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Microbial Dormancy Supports Multi-Species Coexistence Under Resource Fluctuations

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ABSTRACT

The ability for microbes to enter dormant states is adaptive under resource fluctuations and has been linked to the maintenance of diversity. Nevertheless, the mechanism by which microbial dormancy gives rise to the density-dependent feedbacks required for stable coexistence under resource fluctuations is not well understood. Via analysis of consumer-resource models, we show that the stable coexistence of dormancy and non-dormancy strategists is a consequence of the former benefiting more from resource fluctuations while simultaneously reducing overall resource variability, which sets up the requisite negative frequency dependence. Moreover, we find that dormants can coexist alongside gleaner and opportunist strategies in a competitive-exclusion-defying case of three species coexistence on a single resource. This multi-species coexistence is typically characterised by non-simple assembly rules that cannot be predicted from pairwise competition outcomes. The diversity maintained via this three-way trade-off represents a novel phenomenon that is ripe for further theoretical and empirical inquiry.

1 | Introduction

Microbial systems are subject to numerous exogenous and endogenous forces that prevent them from establishing a stable equilibrium. Rather than destabilising ecosystems, theoretical and empirical evidence indicates that fluctuating dynamics can play a critical role in the maintenance of genetic and species diversity (Angert et al. 2009; Chesson 2000; Ellner et al. 2019; Hallett et al. 2019; Letten et al. 2018; Yamamichi, Letten, and Schreiber 2023). Coexistence mechanisms deriving from temporal fluctuations can be grouped into two formally defined classes: the *temporal storage effect* and *relative nonlinearity of competition*, mediated by trade-offs in responses to density-independent (e.g., temperature) and density-dependent (e.g., nutrient resources) factors, respectively (Chesson 1994, 2000). Relative nonlinearity is commonly perceived to be the weaker mechanism in nature since it places putatively narrow constraints on resource acquisition strategies (Xiao and Fussmann 2013; but see Johnson, Godoy, and Hastings 2022, Yamamichi and Letten 2022). It is less widely appreciated, however, that a number of other trade-offs are also capable of promoting coexistence through relative nonlinearity, including sensitivity to predation and disease, adaptive capacity, and, the focus of this study, access to dormant life phases (Kortessis and Chesson 2019; Tan et al. 2020; Yamamichi and Letten 2021, 2022). Explicating the unexplored pathways to coexistence via relative nonlinearity holds promise for a better understanding of diversity maintenance in natural and synthetic microbial ecosystems.

Dormancy is widely recognised to be a beneficial adaptation to environmental variability, providing organisms with a means of

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surviving unfavourable periods, either via separate life stages (e.g., plant seeds and insect pupae/eggs) or via phenotypic switching (e.g., microbes) (Lennon and Jones 2011; Levine and Rees 2004; Măgălie et al. 2023; Venable and Brown 1988). Previous work has shown that in fluctuating environments, organisms that have the capacity to switch between active and dormant states can coexist alongside organisms adopting alternative strategies (Stolpovsky et al. 2016, 2011; Tan et al. 2020; Yamamichi and Letten 2021). This coexistence is routinely attributed to the temporal storage effect (Lennon et al. 2021; Lennon and Jones 2011; Locey 2010; Schwartz et al. 2023; Wisnoski and Lennon 2021), on account of the historical emphasis on dormant life stages in verbal descriptions of the mechanism (Johnson and Hastings 2022; Yamamichi, Letten, and Schreiber 2023). Specifically, diversity maintenance via the temporal storage effect is contingent on two conditions: (i) density-dependence in covariance between environmental favourability and the intensity of competition, which emerges when competitors exhibit trade-offs in responses to density-independent factors (e.g., temperature) that fluctuate through time; and (ii) the adverse effects of competition during unfavourable periods need be buffered to ensure they do not offset the gains made during favourable periods (Chesson 1994, 2000). Dormant life stages offer one well-documented pathway to satisfy this second condition, hence the strong association between dormancy and the temporal storage effect. However, dormancy is neither necessary for buffered growth (Johnson and Hastings 2022, Yamamichi, Letten, and Schreiber 2023), nor is it necessarily limited to the temporal storage effect; it also has the potential to foster the responses to (and impacts on) fluctuations in the intensity of competition that are a signature of relative nonlinearity (Kortessis and Chesson 2019; Tan et al. 2020; Yamamichi and Letten 2021, 2022).

The canonical trade-off facilitating coexistence via relative nonlinearity is between 'gleaner' strategists (characterised by more concave growth responses) that are more competitive when resources are scarce, and therefore benefit from a stable resource supply; and 'opportunist' strategists (characterised by less concave growth responses) that are able to attain higher growth rates when resources are plentiful, and therefore benefit in competition from fluctuating resource supply (Grover 1997; Letten and Yamamichi 2021; Yamamichi and Letten 2022). Critically, the stabilising effect of relative nonlinearity emerges when the gleaner and the opportunist each impact the realised resource variability in a direction that favours the other, irrespective of whether the resource fluctuations are generated endogenously or exogenously. The gleaner-opportunist trade-off is so tightly interwoven with standard explanations of relative nonlinearity, that alternative pathways have gone largely ignored. Yamamichi and Letten (2021) investigated how a trade-off between competitive ability and evolvability can mediate coexistence via relative nonlinearity, but also considered several cognate trade-offs including one in which a plastic consumer with resource-dependant dormancy assumed the role of the rapidly evolving consumer (Tan et al. 2020). The emergence of coexistence via endogenously generated resource cycling implicated relative nonlinearity by analogy, but the phenomenon was not examined further in that work. Here, we explore how the requisite nonlinearity emerges for organisms that alternate between dormant and active life phases under the externally driven fluctuations in resource availability more typical of microbial systems; and the potential for dormancy strategists to occupy a sufficiently differentiated temporal niche that facilitates their coexistence alongside classical gleaner and opportunist strategists.

To investigate the role of dormancy in mediating microbial coexistence, we formulated a consumer-resource ordinary differential equation (ODE) model describing competition between species/genotypes characterised by different resource acquisition strategies and/or the ability to switch between dormant and active phenotypes. The different strategies could represent different species or different genotypes within a species, but for simplicity we hereafter refer to them solely as species. The model is sufficiently general to pertain to a diversity of organisms, but is especially relevant to microbial populations due to their continuous growth dynamics, overlapping generations, and the prevalence of taxa capable of switching interchangeably between dormant and active states (cf. dormancy as a distinct irreversible life stage as in plant seeds or insect eggs). By simulating competition between different species combinations under different frequencies and magnitudes of resource pulsing, we are able to show that: (i) relative nonlinearity can indeed facilitate the coexistence of dormancy and non-dormancy strategists; (ii) dormancy strategists can occupy a separate 'niche' to both gleaners and opportunists, thereby allowing three species to stably persist on a single fluctuating resource and (iii) this three-species coexistence is possible even when not all pairwise subsets are stable.

2 | Methods

2.1 | Model Formulation

All resource competition models implemented in this study take the following classical form:

$$\frac{dN_i}{dt} = N_i\left(\mu_i(R) - m\right) \tag{1}$$

$$\frac{dR}{dt} = \Psi(R) - \sum_{i=1}^{n} \mu_i(R) Q_i N_i \tag{2}$$

where N_i is the population density of consumer i (gleaner, opportunist or dormancy strategist), R is the resource concentration, $\mu_i(R)$ is the per capita consumer functional response of consumer i, m is the density-independent mortality rate common to all consumers, Q_i is the resource quota of consumer i and $\Psi(R)$ is the resource supply function.

The consumer functional response is given by the Monod function,

$$\mu_i(R) = \frac{\mu_{\max,i} R}{K_{s,i} + R} \tag{3}$$

where $\mu_{\max,i}$ is the maximum growth rate and $K_{s,i}$ is the half-saturation constant for consumer i.

The dormancy strategist is unique in the ability to switch, as a function of resource availability, between an active phenotype and a dormant phenotype, where the latter trades off the ability to divide for reduced mortality. To this end, we treat the dormancy strategist as comprising two phenotypes within a structured population, with resource-dependent switching between active, N_a, and dormant, N_d, states as follows:

$$\frac{dN_a}{dt} = N_a\left(\mu_a(R) - m - e^{-\lambda R}\right) + \gamma N_d R \tag{4}$$

$$\frac{dN_d}{dt} = N_a e^{-\lambda R} - \gamma N_d R - m_d N_d \tag{5}$$

where λ denotes the exponentially increasing rate at which the active phenotype switches to the dormant phenotype at low resource concentrations, and γ denotes the corresponding linear rate at which the dormant phenotype switches back to the active state with increasing resource availability. These functions were chosen for their mathematical simplicity and biological realism (i.e., non-negative switching rate across resource fluctuations). Mortality in Equation 5 is indexed, d, to account for reduced mortality compared to the active phenotype and the other growth strategies.

Under continuous resource dynamics, the resource supply function is given by $\Psi(R) = D(S - R)$, where D is the dilution rate and S is the resource supply concentration. Under pulsed resource supply, $\Psi(R)$ is removed from Equation 2 and replaced by discontinuous resource pulsing at fixed intervals:

$$R\left(t^+\right) = R(t^-) + S, t = k\tau, k = 1, 2, \ \ldots \tag{6}$$

where τ is the pulse period and $R\left(t^+\right)$ and $R(t^-)$ represent the respective right and left limits immediately following and preceding a pulse at time t; S is now interpreted as the resource pulse size. Note the resource outflow term, $-DR$, present under continuous resource supply, is absent under pulsed resource supply dynamics.

To quantify the realised per capita growth rate of the dormancy strategist in a fluctuating resource environment, we calculated the log difference in total population size (summed over the active and dormant phases) at each time point over one complete resource pulse cycle (once dynamics were stationary). As such, the shape of the realised per capita growth rate for the dormancy strategist is a combined property of the functional response of the active phenotype, the switching rate between phenotypes and the magnitude and frequency of the resource pulse.

2.2 | Model Parameterisation and Simulation

Except where indicated, resource competition models were parameterised as follows. For the dormancy strategist, $\mu_{\max} = 0.05\,\mathrm{h}^{-1}$, $K_s = 1$ (units of resource), $\lambda = 0.5$, $\gamma = 0.03$. For the gleaner, $\mu_{\max} = 0.07\,\mathrm{h}^{-1}$, $K_s = 0.1$ (units of resource). For the opportunist, $\mu_{\max} = 0.3\ \mathrm{h}^{-1}$, $K_s = 14$ (units of resource). Mortality, m, is $0.025\ \mathrm{h}^{-1}$ for all but the dormant phenotype of the dormancy strategist, for which $m_d = 0.0038\ \mathrm{h}^{-1}$. For all strategists, $Q = 0.01$ (units of resource).

For all pairwise and three-way species iterations, we simulated all combinations of 16 resource pulse sizes, S, evenly spaced from 5 to 20 inclusive, and 14 resource pulse intervals, τ, evenly spaced from 24 to 336, as well as under continuous supply, for a total of 240 unique resource supply size/interval combinations. To account for variation in time to reach stationary dynamics, simulations with longer intervals between resource pulses and/or more species were run for a longer period (total time $= 2000\tau$ or 4000τ for two and three species simulations respectively). Stationarity was confirmed on the basis that the abundances of all consumer species were stationary at a consistent offset in each of the final five pulsing intervals. Simulations were initiated with starting values of 100 for the consumers (dormant phenotype always begins at 0) and 10 for the resource. Any consumer whose population dipped below 10^{-7} in the final τ time steps was treated as having gone extinct. Alongside the core simulations, we also investigated the sensitivity of our results to a range of alternative parameter combinations and model formulations, including perturbations to growth, mortality and dormancy switching parameters; the addition of abiotic resource loss when resources are pulsed; and alternative combinations of resource-dependent switching functions, the details of which are provided in the results and/or figure captions. All models were simulated with the deSolve package (v1.30) (Soetaert, Petzoldt, and Setzer 2010) in R (version 4.1.2).

3 | Results

3.1 | Coexistence of Dormancy and Non-dormancy Strategists Via Relative Nonlinearity

We first consider competitive outcomes between a gleaner strategist and a dormancy strategist under a single resource pulsing regime. Consistent with several previous studies (Stolpovsky et al. 2016, 2011; Tan et al. 2020; Yamamichi and Letten 2021), we observe that in a fluctuating resource environment, a dormancy strategist can coexist with a gleaner that is unable to enter a dormant phase but otherwise has a faster growth rate at all resource concentrations (Figure 1A). This result is robust to the choice of the resource-dependent switching functions (exponential vs. linear; Figure S1) and the inclusion of abiotic resource loss (Figure S2). As is to be expected, however, the outcome of competition (coexistence vs. exclusion) between these two strategies is closely tied to the magnitude of the trade-off between the growth rate of the dormancy strategist during the active phase and its cell mortality during the dormant phase. The greater the growth rate penalty (increasing values on the y-axis of Figure 1B) incurred by the dormancy strategist, the smaller its mortality rate when dormant needs to be to allow for coexistence (decreasing values on the x-axis of Figure 1B). Similarly, coexistence is only possible when the advantage of being able to switch more abruptly to the dormant phenotype at low resource concentrations trades off against: (i) higher mortality during the dormant phase (Figure S3); or (ii) slower switching back to the active phenotype at high-resource concentrations (Figure S4). Note we obtain equivalent results (but with smoother invasion boundaries) via invasion analyses based on Floquet theory (Klausmeier 2008) (Figure S5).

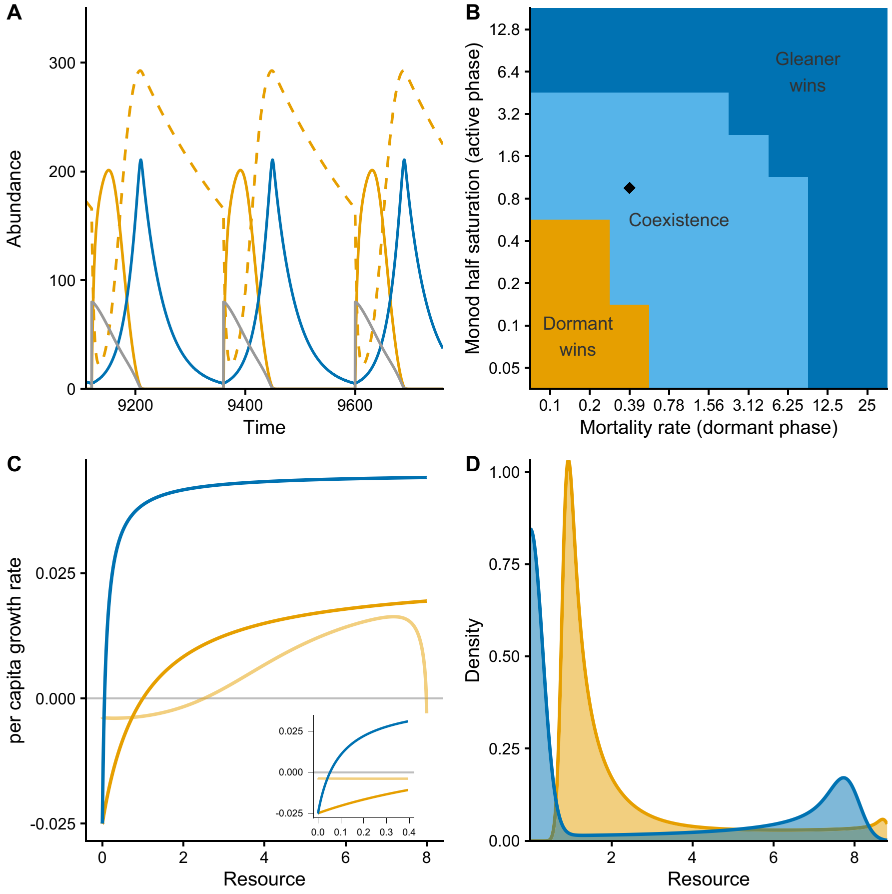

FIGURE 1 | Coexistence of a gleaner and a dormancy strategist under fluctuations in a single resource. (A) Dynamics of the gleaner (blue) and the active (solid orange) and dormant (dashed orange) phenotypes of the dormancy strategist over three successive resource pulses (grey). Resource concentration multiplied by a factor of 10 for visualisation. (B) Outcomes of simulated competition between a gleaner and a dormancy strategist for different parameter combinations of the dormancy strategist's Monod half saturation constant in the active phase and its mortality rate ($\times\ 1000\ \ \mathrm{h}^{-1}$) in the dormant phase. Orange indicates dormancy strategist excluding gleaner; dark blue indicates gleaner excluding dormancy strategist; and light blue indicates coexistence. Diamond denotes parameter space used in other panels. (C) Per capita growth responses of each species, where dark orange depicts the parameterised response for the active phase of the dormancy strategist and light orange is the realised response of the dormancy strategist, time-integrated over both the active and dormant phases. The steep decline in the realised response at high resource concentrations is a consequence of almost all of the dormant strategist cells being in the dormant phase when a new resource pulse is introduced. The inset in (C) is zoomed in on the lowest resource concentrations where the intersection of the functional responses is visible. (D) Kernel density estimates for the resource concentration over one complete cycle of resource pulsing when the dormancy strategist (orange) and the gleaner (blue) are in monoculture. In all panels, resource pulse interval and size of 240 and 8 respectively.

By definition, for relative nonlinearity to be the mechanism facilitating coexistence under this scenario, two criteria must be satisfied. First, there needs to be a trade-off in species' per capita growth responses to resource availability, such that different competitors hold advantages under different degrees of variability in resource concentration (i.e., their growth curves intersect; Chesson 1994; Yamamichi and Letten 2022). Assuming no growth (ignoring mortality) when the limiting resource is completely absent, this first criterion necessitates that at least one competitor in a two-species system has a nonlinear growth function, or that the two species have different nonlinear functions, hence the terminology relative nonlinearity (Barabás, D'Andrea, and Stump 2018). Second, each species, when resident in monoculture, must push resource variability in a direction that favours its competitor. For example, a species that benefits from higher variability in resource concentration must reduce variability in resource concentration relative to its competitor (Chesson 1994, Yamamichi and Letten 2022). The first criterion is notably absent in a direct comparison of functional responses when considering only the active phase of the dormancy strategist (i.e., dark orange response in Figure 1C is completely beneath the blue response of the gleaner across all resource concentrations). The trade-off, however, is evident when the realised per capita growth response is quantified across a complete cycle of resource pulsing, thereby integrating across the active and dormant phases of the dormancy strategist (light orange response in Figure 1C) (see SI and Figure S6 for alternative analytical approximations of the resource-dependent growth rate of the dormancy strategist). At low resource concentrations, the realised per capita growth rate of the dormancy strategist is greater than the per capita growth rate of the gleaner. Moreover, in a similar fashion to a Holling type III growth curve, the per capita growth rate of the dormancy specialist increases more rapidly at high resource concentrations than it does for the gleaner. Thus, relative to the gleaner, the dormancy specialist benefits more from extreme values of resource concentration.

To evaluate the second criterion for coexistence via relative nonlinearity, we can compare the temporal trajectory of the resource concentration when each competitor grows on its own (visualised with kernel density estimates in Figure 1D). Because it is able to persist in the dormant phase through periods of resource scarcity, the dormancy specialist is able to maintain a higher abundance through the pulsing cycle (Figure 1A). As a result, when a resource pulse enters the system, the dormancy specialist is able to rapidly emerge from dormancy and deplete the resource. In contrast, when a resource pulse arrives in the gleaner monoculture, although the gleaner responds by growing comparatively rapidly (Figure 1C), it starts from lower abundance, which means that resources spend longer periods at high concentrations (compared to when the dormancy specialist grows in monoculture). Once the resource reaches low concentrations in the dormancy specialist monoculture, the vast majority of cells have switched to the dormant state, meaning they stop depleting the resource, and therefore resource concentrations never dip as low as they do in the gleaner monoculture (Figure 1D). These differences in variability in resource concentration across the two monocultures are reflected in the variance in resource concentration: when the dormancy strategist grows alone, the variance in resource availability is $\sigma^2 = 4.4$, and when the gleaner grows alone the variance is $\sigma^2 = 10.12$. Thus, the dormancy strategist, which benefits from high variance in resource concentration, reduces the variance to the benefit of the gleaner and vice versa.

Satisfaction of both criteria implicates relative nonlinearity as the driving mechanism underlying the stable coexistence of dormancy and non-dormancy strategists. While dormancy can also contribute to coexistence via the temporal storage effect, we note that not only is it not a necessary condition when generations overlap (e.g., microbial organisms) (Johnson and Hastings 2022; Yamamichi, Letten, and Schreiber 2023), but the temporal storage effect requires fluctuations in non-competitive factors (such as temperature or salinity that, to a first approximation, are not consumed, depleted or modified, but nevertheless regulate organismal fitness). As such, the absence of species-specific responses to a density-independent factor in our model precludes the operation of a temporal storage effect.

3.2 | A Gleaner-Opportunist-Dormancy Trade-Off

We next consider the stability of a three-species system comprising, in addition to the two species already described, a third species that trades off slow growth at low resource concentration with rapid growth at high resource concentration (i.e., an opportunist) (Figure 2A). As such, the two non-dormancy strategists are characterised by a classical gleaner-opportunist trade-off (Grover 1997; Yamamichi and Letten 2022), where opportunists are favoured by resource fluctuations (large $\mu_{\max}$ and K_s in Equation 3) and gleaners are favoured under more continuous resource supply (small $\mu_{\max}$ and K_s in Equation 3).

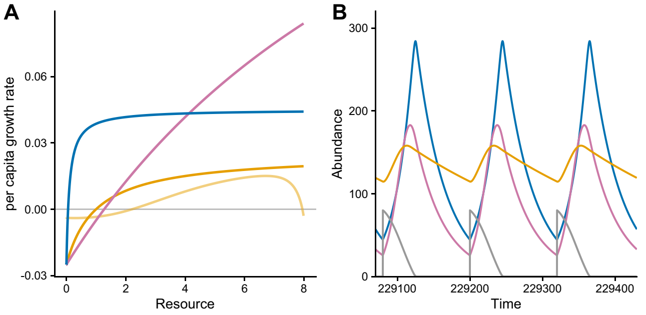

FIGURE 2 | Coexistence of a gleaner, an opportunist and a dormancy strategist under fluctuations in a single resource. (A) Per capita growth responses of a gleaner (blue), an opportunist (pink), active phase of the dormancy strategist (orange) and realised response of the dormancy strategist time-integrated over both the active and dormant phases (light orange). (B) Stationary dynamics of the gleaner, opportunist and the sum of active and dormant phenotypes of the dormancy strategist over three successive resource (grey) pulses (note that large time values on the *x*-axis reflect the need to run simulations for sufficiently long to become stationary). Resource pulse interval and size of 120 and 8 respectively. Resource concentration multiplied by a factor of 10 for visualisation.

For different combinations of resource pulse size and interval, we observe all but one of the seven possible competition outcomes (Figures 2B and 3A). Notably, coexistence of all three strategies is evident across a non-trivial range of intermediate resource pulse sizes and intervals. Although the boundaries and competition outcomes within resource supply space are liable to shift, three species coexistence is still apparent under four out of six independent perturbations to the baseline growth parameters (5% increase or decrease in each species maximum growth rate; Figure S7). To gain deeper insight into observed competitive outcomes in the three-species system, we also investigated the dynamics of all pairwise combinations. Competition between the opportunist and the gleaner alone exhibited familiar dynamics with a substantial coexistence region separating two regions of monodominance; exclusion of the opportunist with small and/or frequent resource pulsing, and exclusion of the gleaner with large or infrequent resource pulsing (Figure 3B, left panel). Competition between the gleaner and the dormancy strategist resulted in broad coexistence except under small and/or frequent resource pulsing where the dormancy strategist is excluded (Figure 3B, centre panel). Finally, competition between the dormancy strategist and the opportunist was again qualitatively similar, but with the opportunist effectively assuming the role of the gleaner and excluding the dormancy strategist when resource pulses are small or frequent (Figure 3B, right panel).

3.3 | Non-Simple Assembly Rules Explain Multi-Species Coexistence

Contrasting the three-way dynamics with the corresponding pairwise dynamics, it is striking that of the 90 (out of 240)

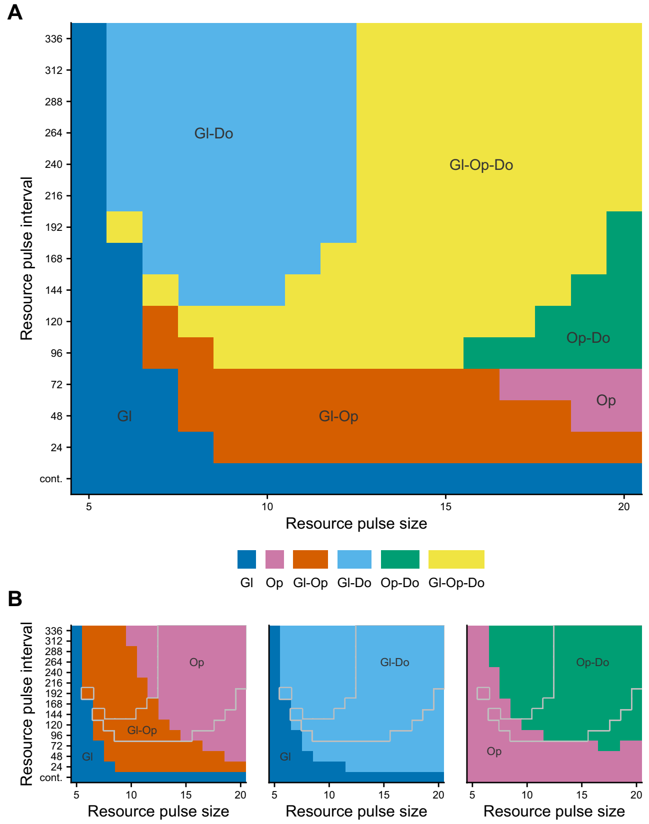

FIGURE 3 | Outcomes of competition between a gleaner, an opportunist, and a dormancy strategist across different patterns of resource supply. (A) All three species together. 'Do', dormancy strategist; Gl, gleaner; Op, opportunist. (B) All pairwise combinations of the three species. Left panel = gleaner versus opportunist, centre panel = gleaner versus dormancy strategist, right panel = opportunist versus dormancy strategist. Grey outline indicates the region of parameter space where all three strategies coexist in (A). 'cont.' denotes continuous resource supply.

combinations of resource pulse interval and resource pulse size that support stable coexistence of all three species, coexistence of all pairs is only found in 10 (e.g., Figure S8). Put another way, in almost 90% of the simulated resource supply scenarios, the three species stably coexist under conditions that do not support the stable coexistence of all constitutive pairs. Close inspection reveals that it is the presence of the dormancy specialist that places sufficient competitive pressure on the opportunist to allow the gleaner to persist in a region of the parameter space (relatively large, infrequent resource pulses) that would otherwise see the opportunist excluding the gleaner in pairwise competition (pink cells within the top right of the grey outline denoting the three species coexistence region in the left panel of Figure 3B). The gleaner then returns the favour, putting sufficient competitive pressure on the opportunist to allow the dormancy strategist to persist in the reciprocal region of parameter space (relatively small, frequent resource pulses) where it would otherwise be excluded by the opportunist in pairwise competition (pink cells within the bottom left of the grey outline denoting the three species coexistence region in the right panel of Figure 3B). Under a more conservative minimum viable population size ($N = 1$), the dominance of the dormancy specialist under large, infrequent resource pulses is more clearly indicated in the exclusion of the gleaner and the opportunist in pairwise competition and its mono-dominance under three-way competition (Figure S9).

4 | Discussion

Our understanding of the rules of diversity maintenance is advancing along several lines, including the formal classification of coexistence mechanisms (Chesson 2000; Ellner et al. 2019; Letten et al. 2018), the identification of niche-defining fitness trade-offs (Duthie, Abbott, and Nason 2015; Ehrlich, Kath, and Gaedke 2020; Gude et al. 2020; Litchman et al. 2007) and the scaling of assembly processes from pairwise to multispecies systems (Angulo et al. 2021; Chang et al. 2023; Friedman, Higgins, and Gore 2017; Vandermeer and Perfecto 2023). Via the integration of a dormancy-growth rate trade-off into a classical model of microbial resource competition, here we have been able to shine a light on each of these lines of inquiry. Specifically, we have shown: (i) how dormancy can trade-off against growth rate to mediate coexistence via relative nonlinearity; (ii) the conditions under which a dormancy strategist can coexist alongside two alternative strategies in a novel example of three species coexisting on a single resource and (iii) the emergence of non-simple assembly rules governing multi-species coexistence in pulsed resource environments.

The subsumption of this dormancy-growth trade-off under the umbrella of relative nonlinearity poses the question of whether relative nonlinearity might also be able to explain stable coexistence in prior studies on diversity maintenance under resource fluctuations. For example, Edwards, Klausmeier, and Litchman (2013) and later Smith and Edwards (2019) obtained the coexistence of three phytoplankton species comprising a resource storage specialist alongside a classical gleaner and opportunist, where the resource specialist favoured resource pulses of intermediate frequency. It is easy to see how resource storage, in spite of comparatively slow growth when resources are plentiful, should give rise to a similarly shaped realised functional response as that found for the dormancy strategist here. As such, it seems highly likely that coexistence of gleaner, opportunist and storage specialists is an example of relative nonlinearity. More recently, Levine, Pacala, and Levine (2024) proposed a new diversity-promoting mechanism, competition for time, to explain the long-term stability of multispecies systems under repeated patterns of succession following disturbance/resource renewal. In their illustrative example, species are described by step-like growth functions (where growth abruptly ceases when resources fall below a critical threshold) and through their own resource consumption hasten the onset of resource conditions favourable to their competitors. While Levine, Pacala, and Levine (2024) describe competition for time as being more similar to relative nonlinearity than the temporal storage effect, it may well be possible to place it wholly under the banner of the former. It is less clear whether this classification naturally extends to earlier work the authors identify as alternative examples of competition for time. Of particular relevance here, the annual plant model presented by Levine and Rees (2004) includes a dormancy-growth trade-off that allows for coexistence under fluctuations in environmental favourability, which the authors originally allied with the temporal storage effect.

Reinterpreting their modelled fluctuations in environmental favourability in terms of fluctuations in resource availability hints at the potential for relative nonlinearity to be operating alongside the temporal storage effect or instead of it. Needless to say, there appear to be a number of opportunities to reassess past empirical and theoretical observations in light of an expanded theory of relative nonlinearity.

The extent to which a growth-dormancy trade-off mediates microbial (or non-microbial) coexistence via relative nonlinearity *ex silico* is an open question. From the animal gut to arid soils, any environment where nutrient availability typically fluctuates through time is a candidate for microbial diversity maintenance via a growth-dormancy trade-off. We might nevertheless anticipate a higher probability of observing growth-dormancy trade-offs in those environments that experience especially prolonged periods of nutrient scarcity, such as oligotrophic lakes and deserts, which are strongly associated with the emergence of dormancy strategists (Aanderud et al. 2016; Leung et al. 2020). At the same time, systems prone to nutrient variability are likely to be subject to fluctuations in a range of other environmental factors (e.g., pH, temperature, salinity, antibiotics). As such, we should generally expect the temporal storage effect to act alongside relative nonlinearity (but not necessarily in synergy) in those systems liable to the emergence of growth-dormancy trade-offs. To date, there has been considerably more empirical research into the temporal storage effect than relative nonlinearity (in microbes and non-microbes alike), at least partly because of the logistical challenges of obtaining high-resolution growth response data. Fortunately, the short generation times and high throughput of microbial systems offer a wealth of opportunities for rigorous tests of coexistence under resource fluctuations. The dormant-spore-forming gram-positive bacteria *Bacillus subtilis* would appear to be an especially tractable candidate organism for exploring the predictions stemming from the current work (Earl, Losick, and Kolter 2008; Shoemaker et al. 2022).

There is a long history of theoretical research in ecology into the modulating influence of resource fluctuations on species coexistence (Armstrong and McGehee 1980; Chesson 1994; Kremer and Klausmeier 2013; Levins 1979). More targeted interest in the impact of resource fluctuations on microbial systems has been building in recent years (Ho, Good, and Huang 2022; Letten et al. 2018; Letten and Ludington 2023; Wortel 2023) and yet it remains a somewhat marginal topic in microbial ecology compared to research on fluctuation-independent processes (Brochet et al. 2021; Ho et al. 2024; Lee, Bloxham, and Gore 2023; Wilson and Lindow 1994) or fluctuations in environmental (density-independent) factors such as temperature (Jiang and Morin 2007; Rodríguez-Verdugo, Vulin, and Ackermann 2019; Tucker and Fukami 2014; Zander, Bersier, and Gray 2017). Several studies have demonstrated the impact of varying dilution rate (e.g., in serial transfer) on coexistence (Abreu et al. 2019; Mancuso et al. 2021), but these have tended to place greater emphasis on fluctuations in density-independent disturbance/mortality rather than the concomitant fluctuations in the availability of resources. However, as recently highlighted in Letten and Ludington (2023), the resource fluctuations rendered by serial-transfer dynamics may well be sufficient to explain these results independent of population bottlenecking. That merely toggling the supply dynamic (magnitude and frequency) of a single resource is sufficient to yield six qualitatively different outcomes among three species serves as another reminder of the regulatory potential of resource dynamics in microbial systems. The silver lining to the peripheral treatment of resource fluctuations in microbial ecology is that there remains a wealth of untrodden paths to new discovery.

Author Contributions

A.D.L, M.Y. and P.-J.K. conceived research. A.D.L, M.Y., J.A.R. and P.-J.K. designed research. A.D.L. and P.-J.K. performed research. A.D.L. wrote first draft. A.D.L., M.Y., J.A.R. and P.-J.K. contributed to revisions.

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Data Availability Statement

Code and simulation outputs are available at Zenodo (https://doi.org/10.5281/zenodo.13324988) and GitHub (https://github.com/andrewletten/dormancy-tradeoff-code).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14507.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.