1}$	Conversion efficiency of bacteria to *P. bursaria*[b]	10^{-7}	11
a_{C,B_1}	ml (cells$_C$ day)$^{-1}$	Attack rate of *Colpidium* on bacteria 1	2.2×10^{-4} (1.7×10^{-4}, 2.9×10^{-4})	8, 9
a_{C,B_2}	ml (cells$_C$ day)$^{-1}$	Attack rate of *Colpidium* on bacteria 2	6.4×10^{-2} (3.5×10^{-2}, 1.2×10^{-1})	8, 9
a_{P,B_1}	ml (cells$_P$ day)$^{-1}$	Attack rate of *P. bursaria* on bacteria 1	3.5×10^{-3} (1.7×10^{-3}, 3.5×10^{-2})	12, 13
a_{P,B_2}	ml (cells$_P$ day)$^{-1}$	Attack rate of *P. bursaria* on bacteria 2	8.3×10^{-3} (4.2×10^{-3}, 1.4×10^{-2})	12, 13
h_C	day (cells$_C$ cells$_B$$^{-1}$)	Handling time of *Colpidium*	1.1×10^{-7} (1.0×10^{-7}, 1.2×10^{-7})	8, 9
h_P	day (cells$_P$ cells$_B$$^{-1}$)	Handling time of *P. bursaria*	3.0×10^{-7} (2.5×10^{-7}, 3.5×10^{-7})	12, 13
m_C	cells$_C$ (cells$_C$ day)$^{-1}$	Biomass turnover of *Colpidium*	0.41 (0.35, 0.47)	6
m_P	cells$_P$ (cells$_P$ day)$^{-1}$	Biomass turnover of *P. bursaria* at no light	0.47 (0.44, 0.52)	10
g_{max}	cells$_P$ (cells$_P$ day)$^{-1}$	Maximal photosynthesis	0.47 ($=m_p$) (0.44, 0.52)	14
k	μmol quanta m^{-2} s^{-1}	Light level at which *P. bursaria* achieves half its maximum photosynthetic growth rate	69 (57, 86)	14
w_1	cells$_B$ ml^{-1} day^{-1}	Rate at which bacteria 1 are generated	9.1×10^8 (6.2×10^8, 1.3×10^9)	15
w_2	cells$_B$ ml^{-1} day^{-1}	Rate at which bacteria 2 are generated	2.9×10^8 (2.0×10^8, 4.0×10^8)	16
δ	cells$_B$ (cells$_B$ day)$^{-1}$	Biomass turnover of bacteria	1.7×10^{-2} (1.2×10^{-2}, 2.2×10^{-2})	15, 16
Initial values				
$C(0)$	cells$_C$ ml^{-1}	Initial *Colpidium* population density	0 or 50	...
$P(0)$	cells$_P$ ml^{-1}	Initial *P. bursaria* population density	0 or 50	...
$B_1(0)$	cells$_B$ ml^{-1}	Initial bacteria 1 population density	w_1/δ	...
$B_2(0)$	cells$_B$ ml^{-1}	Initial bacteria 2 population density	w_2/δ	...

[a]Confidence intervals (CIs) calculated from likelihood profiles as described in Jager and Ashauer (2018).
[b]Estimated from the typical ratio of dry biomass between bacteria and protists (DeLong et al., 2010).

The per capita growth of *Colpidium* due to predation of bacteria (f_C) is the sum of uptake of two species of bacteria. Our model accounts for two types of bacterial prey because this intermediate level of complexity allows us to capture differences in prey preference across the two protists without accounting for all bacterial species present in the system. Such a formulation is consistent with previous studies that have shown that protists differ in bacterial prey preferences (DeLong & Vasseur, 2012; Jiang & Morin, 2004). Therefore, the growth rate of *Colpidium*, f_C, depends upon its consumption (uptake, u) of two pools of bacteria, B_1 and B_2, and the conversion efficiency of bacteria to *Colpidium*, y_C:

$$f_C = y_C(u_{C,B_1} + u_{C,B_2}) \tag{7}$$

Ciliate grazing on bacteria follows a Holling Type II functional response (Fenchel, 1980; Holling, 1959), with a maximum attack rate a_{C,B_1} and a_{C,B_2} for the two bacterial types respectively, and a handling time h_C, that is the same for both bacterial types:

$$u_{C,B_1} = \frac{a_{C,B_1}B_1}{1 + h_C(a_{C,B_1}B_1 + a_{C,B_2}B_2)} \tag{8}$$

$$u_{C,B_2} = \frac{a_{C,B_2}B_2}{1 + h_C(a_{C,B_1}B_1 + a_{C,B_2}B_2)} \tag{9}$$

We formulated the growth of *P. bursaria* (P) similarly, except that this ciliate can also obtain resources through photosynthesis (g). Therefore (using P subscripts to denote species-specific ciliate vital rates) we can describe the change in the density of *P. bursaria* over time as:

$$\frac{dP}{dt} = (f_P - m_P + g)P \tag{10}$$

where:

$$f_P = y_P(u_{P,B_1} + u_{P,B_2}) \tag{11}$$

Hereby the conversion efficiency of bacteria to *P. bursaria* is y_P, and the uptake of each bacteria species is:

$$u_{P,B_1} = \frac{a_{P,B_1}B_1}{1 + h_P(a_{P,B_1}B_1 + a_{P,B_2}B_2)} \tag{12}$$

$$u_{P,B_2} = \frac{a_{P,B_2}B_2}{1 + h_P(a_{P,B_1}B_1 + a_{P,B_2}B_2)} \tag{13}$$

We modeled g, the photosynthetic contribution to growth, as a saturating function of light intensity I (Falkowski & Raven, 2013; Pado, 1965, 1967; Weis, 1974). Specifically, photosynthesis can accelerate growth up to an upper bound g_{max}, with a half-saturation light intensity k:

$$g = g_{max}\frac{I}{k + I} \tag{14}$$

Because *P. bursaria* is obligately heterotrophic (Johnson, 2011; Reisser, 1992), we set $g_{max} = m_P$, such that *P. bursaria* can cover its metabolic costs by photosynthesis but cannot achieve positive growth rates from photosynthesis alone.

Grazing by ciliates feeds back on the population densities of the two pools of bacteria, creating a self-regulating feedback mediated by the depletion of available resources (in this case, bacteria). Because our experimental system included a long-term source of carbon (wheat seeds), we modeled the two bacterial populations as being supplied at the fixed rates w_1 and w_2 respectively. Bacteria are consumed by ciliates according to the uptake functions u_{X,B_i} as described above (where $X = C$ for *Colpidium* grazing and $X = P$ for *P. bursaria* grazing), and also experience per capita turnover at a constant rate δ:

$$\frac{dB_1}{dt} = w_1 - (u_{C,B_1}C + u_{P,B_1}P) - \delta B_1, \tag{15}$$

$$\frac{dB_2}{dt} = w_2 - (u_{C,B_2}C + u_{P,B_2}P) - \delta B_2. \tag{16}$$

## Resource-explicit models recapitulated competition outcomes

As with the Lotka–Volterra formulation, we fit the simplified mechanistic model by minimizing the squared differences between the log-transformed experimental data to the model trajectories. In this case, we fit all treatments and all parameters simultaneously because the mechanistic model has no explicit "competition parameters" that play a role only in the competition experiments (Table 2).

Our resource-explicit model qualitatively recapitulated our empirical findings. In particular, it predicted a transition from heterotroph (*Colpidium*) dominated states, to coexistence, to acquired phototroph (*P. bursaria*) dominated states with increasing light levels (Figure 3). The model also outperformed the Lotka–Volterra formulation statistically (Mechanistic model AIC: 2737 and R^2: 0.44). The AIC difference between the Lotka–Volterra fits and the mechanistic model fits is 208 and 239 for the one-stage and two-stage Lotka–Volterra fits respectively,

indicating that both Lotka–Volterra fits are significantly worse than the mechanistic model fit. Furthermore, the model predicts an increase in terminal population sizes of *P. bursaria* as light level increases (Figure 3), which was also reflected in our empirical findings. Specifically, for monoculture *P. bursaria* experiments, maximum abundances at 100 and 200 µmol quanta m^{-2} s^{-1} were significantly higher than maximum abundances at 50 µmol quanta m^{-2} s^{-1} (Tukey's HSD, $p < 0.05$; Figure 2). However, the model suggests an overshoot in *P. bursaria* populations in monoculture at the two highest light levels before declining to terminal population sizes, which is a qualitative pattern we did not observe in our experiment (Figure 3).

Note that our simulated bacteria abundances can only represent a placeholder for the real resource dynamics because we did not collect data on bacterial abundances over time. Because of these unknown dimensions, our parameter estimates do not represent exact estimates of bacterial vital rates. The model fits are just intended to demonstrate that this type of model can reproduce the observed patterns of protist abundances.

Although bacterial dynamics were poorly constrained empirically, our model's predicted dynamics are consistent with R* theory (Tilman, 1977), in which our protist species with the greatest attack rate drew the bacteria type down to the lowest population size in monoculture (Table 2; Appendix S1: Figures S8 and S9). Except in total
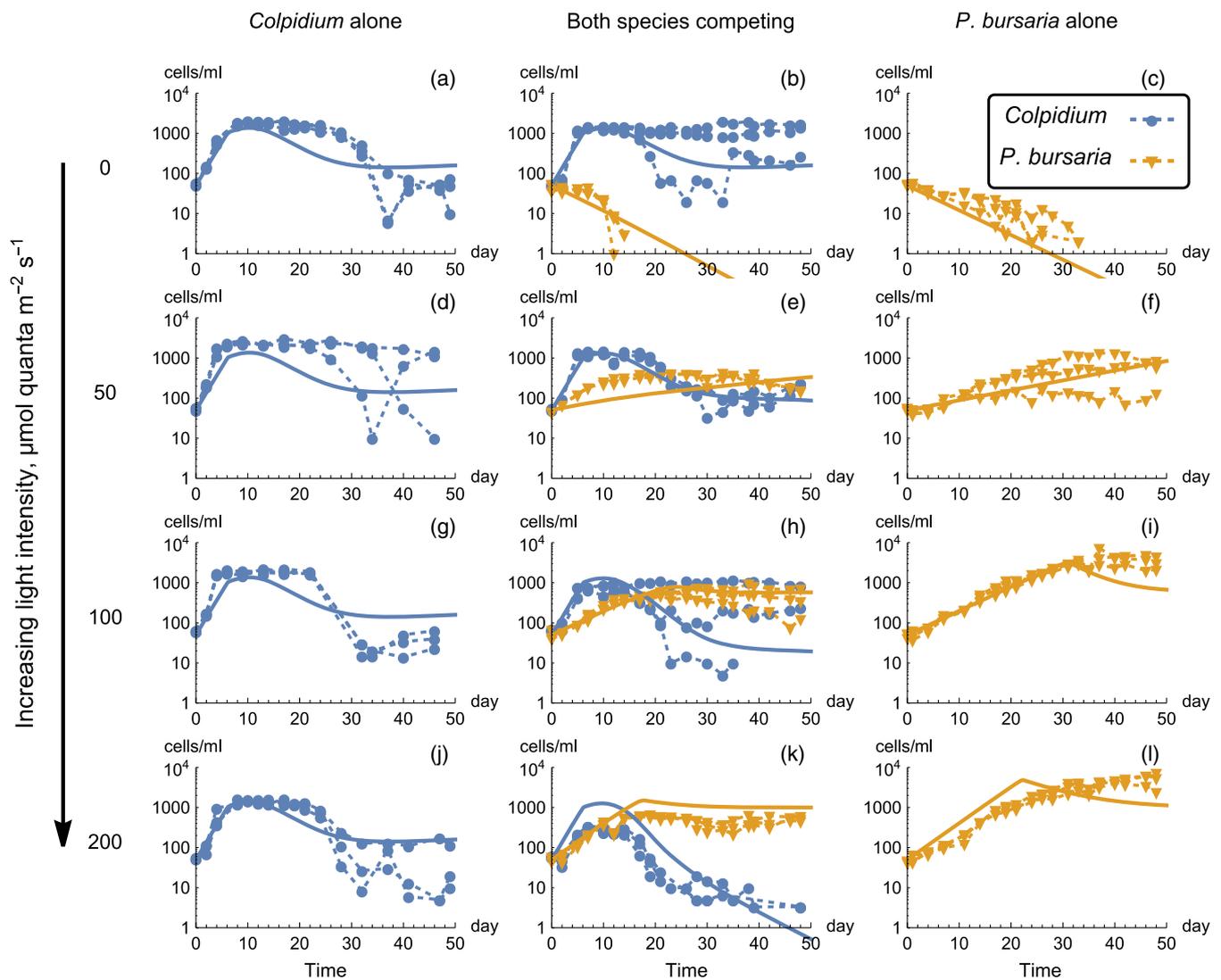
FIGURE 3 Simplified mechanistic model fits (lines) compared with empirical data (points). Please refer to Table 2 for a list of parameters, their units and meanings, and their estimated values from our model fits. Population dynamics of *Colpidium* monocultures (left column), competition cultures (middle column), and *Paramecium bursaria* monocultures (right column) at 0, 50, 100, and 200 µmol quanta m^{-2} s^{-1} light levels (from top to bottom) are shown. Note that the model predicted coexistence at 50 and 100 µmol quanta m^{-2} s^{-1}, which is consistent with experimental findings.

darkness (0 μmol quanta m^{-2} s^{-1}, absence of acquired metabolism) when *P. bursaria* could not obtain sufficient resources to overcome its higher rate of mortality (Table 2), the population of bacteria type 1 was lower in *P. bursaria* monocultures than in *Colpidium* monocultures, and the population of bacteria type 2 was lower in *Colpidium* monocultures. Furthermore, the bacterial populations in "competition" model simulations reflect the trajectories of the bacterial populations in "single-species" simulations for the competitively dominant protists. For example, at 0 μmol quanta m^{-2} s^{-1}, bacterial dynamics in the "competition" simulation are similar to those in the *Colpidium*-only simulation, and at 200 μmol quanta m^{-2} s^{-1}, bacteria reach population sizes similar to those of the *P. bursaria*-only simulations. When coexistence occurred, bacterial populations were a mix of the minimal population sizes shown across the single-species simulations (Appendix S1: Figure S9).

To understand how competitive outcomes depended on acquired metabolism, we generated a bifurcation diagram showing equilibrium population sizes as a function of light availability. Our mechanistic model predicts competitive dominance by *Colpidium* from 0 to 32 μmol quanta m^{-2} s^{-1}, and competitive dominance *P. bursaria* above 108 μmol quanta m^{-2} s^{-1} (Figure 4), consistent with our empirical findings (Figure 3). The model predicts that, as light increases, photosynthesis makes up an increasing proportion of growth strategy for *P. bursaria* due to an increase in photosynthetic contributions, *g* (Figure 4). The equilibrium *P. bursaria* population size increases with light (Figure 4) and, consequently, so does its bacterial uptake (Figure 4). The proportion of photosynthetic growth of *P. bursaria*, which is the ratio of bacterial grazing and photosynthesis, increases with increasing light (Figure 4). Additional light resources allow *P. bursaria* to proliferate, leading to higher consumption of bacteria. Therefore, the extirpation of *Colpidium* at high light levels is driven by the attendant reductions in the bacterial population.

DISCUSSION

Because acquired metabolism enables niche expansion, it can have dramatic effects on the outcomes of competition predicted by niche partitioning. In our system, the acquisition of photosynthetic capacity alleviates competition for bacterial prey resources between *P. bursaria* and *Colpidium* by permitting *P. bursaria* to gain energy from photosynthesis. In high-light environments, this energetic subsidy can give *P. bursaria* enough of a competitive advantage that it excludes *Colpidium*. These findings indicate the significance of non-genomic metabolism to
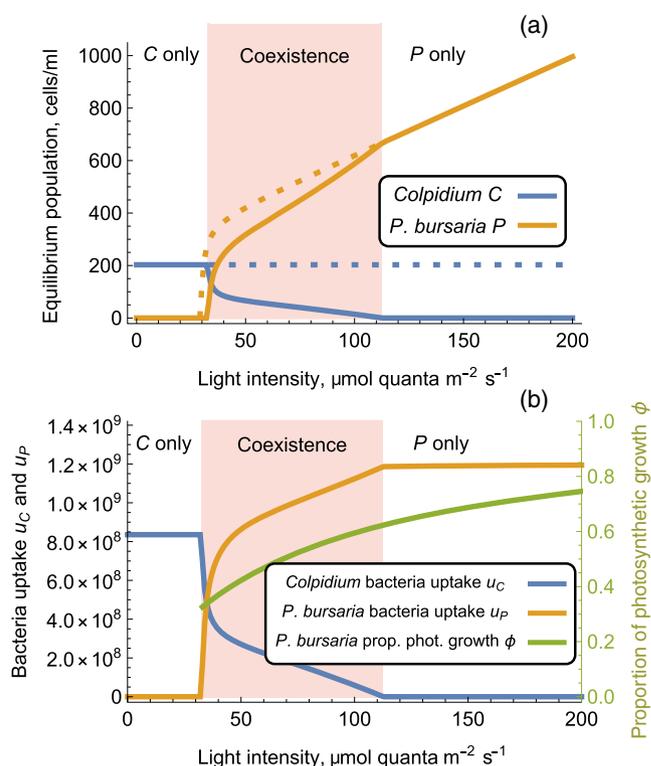
FIGURE 4 Bifurcation of equilibria as a function of light level from 0 to 200 μmol quanta m^{-2} s^{-1} according to the simplified mechanistic model from Figure 3. (a) Equilibria population densities of *Paramecium bursaria* and *Colpidium* across light levels, where dashed lines represent unstable equilibria and the solid line represents stable equilibria. There is species coexistence from 32 to 108 μmol quanta m^{-2} s^{-1}. (b) Uptake of bacteria of *P. bursaria* and *Colpidium* populations, derived from Equations 12 and 13, across increasing light levels. The uptake rates combine the uptake of both bacteria types, $u_C = (u_{C,B_1} + u_{C,B_2})C$ and $u_P = (u_{P,B_1} + u_{P,B_2})P$. Green line represents the proportion of photosynthetic growth φ of *P. bursaria*, which is the ratio of bacterial grazing and photosynthesis, $\phi = \frac{gP}{gP + u_P y_P}$

the outcomes of competition. In protist model systems, other studies have shown that niche partitioning across different bacterial species may allow for coexistence in protists. For example, coexistence of *Colpidium* with *Paramecium tetraurelia* (a heterosporous relative of *P. bursaria*) is primarily due to the differential consumption of heterogeneous bacterial resources (Jiang & Morin, 2004), while *Paramecium aurelia* coexists with *Colpidium* through resource partition of consuming larger bacteria (DeLong & Vasseur, 2012). Our results build on these findings by suggesting that acquired phototrophy allows for coexistence between competitors by means of niche partitioning. The importance of symbionts in competition for resources is also observed in plant communities (Bever et al., 2010). Symbionts, such as mycorrhizal fungi, can allow plants to coexist with

(Smith et al., 1999; van der Heijden, 2003) and competitively exclude other species (Hartnett & Wilson, 1999), or even reverse the outcome of competition (Hetrick et al., 1989). Much like how endosymbionts in *P. bursaria* allows access to light energy, mycorrhizal fungi provide an alternative source of nutrition for plants, changing competition outcomes by means of niche partitioning (Bever et al., 2010).

When we manipulated the value of acquired metabolism by controlling light variability, acquired phototrophs increased in competitive dominance as light availability increased. This appears to occur because light—a resource exclusively available to *P. bursaria* because of its acquired photosynthetic capabilities—subsidizes the growth of *P. bursaria*, increasing its top-down control (via predation) of bacteria. This reduces the bacterial supply for *Colpidium*, which, at the highest light level, is ultimately competitively excluded. Other studies have shown that environmental changes can alter metabolic rates, impacting resource-mediated competition. For example, elevated temperature increases the metabolic requirements of *Colpidium*, with negative effects on competing *P. tetraurelia* (Jiang & Morin, 2007). In phytoplanktonic communities, light-dependent nutrient uptake rates alter competition between phytoplankton and bacteria over the course of daily and seasonal light fluctuations (Kuipers et al., 2000; Litchman et al., 2004). Increases in absolute resource availability can also alter community structure (e.g., the "Paradox of Enrichment" described by Rosenzweig, 1971), and changes in the spatial distribution of resources can permit coexistence among competitors (Amarasekare, 2003). Therefore, our findings add acquired metabolism to a growing list of mechanisms that allow for coexistence of otherwise functionally similar taxa in natural ecosystems.

Our empirical results were well described by our mathematical model, but only when we accounted for the availability of light and prey (bacteria) resources. Therefore, our findings emphasize the importance of an explicit accounting for resource competition, especially when developing theory around acquired metabolism, which is fundamentally linked to niche expansion via extended resource use. Although our model accurately predicted a qualitative shift in competitive dominance from *Colpidium* to *P. bursaria* with increasing light levels, it nonetheless was unable to perfectly capture the quantitative dynamics of our empirical system, especially for *P. bursaria* in monoculture. For example, our model predicts a general increase in equilibrium population sizes to increase with increasing light (Figure 3). While this upward trend is also reflected in the *P. bursaria* monoculture experiments, the maximum populations sizes at 100 and 200 μmol quanta m^{-2} s^{-1} are higher than the

values from the model (Figure 2). Seeing that our model predicts an initial overshoot in population size followed by a decline to equilibrium population sizes, it is possible that, given additional experimental time, *P. bursaria* populations from the monoculture experiments might also decline and persist at a lower carrying capacity more similar to our model's predictions.

A suite of different mechanisms could also account for the resource-based competitive outcomes that we observed in our study. For example, coexistence between the two protist species could also be facilitated by self-shading of *P. bursaria* causing self-limitation of population size. We tested a model variant that accounts for self-shading as described in Huisman & Weissing (1994) (Appendix S3). The fits show that by including self-shading effects, the two protist species can coexist on a single bacteria species. We note, however, that this mechanism was unlikely to be exclusively responsible for the observed coexistence patterns for two reasons: First, even at the highest *P. bursaria* densities, flasks were not visibly green suggesting that densities were still relatively low. Second, occasional measurements of cellular chlorophyll-*a* content (related to other projects; H. V. Moeller, personal communication) showed that *P. bursaria* chlorophyll content did not increase with density, so there was no evidence for a self-shading acclimation response (Flynn & Raven, 2017). Of course, alternative formulations of bacterial dynamics could account for more than two bacterial species and for more complex feedbacks between the protists and the bacterial communities (e.g., production of dissolved organic matter by *P. bursaria* that could accelerate population growth). Critically, coexistence can be observed only when accounting for at least two different resources or other mechanisms that enhance intraspecific competition (and, consequently, self-regulation of population sizes).

In our experiment, we did not measure bacterial abundance or community composition. Therefore, although we inoculated all experiments with the same initial complement of bacteria, we cannot exclude the possibility that our results are driven by more nuanced partitioning of the bacterial community (e.g., preferences among bacterial types by *P. bursaria* and *Colpidium*). Indeed, because of a lack of bacterial data, our model parameterization of bacteria (and its subsequent predictions of bacterial dynamics) is poorly constrained. Studies that quantify bacterial dynamics over time would enable more biologically realistic formulations of bacterial dynamics, and a quantitative evaluation of the various mechanisms proposed above. A better experiment could be to compete chlorotic (symbiont-bearing) *P. bursaria* with apochlorotic (symbiont-lacking) *P. bursaria* (Salsbery & DeLong, 2018) to control for differences in ciliate physiology and ecology.

Our experimental results validated previous work quantifying abundance of phototrophs, mixotrophs, and heterotrophic nanoflagellates in the ocean, which found that mixotrophy is favored relative to specialist strategies with increased irradiance (Edwards, 2019). Due to their competitive success in open oceans, the major limiting factor of mixotrophic success is attributed to availability of light and nutrients rather than competition against heterotrophs or phototrophs (Edwards, 2019). Although our experiments were conducted on freshwater protists, our results showed that competitive outcomes shifted over ecologically relevant light environments. While low latitude, surface water light levels can be much higher (more than 2000 μmol quanta m^{-2} s^{-1}) than our experimental light levels, the transition from competitive exclusion of *P. bursaria* to its competitive dominance occurred over the range of light levels within which its growth was saturated (Figure 2).

In conclusion, our results show that acquired metabolism can affect community dynamics because it allows organisms to expand their niches and alleviate competition of a shared resource through niche partitioning. Indeed, our iterative modeling approach highlights the significance of explicitly accounting for these resources, as a mechanistic way of predicting the outcomes of competition. Environmental conditions also shape resource availability and metabolic requirements (Brown et al., 2004; Salsbery & DeLong, 2018), which leads to varying coexistence and extinction patterns of acquired phototrophs. Acquired phototrophs are present in all water systems and modulate primary production, especially in oligotrophic open oceans (Leles et al., 2017). However, this is just one example of acquired metabolic potential. Acquired metabolism can have profound impacts on community dynamics by accessing metabolic potential not encoded in their own genomes, and therefore highlights their importance and the need for more empirical and theoretical studies of their ecology.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data and code (ferdi-P & Moeller, 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.5908706.

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REFERENCES

Amarasekare, P. 2003. "Competitive Coexistence in Spatially Structured Environments: A Synthesis." *Ecology Letters* 6(12): 1109–22. https://doi.org/10.1046/j.1461-0248.2003.00530.x.

Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. "Rooting Theories of Plant Community Ecology in Microbial Interactions." *Trends in Ecology & Evolution* 25(8): 468–78. https://doi.org/10.1016/j.tree.2010.05.004.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85(7): 1771–89. https://doi.org/10.1890/03-9000.

Chesson, P. 2000. "Mechanisms of Maintenance of Species Diversity." *Annual Review of Ecology and Systematics* 31(1): 343–66. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

DeLong, J. P., J. G. Okie, M. E. Moses, R. M. Sibly, and J. H. Brown. 2010. "Shifts in Metabolic Scaling, Production, and Efficiency across Major Evolutionary Transitions of Life." *Proceedings of the National Academy of Sciences* 107(29): 12941–5.

DeLong, J. P., and D. A. Vasseur. 2012. "Coexistence Via Resource Partitioning Fails to Generate an Increase in Community Function." *PLoS One* 7(1): e30081. https://doi.org/10.1371/journal.pone.0030081.

Edwards, K. F. 2019. "Mixotrophy in Nanoflagellates across Environmental Gradients in the Ocean." *Proceedings of the National Academy of Sciences* 116(13): 6211–20. https://doi.org/10.1073/pnas.1814860116.

Falkowski, P. G., T. Fenchel, and E. F. Delong. 2008. "The Microbial Engines that Drive Earth's Biogeochemical Cycles." *Science (New York, N.Y.)* 320(5879): 1034–9. https://doi.org/10.1126/science.1153213.

Falkowski, P. G., and J. A. Raven. 2013. *Aquatic Photosynthesis*, 2nd ed. Princeton, NJ: Princeton University Press.

Fenchel, T. 1980. "Suspension Feeding in Ciliated Protozoa: Functional Response and Particle Size Selection." *Microbial Ecology* 6(1): 1–11. https://doi.org/10.1007/BF02020370.

ferdi-P, and H. Moeller. 2022. "hollymoeller/Hsu_etal_CompetitionModels: Hsu_etal_CompetitionModels (v1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.5908706.

Flynn, K. J., and J. A. Raven. 2017. "What Is the Limit for Photoautotrophic Plankton Growth Rates?" *Journal of Plankton Research* 39(1): 13–22. https://doi.org/10.1093/plankt/fbw067.

Fox, J., and P. Morin. 2001. "Effects of Intra- and Interspecific Interactions on Species Responses to Environmental Change." *Journal of Animal Ecology* 70(1): 80–90. https://doi.org/10.1111/j.1365-2656.2001.00478.x.

Gause, G. F., and A. A. Witt. 1935. "Behavior of Mixed Populations and the Problem of Natural Selection." *The American Naturalist* 69(725): 596–609.

Gill, D. E., and N. G. Hairston. 1972. "The Dynamics of a Natural Population of Paramecium and the Rôle of Interspecific Competition in Community Structure." *Journal of Animal Ecology* 41(1): 137–51. https://doi.org/10.2307/3509.

González, M. B. R., and J. Gonzalez-López. 2013. *Beneficial Plant-Microbial Interactions: Ecology and Applications*. Boca Raton, FL: CRC Press.

Grinnell, J. 1928. "Presence and Absence of Animals." In *Joseph Grinnell's Philosophy of Nature: Selected Writings of a Western Naturalist*, edited by J. Grinnell, 195–216. Berkeley, CA: University of California Press.

Hardin, G. 1960. "The Competitive Exclusion Principle." *Science* 131(3409): 1292–7. https://doi.org/10.1126/science.131.3409.1292.

Hartnett, D. C., and G. W. T. Wilson. 1999. "Mycorrhizae Influence Plant Community Structure and Diversity in Tallgrass Prairie." *Ecology* 80(4): 1187–95. https://doi.org/10.1890/0012-9658(1999)080[1187:MIPCSA]2.0.CO;2.

Hetrick, B. A. D., G. W. T. Wilson, and D. C. Hartnett. 1989. "Relationship between Mycorrhizal Dependence and Competitive Ability of Two Tallgrass Prairie Grasses." *Canadian Journal of Botany-Revue Canadienne De Botanique* 67: 2608–15.

Hirzel, A. H., and G. Le Lay. 2008. "Habitat Suitability Modelling and Niche Theory." *Journal of Applied Ecology* 45(5): 1372–81. https://doi.org/10.1111/j.1365-2664.2008.01524.x.

Holling, C. S. 1959. "Some Characteristics of Simple Types of Predation and Parasitism." *The Canadian Entomologist* 91(7): 385–98. https://doi.org/10.4039/Ent91385-7.

Holyoak, M., and S. P. Lawler. 2005. "The Contribution of Laboratory Experiments on Protists to Understanding Population and Metapopulation Dynamics." *Advances in Ecological Research* 37: 245–71. https://doi.org/10.1016/S0065-2504(04)37008-X.

Huisman, J., and F. J. Weissing. 1994. "Light-Limited Growth and Competition for Light in Well-Mixed Aquatic Environments: An Elementary Model." *Ecology* 75(2): 507–20. https://doi.org/10.2307/1939554.

Hurlbert, S. H. 1978. "The Measurement of Niche Overlap and Some Relatives." *Ecology* 59(1): 67–77. https://doi.org/10.2307/1936632.

Jager, T., and R. Ashauer. 2018. "Modelling Survival under Chemical Stress: A Comprehensive Guide to the GUTS Framework." Version 1.0, Leanpub. https://leanpub.com/guts_book

Jiang, L., and P. J. Morin. 2004. "Temperature-Dependent Interactions Explain Unexpected Responses to Environmental Warming in Communities of Competitors." *Journal of Animal Ecology* 73(3): 569–76. https://doi.org/10.1111/j.0021-8790.2004.00830.x.

Jiang, L., and P. J. Morin. 2007. "Temperature Fluctuation Facilitates Coexistence of Competing Species in Experimental Microbial Communities." *Journal of Animal Ecology* 76(4): 660–8. https://doi.org/10.1111/j.1365-2656.2007.01252.x.

Johnson, M. D. 2011. "The Acquisition of Phototrophy: Adaptive Strategies of Hosting Endosymbionts and Organelles." *Photosynthesis Research* 107(1): 117–32. https://doi.org/10.1007/s11120-010-9546-8.

Karakashian, M. W. 1975. "Symbiosis in *Paramecium bursaria*." *Symposia of the Society for Experimental Biology* 29: 145–73.

Karakashian, S. J. 1963. "Growth of *Paramecium bursaria* as Influenced by the Presence of Algal Symbionts." *Physiological Zoology* 36(1): 52–68. https://doi.org/10.1086/physzool.36.1.30152738.

Kuipers, B., G. J. van Noort, J. Vosjan, and G. J. Herndl. 2000. "Diel Periodicity of Bacterioplankton in the Euphotic Zone of the Subtropical Atlantic Ocean." *Marine Ecology Progress Series* 201(August): 13–25. https://doi.org/10.3354/meps201013.

Leles, S. G., A. Mitra, K. J. Flynn, D. K. Stoecker, P. J. Hansen, A. Calbet, G. B. McManus, et al. 2017. "Oceanic Protists with Different Forms of Acquired Phototrophy Display Contrasting Biogeographies and Abundance." *Proceedings of the Royal Society B: Biological Sciences* 284(1860): 20170664. https://doi.org/10.1098/rspb.2017.0664.

Levine, J. M., and J. HilleRisLambers. 2009. "The Importance of Niches for the Maintenance of Species Diversity." *Nature* 461(7261): 254–7. https://doi.org/10.1038/nature08251.

Litchman, E., C. A. Klausmeier, and P. Bossard. 2004. "Phytoplankton Nutrient Competition Under Dynamic Light Regimes." *Limnology and Oceanography* 49(4part2): 1457–62. https://doi.org/10.4319/lo.2004.49.4_part_2.1457.

Lotka, A. J. 1932. "The Growth of Mixed Populations: Two Species Competing for a Common Food Supply." *Journal of the Washington Academy of Sciences* 22(16/17): 461–9.

Lowe, C. D., E. J. Minter, D. D. Cameron, and M. A. Brockhurst. 2016. "Shining a Light on Exploitative Host Control in a Photosynthetic Endosymbiosis." *Current Biology* 26(2): 207–11. https://doi.org/10.1016/j.cub.2015.11.052.

MacArthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *The American Naturalist* 101(921): 377–85. https://doi.org/10.1086/282505.

May, R. M., and R. H. MacArthur. 1972. "Niche Overlap as a Function of Environmental Variability." *Proceedings of the National Academy of Sciences* 69(5): 1109–13. https://doi.org/10.1073/pnas.69.5.1109.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. "Rebuilding Community Ecology from Functional Traits." *Trends in Ecology & Evolution* 21(4): 178–85. https://doi.org/10.1016/j.tree.2006.02.002.

Moeller, H. V., E. Peltomaa, M. D. Johnson, and M. G. Neubert. 2016. "Acquired Phototrophy Stabilises Coexistence and Shapes Intrinsic Dynamics of an Intraguild Predator and Its Prey." *Ecology Letters* 19(4): 393–402. https://doi.org/10.1111/ele.12572.

Müller, J. P., C. Hauzy, and F. D. Hulot. 2012. "Ingredients for Protist Coexistence: Competition, Endosymbiosis and a Pinch of Biochemical Interactions." *Journal of Animal Ecology* 81(1): 222–32. https://doi.org/10.1111/j.1365-2656.2011.01894.x.

Ochman, H., J. G. Lawrence, and E. A. Groisman. 2000. "Lateral Gene Transfer and the Nature of Bacterial Innovation." *Nature* 405(6784): 299–304. https://doi.org/10.1038/35012500.

Pado, R. 1965. "Mutual Relation of Protozoans and Symbiotic Algae in *Paramaecium bursaria*. I. the Influence of Light on the Growth of Symbionts." *Folia Biologica* 13(2): 173–82.

Pado, R. 1967. "Mutual Relation of Protozoans and Symbiotic Algae in *Paramaecium bursaria*. II. Photosynthesis." *Acta Societatis Potanicorum Poloniae* 36(1): 97–108.

Park, M. G., M. Kim, and S. Kim. 2014. "The Acquisition of Plastids/Phototrophy in Heterotrophic Dinoflagellates." *Acta Protozzoologica* 53(1): 39–50.

Reisser, W. 1980. "The Metabolic Interactions Between *Paramecium bursaria* Ehrbg. and *Chlorella* Spec. In the *Paramecium bursaria*-Symbiosis." *Archives of Microbiology* 125(3): 291–3. https://doi.org/10.1007/BF00446890.

Reisser, W. 1992. "Endosymbiotic Associations of Algae with Freshwater Protozoa and Invertebrates." In *Algae and Symbioses: Plants, Animlals, Fungi, Viruses, Interactions Explored*, edited by J. Kristiansen and Ø. Moestrup, 1–19. Bristol: Biopress Limited.

Reisser, W., and D.-P. Häder. 1984. "Role of Endosymbiotic Algae in Photokinesis and Photophobic Responses of Ciliates." *Photochemistry and Photobiology* 39(5): 673–8. https://doi.org/10.1111/j.1751-1097.1984.tb03908.x.

Rosenzweig, M. L. 1971. "Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time." *Science* 171(3969): 385–7. https://doi.org/10.1126/science.171.3969.385.

Rothhaupt, K. O. 1996. "Laboratorary Experiments with a Mixotrophic Chrysophyte and Obligately Phagotrophic and Photographic Competitors." *Ecology* 77(3): 716–24. https://doi.org/10.2307/2265496.

RStudio Team. 2018. *RStudio: Integrated Development for R*. Boston, MA: RStudio, PBC. http://www.rstudio.com/.

Salsbery, M. E., and J. P. DeLong. 2018. "The Benefit of Algae Endosymbionts in *Paramecium bursaria* Is Temperature Dependent." *Evolutionary Ecology Research* 19(6): 669–78.

Scott, K. M., and C. R. Fisher. 1995. "Physiological Ecology of Sulfide Metabolism in Hydrothermal Vent and Cold Seep Vesicomyid Clams and Vestimentiferan Tube Worms." *Integrative and Comparative Biology* 35(2): 102–11. https://doi.org/10.1093/icb/35.2.102.

Siegel, R. W. 1960. "Hereditary Endosymbiosis in *Paramecium bursaria*." *Experimental Cell Research* 19(2): 239–52. https://doi.org/10.1016/0014-4827(60)90005-7.

Smith, M. D., D. C. Hartnett, and G. W. T. Wilson. 1999. "Interacting Influence of Mycorrhizal Symbiosis and Competition on Plant Diversity in Tallgrass Prairie." *Oecologia* 121(4): 574–82. https://doi.org/10.1007/s004420050964.

Stoecker, D. K., M. D. Johnson, C. de Vargas, and F. Not. 2009. "Acquired Phototrophy in Aquatic Protists." *Aquatic Microbial Ecology* 57(3): 279–310. https://doi.org/10.3354/ame01340.

Stoecker, D. K., A. E. Michaels, and L. H. Davis. 1987. "Large Proportion of Marine Planktonic Ciliates Found to Contain Functional Chloroplasts." *Nature* 326(6115): 790–2. https://doi.org/10.1038/326790a0.

Tilman, D. 1977. "Resource Competition between Plankton Algae: An Experimental and Theoretical Approach." *Ecology* 58(2): 338–48. https://doi.org/10.2307/1935608.

Tonooka, Y., and T. Watanabe. 2002. "A Natural Strain of *Paramecium bursaria* Lacking Symbiotic Algae." *European Journal of Protistology* 38(1): 55–8. https://doi.org/10.1078/0932-4739-00846.

Vacher, C., A. Tamaddoni-Nezhad, S. Kamenova, N. Peyrard, Y. Moalic, R. Sabbadin, L. Schwaller, et al. 2016. "Chapter One - Learning Ecological Networks from Next-Generation Sequencing Data." In *Advances in Ecological Research*, Vol 54, edited by G. Woodward and D. A. Bohan, 1–39. Cambridge, MA: Academic Press. https://doi.org/10.1016/bs.aecr.2015.10.004.

van der Heijden, M. G. A. 2003. "Arbuscular Mycorrhizal Fungi as a Determinant of Plant Diversity: In Search of Underlying Mechanisms and General Principles." In *Mycorrhizal Ecology*, edited by M. G. A. van der Heijden and I. R. Sanders, 243–65. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-38364-2_10.

Vandermeer, J. H. 1972. "Niche Theory." *Annual Review of Ecology and Systematics* 3(1): 107–32. https://doi.org/10.1146/annurev.es.03.110172.000543.

Volterra, V. 1926. "Variazioni E Fluttuazioni Del Numero D'individui in Specie Animali Conviventi." *Memoria della Reale Accademia Nazionale dei Lincei* 2: 31–113.

Weis, D. S. 1974. "Sparing Effect of Light on Bacterial Consumption of *Paramecium bursaria*." *Transactions of the American Microscopical Society* 93(1): 135–40. https://doi.org/10.2307/3225232.

Wolfram Research, Inc. 2020. *Mathematica, Version 12.2*. Champaign, IL: Wolfram Research, Inc.

Zientz, E., T. Dandekar, and R. Gross. 2004. "Metabolic Interdependence of Obligate Intracellular Bacteria and Their Insect Hosts." *Microbiology and Molecular Biology Reviews* 68(4): 745–70. https://doi.org/10.1128/MMBR.68.4.745-770.2004.

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