

## Research

### Effects of multiple timescales of resource supply on the maintenance of species and functional diversity

Alaina N. Smith and Kyle F. Edwards

A. N. Smith (<https://orcid.org/0000-0002-5622-202X>) ✉ ([asmith21@hawaii.edu](mailto:asmith21@hawaii.edu)) and K. F. Edwards (<https://orcid.org/0000-0002-0661-3903>), Dept of Oceanography, Univ. of Hawai'i at Mānoa, 1000 Pope Rd, Honolulu, HI 96822, USA.

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It is well known that variable resource supply can allow competitors to coexist on a single limiting resource, and this is one mechanism that may explain the maintenance of diversity in paradoxically speciose communities. Ecosystems experience fluctuations in resource supply on a range of timescales, but we have a poor understanding of how multiple frequencies of resource supply affect the maintenance of diversity and community structure. Here we explore this question using a model of phytoplankton competition for a limiting nutrient, parameterized using empirical tradeoffs between rapid growth, nutrient storage capacity and nutrient uptake affinity. Compared to a single frequency of nutrient supply, we find that multiple frequencies of nutrient supply increase functional diversity, by permitting the coexistence of strategies adapted to different frequencies of supply. Species richness is also promoted by multiple modes of nutrient supply, but not as consistently as functional diversity. Although this model is parameterized for phytoplankton, the fundamental dynamics and tradeoffs likely occur in a variety of ecosystems. Our results suggest that the spectrum of temporal variation driving communities should be further investigated in the context of the maintenance of diversity and the functional composition of communities under different environmental regimes.

Keywords: coexistence, nutrients, phytoplankton, resource pulse, tradeoffs, traits

## Introduction

One of the fundamental questions in ecology is: how is species diversity maintained? This is an especially challenging question for diverse communities that compete for a small number of resources, such as phytoplankton, coral reefs and forests (Petraitis et al. 1989). Diversity is one of the main components of ecosystem functionality, controlling the magnitude and efficiency of ecosystem processes, and as such, understanding how diversity is maintained is important for understanding ecosystem processes (Hooper et al. 2012). There are a large number of potential mechanisms by which competitors may coexist, such as resource partitioning, competition–defense tradeoffs, specialist enemies and spatial or temporal variation in competitive ability (Hutchinson 1959, Leibold 1996, Chesson 2000, Thingstad 2000). Here we focus on the role of temporal variation in resource supply.

Theory shows that diversity can be maintained when resource supply varies and species differ in performance between low and high resource levels (Armstrong and McGehee 1980, Chesson 2000). In aquatic systems nutrient limitation is very common (Hecky and Kilham 1988, Moore et al. 2003, Edwards and Litchman 2014), but there are physical processes that create fluctuations in nutrient supply, such as upwelling, seasonal cycles in mixed layer depth, storms, fronts and eddies (Cullen et al. 2002, Leichter et al. 2003, Lévy et al. 2015). Likewise, in arid terrestrial systems variability in rainfall may promote diversity, as has been argued for desert plant communities (Chesson et al. 2004).

Here we investigate a model of fluctuating resource supply designed to represent phytoplankton competition for nutrients. Phytoplankton are the base of pelagic aquatic ecosystems, and globally they account for about half of net primary production (Falkowski et al. 2004). Therefore, understanding how phytoplankton communities are affected by changes in the physical environment is important, especially in the context of climate change (Leichter et al. 2003, Moore et al. 2003). Phytoplankton rely on a variety of nutrients to grow, and nutrient supply limits primary production either seasonally or chronically in most aquatic ecosystems (Reynolds 2006, Sarmiento and Gruber 2006). Phytoplankton have been shown to adopt a range of strategies for nutrient acquisition, and these strategies have been categorized in terms of three major axes: competitive ability under chronically low nutrient concentration, ability to store nutrients when they increase transiently, and ability to grow rapidly under nutrient-rich conditions (Sommer 1984). These strategies can be quantified using three ecophysiological traits that are often measured in the laboratory: specific nutrient uptake affinity, nutrient storage capacity and maximum growth rate (Litchman et al. 2009, Edwards et al. 2013a). Previous work found evidence for a three-way tradeoff among these traits, such that an increase in performance along one axis results in a decline along the other two axes (Edwards et al. 2013a). Among freshwater species cyanobacteria tend to have high nutrient affinity, desmids tend to have high storage capacity, green algae tend to have rapid growth rate and diatoms tend to have intermediate trait values (Edwards et al. 2013a). Among marine species the highest nutrient affinity is found among picocyanobacteria (Lomas et al. 2014), the most rapid growth is often found among smaller diatoms and other nanoeukaryotes (Edwards et al. 2012, Marañon et al. 2013), and large diatoms may be storage specialists (Stolte and Riegman 1995, Litchman et al. 2009).

A model parameterized with the empirical tradeoff among nutrient affinity, rapid growth and storage capacity showed that this tradeoff can permit coexistence under pulsed nutrient supply, with the structure of the community depending on the frequency of the pulses, and there was evidence that multiple modes of nutrient supply could further enhance diversity (Edwards et al. 2013a). These results were consistent with experiments showing that pulsed nutrient supply could alter community structure, and in some cases

increase phytoplankton diversity (Turpin and Harrison 1980, Sommer 1984, Gaedke and Sommer 1986, Ducobu et al. 1998, Cermeño et al. 2011). Although the role of resource fluctuations in maintaining diversity has been investigated in many studies, previous theory and experiments have focused on a single timescale of resource fluctuations (Gaedke and Sommer 1986, Hay 1986, Grover 1991, Cermeño et al. 2011). In natural ecosystems there are multiple timescales and magnitudes of resource fluctuations occurring simultaneously (Sousa 1984, Lévy and Martin 2013). For example, seasonally stratified waters tend to have spring and fall ‘blooms’ when both nutrients and light are relatively available, while stratified summer conditions are nutrient-limited and deeply-mixed winter conditions are light-limited (Sarmiento and Gruber 2006). At the same time, in both seasonally stratified and permanently stratified waters there are more frequent events that can bring nutrients into the photic zone. These include the formation of mesoscale eddies in the ocean (timescale~months), wind-driven upwelling and relaxation (timescale~weeks), entrainment of deep water or sediments under high wind events (timescale~weeks–months), rainfall events leading to runoff in lakes or the coastal ocean (timescale~weeks–months), and formation of submesoscale fronts (timescale~days) (Soranno et al. 1997, Robarts et al. 1998, Istvanovics et al. 2004, Kamarainen et al. 2009, Lévy et al. 2015). It is possible that these multiple frequencies of resource supply allow for a greater diversity of coexisting species than a single frequency of resource supply. Furthermore, the particular timescales of fluctuations could be important, and a greater disparity in timescales could permit a greater diversity of species, if there are tradeoffs that cause each species to be best adapted to a specific timescale of fluctuations. In addition, understanding how multiple timescales of fluctuation influence coexistence could also yield insights into community dynamics and the question of whether competitors tend to show synchronous or compensatory dynamics (Houlahan et al. 2007, Loreau and de Mazancourt 2008). For example, previous work has found that co-occurring phytoplankton populations may be largely synchronized at annual scales but with compensatory dynamics at shorter timescales (Vasseur and Gaedke 2007). There is also a tendency for morphologically similar species to have more similar temporal dynamics (Rocha et al. 2011), and for species with similar physiological traits to respond similarly to variation in light and dissolved nitrogen (Edwards et al. 2013b). Because nutrient fluctuation engenders successional dynamics, it may synchronize competitors with similar traits while leading to compensatory dynamics among competitors with divergent traits. In this study, we use a mechanistic model of competition to explore how multiple timescales of resource fluctuations affect community structure, and we ask whether multiple timescales increase diversity relative to a single timescale. The model is parameterized for phytoplankton using empirically observed tradeoffs, but the structure of the model is relatively simple and the major results are likely relevant to a broader range of ecosystems.

## Methods

We analyze whether multiple frequencies of resource supply alter community structure and diversity relative to a single frequency. We adapt a previously developed model (Grover 1991) of phytoplankton competition, which is designed for nutrient-limited growth under variable nutrient supply.

### Model structure

The model is the following system of ordinary differential equations, which describe mixed-layer abundance  $N_i$  (cells  $l^{-1}$ ) and internal phosphorus quota  $Q_i$  ( $\mu\text{mol P cell}^{-1}$ ) for  $n$  species that compete for inorganic phosphorus  $R$  ( $\mu\text{mol P l}^{-1}$ ):

$$\frac{dQ_i}{dt} = \left[ V_{\max hi} - (V_{\max hi} - V_{\max lo, i}) \left( \frac{Q_i - Q_{\min}}{Q_{\max, i} - Q_{\min}} \right) \right] \left( \frac{R}{R + K_i} \right) - \mu_{\infty, i} \left( 1 - \frac{Q_{\min}}{Q_i} \right) Q_i \quad (1)$$

$$\frac{dN_i}{dt} = \mu_{\infty, i} \left( 1 - \frac{Q_{\min}}{Q_i} \right) N_i - mN_i - aN_i \quad (2)$$

$$\frac{dR}{dt} = a(S - R) - \sum_i \left[ V_{\max hi} - (V_{\max hi} - V_{\max lo, i}) \left( \frac{Q_i - Q_{\min}}{Q_{\max, i} - Q_{\min}} \right) \right] \left( \frac{R}{R + K_i} \right) N_i + \sum_i f m N_i Q_i \quad (3)$$

Equation 1 describes dynamics of the quota  $Q_i$  for species  $i$ , which is gained through uptake of the nutrient from the environment and utilized by cell growth. Uptake follows Michaelis–Menten kinetics, with half-saturation constant  $K_i$  ( $\mu\text{mol P l}^{-1}$ ) and maximum uptake rate that declines from  $V_{\max hi}$  ( $\mu\text{mol P cell}^{-1} \text{ day}^{-1}$ ) when  $Q_i = Q_{\min}$  to  $V_{\max lo, i}$  when  $Q_i = Q_{\max, i}$  (parameters that are constant across species are presented without ‘ $i$ ’ subscripts). We assume that growth increases with internal nutrient concentration, following the Droop quota model (Droop 1973), with a minimum quota  $Q_{\min}$  ( $\mu\text{mol P cell}^{-1}$ ) and asymptotic growth at infinite quota  $\mu_{\infty, i}$  ( $\text{d}^{-1}$ ). Equation 2 describes change in biomass  $N_i$  for species  $i$ , which grows as a function of the nutrient quota, and is diminished through mortality at rate  $m$  ( $\text{day}^{-1}$ ) and mixing with deep water at rate  $a$  ( $\text{d}^{-1}$ ). Equation 3 describes change in ambient nutrient  $R$ , which is mixed into the mixed layer from deep water at rate  $a$ , consumed by cells and replenished through the recycling of a portion  $f$  of dead matter. Nutrients are also introduced, and cells lost, through periodic pulsed mixing events such that

$$R(jT^+) = (1 - p)R(jT^-) + pS \quad (4)$$

$$N(jT^+) = (1 - p)N(jT^-) \quad (5)$$

for all positive integers  $j$  (which counts time in pulses), where  $T^-$  indicates conditions immediately before the pulse and  $T^+$  indicates conditions immediately after the pulse. Here  $p$  is the fraction of the mixed layer that is instantaneously replaced with deep water that has nutrient concentration  $S$ , and at the same time the phytoplankton are diluted because they are assumed to be absent below the mixed layer. The model was solved numerically using the lsoda algorithm in the deSolve R package (Soetaert et al. 2010).

The model was parameterized with values from previous experiments that reflect empirical values for phytoplankton limited by phosphorus (Table 1). We chose phosphorus as the limiting nutrient because data was available from a sufficient number of species to quantify tradeoffs among the focal traits (Edwards et al. 2013a). Parameters that are constant across species include those for minimum phosphorous quota  $Q_{\min}$  ( $1.74 \times 10^{-9} \mu\text{mol P cell}^{-1}$ ), the upper limit for maximum cell-specific phosphate uptake rate  $V_{\max hi}$  ( $3.89 \times 10^{-7} \mu\text{mol P cell}^{-1} \text{ day}^{-1}$ ), and the mortality rate  $m$  ( $0.01 \text{ day}^{-1}$ ). Environmental parameters include the rate of mixing across the thermocline  $a$  ( $0.1 \text{ day}^{-1}$ ), the fixed deep-water concentration of phosphate  $S$  ( $3 \mu\text{mol l}^{-1}$ ), and the fraction of phytoplankton mortality that is recycled by remineralization in the mixed layer  $f$  ( $0.7$ ).

There is evidence for tradeoffs between strategies that allow species to grow quickly under high phosphorus supply, store phosphorus after a pulse event, or compete better under chronically limited phosphorus. The tradeoff is dependent upon three parameters: the specific uptake affinity for phosphorus  $P_{\text{saff}, i}$  (equal to  $V_{\max hi} / K_i Q_{\min}$ ), the maximum growth rate  $\mu_{\max, i}$  and the maximum phosphorus quota  $Q_{\max, i}$  (Edwards et al. 2013a). Under steady-state nutrient limitation competitive ability is determined by the nutrient concentration at which growth equals mortality ( $R^*$ ; Tilman 1982); a species with a lower  $R^*$  will exclude a species with a higher  $R^*$ . It can be shown that as mortality  $\rightarrow 0$ ,  $R_i^* \rightarrow m K_i Q_{\min} / V_{\max hi}$  (Litchman et al. 2007). This means that for species with equal mortality, competitive ability under chronic nutrient limitation is proportional to the specific uptake affinity. Even when mortality is non-zero the specific uptake affinity is a good predictor of competitive outcomes in chemostat experiments (Edwards et al. 2011), and in a natural marine system specific nitrate affinity predicts how species respond to seasonal nitrogen depletion (Edwards et al. 2013b). Under prolonged saturating nutrient concentrations population growth rate will approach  $\mu_{\max, i}$  and therefore relative fitness of competitors will depend on differences in  $\mu_{\max}$  and the proportion of time during which growth is nutrient saturated (Litchman and Klausmeier 2001). It has also been shown that species with high  $\mu_{\max}$  are selected for under conditions of high resource concentrations, in lakes and in the ocean

Table 1. Definition of model parameters and state variables.

Variable	Description	Units	Values
State variables			
$N$	Phytoplankton biomass	cell l <sup>-1</sup>	–
$R$	External nutrient concentration	μmol P l <sup>-1</sup>	–
$Q$	Internal cellular nutrient concentration	μmol P cell <sup>-1</sup>	–
Model parameters			
$\mu_{\max}$	Maximum growth rate	day <sup>-1</sup>	0.2–3.5
$P_{\text{saff}}$	Specific affinity for phosphate uptake	l μmol P <sup>-1</sup> day <sup>-1</sup>	10 <sup>0</sup> –10 <sup>6</sup>
$\mu_{\infty}$	Asymptotic growth at infinite quota	day <sup>-1</sup>	0.2–9.74
$K$	Half-saturation constant	μmol l <sup>-1</sup>	0.04–4.97
$Q_{\min}$	Minimum cell quota	μmol P cell <sup>-1</sup>	1.74 × 10 <sup>-9</sup>
$V_{\text{maxhi}}$	Upper limit of max cell-specific phosphate uptake rate	μmol P cell <sup>-1</sup> day <sup>-1</sup>	3.89 × 10 <sup>-7</sup>
$V_{\text{maxlo}}$	Lower limit of max cell-specific phosphate uptake rate	μmol P cell <sup>-1</sup> day <sup>-1</sup>	1.73 × 10 <sup>-16</sup> to $V_{\text{maxhi}}$
$m$	Rate of mortality	day <sup>-1</sup>	0.01
$d$	Integrated mortality rate	day <sup>-1</sup>	0.0255
$S$	Fixed deep-water concentration of phosphate	μmol l <sup>-1</sup>	3
$a$	Mixing with deep water	day <sup>-1</sup>	0.1
$f$	Proportion of dead matter recycled		0.7

(Edwards et al. 2013b, c). Finally,  $Q_{\max}$  appears to be most important for fitness when nutrient fluctuation occurs on the timescale of several generations (Edwards et al. 2013a). This is sensible because the ratio  $Q_{\max}/Q_{\min}$  determines how many cell divisions are possible if a nutrient pulse has saturated cellular storage capacity but in the process ambient nutrients were depleted.

In our model these parameters vary across species and are constrained by a three-way tradeoff. In order to approximate a continuous plane of strategies, a matrix of trait values for 400 species was created. Species are assigned a value for  $\mu_{\max,i}$  ranging between 0.2 and 3.5 day<sup>-1</sup>, and a value for  $P_{\text{saff},i}$  ranging between 10<sup>0</sup> and 10<sup>6</sup> l μmol P<sup>-1</sup> day<sup>-1</sup>. The three-way tradeoff is imposed by solving for  $Q_{\max,i}$  as the third axis on the tradeoff plane:  $\log_{10} Q_{\max,i} = -5.77 - 1.22 \times \log_{10} P_{\text{saff},i} - 5.91 \times \log_{10} \mu_{\max,i}$  (Edwards et al. 2013a). Sufficiently large values of  $P_{\text{saff},i}$  and/or  $\mu_{\max,i}$  lead to  $-Q_{\max,i} < Q_{\min}$ , and these species are discarded as infeasible. Specific  $P$  affinity is a composite trait involving  $V_{\text{maxhi}}$ ,  $K_i$  and  $Q_{\min}$ , and therefore we must translate from  $P_{\text{saff}}$  to these component traits. We hold  $V_{\text{maxhi}}$  and  $Q_{\min}$  constant at intermediate values (3.89 × 10<sup>-7</sup> μmol cell<sup>-1</sup> day<sup>-1</sup> and 1.74 × 10<sup>-9</sup> μmol cell<sup>-1</sup>, respectively), and vary  $K$  across species to obtain the appropriate values of  $P_{\text{saff}}$ , i.e.  $K_i = V_{\text{maxhi}} / P_{\text{saff},i} Q_{\min}$ . This choice is sensible because among the three component traits,  $P_{\text{saff}}$  covaries most strongly with  $K$ , and is not significantly correlated with  $V_{\text{max}}$  or  $Q_{\min}$  (Edwards et al. 2013a). The assigned parameter values were used in the following equations to solve for the additional parameters  $\mu_{\infty,i}$  and  $V_{\text{maxlo},i}$  (Grover 1991):

$$\mu_{\infty,i} = \frac{\mu_{\max,i} \times Q_{\max,i}}{(Q_{\max,i} - Q_{\min})} \quad (6)$$

$$V_{\text{maxlo},i} = \mu_{\max,i} \times Q_{\max,i} \quad (7)$$

## Implementation of nutrient pulses

Previous work (Litchman et al. 2009, Edwards et al. 2013a) has shown that pulsed nutrient supply can allow multiple species to coexist in this model under the appropriate tradeoffs, but the number of surviving species is still small (about 2–4). We used the model to test if diversity changes when multiple time scales of variation occur at the same time, and we hypothesize that multiple time scales of pulsed nutrient supply will permit a greater number of species to coexist. Large pulse events tend to be rarer than those of smaller magnitude, and so we compare frequent events of smaller magnitude and rarer events of larger magnitude. We therefore implemented multiple pulse frequencies by varying the pulse period from 1 to 256 days while simultaneously including a ‘background’ period of 4, 16, or 64 days (Fig. 1). This allowed us to test the hypothesis that larger differences in period length would allow for greater community diversity.

Nutrient pulses were added to the model by replacing a fraction of the mixed layer with deep water (Eq. 4, 5). The magnitude for each pulse, i.e. the replacement fraction, was defined using the equation  $p = 1 - e^{-d \times T}$ . The fraction  $p$  is a function of the pulse period  $T$  (days) and instantaneous dilution rate  $d$  (day<sup>-1</sup>). The pulse therefore removes a fraction of the biomass every  $T$  days equivalent to the integrated instantaneous dilution rate  $d$  (set to 0.0255 day<sup>-1</sup>), in order to vary the frequency of nutrient pulses while holding constant the total loss rate and total nutrient supply. Because each pulse period is paired with a pulse magnitude, during occasions when two pulse events coincide, the magnitude of the combined pulse was calculated to be  $p_{1+2} = 1 - e^{-d \times (T_1 + T_2)}$  (Fig. 1).

Competitive dynamics were simulated by initializing the pool of 400 species at equal low density, and running the model until it converged on a periodic attractor (Fig. 2). Species whose maximum abundance over one pulse period (i.e. the longer pulse period if two frequencies are present) was less than 10<sup>-3</sup> ml<sup>-1</sup> were declared extinct and removed.



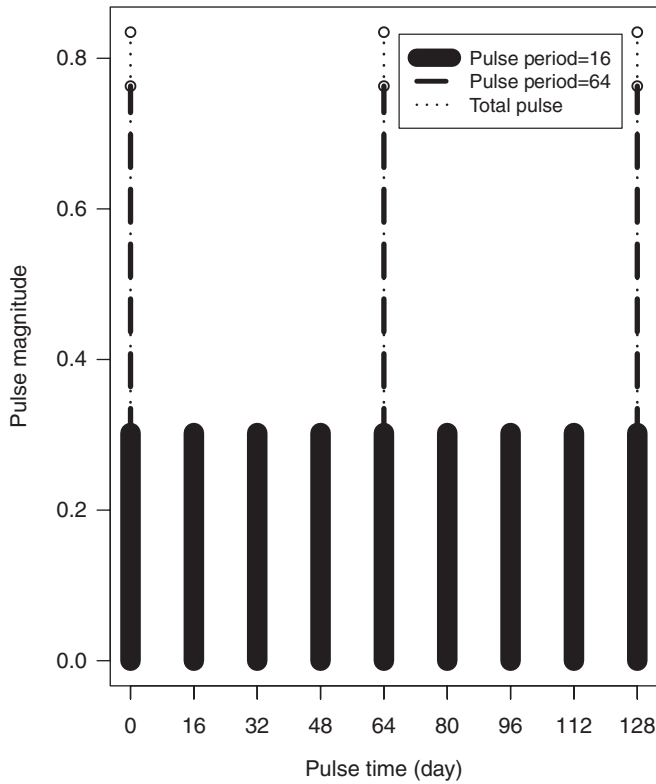


Figure 1. An example of how multiple frequencies of pulsed nutrients are combined. The pulse times (x-axis) are the days at which pulses were introduced into the system. Pulse magnitude, on the y-axis, is the proportion of the mixed layer replaced with deep water. In this example pulses occurred with periods of 16 days and 64 days.

We confirmed that species previously declared extinct were unable to invade the ‘final’ set of species, which was also found in the previous study that used a similar algorithm (Edwards et al. 2013a).

The model was run under several additional conditions to better understand the dynamics. To explore how the effect of multiple frequencies of resource supply might depend on the magnitude of the resource pulses, we reduced  $d$ , which controls the magnitude of the pulsed mixing events, by 25, 50 and 75%. We also explored whether the effect of multiple frequencies depends on multiple dimensions of trait variation, by constraining species to vary according to two-way tradeoffs, rather than the full three-way tradeoff. For the tradeoff between  $\mu_{\max}$  and  $P_{\text{saff}}$ , trait values were defined as described above, but with  $Q_{\max}$  held constant across species at a low value of  $2.00 \times 10^{-9} \mu\text{mol P cell}^{-1}$ . For the tradeoff between  $P_{\text{saff}}$  and  $Q_{\max}$ ,  $\mu_{\max}$  was held constant at an intermediate value of  $0.88 \text{ day}^{-1}$  or a low value of  $0.3 \text{ day}^{-1}$ . For the tradeoff between  $\mu_{\max}$  and  $Q_{\max}$ ,  $P_{\text{saff}}$  was held constant at an intermediate value of  $10001 \mu\text{mol P}^{-1} \text{ day}^{-1}$  or a low value of  $1001 \mu\text{mol P}^{-1} \text{ day}^{-1}$ . Finally, the model was run with the turbulent diffusion term ( $a$ ) set to zero in order to simulate a set of conditions where there is no steady background flux of nutrients, and therefore the only supply of nutrients is

through the pulsed mixing events. The recycling term ( $f$ ) was also set to zero because recycling also results in a steady release of dissolved nutrients.

To analyze the model results we visualize patterns of community structure in trait space, and we also analyze species richness and functional diversity under different scenarios. Functional diversity is quantified using functional dispersion, which we define as the mean Euclidean distance in log trait space between each coexisting species and the centroid of the coexisting species (Anderson et al. 2006). To weight the three traits equally, trait values were standardized such that each trait had a variance of 1 on a log scale.

## Results

### One frequency of pulsed nutrient supply

Under a single frequency of pulsed nutrient supply, community structure varied as found previously (Edwards et al. 2013a), which we review here. Across a gradient of pulse frequencies, there were clear differences in which strategies persisted. Under pulse periods of 1 and 2 days only species with high affinity for phosphorus uptake ( $P_{\text{saff}}$ ) persisted (Fig. 3A). Under periods of 4–16 days a strategy of high storage capacity ( $Q_{\max}$ ) and low  $P_{\text{saff}}$  coexists with a strategy of high  $P_{\text{saff}}$  and low  $Q_{\max}$ ; maximum growth rates ( $\mu_{\max}$ ) are low for both of these types. When the pulse period increases to 32 days the community shifts such that the storage strategy is absent, while a strategy of high  $\mu_{\max}$  and low  $P_{\text{saff}}$  coexists with a strategy of high  $P_{\text{saff}}$  and low  $\mu_{\max}$ . For pulse periods of 64–256 days, strategies with intermediate  $\mu_{\max}$  and  $P_{\text{saff}}$  values can also coexist.

### Two frequencies of pulsed nutrient supply

Under two frequencies of pulsed nutrient supply the coexistence of strategies mirrored what was found under a single frequency: a high affinity strategy persists under all conditions, while a storage strategy persists under periods of 4–16 days, and rapid growth strategies persist under periods of 32–256 days (Fig. 3B–D). Thus, when the background period is 16 days a species with high  $Q_{\max}$  (and low  $P_{\text{saff}}$  and  $\mu_{\max}$ ) always persists, regardless of the secondary period (Fig. 3C). Likewise, when the background period is 64 days a species with high  $\mu_{\max}$  (and low  $P_{\text{saff}}$  and  $Q_{\max}$ ) always persists, regardless of the secondary period (Fig. 3D). The novel effect of multiple pulse frequencies is that all three strategies can persist simultaneously, if pulses of the appropriate frequency are present. This can be seen when the background period is 16 days and the secondary period is 64–256 days (Fig. 3C), and when the background period is 64 days and the secondary period is 8–16 days (Fig. 3D).

However, some of the community patterns show that community structure under two frequencies of supply is not simply the sum of the communities that occur under each individual frequency. For example, under a background

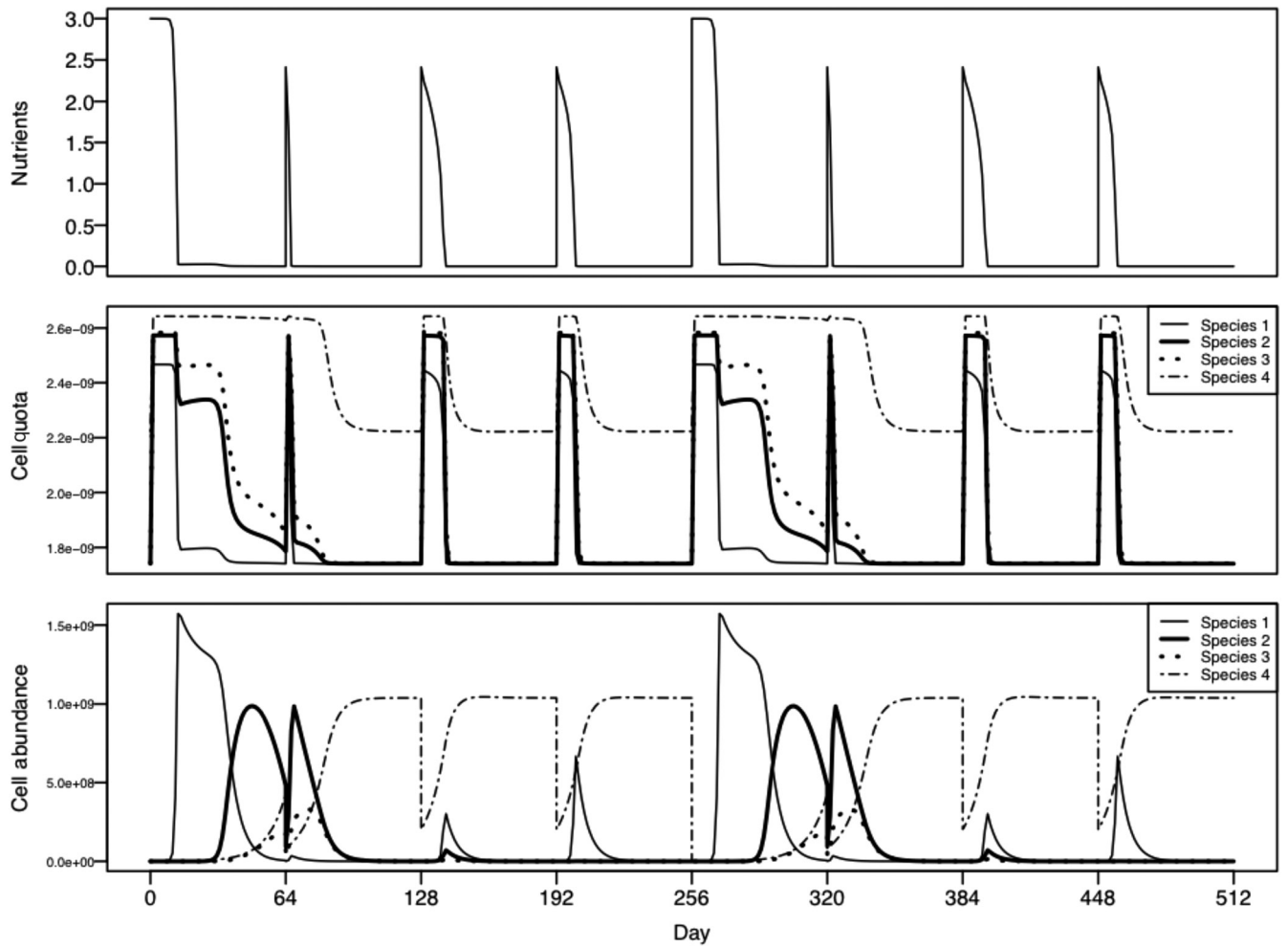


Figure 2. Example model dynamics after convergence to the periodic attractor. In this example, the pulse periods were 64 and 256 days. The top panel shows nutrient dynamics, with a large pulse every 256 days and a smaller pulse every 64 days. The middle panel shows quota dynamics for four coexisting species. The bottom panel shows the abundances of the four species. Species 1 has the highest  $\mu_{\max}$  and lowest  $P_{\text{saff}}$ , species 4 has the highest  $P_{\text{saff}}$  and lowest  $\mu_{\max}$ , and species 2 and 3 have intermediate values of these traits. The units for the axes: nutrient is  $\mu\text{mol P l}^{-1}$ , cell quota is  $\mu\text{mol P cell}^{-1}$ , cell abundance is  $\text{cells l}^{-1}$ .

period of 2 days a species with high  $\mu_{\max}$  does not appear when the secondary pulse period is 32 days, in contrast to the single-frequency results (Fig. 3B). In addition, under periods of 128–256 days there are fewer species with intermediate  $\mu_{\max}$  and  $P_{\text{saff}}$  values (Fig. 3B), and this is true to a lesser extent under background frequencies of 16 and 64 days (Fig. 3C–D).

To summarize how multiple frequencies of nutrient supply affect species diversity and functional diversity, we plotted the distribution of species richness and functional diversity across all pulse frequencies, comparing the four scenarios in Fig. 3: single pulse frequency, additional pulse every 2 days, additional pulse every 16 days, and additional pulse every 64 days (Fig. 4). The results show that multiple pulse frequencies do not consistently increase the number of coexisting species, relative to a single pulse frequency (Fig. 4A–D). In contrast, functional diversity is about 50% greater when there is a second pulse every 16 or 64 days (Fig. 4E–H). The increase

in functional diversity is essentially due to the coexistence of three kinds of strategies (affinity, storage, rapid growth), because this diversity of strategies cannot simultaneously coexist under a single pulse frequency (Fig. 3A).

## Two-way tradeoffs

### $\mu_{\max}$ versus $P_{\text{saff}}$

We also analyzed the model with the focal traits constrained by two-way tradeoffs, instead of a three-way tradeoff, to explore whether the effect of multiple pulse frequencies depends on multiple dimensions of trait variation. Under a two-way tradeoff between  $\mu_{\max}$  and  $P_{\text{saff}}$  ( $Q_{\max}$  held constant), a rapid growth strategy (high  $\mu_{\max}$  and low  $P_{\text{saff}}$ ) is favored by intermediate pulse periods (4–16 days), where previously a storage strategy was favored by those periods (Supplementary material Appendix 1 Fig. A1). This implies that a storage strategy, when present, outcompetes a rapid growth strategy

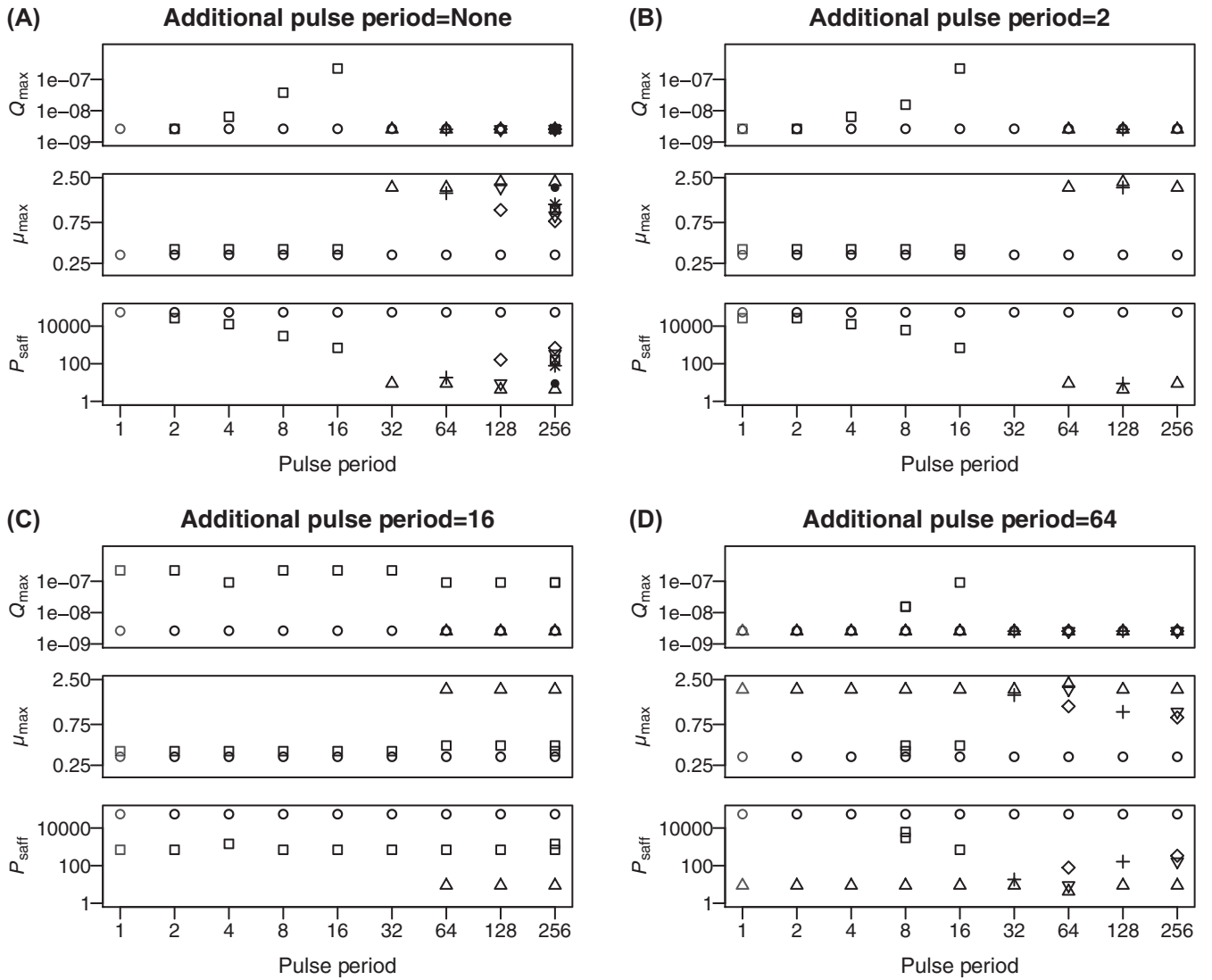


Figure 3. Community structure as a function of pulse frequency (or frequencies). Each point represents the trait value for a single species that persisted during that trial. For each pulse period on the x-axis, the values for each trait of all coexisting species are plotted. The units for the axes are:  $Q_{\max}$ ,  $\mu\text{mol P cell}^{-1}$ ;  $\mu_{\max}$ ,  $\text{d}^{-1}$ ;  $P_{\text{saff}}$ ,  $\mu\text{mol P}^{-1} \text{ day}^{-1}$ . (A) Community structure under a single pulse frequency, with pulse period ranging from 1 to 256 days. (B) Community structure under two simultaneous pulse frequencies. All communities experience a ‘background’ pulse every 2 days, and a second pulse with period ranging from 1 to 256 days. (C) As in (B), but with a background pulse every 16 days. (D) As in (B), but with a background pulse every 64 days.

at those periods. However, multiple pulse frequencies do not increase species richness or functional diversity beyond what is seen under a single pulse frequency (Fig. 5), and a background pulse periods of 2 days causes the loss of the rapid growth strategy under secondary periods of 4–16 days (Supplementary material Appendix 1 Fig. A1). This may occur because the smaller, more frequent pulses give a relative advantage to the high affinity strategy.

#### $P_{\text{saff}}$ versus $Q_{\max}$

Under a two-way tradeoff between specific uptake affinity and storage capacity, if  $\mu_{\max}$  is held constant at an intermediate value ( $0.88 \text{ day}^{-1}$ ), a single strategy with relatively low  $Q_{\max}$  and intermediate  $P_{\text{saff}}$  excludes the other species under all conditions (Supplementary material Appendix 1 Fig. A2).

If  $\mu_{\max}$  is reduced to a lower value ( $0.3 \text{ day}^{-1}$ ) that permits a relatively high  $P_{\text{saff}}$ , then coexistence between high affinity and high storage strategies is possible under periods of 4–32 days (Supplementary material Appendix 1 Fig. A3). However, multiple pulse frequencies do not enhance functional or species diversity relative to a single pulse frequency (Supplementary material Appendix 1 Fig. A4).

#### $\mu_{\max}$ versus $Q_{\max}$

Finally, under a two-way tradeoff between maximum growth rate and storage capacity, little coexistence occurs. Pulse periods from 8 to 32 days allow two species to coexist that differ slightly in the two traits (Supplementary material Appendix 1 Fig. A5). A similar outcome is found whether  $P_{\text{saff}}$  is held constant at an intermediate value ( $1000 \mu\text{mol P}^{-1} \text{ day}^{-1}$ )

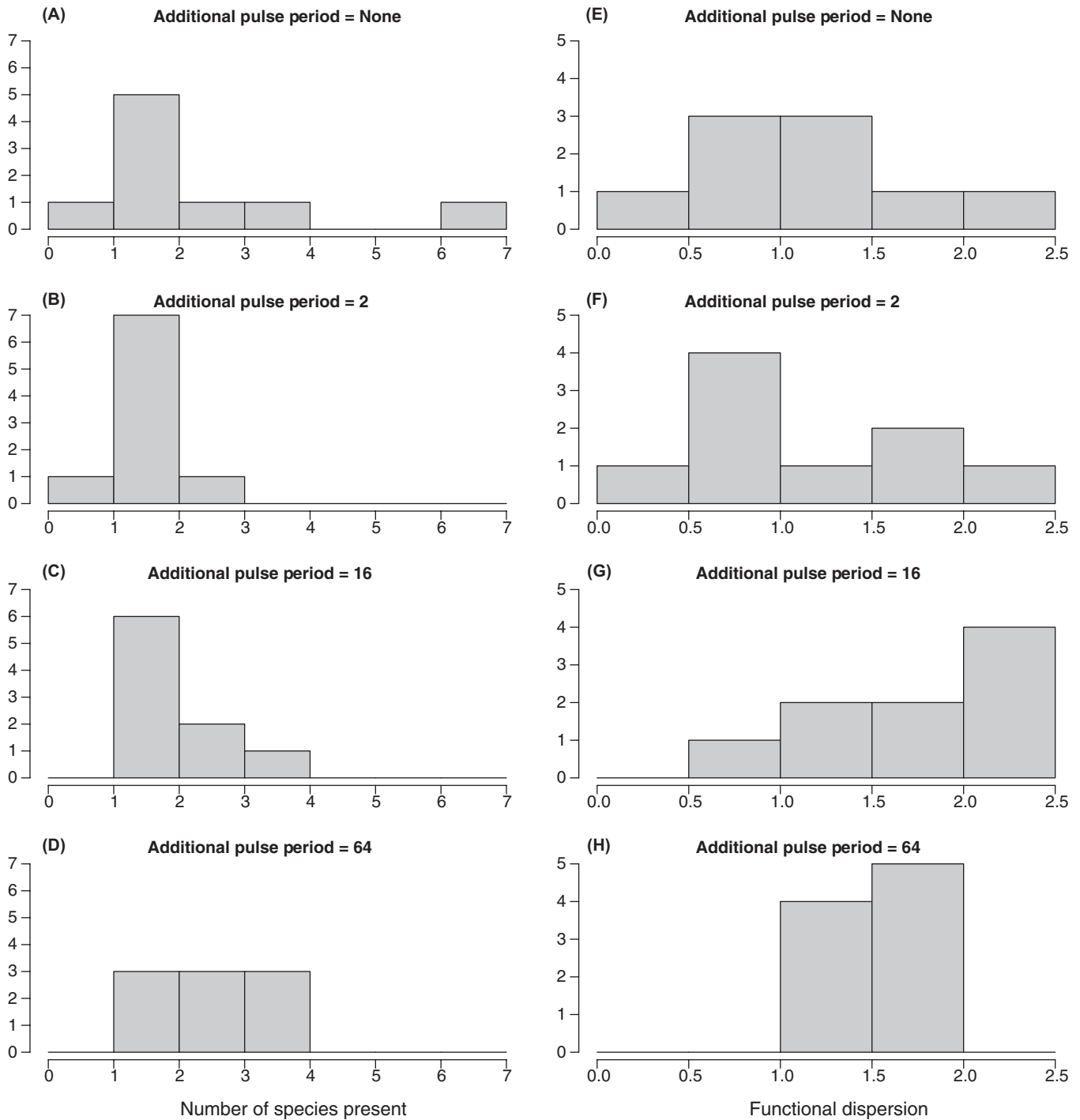


Figure 4. Effects of one versus two pulse frequencies on species and functional diversity. (A–D) show the distribution of species richness across all model runs displayed in Fig. 3, for panel (A–D) respectively. (E–H) show the distribution of functional dispersion across all model runs in Fig. 3, for panel (A–D) respectively.

or a relatively low value ( $100 \mu\text{mol P}^{-1} \text{ day}^{-1}$ ) (results not shown).

### Altered pulse magnitude

Reducing the magnitude of the nutrient pulses by 25–50% causes only minor shifts in the patterns of community structure

already described (Supplementary material Appendix 1 Fig. A6, A7). In contrast, reducing the magnitude by 75% affects the ability of multiple strategies to coexist, such that affinity and storage strategies coexist under periods of 4–16 days, and affinity and rapid growth strategies coexist under periods of 32–256 days, but storage and rapid growth strategies do not occur simultaneously (Supplementary material Appendix 1 Fig. A8).



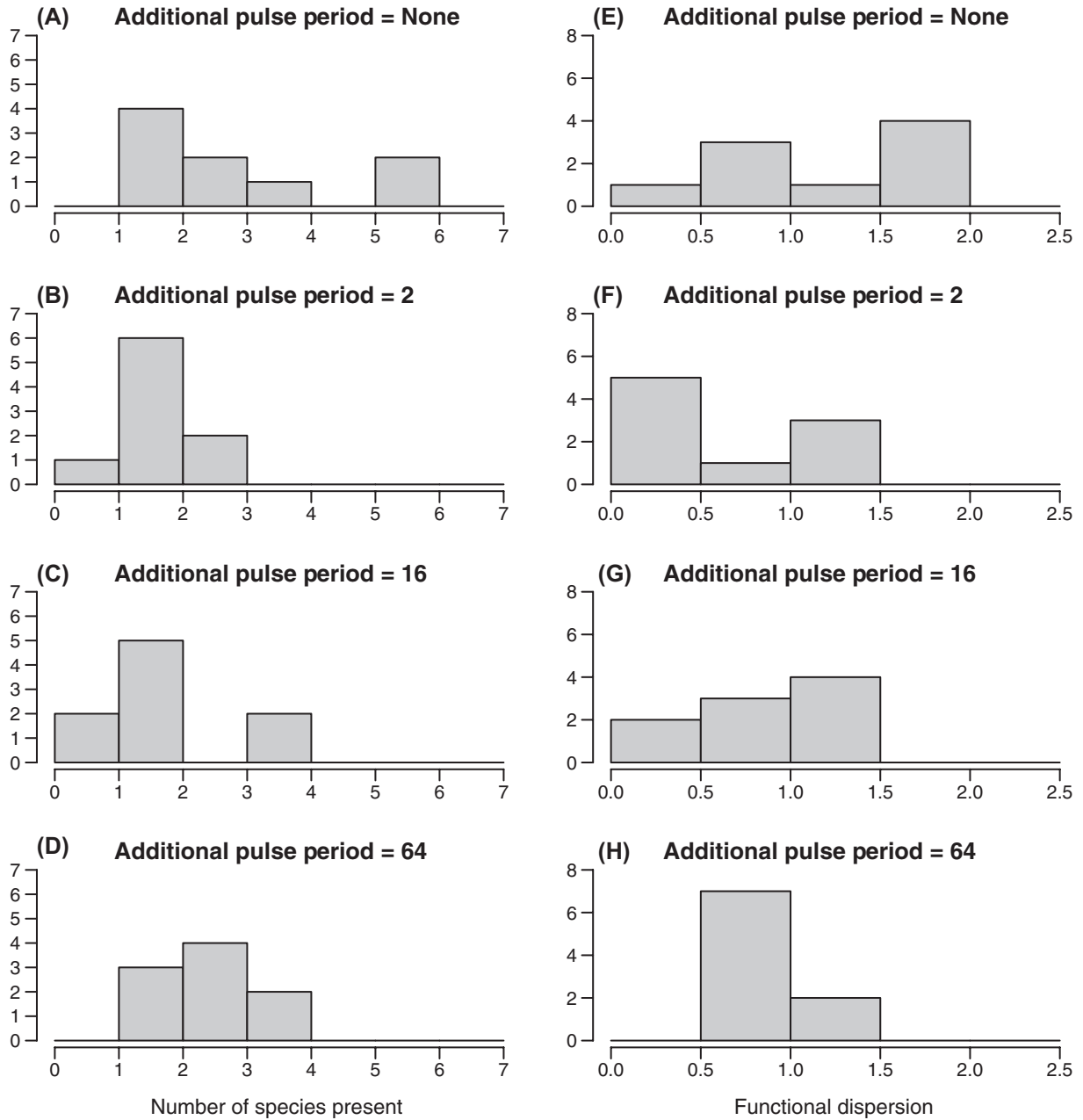


Figure 5. Two-way tradeoff between  $\mu_{\max}$  and  $P_{\text{saff}}$ . Effects of one versus two pulse frequencies on species and functional diversity, under a two-way tradeoff between maximum growth rate and phosphate affinity. (A–D) show the distribution of species richness across all model runs displayed in Supplementary material Appendix 1 Fig. A1, for panel (A–D) respectively. (E–H) show the distribution of functional dispersion across all model runs in Supplementary material Appendix 1 Fig. A1, for panel (A–D) respectively.

### Continuous nutrient supply

Removing continuous nutrient supply (mixing and recycling) has a large effect on community structure and diversity. A strategy of high  $P_{\text{saff}}$  (and low  $\mu_{\max}$  and  $Q_{\max}$ ), which previously persisted under all conditions, is now present only under pulse periods of 1–2 days (Supplementary material Appendix 1 Fig. A9). This leads to a substantial reduction

in species richness and functional diversity (Supplementary material Appendix 1 Fig. A10). Under these conditions, multiple pulse frequencies slightly increase species richness and functional diversity (Supplementary material Appendix 1 Fig. A10), primarily because a combination of short periods (1–2 days) and long periods (64–256 days) allows a high  $P_{\text{saff}}$ /low  $\mu_{\max}$  strategy to coexist with a high  $\mu_{\max}$ /low  $P_{\text{saff}}$  strategy (Supplementary material Appendix 1 Fig. A10).

## Spectral analysis

Although the focus of the current study is coexistence, we analyzed cross-correlation of coexisting competitors when pulses are added every 16 and 64 days, which permits species with high affinity, high storage capacity, and rapid growth to coexist (Fig. 2C). At a lag of zero days, the cross-correlation of the high affinity and rapid growth strategists is negative ( $-0.44$ ), while for the affinity and storage strategies the correlation is positive ( $0.47$ ), and for the storage and rapid growth strategies the correlation is near zero ( $-0.058$ ) (Supplementary material Appendix 1 Fig. A11). Analysis of cross-wavelet power exhibits more complex patterns. For example, the rapid growth and affinity strategies covary negatively at  $\sim 64$  day period but positively at a  $\sim 16$  day period. The storage and affinity strategies are out of phase by  $\sim 90$  radians at the 64 day period but positively correlated at  $\sim 32$  days. In general these patterns suggest that coexisting competitors can exhibit positively or negatively correlated dynamics, and the sign of the correlation can switch for different timescales.

## Discussion

### Effects of multiple frequencies of nutrient supply

As shown previously, under a single frequency of nutrient supply, changing the period/magnitude of the pulse causes large shifts in community structure, with multiple strategies often coexisting (Fig. 3A). When pulse periods are small (every day or two), the dominant strategy is high uptake affinity (and low storage and max. growth rate). Because these pulses are frequent and only deliver a small amount of nutrients, these conditions are similar to a steady stream of nutrients. Therefore, it is advantageous to have high uptake affinity. For periods of 4–16 days, the time between pulses is great enough that a strategy of storing nutrients becomes beneficial. The advantage of storing nutrients declines under longer pulse periods, because the amount of time between nutrient introductions is so long that stored nutrients are exhausted during growth, before the next pulse arrives. Therefore, it becomes more advantageous to grow as fast as possible while the nutrients are available. Thus there is a shift toward the third strategy of maximizing the nutrient-sufficient growth rate.

We initially expected that incorporating multiple pulse frequencies would cause an overall increase in the number of species able to coexist. However, there was no clear difference in the number of species able to coexist between one pulse frequency and two pulse frequencies (usually 2–4 species; Fig. 4). Instead, what differed was the functional diversity of strategies that coexist. Under one frequency there were pulse periods where the coexisting species had distinct strategies, and there are clear shifts between these strategies across conditions. Under two frequencies, the coexisting community is in some ways the sum of the communities that emerge under each individual frequency. Pulse periods of  $\sim 1$ –2 weeks favor

species with high  $Q_{\max}$ , and pulse periods  $>1$  month favor species with high  $\mu_{\max}$ . When frequencies in both of these ranges are present, both strategies occur (Fig. 3B–D). In addition, species with high  $P_{\text{saff}}$  can persist under all conditions, which is discussed further below. It should be noted that combining two frequencies of nutrient supply does not exactly result in a community that is the sum of the communities that emerge under the individual frequencies. For example, under the longest pulse periods, species with intermediate  $\mu_{\max}$  can coexist with high  $\mu_{\max}$  and high  $P_{\text{saff}}$  species (Fig. 3A), but when a pulse period of 16 days is added a high  $Q_{\max}$  species is added and appears to exclude the intermediate  $\mu_{\max}$  species.

Our model design actually includes three different frequencies of nutrient input: the first pulse frequency, the second pulse frequency and the mixing and recycling that acts as a constant influx of nutrients into the system. When mixing and recycling are removed the species with the highest  $P_{\text{saff}}$  (and low  $Q_{\max}$  and  $\mu_{\max}$ ), which previously persisted under all conditions, now only occurs under pulse periods of 1–4 days (Supplementary material Appendix 1 Fig. A9). Therefore, the persistence of this species is another example of how species with different strategies can coexist when supply frequencies that select for those strategies are combined. When mixing and recycling are removed, the species best adapted to steady nutrient supply can only persist when pulse periods are small enough to approximate continuous supply.

Our exploration of two-way tradeoffs shows that multiple frequencies of nutrient supply only increase functional diversity when species' traits can vary in multiple dimensions (i.e. under a three-way tradeoff). Under a two-way tradeoff between  $\mu_{\max}$  and  $P_{\text{saff}}$ , multiple pulse frequencies did not increase species richness or functional diversity (Fig. 5). Rather, the greatest functional diversity and species richness is seen under the longest periods with the largest pulses (Supplementary material Appendix 1 Fig. A1), and multiple pulse frequencies exhibit similar or lower diversity than is found under the single component frequencies. This difference, compared to the three-way tradeoff, is likely because this scenario removes the storage strategy that is best adapted to pulses of intermediate frequency. The other two-way tradeoffs are generally less effective at promoting coexistence: a tradeoff between  $Q_{\max}$  and  $P_{\text{saff}}$  only maintains coexistence when  $\mu_{\max}$  is set to a low value of  $0.3 \text{ day}^{-1}$  (Supplementary material Appendix 1 Fig. A2, A3), and a tradeoff between  $\mu_{\max}$  and  $Q_{\max}$  only leads to coexistence of very similar strategies under restricted conditions (Supplementary material Appendix 1 Fig. A5). Overall these results suggest that community responses to resource fluctuation will depend on the both the dimensionality of trait variation and the major frequencies at which resources fluctuate.

A number of lab experiments have tested whether pulsed nutrient supply alters community structure and promotes coexistence of phytoplankton (Sommer 1984, Ducobo et al. 1998, Cermeño et al. 2011). Future experiments with phytoplankton or other experimentally tractable organisms could

test whether multiple frequencies of supply allow for greater diversity, and including/excluding a continuous source of nutrients would be an important comparison. Our results may also be useful for interpreting or guiding work that combines plankton ecosystem models with high resolution physical models (Lévy et al. 2015), perhaps by informing why community structure changes under physical regimes that have different characteristic frequencies of nutrient fluctuation. Comparing our model predictions to observational community patterns will require new data on trait distributions within communities, because data on the relevant traits (specific uptake affinities, maximum growth rates, nutrient quotas) is currently too sparse to quantify patterns of functional diversity (Edwards 2016).

## Implications

Although our model is parameterized for phytoplankton limited by phosphorus, the structure of the model is relatively simple and the results may apply to a broad range of systems where resources vary over time. The model is parameterized for phosphorus due to the amount of data on the relevant tradeoffs, but similar dynamics could occur for nitrogen, which is often limiting in the ocean as well as lakes (Litchman et al. 2009). Shifts in community composition and functional diversity could have a range of biogeochemical effects, ultimately driven by episodic events of nutrient supply that are poorly understood at this point (Johnson et al. 2010, Lévy and Martin 2013). One possibility is that nitrogen utilization strategies vary with size, such that the smallest phytoplankton have the highest nitrogen affinity, intermediate-sized species have the fastest growth rates, and the largest species have the greatest storage capability (Litchman et al. 2009, Marañón et al. 2013). In this case frequencies of nitrogen supply may be linked to community size diversity, and potentially to biogeochemical processes such as carbon flux to the deep ocean (Boyd et al. 2010). It will also be important to put multiple frequencies of resource variation into a meta-community context, because temporal forcing will likely differ across space, and effects on local and regional diversity will depend on the degree of spatial differences and rates of mixing between environmentally distinct habitats (Mouquet and Loreau 2003, Lévy et al. 2015).

Our results may also be relevant for other kinds of ecosystems, such as arid or forest plant communities. In arid and semi-arid environments, the frequency of rainfall events alters plant diversity. Rainfall events of small magnitude are common, with medium-sized events that occur less frequently, and large events that are highly variable (Schwinning and Sala 2004). This spectrum is similar to pulses of phosphorus in our model, where there are smaller, more frequent events and larger, less frequent events. During smaller rainfall events the water only penetrates the top soil, benefitting species with shorter roots, while larger rainfall events benefit species with deep roots (Chesson et al. 2004). Therefore, diversity in arid environments could possibly be maintained through the pairing of high frequency and low frequency rainfall events.

Spatial competition among sessile organisms could also lead to similar community dynamics. In terrestrial environments, fires and droughts can be an important source of disturbance to which some species are well-adapted. Fires spark succession in plant communities, with a temporal sequence of species that can grow and occupy space the fastest, hardier plants that can survive in the altered soil and eventually weed out the primary successor, and widespread tertiary successors that ultimately outcompete the secondary successors (Connell and Slatyer 1977, Ellsworth et al. 2013). If there are multiple frequencies of fire events (of different magnitude), there could be a mixture of all three successional types in the landscape. Similar dynamics could operate in hard substrate benthic marine communities, for which disturbance commonly drives successional dynamics, and disturbance of different frequencies and spatial scales can favor different species (Sousa 1984).

Analysis of cross-correlation and cross-wavelet power showed that coexisting competitors can be positively correlated, negatively correlated, or uncorrelated over time. In addition, the sign of these correlations can switch across timescales (Supplementary material Appendix 1 Fig. A11). These results are relevant when considering whether natural populations exhibit synchronous or compensatory dynamics, and whether compensatory dynamics are expected when species compete (Vasseur and Gaedke 2007, Loreau and de Mazancourt 2008). In the current model the mix of forces affecting synchrony are complex; nutrient flux and associated population dilution will tend to synchronize competitors, but differential responses to periods of nutrient abundance versus scarcity will tend to cause more compensatory dynamics, and both of these processes are happening at multiple timescales. The final result is that patterns of correlation and covariance are variable enough that it would be difficult to infer underlying community processes from these signals.

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- Supplementary material (available online as Appendix oik.04937 at <[www.oikosjournal.org/appendix/oik-04937](http://www.oikosjournal.org/appendix/oik-04937)>). Appendix 1.