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E-Article

Mechanistic Models of Trophic Interactions: Opportunities for Species Richness and Challenges for Modern Coexistence Theory

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abstract: Many potential mechanisms promote species coexistence, but we know little about their relative importance. To compare multiple mechanisms, we modeled a two-trophic planktonic food web based on mechanistic species interactions and empirically measured species traits. We simulated thousands of possible communities under realistic and altered interaction strengths to assess the relative importance of three potential drivers of phytoplankton and zooplankton species richness: resource-mediated coexistence mechanisms, predator-prey interactions, and trait trade-offs. Next, we computed niche and fitness differences of competing zooplankton to obtain a deeper understanding of how these mechanisms determine species richness. We found that predator-prey interactions were the most important driver of phytoplankton and zooplankton species richness and that large zooplankton fitness differences were associated with low species richness, but zooplankton niche differences were not associated with species richness. However, for many communities we could not apply modern coexistence theory to compute niche and fitness differences of zooplankton because of conceptual issues with the invasion growth rates arising from trophic interactions. We therefore need to expand modern coexistence theory to fully investigate multitrophic-level communities.

Keywords: species richness, coexistence, ecological modeling, community assembly, food web.

Introduction

When Hutchinson coined the term “paradox of the plankton,” he was emphasizing that plankton all seem to belong to the same niche, at least to a naive observer, yet hundreds of plankton species appear to coexist (Hutchinson 1959). But 60 years of research has produced a long list of the different limiting factors that could promote stable coexistence in plankton communities and the diversity of primary producers in general. For example, different species may be limited by different resources, such as light, nitrogen, or phosphorus (Litchman et al. 2007; Litchman and Klausmeier 2008; Edwards et al. 2011; Kraft et al. 2015). Alternatively, different species could be limited by different predators or pathogens (Janzen 1970; Olff and Ritchie 1998; Bagchi et al. 2014; Becerra 2015; Ehrlich et al. 2020) or could adopt different strategies for dealing with generalist enemies, as in the growth-defense trade-off (Finkel et al. 2010; Lind et al. 2013; Branco et al. 2020). Finally, some mechanisms depend on external environmental fluctuations (Litchman 2003; Letten et al. 2018; Ellner et al. 2019; Zepeda and Martorell 2019) or internally generated biotic fluctuations (Huisman et al. 2006); a well-known example is the gleaner-opportunist trade-off (Litchman and Klausmeier 2001; Kiørboe et al. 2018). In a sense, we now may have too many explanations for diversity rather than too few, as we know little about the relative importance of all of these mechanisms (Shoemaker et al. 2020*a*).

Modern coexistence theory is a general framework designed to quantify and compare the strength of multiple mechanisms maintaining species richness (Chesson 2000; Carroll et al. 2011; Barabás et al. 2018; Ellner et al. 2019; Spaak and De Laender 2020; Spaak et al. 2021*c*). However, modern coexistence theory predominantly focuses on species within a single trophic level, either competing

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for abiotic resources or modeled with phenomenological interactions (Narwani et al. 2013; Godoy and Levine 2014; Germain et al. 2016). While some theoretical work exists on competition for biotic resources, typically modeled with logistic growth rates (Chesson 1990; Chesson and Kuang 2008; Letten et al. 2017), these biotic resources never have interactions with other resources or compete among themselves for resources at a lower trophic level. Additionally, modern coexistence theory is often applied to models with phenomenological species interactions (Germain et al. 2016; Chesson 2018; Pérez-Ramos et al. 2019; but see Letten and Stouffer 2019; Shoemaker et al. 2020*a*; Spaak and De Laender 2021; Spaak et al. 2021*a*). Consequentially, we have only limited understanding of the drivers and mechanisms of species coexistence in communities with multiple trophic levels and mechanistic species interactions (Godoy et al. 2018).

Originally, modern coexistence theory was developed to better understand the importance of fluctuation-dependent coexistence mechanisms (Chesson 1994; Chesson and Huntly 1997). It distinguishes fluctuation-dependent from fluctuation-independent mechanisms and further decomposes the fluctuation-dependent mechanisms into storage effect, relative nonlinearity, and growth-density covariance (Chesson 2003; Barabás et al. 2018) or other components of interest (Ellner et al. 2019). However, empirical applications of modern coexistence theory investigating both fluctuation-dependent and fluctuation-independent mechanisms tend to show that fluctuation-independent mechanisms are stronger than fluctuation-dependent mechanisms (Chu and Adler 2015; Zepeda and Martorell 2019; Shoemaker et al. 2020*b*). Further decomposition of the fluctuation-independent term into contributions from specific biological mechanisms, such as resource-mediated (Tilman et al. 1982) or predator-mediated (Chesson and Kuang 2008) niche differences, would be informative but is possible only when competition is modeled mechanistically rather than phenomenologically.

In this article, we investigate the relative importance of resource- and predator-mediated coexistence mechanisms for phytoplankton and zooplankton species richness in an empirically parameterized model for an aquatic food web consisting of nutrients, phytoplankton, and zooplankton. We then ask whether modern coexistence theory—specifically the quantification of niche and fitness differences—helps us to understand our results or leads to additional insights that we would not otherwise have obtained. We chose planktonic food webs for our model system because the mechanisms of how phytoplankton compete for resources and how zooplankton graze on phytoplankton are well understood and have been studied and modeled for many decades (e.g., Tilman et al. 1982; Brun et al. 2017). Additionally, the models can be parameterized empirically using databases of measured phytoplankton and zooplankton traits. Using these trait databases, we can generate a species pool consisting of many thousands of hypothetical phytoplankton and zooplankton species and then search for generalities as opposed to special cases (Litchman and Klausmeier 2008; Litchman et al. 2013). Understanding planktonic food webs is also practically important, as they form the basis of every aquatic food web and are responsible for roughly 50% of the world's primary production (Field 1998).

To investigate the relative importance of resource- versus predator-mediated coexistence mechanisms for these simulated communities, we manipulated species traits and observed the resulting changes in phytoplankton and zooplankton species richness. Intuitively, if predator-mediated coexistence mechanisms are driving species richness, then changes to traits governing predator-mediated coexistence mechanisms should strongly affect species richness. Conversely, if changes to traits driving predation have no effect on species richness, we will conclude that predator-mediated coexistence mechanisms are not driving species richness. Specifically, we manipulated traits in two ways. First, we (independently) altered the underlying mean and variance of all 15 trait distributions (nine phytoplankton traits, four zooplankton traits, and two joint traits) to understand how these traits individually influenced species richness. Second, we altered all of the 42 possible trait-trait correlations (36 phytoplankton traits, six zooplankton traits, and no joint traits) to understand which trade-offs are most important for coexistence. Because several traits and trait correlations are critical to resource- and/or predator-mediated coexistence mechanisms, this allowed us to explore the importance of some coexistence mechanisms for species richness (for specific expectations, see tables 1, S1). We found in these two trait manipulations that species richness was primarily driven by the trophic interaction between phytoplankton and zooplankton. Competition of phytoplankton for nutrients was less important for phytoplankton species richness. Finally, when we applied methods from modern coexistence theory to gain a more general understanding of the drivers of species richness, we found that in many cases we could not compute invasion growth rates even in two-species communities. Often, one of two coexisting zooplankton species could not survive without its "competitor" zooplankton, a phenomenon known from obligatory mutualists but new to competitive interactions. This led to an unexpected third objective: under which conditions can the methods of modern coexistence theory be applied to multitrophic communities? We found that even for simple communities consisting of two phytoplankton and two zooplankton species, modern coexistence theory is often not be applicable because

Table 1: Summary of model notation and allometric scalings of plankton traits (Finkel et al. 2010; Brun et al. 2017; Ehrlich et al. 2020)

Variable	Description	Unit	Allometric scaling
Environment:			
d	Dilution rate	day^{-1}	…
S_N, S_P	Resource supply	μmol L^{-1}	…
I	Incoming light	μmol quanta m^{-2} s^{-1}	…
z_m	Epilimnion depth	m	…
Phytoplankton traits:			
μ_i^P	Maximum growth rate	day^{-1}	$\sim (V_i^P)^{-.25}$
k_{iP}^P, k_{iN}^P	Half-saturation constant for N and P	μmol L^{-1}	$\sim (V_i^P)^{.5}$
c_{iP}, c_{iN}	Resource uptake	μmol cell^{-1} day^{-1}	$\sim (V_i^P)^{.667}$
a_i	Absorption coefficient	mm^2 cell^{-1}	$\sim (V_i^P)^{.77}$
k_{iL}^P	Half-saturation constant for light	μmol quanta m^{-2} s^{-1}	$\sim (V_i^P)^{-.08}$
w_i^P	Nutritional value of phytoplankton	μmol cell^{-1}	$\sim (V_i^P)^{.80}$
e_i^P	Edibility of phytoplankton	1	$\sim (V_i^P)^{-.21}$
Zooplankton traits:			
μ_j^Z	Maximum growth rate	day^{-1}	…
c_j^Z	Clearance rate	mL h^{-1} ind^{-1}	$\sim (V_j^Z)^{1.0}$
m_j^Z	Mortality rate	day^{-1}	$\sim (V_j^Z)^{.092}$
k_j^Z	Half-saturation constant for nutrients	μmol R ind^{-1} h^{-1}	$\sim (V_j^Z)^{1.0}(\mu_j^Z)^{1.0}$
Joint traits:			
h_{ji}	Handling time	h cell^{-1} ind	$\sim (V_i^P)^{1.0}(V_j^Z)^{-.61}$
s_{ji}	Selectivity	1	See text
Other variables:			
N_i^P	Phytoplankton density	cells mL^{-1}	…
V_i^P	Phytoplankton biovolume	μm^3	…
N_j^Z	Zooplankton density	ind L^{-1}	…
V_j^Z	Zooplankton size	mg C	…

invasion growth rates of the zooplankton species are not always defined.

Methods

Growth Dynamics

We modeled an aquatic food web with two trophic levels, phytoplankton and zooplankton (fig. 1). We did not consider higher trophic levels because we lacked empirical data for their parametrization. We use superscript "P" for phytoplankton-related terms and a superscript "Z" for zooplankton-related terms. Additionally, a subscript i indicates the identity of a focal phytoplankton species, n is a summation index of phytoplankton species, and j indicates the identity of a zooplankton species. Notation for the model is defined in the text and summarized in table 1.

We assume that phytoplankton compete for the essential resources nitrogen, phosphorus, and light, all of which influence their growth (Tilman et al. 1982; Huisman and Weissing 1994). The equations for these three essential resources are, respectively,

$$G_{iN}^P(R_N) = \frac{R_N}{R_N + k_{iN}^P}, \tag{1}$$

$$G_{iP}^P(R_P) = \frac{R_P}{R_P + k_{iP}^P}, \tag{2}$$

$$I(s) = I(0)\exp\left(-s\sum_n a_n N_n^P\right), \tag{3}$$

$$\begin{aligned} G_{iL}^P &= \int_0^{z_m} \frac{I(s)}{I(s) + k_{iL}^P}\, ds \\ &= \frac{\mu_i^P}{z_m \sum_n a_n N_n^P} \\ &\quad \times \log\left(\frac{k_{iL}^P + I(0)}{k_{iL}^P + I(0)\exp(-z_m \sum_n a_n N_n^P)}\right), \end{aligned} \tag{4}$$

$$G_i^P = \mu_i^P \min(G_{iN}^P, G_{iP}^P, G_{iL}^P), \tag{5}$$

where G_{iN}^P, G_{iP}^P, and G_{iL}^P correspond to the growth rate of the phytoplankton if they were limited by nitrogen, phosphorus, or light. The terms $G_{iN}^P(R_N)$ and $G_{iP}^P(R_P)$ are Holling type 2 responses to the resource concentration of nitrogen (R_N; μmol L^{-1}) and phosphorus (R_P) with half-saturation constant k_{iN}^P (μmol L^{-1}) and k_{iP}^P, respectively. Similarly, light-limited growth at depth s (m) is a Holling

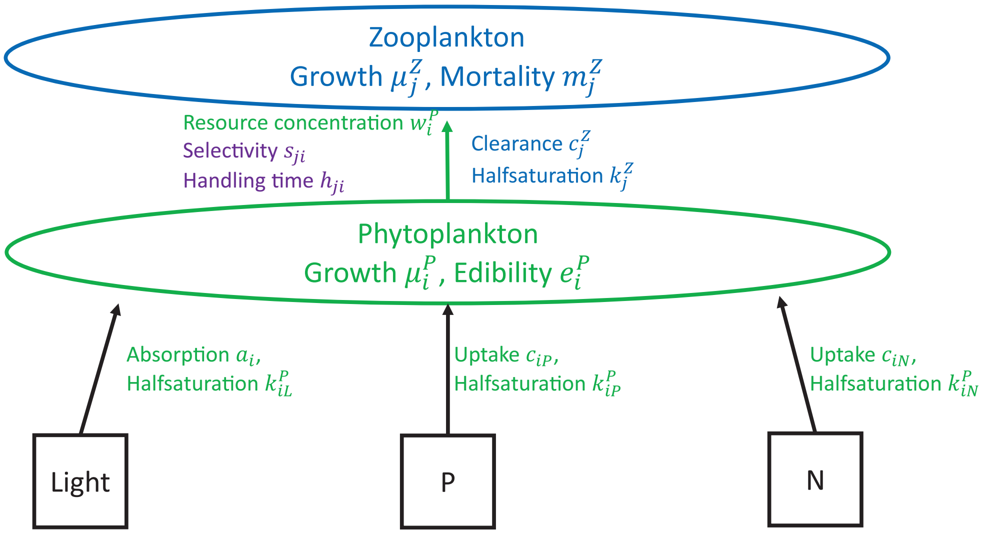

Figure 1: Each phytoplankton species consumes three essential resources: light, phosphorus, and nitrogen. Their growth rates saturate in resource availability (Holling type 2). The growth rates of the phytoplankton are governed by resource uptake traits (a_i, $c_{i\mathrm{N}}$, and $c_{i\mathrm{P}}$), half-saturation constants ($k_{i\mathrm{L}}$, $k_{i\mathrm{P}}$, and $k_{i\mathrm{N}}$), and their maximum growth rates μ_i^{P}. The consumption of phytoplankton is governed by their edibility e_i^{P}, the zooplankton's clearance rate c_j^{Z}, the handling time h_{ji}, and the selectivity s_{ji}, which depend on the identity of both each phytoplankton and each zooplankton species. Given this consumption, the zooplankton growth rate is governed by the resource concentration of the phytoplankton w_i^{P}, the half-saturation constant k_j^{Z}, and the maximum growth rate μ_j^{Z} of the zooplankton. Finally, each zooplankton has a mortality rate m_j.

type 2 response to the light availability $I(s)$, which depends exponentially on the depth s and the light absorption coefficient a_i of species i (mm^2 cell^{-1}). The overall light-limited growth is the integral over the total mixing depth or epilimnion depth z_{m} (Huisman and Weissing 1994). The term $I(0)$ is the incoming light intensity at surface level (μmol quanta m^{-2} s^{-1}). The actual growth rate of the phytoplankton G_i^{P} is the minimum of these three resource-specific growth rates multiplied by the maximum growth rate μ_i^{P} (day^{-1}).

The resource dynamics are given by

$$\frac{dR_{\mathrm{N}}}{dt} = d(S_{\mathrm{N}} - R_{\mathrm{N}}) - \sum_n c_{n\mathrm{N}} G_n^{\mathrm{P}} N_n^{\mathrm{P}}, \tag{6}$$

$$\frac{dR_{\mathrm{P}}}{dt} = d(S_{\mathrm{P}} - R_{\mathrm{P}}) - \sum_n c_{n\mathrm{P}} G_n^{\mathrm{P}} N_n^{\mathrm{P}}, \tag{7}$$

where the first term corresponds to the influx of new nutrients and the second term corresponds to the uptake of resources by phytoplankton. The term d is the dilution rate of the system (day^{-1}), S_{N} and S_{P} are the incoming resource concentrations of nitrogen and phosphorus (μmol L^{-1}), $c_{n\mathrm{N}}$ and $c_{n\mathrm{P}}$ are the maximal resource uptake traits for nitrogen and phosphorus (μmol cell^{-1} day^{-1}), and N_n^{P} is the density of phytoplankton (cells mL^{-1}). The phytoplankton consume only the resources used directly for growth; we exclude any internal storage of resources, or, equivalently, we assume that the internal resource dynamics of the phytoplankton are fast, so that internal resource store is a function of the current nutrient uptake rate. There is no corresponding equation for light dynamics, as light is not stored in the water like nitrogen and phosphorus resources are. Rather, the current light level depends on the incoming light intensity $I(0)$ and the depth of the water column (Huisman and Weissing 1994); this is captured in equation (4).

The zooplankton consume the phytoplankton. Each zooplankton has a clearance rate c_j^{Z}, which describes the rate at which it searches for phytoplankton (mL h^{-1} ind^{-1}). Zooplankton select for phytoplankton on the basis of their size, described by a selectivity coefficient s_{ji} (dimensionless). Zooplankton j therefore encounter a phytoplankton i at rate $c_j^{\mathrm{Z}} s_{ji} N_i^{\mathrm{P}}$, which are handled in time h_{ji} (h cell^{-1} ind). Additionally, certain phytoplankton are defended, making them less edible and harder to digest, represented by dimensionless edibility coefficient e_i^{P} (Ehrlich et al. 2020). A zooplankton consumes phytoplankton at rate (Branco et al. 2020)

$$C_{ji}^{\mathrm{Z}}(N_i^{\mathrm{P}}) = e_i^{\mathrm{P}} \frac{c_j^{\mathrm{Z}} s_{ji} N_i^{\mathrm{P}}}{1 + \sum_n c_j^{\mathrm{Z}} h_{jn} s_{jn} N_n^{\mathrm{P}}}. \tag{8}$$

The dynamics of phytoplankton are given by

$$\frac{dN_i^{\mathrm{P}}}{dt} = N_i^{\mathrm{P}} G_i^{\mathrm{P}} - \sum_j C_{ji}^{\mathrm{Z}}(N_i^{\mathrm{P}}) N_j^{\mathrm{Z}} - dN_i^{\mathrm{P}}, \tag{9}$$

where the three terms stand for growth, grazing, and dilution of the system.

Zooplankton take up resources via consumption, so resource uptake depends on the nutritional value w_n^{P} of the phytoplankton (μmol R cell^{-1}). The term w_n^{P} denotes the general nutritional value of the phytoplankton, and we do not distinguish between phosphorus, nitrogen, or other potentially limiting resources. We assume that the nutritional value of phytoplankton does not depend on external nutrient concentrations, as the stoichiometry of the phytoplankton is approximately constant. Rather, external nutrient concentrations only affect phytoplankton growth rates. The zooplankton growth rate is a Holling type 2 response to the nutrient intake, which is given by the amount of phytoplankton consumed ($C_{jn}^{\mathrm{Z}}(N_n^{\mathrm{P}})$) multiplied by the nutrient concentration w_n^{P} (μmol cell^{-1}) of said phytoplankton species, that is,

$$\frac{dN_j^{\mathrm{Z}}}{dt} = \mu_j^{\mathrm{Z}} N_j^{\mathrm{Z}} \frac{\sum_n w_n^{\mathrm{P}} C_{jn}^{\mathrm{Z}}(N_n^{\mathrm{P}})}{k_j^{\mathrm{Z}} + \sum_n w_n^{\mathrm{P}} C_{jn}^{\mathrm{Z}}(N_n^{\mathrm{P}})} - m_j^{\mathrm{Z}} N_j^{\mathrm{Z}}, \tag{10}$$

where N_j^{Z} is the density of zooplankton (ind L^{-1}), μ_j^{Z} is the maximum growth rate of zooplankton (day^{-1}), k_j^{Z} is the half-saturation constant for zooplankton growth (μmol R ind^{-1} h^{-1}), and m_j^{Z} is the mortality rate of zooplankton j (day^{-1}).

Allometric Scaling and Parameter Definitions

The nine phytoplankton traits (μ_i^{P}, $c_{i\mathrm{N}}$, $c_{i\mathrm{P}}$, $k_{i\mathrm{N}}^{\mathrm{P}}$, $k_{i\mathrm{P}}^{\mathrm{P}}$, $k_{i\mathrm{L}}^{\mathrm{P}}$, a_i, w_i^{P}, e_i^{P}) and the four zooplankton traits (μ_j^{Z}, m_j^{Z}, c_j^{Z}, k_j^{Z}) were randomly drawn from a multivariate lognormal distribution fitted to empirical data. All of the multivariate lognormal distributions were fitted to empirical data from the literature (Uye 1982; Agustí 1991; Edwards et al. 2012, 2015; Brun et al. 2017; Ehrlich et al. 2020). For each trait T, we first fitted a lognormal distribution to the empirically measured data, fitting mean μ_T and standard deviation σ_T, that is, $\log(T) \sim \mathcal{N}(\mu_T, \sigma_T)$ (figs. S9, S10, diagonal). Unfortunately, the datasets did not contain sufficient data points to empirically estimate many of the correlations between the log distribution of the traits.

Therefore, we estimated the correlation of the lognormal trait distributions using allometric scaling. Importantly, where empirical data on the trade-offs were available, the estimates through allometric scaling aligned well with the empirically measured trade-offs. We compiled allometric scaling parameters for each of the traits (Litchman et al. 2007; Finkel et al. 2010; Brun et al. 2017; Ehrlich et al. 2020), that is, $\log(T) \sim \beta_T \log(V)$, where V is the volume of the phytoplankton or zooplankton. We then computed the correlation between two traits T_1 and T_2 as

$$\rho(\log(T_1), \log(T_2)) = \beta_{T_1} \beta_{T_2} \frac{\sigma_V^2}{\sigma_{T_1} \sigma_{T_2}}, \tag{11}$$

where σ_V is the standard deviation of $\log(V)$.

Given the correlation matrix ρ of log plankton traits, we computed the covariance matrix $\Sigma = \sigma \rho \sigma^T$, where σ is the vector of standard deviations of the log trait distributions. The log plankton traits were assumed to have a multivariate normal distribution with mean μ_T and covariance matrix Σ. We used one multivariate normal distribution for the log of the nine phytoplankton traits (μ_i^{P}, $c_{i\mathrm{N}}$, $c_{i\mathrm{P}}$, $k_{i\mathrm{N}}^{\mathrm{P}}$, $k_{i\mathrm{P}}^{\mathrm{P}}$, $k_{i\mathrm{L}}^{\mathrm{P}}$, a_i, w_i^{P}, e_i^{P}) and another for the four zooplankton traits (μ_j^{Z}, m_j^{Z}, c_j^{Z}, k_j^{Z}). For the half-saturation constant k_j^{Z} we found that $k_j^{\mathrm{Z}} = q_j^{\mathrm{Z}} \mu_j^{\mathrm{Z}}$, where q_j^{Z} is the minimal resource concentration of zooplankton j (μmol R mg C^{-1}; see sec. S2 of the supplemental PDF).

The joint traits h_{ji} and s_{ji} were defined via the body sizes of the phytoplankton and zooplankton species. Empirical data show that the handling time h_{ji} and the selectivity s_{ji} depended on the traits of both species in a phytoplankton-zooplankton pair and therefore could not be determined with the above-described method. Empirically, the handling time decreases with zooplankton size and increases with phytoplankton size and was defined as $\log(h_{ji}) = \alpha_h + 1.0 \log(V_i^{\mathrm{P}}) - 0.61 \log(V_j^{\mathrm{Z}})$ (Uye 1982; Branco et al. 2020). Selectivity s_{ji} was a decreasing function of the difference between phytoplankton size and preference of size by zooplankton. We set the size preference of the zooplankton to $V_{\mathrm{pref}} = \mu_{V_i^{\mathrm{P}}} / \mu_{V_j^{\mathrm{Z}}} \approx 322\ \mu\mathrm{L} / 2.61 \times 10^6\ \mu\mathrm{L} \approx 1/20^3$; that is, a zooplankton of mean size would prefer phytoplankton of mean size. This is close to the empirical measurement in the copepod *Acartia tonsa*, which has a size preference of $1/40^3$ (Berggreen et al. 1988). Given this, we defined the relative selectivity of zooplankton to be

$$s'_{ji} = \exp\left(-\frac{(V_i^{\mathrm{P}} - V_{\mathrm{pref}} V_j^{\mathrm{Z}})^2}{2\sigma_s^2}\right), \tag{12}$$

where σ_s is the selectivity breadth, which was set to $\sqrt{0.5}$ in accordance with the theoretical estimates of Branco et al. (2020). We then normalized these relative selectivities such that their total for each zooplankton is 1, that is, $s_{ji} = s'_{ji} / \sum_n s'_{ji}$.

Simulations

To assess the relative importance of trophic interactions, resource competition, and trait trade-offs for phytoplankton and zooplankton species richness, we conducted simulations that mimic community assembly in which each year one new phytoplankton and zooplankton species try to invade. To do so we first generated 1,000 species pools each consisting of 20 phytoplankton and 20 zooplankton species. For each species pool, we started community assembly with one randomly chosen phytoplankton species at its monoculture equilibrium density and one randomly chosen zooplankton species at low density. We then simulated the community dynamics over time for one year, removed any species that became extinct (below 0.01% of total community biomass), and then introduced one new phytoplankton and zooplankton species at low density. All simulations were performed in Python 3.8.5, and all scripts are available in Zenodo (https://doi.org/10.5281/zenodo.7462012; Spaak 2022). Our analyses are based on the resulting species richness after 20 years (longer times did not increase species richness; supplemental PDF, sec. S1; fig. S1). Strictly speaking, we assessed co-occurrence rather than coexistence, as we simply observed the presence of species at the end of the simulation. We assessed co-occurrence because the invasion approach typically used in modern coexistence theory to assess coexistence was not feasible, as often the subcommunities with one species removed did not form a stable equilibrium, so that computing invasion growth rates was not possible (see "Niche and Fitness Differences" below).

We assessed the importance of the drivers of species richness by simulating community assemblies of plankton with altered traits. Specifically, we independently altered the mean μ_T, the standard deviation σ_T, or the correlation $\rho(T_1, T_2)$ of the multivariate log distribution of the traits. Generally, increasing or decreasing the mean μ_T of a trait can affect the strength of the mechanism governed by the specific trait (e.g., resource competition for resource uptake traits or predator-mediated effects for the attack rate). For example, decreasing the mean of the half-saturation constant for nitrogen growth $k_{i\mathrm{N}}^{\mathrm{P}}$ will make all species more nitrogen adapted, hence making nitrogen competition less important. Increasing the standard deviation σ_T of a trait increases the variation of that trait across species, potentially increasing fitness differences (e.g., in the case of μ_i^{P}, μ_j^{P}, and m_j^{P}) but also potentially creating new niches (e.g., in the case of s_{ji}). For example, increasing the standard deviation of edibility e_i^{P} will increase the difference between the most edible and least edible species but might also increase the strength of growth-defense trade-offs. Altering the correlation between two traits will affect the strength of the corresponding trade-off. However, we want to emphasize that we did not have a priori expectations about how all of the trait changes would affect phytoplankton or zooplankton species richness. Instead, we explored all of the possibilities to ensure we found the correlations with the strongest effects (e.g., $\rho(w_i^{\mathrm{P}}, \mu_i^{\mathrm{P}})$) as well as those that differ from our expectations (e.g., $\rho(c_{i\mathrm{N}}^{\mathrm{P}}, c_{i\mathrm{P}}^{\mathrm{P}})$). For an overview of all expectations and the underlying intuition, see tables S1–S3.

We increased or decreased μ_T by 1 standard deviation σ_T, and we increased or decreased the standard deviation σ_T by a factor of 4 (corresponding to a change in variance by a factor of 2). With these altered traits, we performed the same community assembly process (fig. S2). We investigated the effect of the standard deviation of the handling time h_{jn} by setting $h'_{jn} = \sqrt{\lambda}(h_{jn} - \mu_{h_{jn}}) + \mu_{h_{jn}}$, where λ is the factor by which we increased or decreased the standard deviation and $\mu_{h_{jn}}$ is the mean of the handling time. We investigated the effect of the standard deviation of the selectivity by setting $\sigma'_s = \lambda\sigma_s$. Because the total selectivity of a zooplankton must sum to 1 ($\sum_n s_{jn} = 1$), we did not investigate the effect of mean selectivity on phytoplankton and zooplankton species richness.

We investigated the effect of trait trade-offs by altering the correlation $\rho(T_1, T_2)$ between two traits. However, the correlation $\rho(T_1, T_3)$ and the correlation $\rho(T_2, T_3)$ set a constraint for the correlation $\rho(T_1, T_2)$, such that we could not choose the correlation freely in the interval $[-1, 1]$. More generally, the resulting correlation matrix ρ must be semipositive definite. We simulated communities with the minimal and maximal possible value for correlation $\rho(T_i, T_j)$, which depended on the specific traits involved.

Niche and Fitness Differences

To better understand how the mechanisms affected coexistence, we computed niche and fitness differences for zooplankton species competing for phytoplankton using the method of Spaak et al. (2021*c*). They define niche and fitness differences on the basis of the intrinsic, the invasion, and the no-niche growth rates. These were defined as the growth rates of the zooplankton "invading" three different scenarios. The intrinsic growth rate, denoted μ_j, describes the growth rate of a zooplankton invading an empty community, where no zooplankton are present and phytoplankton are at their equilibrium. Note that the intrinsic growth rate μ_j is lower than the maximal growth rate μ_j^{Z}, as μ_j^{Z} is the growth rate when resource abundance for the zooplankton is infinite. The invasion growth rate r_j is the growth rate of a zooplankton invading a community with the competitor zooplankton at their equilibrium densities and phytoplankton at their corresponding densities. Finally, the no-niche growth rate η_j is the growth rate of the zooplankton invading a community with itself as a resident, but at a density equivalent to the combined equilibrium density of its competitors.

We computed niche and fitness differences only for the zooplankton species, not for phytoplankton. We could not compute the niche and fitness differences for competing phytoplankton, as this would have required setting the zooplankton densities at equilibrium for a given density of phytoplankton N_i^{P} (Spaak and De Laender 2020). However, the growth rate of zooplankton is independent of zooplankton density, and hence such an equilibrium of zooplankton is not defined in general. To compute the niche and fitness differences for the zooplankton species, we considered the phytoplankton species as resources.

Given these growth rates, we defined niche and fitness differences of zooplankton as

$$\begin{aligned} \mathcal{N}_j &= \frac{r_j - \eta_j}{\mu_j - \eta_j}, \\ \mathcal{F}_j &= \frac{-\eta_j}{\mu_j - \eta_j}. \end{aligned} \tag{13}$$

Importantly, these definitions of niche and fitness differences depend on the invasion growth rate and can therefore be computed only for communities in which both species in monoculture reach a stable, nonzero equilibrium density.

Results

In simulations with unaltered trait distributions (i.e., the distributions estimated from empirical measurements), phytoplankton species richness ranged from 1 to 5 with an average of 2.4, and zooplankton species richness ranged from 0 to 5 with an average of 2.2 (fig. 2). Phytoplankton and zooplankton richness were strongly correlated ($\rho = 0.71$); roughly 50% of communities had equal phytoplankton and zooplankton species richness, and zooplankton richness exceeded phytoplankton richness in only 15% of the communities.

Generally, phytoplankton and zooplankton species richness responded very similarly to changes in trait distribution. Simulations with altered trait distribution showed that changes in the mean or variance of many trait distributions had little or no effect on phytoplankton or zooplankton species richness (figs. 2*A*, 2*B*, 2*D*, 2*E*, S2). Traits associated with species growth rates (μ^{P}, μ^{Z}, and m^{Z}) were unimportant for phytoplankton or zooplankton species richness (fig. 2*A*, 2*D*). Similarly, phytoplankton resource uptake traits (c_n, c_p, and a) as well as half-saturation constants for these resources (k_n, k_p, and k_l) had only minor effects on phytoplankton or zooplankton species richness. When these traits had very large values, species richness of zooplankton declined (fig. 2*E*), likely because many zooplankton species did not have enough phytoplankton to consume, as high resource uptake as well as a high half-saturation constant implies lower equilibrium densities of phytoplankton.

Changes in traits regulating the phytoplankton-zooplankton interactions had the strongest effect on phytoplankton and zooplankton species richness (fig. 2*C*, 2*F*). This matches findings from observational data in a temperate lake (Merkli 2021). The effects of these trait changes on species richness are likely due to a combination of the following three explanations.

First, the trait changes affected the amount of resources taken up by zooplankton. If this amount was to low—for example, because consuming one phytoplankton cell takes too long (high handling time h_{ji}, brown line, fig. 2*C*, 2*F*)—then zooplankton starved and species richness dropped. Conversely, if this amount increased, then more zooplankton had sufficient food to survive. This is a possible explanation for the effects of handling time h_{ji} and edibility e_i^{P} on phytoplankton and zooplankton species richness. However, this explanation ignores competition between zooplankton and leads to the prediction that the trait changes monotonically affect species richness.

Second, the trait changes affected the underlying trait trade-offs and allowed the creation of superspecies. This may explain why changes in three of the traits showed a unimodal effect on zooplankton species richness (nutritional value w_i^{P}, half-saturation constant k_j^{Z}, and clearance rate c_j^{Z}; fig. S3*C*, S3*F*). For example, the positive correlation between half-saturation constant k_j^{Z} and clearance rate c_j^{Z} created a gleaner-opportunist trade-off. However, if all species had increased clearance rates, then growth was limited not by the amount of phytoplankton consumed (which was driven by the clearance rate) but only by the half-saturation constant, which effectively destroyed the trade-off.

Third, phytoplankton species richness follows zooplankton species richness because phytoplankton richness is maintained by the trophic interaction with zooplankton. Consequentially, a decline in zooplankton species richness decreases the stabilizing effect of zooplankton on phytoplankton, and their richness declines as well (fig. S6). This explains why resource competition traits had little effect on phytoplankton richness as well as the strong correlation between phytoplankton and zooplankton species richness. It also explains why effects of trait changes more strongly affected zooplankton richness than phytoplankton richness.

The effects of altered trait correlations (fig. 3) were consistent with the effects of changes in trait means. First, many trait correlations had no strong effect on species phytoplankton and zooplankton richness (fig. S5). Second, many of the trait correlations that had a strong effect on phytoplankton and zooplankton richness were linked to the trophic interactions between phytoplankton and zooplankton. Third, zooplankton species richness was more sensitive than phytoplankton species richness to changes in trait correlations (compare fig. 3*B* with 3*F* and 3*C* with 3*G*).

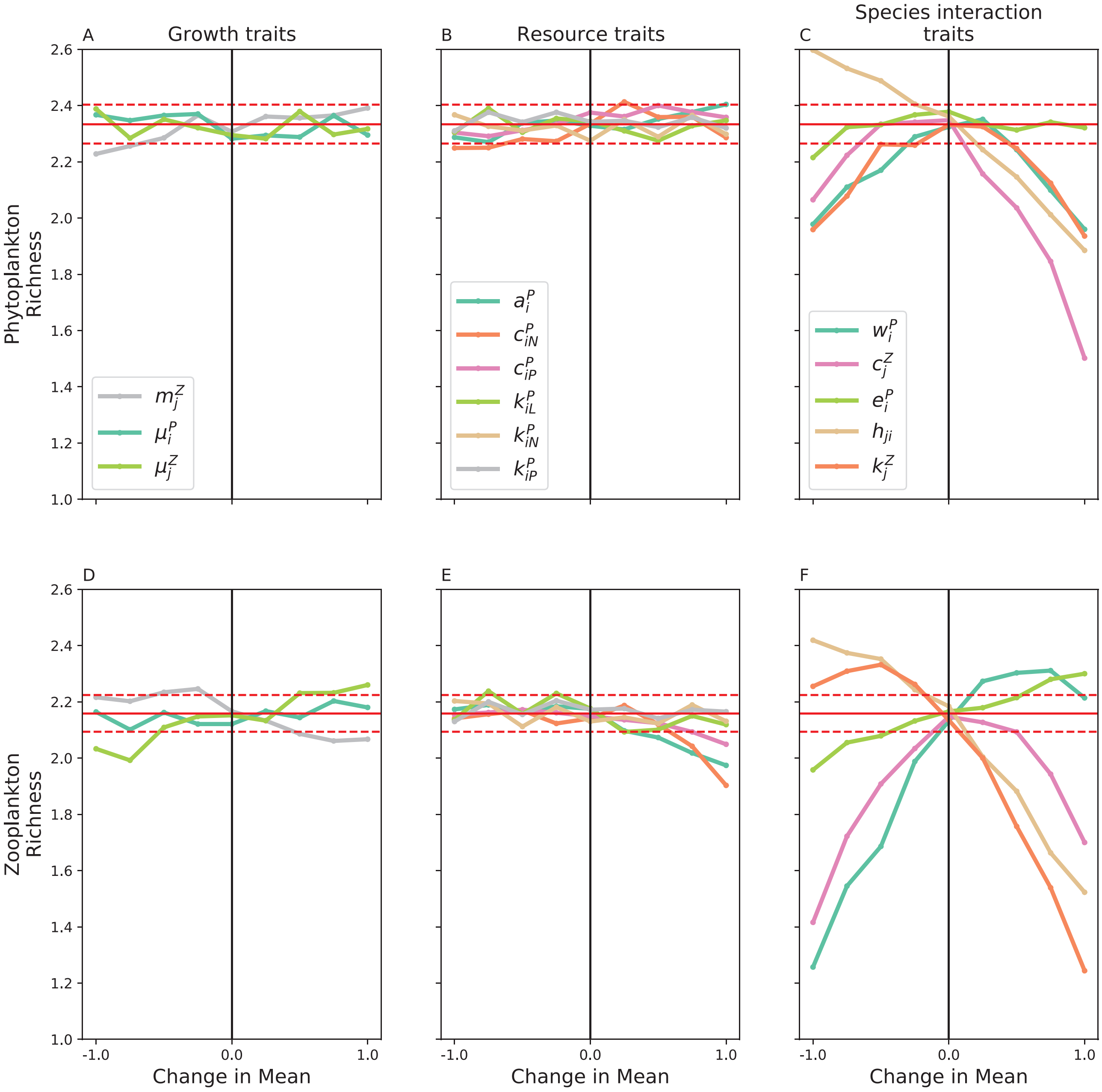

Figure 2: We changed the means of growth traits (*A*, *D*), resource traits (*B*, *E*), and species interaction traits (*C*, *F*) and investigated their effect on phytoplankton (*A*–*C*) and zooplankton (*D*–*F*) species richness. The mean values of the growth traits (*A*, *D*) and of the traits governing the competition of phytoplankton for resources (*B*, *E*) had little effect on species richness; conversely, altering the traits governing the interaction between phytoplankton and zooplankton (*C*, *F*) had a strong effect on species richness. In all panels, the black vertical line indicates the empirical values of the traits, and the red horizontal lines show the mean (solid) and 99% confidence interval (dashed) of the respective values for communities generated with the empirical trait values.

Six of the 10 trade-offs with the strongest effect can be categorized as gleaner-opportunist trade-offs—that is, one species benefits from high resource availabilities and the other from low resource availabilities (fig. 3*A*, 3*E*). Two of these trade-offs are competition for nitrogen (green line in fig. 3) and phosphorus (brown line in fig. 3), and the other four concerned the trophic interactions. The other trade-offs all concerned the nutritional value w_i^P of the phytoplankton. Two of these are conceptually similar to a growth-defense trade-off (fig. 3*B*, 3*F*). Low nutritional

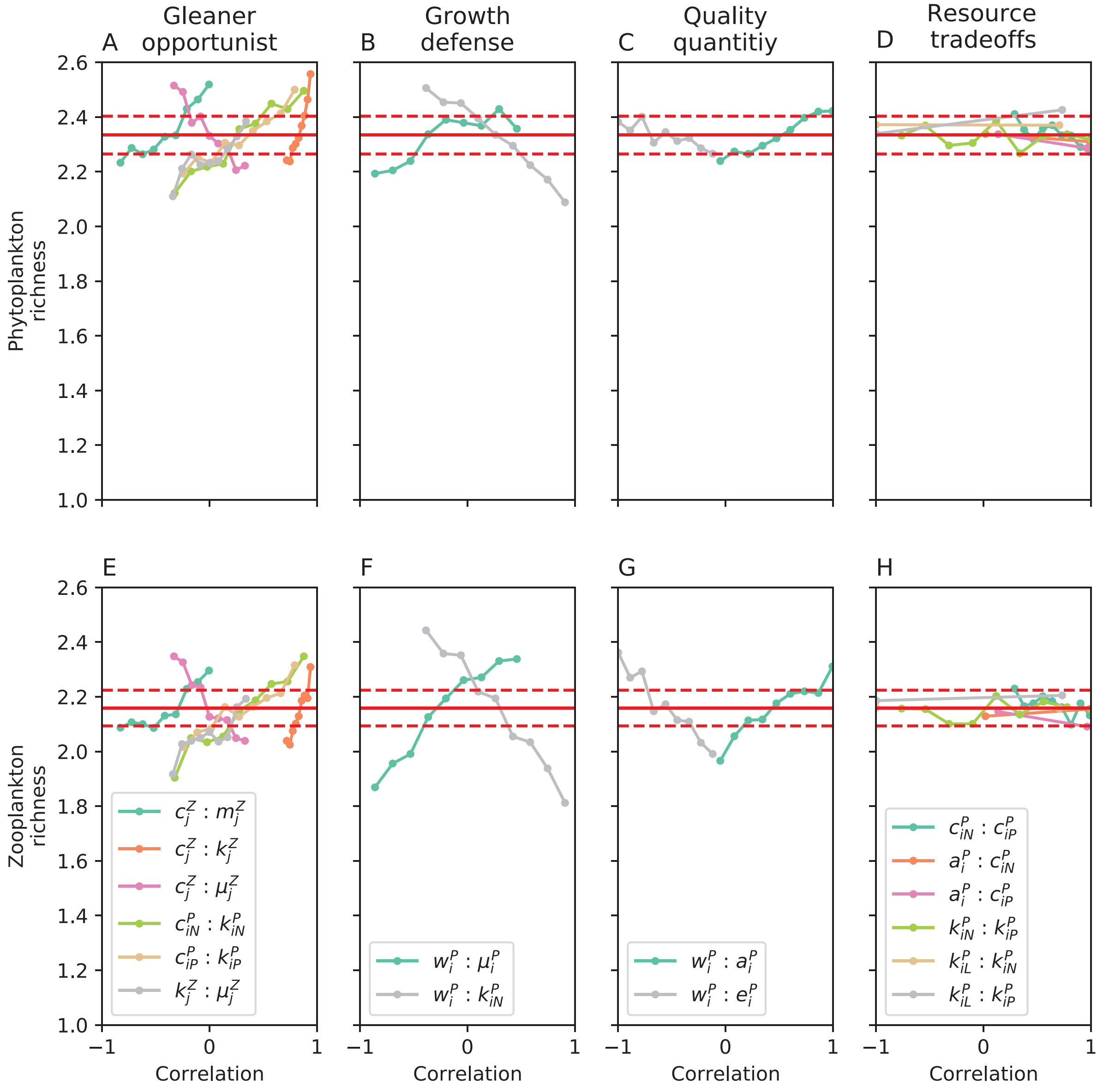

Figure 3: We changed the trade-offs (correlation matrix) between traits and investigated the effects on phytoplankton (*A*–*D*) and zooplankton (*E*–*H*) species richness. The trade-offs with the strongest effects are grouped into gleaner-opportunist (*A*, *E*), growth-defense (*B*, *F*), and superresource (*C*, *G*) trade-offs. Resource competition trade-offs had no strong effect on phytoplankton or zooplankton species richness (*D*, *H*). In all panels, the red horizontal lines show the mean (solid) and 99% confidence interval (dashed) of the respective values for communities generated with the empirical trait values. The correlation cannot be chosen freely for each trade-off; rather, the maximal and minimal possible values for each trait pair are determined by the requirement that the entire trait correlation matrix must be positive definite (see "Methods"). This figure shows only 16 of the possible 42 trait correlations. We chose all of the trait correlations with the strongest effects (*A*–*C*) as well as the resource trait correlations because of a priori expectations (see table S2). For an overview of all traits, we refer the reader to figure S5.

value w_i^{P} does not provide immediate protection against predation; however, it limits the growth rates of the predator and therefore protects against future predation. Both high intrinsic growth rate μ_i^{P} and low half-saturation constant k_i^{P} contribute to high growth rates, so these trade-offs are therefore similar to the familiar growth-defense trade-offs. However, the growth-defense trade-off between edibility e_i^{P} and intrinsic growth rate μ_i^{P} did not have a strong effect on phytoplankton and zooplankton species richness.

The last two are trade-offs between high-quality food for zooplankton (i.e. high nutritional value w_i^{P}) and high-quantity food for zooplankton, either high abundance because of low absorption rates a_i^{P} or high edibility e_i^{P}. Reducing the strength of this trade-off will create phytoplankton having both high quality and high quantity. Zooplankton species that consume these abundant high-quality phytoplankton will have a competitive advantage over zooplankton consuming low-quality and low-quantity phytoplankton, and that competitive advantage will decrease zooplankton richness.

Interestingly, none of the six possible resource trade-offs had a strong effect on phytoplankton and zooplankton species richness (fig. 3*D*, 3*H*). This supports our hypothesis that differences among phytoplankton species in resource requirements or response to limiting resources are not important drivers of phytoplankton and zooplankton species richness in this community.

Niche and Fitness Differences

Changes in fitness differences were the underlying cause for the change in zooplankton species richness for most changes in trait distributions (fig. 4*D*). The trait changes that lead to starving zooplankton (increasing half-saturation constant k_{Z}, increasing handling time h_{jp}, decreasing resource availability R_{P}, and decreasing clearance rate c_{Z}) all increased fitness differences between the competing zooplankton (figs. S3, S4). The closer a zooplankton was to the starvation boundary, the lower its fitness and the stronger fitness differences became, explaining the decrease in zooplankton species richness. Similarly, relaxing gleaner-opportunist trade-offs created superspecies with increased fitness (fig. 3*E*); the growth-defense trade-offs and the quality-quantity trade-offs create superresources, and zooplankton consuming these superresources had a fitness advantage (fig. 3*F*, 3*G*). Niche differences between zooplankton were not correlated with zooplankton species richness (fig. 4*C*). Similarly, niche and fitness differences between competing zooplankton were not strongly associated with phytoplankton species richness.

We often observed negative niche differences for one of the two competing zooplankton species, despite the two species coexisting (fig. 4*A*, 4*C*). This is possible in the case of an asymmetric species interaction (i.e., species 1 positively affects species 2 while species 2 negatively affects species 1). In this case, species 2 has $\mathcal{N}_2 > 1$, indicating facilitation (Spaak et al. 2021*c*); conversely, species 1 must have $\mathcal{N}_1 < 1$, as it is not facilitated. Additionally, as shown by Spaak and De Laender (2020), we must have $|1 - \mathcal{N}_2| = |1 - \mathcal{N}_1|$, which yields $\mathcal{N}_1 < 0$. This is consistent with the typical interpretation of negative niche differences that interspecific interactions are stronger than intraspecific interactions (Ke and Letten 2018), although in this case only for species 1.

However, the relevance of these findings is not entirely clear because we were able to compute niche and fitness differences only for a small fraction of all assembled communities (~10%). For the remaining 90% of the communities, we encountered different conceptual and computational challenges in calculating niche and fitness differences, as we describe below. To compute niche and fitness differences, one has to numerically solve the equation $|(\mu_i - r_i)/(\mu_i - \eta_i(c_{ij}))| = |(\mu_j - r_j)/(\mu_j - \eta_j(1/c_{ji}))|$ for c_{ij}, which is guaranteed to have a solution if μ_i, r_i, and $\eta_i(c_{ij})$ are well defined and $\eta_i(c_{ij})$ depends continuously on c_{ij} (Spaak and De Laender 2020).

In roughly 50% of communities, one of the two zooplankton was not able to persist at all in the absence of the other zooplankton, which implies that r_i is not defined for one of the two species. This occurred when the two zooplankton behaved similarly to obligatory mutualists. As an illustrative example, consider a large and a small zooplankton that predominantly feed on a large or a small phytoplankton species, respectively (fig. 5*B*). In the absence of any zooplankton, suppose that the smaller phytoplankton has an advantage in competition for the abiotic resources and competitively excludes the larger phytoplankton species. If the larger zooplankton is an inefficient predator of the small phytoplankton and therefore cannot invade a community where only small phytoplankton are present, it will not have a monoculture equilibrium density. Consequently, we cannot compute an invasion growth rate of the smaller zooplankton invading the larger zooplankton in monoculture, and computation of niche and fitness differences is not possible.

Nonetheless, the two zooplankton might be able to coexist. The smaller zooplankton will predominantly consume the smaller phytoplankton. If we first introduce the smaller zooplankton it will decrease the density of the smaller phytoplankton and reduce its competitive strength. The larger phytoplankton will invade and persist in the presence of the smaller zooplankton. Then the larger zooplankton will have a prey to consume and may be able to invade. Even though all species interactions result from resource competition, this scenario resembles the cases of obligatory mutualism or keystone species and cannot be analyzed using any of the existing definitions of niche and fitness differences (Spaak and De Laender 2020; Spaak et al. 2021*c*).

In roughly 10% of the communities, the phytoplankton on their own were driven by priority effects (i.e., the phytoplankton community had two distinct stable equilibria). In this case the intrinsic growth rate of the zooplankton species is not unique, and different choices of the intrinsic growth rates would lead to different niche and fitness differences. In this case one could still define niche and fitness differences, but they would be nonunique.

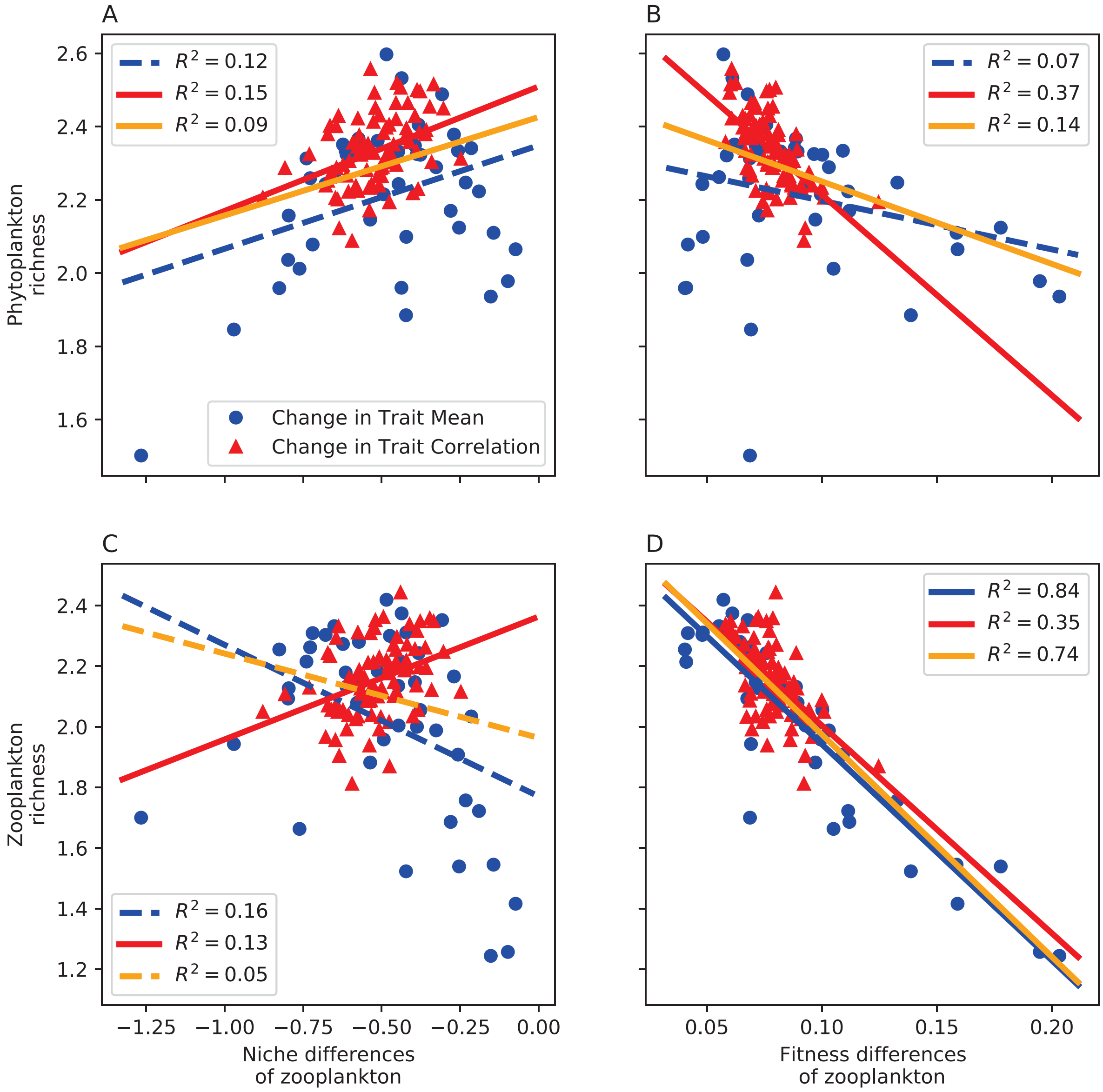

Figure 4: Overall, niche differences were not strongly correlated with phytoplankton (*A*) or zooplankton richness (*C*). Fitness differences were strongly correlated with zooplankton richness (*D*). The correlation between fitness differences and phytoplankton richness (*B*) likely stems from the correlation between phytoplankton and zooplankton richness and not from a direct effect of fitness differences on phytoplankton richness. Blue circles show average species richness from changes in mean traits (i.e., corresponding to fig. 2*C* or 2*F*) versus the niche or fitness differences from changes in mean traits (fig. 2*H* or 2*I*). Red triangles show the corresponding data for changes in trade-offs (fig. 3). Lines show the best linear fit based on least R^2, with the orange line showing the best linear fit for all data. Dashed lines indicate that the linear fit was not significant at the $P = .01$ level.

In roughly 10% of the communities, the no-niche growth rate was discontinuous. Effectively, c_{ij} increases the mortality of the phytoplankton; this can change the coexistence state of the two phytoplankton from coexisting to monodominance of one species. This qualitative change of the underlying phytoplankton community causes a discontinuity of $\eta_i(c_{ij})$.

In roughly 15% of the communities, we observed Allee effects in the zooplankton species (i.e., $\eta_i(c_{ij}) > \mu_i$). This can happen in a similar way as the facilitation between zooplankton species described above. However, in this case the zooplankton has stronger predation pressure on the species, which is less favorable for its growth rate. Mathematically, niche and fitness differences may

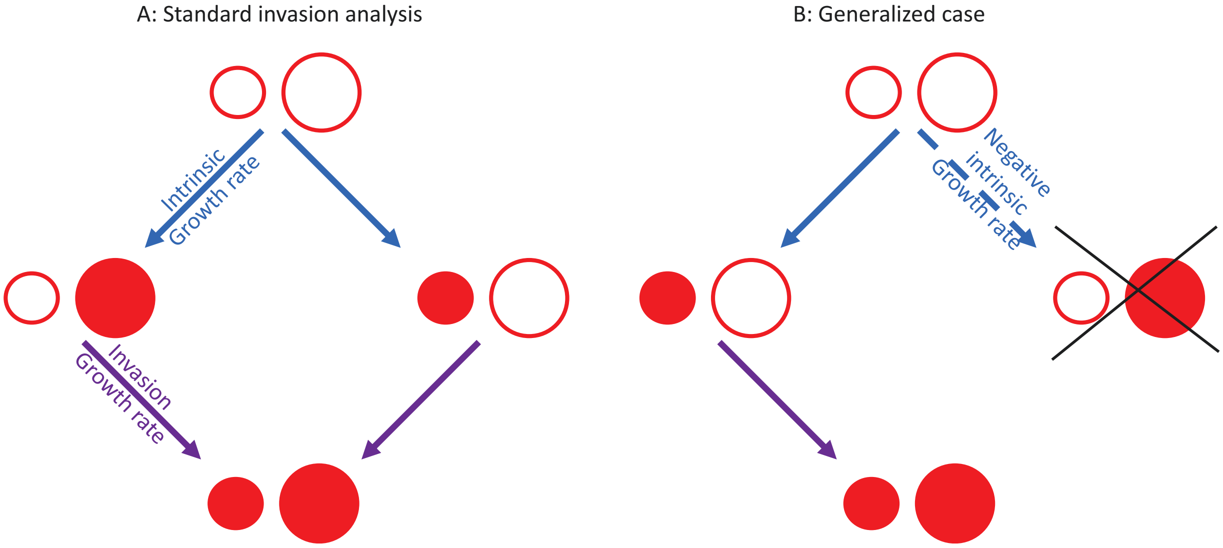

Figure 5: The standard community assembly process of a small and a large zooplankton competing for phytoplankton is shown in *A*. Initially, both zooplankton species are absent (*top*), and both have a positive intrinsic growth rate. Either of the two zooplankton will arrive and successfully invade the empty ecosystem, as both have a positive intrinsic growth rate (blue arrow), leading to an ecosystem in monoculture (*middle*). Finally, the other zooplankton species can invade the monoculture of its competitor, as both have a positive invasion growth rate (purple arrow), leading to coexistence (*bottom*). As shown in *B*, however, if we assume that the lower trophic level of phytoplankton cannot coexist in the absence of zooplankton, only one of the zooplankton (here, the smaller) will have a positive intrinsic growth rate, as the other zooplankton will (potentially) not have enough food. Consequentially, the larger zooplankton will not be able to survive in monoculture. The usual invasion analysis for the smaller zooplankton species—which would ask whether it can invade a community dominated by the larger species—is therefore not possible. However, coexistence might still be possible, as the large zooplankton can invade the monoculture of the small zooplankton. This is possible because the small zooplankton reduces the competitive ability of the small phytoplankton such that the small and the large phytoplankton can coexist in the presence of zooplankton.

still be defined in this case; however, the biological interpretation of niche and fitness differences in the presence of Allee effects is unclear (Spaak et al. 2021*c*).

For the remaining 5% of the communities, computation of niche and fitness differences was conceptually possible but difficult because of computational limitations. In these cases zooplankton species had no stable equilibrium density in monoculture but rather fluctuated periodically. This implies that for each iteration of the numerical solver of $|(\mu_i - r_i)/(\mu_i - \eta_i(c_{ij}))| = |(\mu_j - r_j)/(\mu_j - \eta_j(c_{ji}))|$, we had to recompute the equilibrium distribution given the new c_{ij}. Consequentially, the computation of niche and fitness differences for these communities was computationally very expensive and imprecise.

Discussion

We investigated the relative importance of resource- and predator-mediated coexistence mechanisms on species richness in phytoplankton-zooplankton communities based on mechanistic species interactions and empirical trait data (for an overview of the effects, see table S4). We altered several parameters of the trait distributions governing phytoplankton and zooplankton growth and found that changes in traits associated with the trophic interaction between phytoplankton and zooplankton had strong effects on species richness (figs. 2*C*, 2*F*, 3*A*–3*C*, 3*E*, 3*F*). However, changes in traits related to resource-mediated coexistence mechanisms had much weaker effects on species richness. We conclude that phytoplankton and zooplankton species richness in our model is primarily determined by predator-mediated coexistence mechanisms. Additionally, by applying the methods of modern coexistence theory we found that the changes in phytoplankton and zooplankton species richness caused by changes in trait means or correlations were largely driven by altered fitness differences (fig. 4). However, we also found that modern coexistence theory often does not apply to these simple multitrophic communities.

Trade-offs in resource affinities of phytoplankton did not have a strong effect on species richness of phytoplankton or zooplankton in our model (fig. 3*D*), for two reasons. First, while the potential benefits of such trade-offs for species richness are clear (Tilman et al. 1982; Huisman and Weissing 1994; Letten et al. 2017), those benefits may be quite weak in this complex system, which also includes predator-prey dynamics. In our model, two randomly chosen phytoplankton are unlikely to have a sufficiently strong trade-off in their resource affinities to stably coexist. Often, the smaller phytoplankton have better resource uptake traits and will outcompete its larger competitor based on resource competition alone (Edwards et al. 2012; Bernhardt et al. 2020). Second, the relative importance of a certain mechanism may depend on the presence of other mechanisms (Letten et al. 2018; Zepeda and Martorell 2019; Shoemaker et al. 2020*a*). Most work on resource-mediated niche differences has been done in the absence of predators. If we exclude predator-mediated coexistence mechanisms, we do find that resource-mediated coexistence mechanisms have a small positive effect on species richness (supplemental PDF, sec. S1; fig. S7). However, in the presence of predator-mediated coexistence mechanisms, the positive effect of resource-mediated coexistence mechanisms on species richness is unimportant. These results demonstrate that instead of asking whether a mechanism operating in isolation can affect species richness, we should investigate both the magnitude and the relative importance of different mechanisms operating simultaneously. Consideration of multiple mechanisms also makes it possible to study interactions among them. In our model, the effects of resource partitioning and predation on species richness were not additive.

We found that zooplankton fitness differences were correlated with zooplankton richness (fig. 4*D*) and, to a lesser extent, with phytoplankton richness (fig. 4*B*). Conversely, zooplankton niche differences were only weakly correlated with phytoplankton or zooplankton richness. This differs from earlier findings in phytoplankton or plant communities, which mostly found that niche differences were more strongly associated with species richness (Levine and HilleRisLambers 2009; Adler et al. 2010; Narwani et al. 2017; Buche et al. 2022). This difference may stem from many different sources, such as model complexity, the two trophic levels in our model, or our inability to compute niche and fitness differences for all communities (see the next section). Additionally, we used a different method than in most of the previous work, which may affect our interpretation of coexistence (Spaak et al. 2021*d*).

Our model is based on mechanistic species interactions and empirically measured traits, yet it lacks certain key features from the natural world. First and foremost, we did not include any external fluctuations, either random or deterministic (e.g., seasonality), and as such we excluded many potential coexistence mechanisms (Chesson 1994; Barabás et al. 2018; Letten et al. 2018; Ellner et al. 2019; Shoemaker et al. 2020*b*). Fluctuations would likely increase species richness and potentially affect the importance of resource competition. Yet many empirical studies have shown that fluctuation-dependent mechanisms appear to be less important than fluctuation-independent mechanisms for coexistence (Chu and Adler 2015; Letten et al. 2018; Zepeda and Martorell 2019). Second, phytoplankton and zooplankton species richness was generally low compared with that in natural communities. The relative importance of different coexistence mechanisms might depend on species richness. For example, Spaak et al. (2021*a*) have shown that increasing species richness increases the importance of fitness differences compared with niche differences. Third, the trophic structure was simple and excluded any higher trophic level and any mixotrophs. As we found that trophic interactions are the most relevant factor for phytoplankton and zooplankton species richness, it would be interesting to see whether higher trophic levels are even more important. Fourth, the traits were measured in laboratory environments and may be biased toward fast-growing species, which are simple to grow in culture. Our trait distributions may therefore differ from trait distributions observed in nature. Unfortunately, we do not have any empirical data to assess how strongly our empirically measured traits differ.

Implications for Modern Coexistence Theory

We were not able to compute niche and fitness differences for many of our simulated communities. This is not solely a limitation of the niche and fitness differences method we chose to apply but is more generally a conceptual limitation of modern coexistence theory in its current formulation based on invasion growth rates. It is now well known that invasion analysis can fail (Schreiber 2000; Barabás et al. 2018), especially in multispecies communities (Saavedra et al. 2017; Spaak et al. 2021*b*) or in models including Allee effects (Schreiber et al. 2019). However, we were surprised that invasion analysis failed in such a simple community of two zooplankton species competing for phytoplankton as a resource. In our model, these difficulties are a natural consequence of the increased complexity of the underlying community. It is not solely a limitation of the model investigated here; rather, similar issues are likely to emerge in any community with multiple trophic levels, whether the model is mechanistic or phenomenological. For example, Huisman and Olff (1998) and Arsenault and Owen-Smith (2002) found that small herbivores can persist only in the presence of larger herbivores. Another typical example are keystone species, where the presence of these keystone species has large effects on the biodiversity of the ecosystem (Creed 2000).

Much of the work of modern coexistence theory is based on invasion growth rates, with the presumption that invasion growth rates are well defined and that their signs give insight into coexistence (Schreiber 2000; Barabás et al.

2018; Ellner et al. 2019; Pande et al. 2020; Spaak and De Laender 2020). However, we observed communities in which the invasion growth rate is not well defined or does not exist (fig. 5). These communities behaved similarly to communities driven by Allee effects or communities driven by obligatory mutualism. It was not previously recognized that these communities can arise from simple resource competition, a well-understood mechanism that is fundamental for coexistence (Chesson 1990; Chesson and Kuang 2008; Letten et al. 2017; Letten and Stouffer 2019; Spaak et al. 2021*a*, 2021*b*).

Schreiber (2000) proposed a generalized version of invasion growth rate analysis. The traditional invasion growth rate approach tests whether each species can invade the subcommunity from which it alone is absent (fig. 5*A*). In contrast, the generalized invasion analysis investigates for each possible subcommunity which species can invade (fig. 5*B*), as shown by the sign of their invasion growth rate when introduced into that subcommunity. Recently, Hofbauer and Schreiber (2022) proved that under certain assumptions, coexistence is guaranteed if the graph of possible community transitions is acyclic (e.g., rock-paper-scissors-type situations are ruled out), and all subcommunities from which any one species has been removed can be invaded at steady state (which may involve extinction of additional species). A complete theory is not yet in hand, as Hofbauer and Schreiber (2022) discuss; for example, the current results are not applicable when some subcommunities have alternate stable states that can be invaded by different sets of species. Nonetheless, Hofbauer and Schreiber (2022) already allow the extension to some situations (such as those in fig. 5*B*) of the strand of modern coexistence theory that focuses on calculating invasion growth rates and decomposing them into contributions from different coexistence mechanisms (e.g., Chesson 1994, 2003; Ellner et al. 2019). These advances for deterministic models are complemented by progress on coexistence theory for stochastic models based on invasion analysis (e.g., Benaïm and Schreiber 2019; Hening et al. 2021). The theory for stochastic models requires quantitative information about invasion growth rates (the Hofbauer criterion; eq. [3.4] in Benaïm and Schreiber 2019), not just their signs, but there are reasons to hope that this situation is temporary (Hofbauer and Schreiber 2022).

These new and more widely applicable approaches to invasion analysis have not yet percolated across to the thread of modern coexistence theory where the key concepts are the parallel dichotomies of stabilizing versus equalizing mechanisms and niche differences versus fitness differences. These ideas were very important conceptually, in particular for clarifying how different biological mechanisms can contribute to coexistence in different ways. But approaches for making them quantitative have largely been based on pairwise interactions, on phenomenological models for species competition, and on the assumption that the traditional invasion analysis completely characterizes coexistence. Where simple invasion analysis fails, the available methods to compute niche and fitness differences (Carroll et al. 2011; Spaak and De Laender 2020; Spaak et al. 2021*c*) also rarely yield insights, as they result in $\mathcal{N} = 1$ and $\mathcal{F} = \pm\infty$. Conceptually, it seems evident that coexisting species must have some degree of niche differences sufficient to overcome their fitness differences, but exactly how to quantify those differences in situations requiring the generalized version of invasion analysis remains a challenge, and our results suggest that such situations may be common in communities with multiple trophic levels.

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Statement of Authorship

Conceptual study design: J.W.S., P.B.A., S.P.E.; funding acquisition: J.W.S., P.B.A., S.P.E.; coding simulations and visualization: J.W.S.; writing—original draft: J.W.S.; writing—review and editing: J.W.S., P.B.A., S.P.E.

Data and Code Availability

All code is publicly available on Zenodo (https://doi.org/10.5281/zenodo.7462012; Spaak 2022).

References

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters 13:1019–1029.

Agustí, S. 1991. Allometric scaling of light absorption and scattering by phytoplankton cells. Canadian Journal of Fisheries and Aquatic Sciences 48:763–767.

Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313–318.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506:85–88.

Barabás, G., R. D'Andrea, and S. M. Stump. 2018. Chesson's coexistence theory. Ecological Monographs 88:277–303.

Becerra, J. X. 2015. On the factors that promote the diversity of herbivorous insects and plants in tropical forests. Proceedings of the National Academy of Sciences of the USA 112:6098–6103.

Benaïm, M., and S. J. Schreiber. 2019. Persistence and extinction for stochastic ecological models with internal and external variables. Journal of Mathematical Biology 79:393–431.

Berggreen, U., B. Hansen, and T. Kiørboe. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology 99:341–352.

Bernhardt, J. R., P. Kratina, A. L. Pereira, M. Tamminen, M. K. Thomas, and A. Narwani. 2020. The evolution of competitive ability for essential resources. Philosophical Transactions of the Royal Society B 375:20190247.

Branco, P., M. Egas, S. R. Hall, and J. Huisman. 2020. Why do phytoplankton evolve large size in response to grazing? American Naturalist 195:E20–E37.

Brun, P., M. R. Payne, and T. Kiørboe. 2017. A trait database for marine copepods. Earth System Science Data 9:99–113. https://doi.org/10.5194/essd-9-99-2017.

Buche, L., J. W. Spaak, J. Jarillo, and F. De Laender. 2022. Niche differences, not fitness differences, explain predicted coexistence across ecological groups. Journal of Ecology 110:2785–2796.

Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology 92:1157–1165.

Chesson, P. 1990. MacArthur's consumer-resource model. Theoretical Population Biology 37:26–38.

———. 1994. Multispecies competition in variable environments. Theoretical Population Biology 45:227–276.

———. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

———. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical Population Biology 64:345–357.

———. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology 106:1773–1794.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. Nature 456:235–238.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs 85:373–392.

Creed, R. P. 2000. Is there a new keystone species in North American lakes and rivers? Oikos 91:405–408.

Edwards, K. F., C. A. Klausmeier, and E. Litchman. 2011. Evidence for a three-way trade-off between nitrogen and phosphorus competitive abilities and cell size in phytoplankton. Ecology 92:2085–2095.

———. 2015. Nutrient utilization traits of phytoplankton: ecological archives E096-202. Ecology 96:2311–2311.

Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. Limnology and Oceanography 57:554–566.

Ehrlich, E., N. J. Kath, and U. Gaedke. 2020. The shape of a defense-growth trade-off governs seasonal trait dynamics in natural phytoplankton. ISME Journal 14:1451–1462.

Ellner, S. P., R. E. Snyder, P. B. Adler, and G. Hooker. 2019. An expanded modern coexistence theory for empirical applications. Ecology Letters 22:3–18.

Field, C. B. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240.

Finkel, Z. V., J. Beardall, K. J. Flynn, A. Quigg, T. A. V. Rees, and J. A. Raven. 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry. Journal of Plankton Research 32:119–137.

Germain, R. M., J. T. Weir, and B. Gilbert. 2016. Species coexistence: macroevolutionary relationships and the contingency of historical interactions. Proceedings of the Royal Society B 283:20160047.

Godoy, O., I. Bartomeus, R. P. Rohr, and S. Saavedra. 2018. Towards the integration of niche and network theories. Trends in Ecology and Evolution 33:287–300.

Godoy, O., and J. M. Levine. 2014. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

Hening, A., D. H. Nguyen, and P. Chesson. 2021. A general theory of coexistence and extinction for stochastic ecological communities. Journal of Mathematical Biology 82:56.

Hofbauer, J., and S. J. Schreiber. 2022. Permanence via invasion graphs: incorporating community assembly into modern coexistence theory. Journal of Mathematical Biology 85:54.

Huisman, J., and H. Olff. 1998. Competition and facilitation in multispecies plant-herbivore systems of productive environments. Ecology Letters 1998:25–29.

Huisman, J., N. N. Pham Thi, D. M. Karl, and B. Sommeijer. 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439:322–325.

Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology 75:507–520.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Ke, P.-J., and A. D. Letten. 2018. Coexistence theory and the frequency-dependence of priority effects. Nature Ecology and Evolution 2:1691–1695.

Kiørboe, T., A. Visser, and K. H. Andersen. 2018. A trait-based approach to ocean ecology. ICES Journal of Marine Science 75:1849–1863.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the USA 112:797–802.

Letten, A. D., M. K. Dhami, P.-J. Ke, and T. Fukami. 2018. Species coexistence through simultaneous fluctuation-dependent mechanisms. Proceedings of the National Academy of Sciences of the USA 115:6745–6750.

Letten, A. D., P.-J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and contemporary niche theory. Ecological Monographs 87:161–177.

Letten, A. D., and D. B. Stouffer. 2019. The mechanistic basis for higher-order interactions and non-additivity in competitive communities. Ecology Letters 22:423–436.

Levine, J. M., and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. Nature 461:254–257.

Lind, E. M., E. T. Borer, E. Seabloom, P. B. Adler, J. D. Bakker, D. M. Blumenthal, M. Crawley, et al. 2013. Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. Ecology Letters 2019:513–521.

Litchman, E. 2003. Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria. Aquatic Microbial Ecology 31:241–248.

Litchman, E., and C. A. Klausmeier. 2001. Competition of phytoplankton under fluctuating light. American Naturalist 157:170–187.

———. 2008. Trait-based community ecology of phytoplankton. Annual Review of Ecology, Evolution, and Systematics 39:615–639.

Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecology Letters 10:1170–1181.

Litchman, E., M. D. Ohman, and T. Kiørboe. 2013. Trait-based approaches to zooplankton communities. Journal of Plankton Research 35:473–484.

Merkli, S. 2021. The relative importance of top-down and bottom-up controls on the growth rate of phytoplankton trait-based groups. MS thesis. University of Zurich.

Narwani, A., M. A. Alexandrou, T. H. Oakley, I. T. Carroll, and B. J. Cardinale. 2013. Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. Ecology Letters 16:1373–1381.

Narwani, A., B. Bentlage, M. A. Alexandrou, K. J. Fritschie, C. Delwiche, T. H. Oakley, and B. J. Cardinale. 2017. Ecological interactions and coexistence are predicted by gene expression similarity in freshwater green algae. Journal of Ecology 105:580–591.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13:261–265.

Pande, J., T. Fung, R. Chisholm, and N. M. Shnerb. 2020. Mean growth rate when rare is not a reliable metric for persistence of species. Ecology Letters 23:274–282.

Pérez-Ramos, I. M., L. Matías, L. Gómez-Aparicio, and O. Godoy. 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nature Communications 10:2555.

Saavedra, S., R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine. 2017. A structural approach for understanding multispecies coexistence. Ecological Monographs 87:470–486.

Schreiber, S. J. 2000. Criteria for C^r robust permanence. Journal of Differential Equations 162:400–426.

Schreiber, S. J., M. Yamamichi, and S. Y. Strauss. 2019. When rarity has costs: coexistence under positive frequency-dependence and environmental stochasticity. Ecology 100:e02664.

Shoemaker, L. G., A. K. Barner, L. S. Bittleston, and A. I. Teufel. 2020*a*. Quantifying the relative importance of variation in predation and the environment for species coexistence. Ecology Letters 23:939–950.

Shoemaker, L. G., L. L. Sullivan, I. Donohue, J. S. Cabral, R. J. Williams, M. M. Mayfield, J. M. Chase, et al. 2020*b*. Integrating the underlying structure of stochasticity into community ecology. Ecology 101:e02922.

Spaak, J. W. 2022. juergspaak/plankton_foodweb: Mechanistic models of trophic interactions: opportunities for species richness and challenges for modern coexistence theory. Zenodo, American Naturalist, https://doi.org/10.5281/zenodo.7462012.

Spaak, J., R. Millet, P.-J. Ke, A. D. Letten, and F. De Laender. 2021*a*. The effect of non-linear competitive interactions on quantifying niche and fitness differences. bioRxiv, https://doi.org/10.1101/2021.08.30.458252.

Spaak, J. W., C. Carpentier, and F. De Laender. 2021*b*. Species richness increases fitness differences, but does not affect niche differences. Ecology Letters 24:2611–2623.

Spaak, J. W., and F. De Laender. 2020. Intuitive and broadly applicable definitions of niche and fitness differences. Ecology Letters 23:1117–1128.

———. 2021. Effects of pigment richness and size variation on coexistence, richness and function in light-limited phytoplankton. Journal of Ecology 109:2385–2394.

Spaak, J. W., O. Godoy, and F. De Laender. 2021*c*. Mapping species niche and fitness differences for communities with multiple interaction types. Oikos 130:2065–2077.

Spaak, J. W., P.-J. Ke, A. D. Letten, and F. De Laender. 2021*d*. Different methods for niche and fitness differences computation offer contrasting explanations of species coexistence. bioRxiv, https://doi.org/10.1101/2021.09.28.462166.

Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annual Review of Ecology and Systematics 13:349–372.

Uye, S.-i. 1982. Length-weight relationships of important zooplankton from the inland sea of Japan. Journal of the Oceanographical Society of Japan 38:149–158.

Zepeda, V., and C. Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. Ecology 100:e02726.

References Cited Only in the Online Enhancements

Barabás, G., and G. Meszéna. 2009. When the exception becomes the rule: the disappearance of limiting similarity in the Lotka–Volterra model. Journal of Theoretical Biology 258:89–94.

Barbier, M., J.-F. Arnoldi, G. Bunin, and M. Loreau. 2018. Generic assembly patterns in complex ecological communities. Proceedings of the National Academy of Sciences of the USA 115:2156–2161.

Droop, M. R. 1973. Some thoughts on nutrient limitation in algae. Journal of Phycology 9:264–272.

Kiørboe, T., and M. K. Thomas. 2020. Heterotrophic eukaryotes show a slow-fast continuum, not a gleaner–exploiter trade-off. Proceedings of the National Academy of Sciences of the USA 117:24893–24899.

Macarthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

Pastore, A. I., G. Barabás, M. D. Bimler, M. M. Mayfield, and T. E. Miller. 2021. The evolution of niche overlap and competitive differences. Nature Ecology and Evolution 5:330–337.

Song, C., G. Barabás, and S. Saavedra. 2019. On the consequences of the interdependence of stabilizing and equalizing mechanisms. American Naturalist 194:627–639.

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