Recycling and complementary food sources hinder oscillatory dynamics in a microbial population

Benedetta Ciarmoli[1] and Sophie Marbach[1,*]

[1] *CNRS, Sorbonne Université, Physicochimie des Electrolytes et Nanosystèmes Interfaciaux, F-75005 Paris, France*

(Dated: September 22, 2025)

Microbes constantly interact with their environment by depleting and transforming food sources. Theoretical studies have mainly focused on Lotka-Volterra models, which do not account for food source dynamics. In contrast, consumer-resource models, which consider food source dynamics, are less explored. In particular, it is still unclear what physical mechanisms control oscillatory dynamics at a single population level, a phenomenon which can only be captured by a consumer-resource model. Here, we present a minimalistic consumer-resource model of a single microbial population with growth and death dynamics, consuming a continuously replenishing substrate. Our model reveals that decaying oscillations can occur if and only if the timescale of microbial adaptation to food supply changes exceeds the death timescale. This general rule allows us to easily examine additional physical phenomena. We find that microbial necromass recycling or complementary use of multiple food sources reduces the parameter range for oscillations and increases the decay rate of oscillations, stabilizing the dynamical system. Conversely, requiring multiple simultaneous food sources destabilizes the system. Essentially, facilitating growth reduces the likelihood of oscillations. We hope our work will motivate further investigations of consumer-resource models to improve descriptions of environments where food source distributions vary in space and time.

Microbes are at the root of diverse and essential physico-chemical reactions. In soils, as a canonical example, microbial decomposition is a first step towards carbon sequestration [1–5]. Microbes also act as water filters, pollutant removers, promote plant growth, and participate in the fixation of numerous chemical compounds such as nitrogen [2–7]. Beyond soils, microbes play key roles in carbon cycling in the ocean [8, 9]. From a biomedical perspective, a canonical example is their role on healthy gut function [10]. From an industrial perspective, microbial metabolism is also useful for the large scale bioproduction of chemicals [11].

In this context, one must understand the impact of food source abundance on microbial density and function, and reciprocally how microbes affect food source abundance. For instance, slight variations in local oxygen concentration can modify the emission of methane by microbes [12]. In soils, community diversity might not be the most important parameter for nutrient cycling, because nutrients are always cycled by some other species, rather, diversity might be conditioned mostly by nutrient availability [6]. Still, there are many nutrients whose cycle is not investigated [6]. From an industrial perspective, there are still open challenges in maximizing the efficiency of bioproduction or detoxification by tuning *e.g.* nutrient or toxin supply conditions [11, 13]. The balance between the relative abundance of food sources and the living microbes is thus subtle, calling for fundamental insights.

From a theoretical perspective, most efforts have focused on microbe-level population dynamics, described via Lotka Volterra or Macarthur models and derivatives [14–21]. In these models, all species are biotic, *i.e.* living and reproducing. While fundamental to predict and understand biodiversity in microbial communities, such theories do not account for the underlying abundance of food sources and interactions mediated by these relative abundances. In this context, food sources refer to abiotic, non-living compounds. This means that under different initial food source conditions, LV type models may not be able to predict correct microbial dynamics [22, 23]. Phenomena like resilience, niche expansion, and spatial self-organisation cannot be accounted for without considering local couplings and/or underlying food source dynamics [24, 25]. Finally, LV-type models can not inform on nutrient cycling dynamics.

In contrast, consumer-resource (CR) models, where food sources are governed by abiotic growth laws, have allowed us to progress on microbe mediated nutrient cycling [22, 26]. Unlike the Macarthur model [14], which is puzzlingly also called "consumer-resource model", here the limiting food source for microbial growth is an abiotic (non-reproducing) species [22, 26]. CR models have investigated the role of switching environment parameters or toxin levels on population diversity and growth [27, 28]. Comparing CR models to experiments has allowed us to explain denitrification rates in large communities [7], community diversity [29], and degradation rates in the ocean [9]. Even at larger scales, accounting explicitly for food sources is key to understand pattern arrangements of for instance sessile organisms like trees [30]. Yet, in comparison with LV models, there is still much less fundamental insight on the variety of dynamics that CR models can lead to [23].

One fascinating fundamental feature of CR models is the possibility of observing oscillatory dynamics on the abundance of one or more species caused by oscillations of food source content [31, 32]. Strikingly, even in the simplest CR setting, with 1 species and 1 limiting food

* sophie.marbach@cnrs.fr

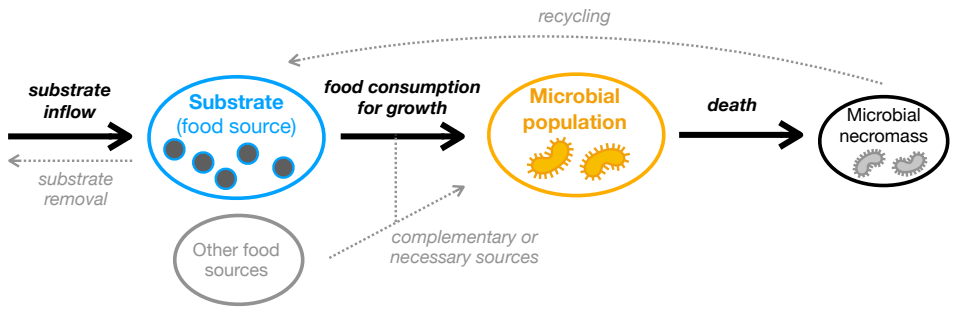

FIG. 1. Schematic of the minimal consumer-resource (CR) model considered in this study involving a single abiotic resource – the substrate in blue – and a single consumer – the microbial population in yellow. Black arrows indicate the main physical processes at play. Here, we study the emergence of oscillatory dynamics in this minimal model and common model extensions corresponding to further bio-physical ingredients in gray.

source, under low food source supply rates, the abundance of microbes can undergo decaying oscillatory dynamics [33]. While oscillations of microbial population are quite universal for LV dynamics, they involve always at least 2 reproducing species. Since only few works have higlighted the presence of oscillations for a single species, theoretically [33, 34], or in continuous culture experiments [35, 36], it is still not clear what minimal ingredients are required for oscillations of a single microbe species, or how these oscillations are modified by diverse physical phenomena. We lack physical intuition on the underlying mechanism which determine oscillation features: the parameter range over which they occur and the decay rate which sets how fast the system reaches equilibrium.

Here we establish the simplest possible model of a consumer growing on single food source which exhibits oscillatory dynamics – see Fig. 1 – and perform analytical and numerical investigations of the model. We find oscillations occur for a certain range of parameters. Oscillations also increase the time to reach a stable steady state compared to non-oscillatory solutions (Sec. I). From this starting point, we consider the impact of common physical features: recycling of waste microbes, multiple resources being either necessary or complementary for growth, and substrate removal. In all cases, the emergence of oscillatory behavior, and the magnitude of the decay rate of oscillations, are characterized by a balance of only two timescales: the timescale to adapt to changes in food supply τ_{food}, and the timescale to recover from excess population numbers, from death or predators, τ_{death}. When $\tau_{\text{food}} \leq \tau_{\text{death}}$, the system adapts sufficiently rapidly to changes in food supply rates that no oscillations are seen and the system converges rapidly to steady state. Reciprocally, when $\tau_{\text{food}} \geq \tau_{\text{death}}$, these mechanisms become out of phase, oscillations occur, and the system converges more slowly towards its steady state. Changes to the physical model modify these timescales and thus the balance of competing phenomena and the dynamics. In particular, phenomena that facilitate growth such as recycling, complementary food sources decrease the time to respond to changes in food supply, reduce the range over which oscillations occur and the timescale for oscillations to relax and therefore stabilize the system (Sec. II). Finally, we discuss how these oscillations might affect a microbes environment by assessing waste production rates (Sec. III).

I. GENERAL FRAMEWORK TO STUDY OSCILLATIONS IN A SINGLE MICROBIAL POPULATION

A. Consumer-resource model

Our starting point is a consumer-resource model with minimal ingredients. We let $X(t)$ and $S(t)$ be the microbial population and food source – sometimes called substrate – concentration, respectively, with time t. Throughout this work, we do not specify precisely the units of all quantities, but we note that the units of $X(t)$ and $S(t)$ may be chosen with no change in the equations – $X(t)$ can therefore be measured *e.g.* in optical units as common for fluorescent species and $S(t)$ in mol/L. The food source can represent, for instance, a carbon source – see Fig. 1. Since the model should represent microorganisms, they should at least consume food sources that allow them to grow and reproduce. Then, we require two necessary conditions to reach non-trivial steady states. First, food sources should be constantly supplied through a substrate inflow, otherwise microorganisms would run out of supplies. This supply could originate from incoming flows in their environment. Second, there must be a mechanism by which the population of microorganisms diminishes, otherwise the population would indefinitely grow. This may be due to external conditions like flows which carry microorganisms away from the considered pool, external predators, or simply death. The kinetics of a single species $X(t)$ and its food source $S(t)$ are thus

minimally described by

$$\frac{\mathrm{d}X}{\mathrm{d}t} = r\mu(S)X - \lambda X \tag{1}$$
$$\frac{\mathrm{d}S}{\mathrm{d}t} = nK_S - \gamma r\mu(S)X \tag{2}$$

where $\mu(S)$ is nondimensional and quantifies the efficiency of reproduction depending on the amount of available food sources, r is a reproduction rate, λ is a death rate, n is an inflow rate relative to a reference concentration K_S of supplied substrate, and γ is a conversion factor quantifying the amount of substrate needed per microorganism to sustain reproduction and growth.

The ingredients of the model described by Eqs. (1-2) and illustrated in Fig. 2 are generic and broadly used, albeit often with additional terms [22, 23, 33, 37, 38]. In particular, these modeling ingredients have been shown to describe well the response of even a heterogeneous system in diverse conditions so are a priori a good coarse-graining of the underlying microscopic dynamics [39].

A few aspects of the model merit discussion, for the sake of generality. In practice, one could assume Monod kinetics for substrate consumption, as is common, as $\mu(S) = \frac{S}{K_S+S}$, see *e.g.* Refs. [2, 31–33, 40]. For now, however, we keep the derivation general and assume $\mu(S)$ is simply a continuous function of S. This function, in our minimal model, should nonetheless be increasing as one expects that more resources should favor growth. Different authors place γ either in the species equation [2] or, like here, in the substrate's equation [33], and thus γ can assume very different values depending on the definition. Note that we do not assume equal rates of substrate and biomass removal from the system, which would be the case to model a chemostat growth setup [22, 33] but we will review the impact of substrate removal in Sec. II D. However, Eqs. (1-2) represent well systems where the inflow of some food sources is different from the dilution rate of the chemostat. This is the case for instance for oxygen supply, since it is often provided via a gazeous pump, and in this context, single species oscillations have been observed [35, 36].

Our goal in this paper is to study the minimal model described by Eqs. (1-2) and simple extensions, so as to understand how and why oscillations might arise in the microbial and substrate concentrations, how they might be suppressed or enhanced, and how their temporal features, decay rate and oscillation frequency, depend on parameters.

B. Non-dimensionalization and essential system parameters.

To make progress, it is useful to notice a natural non-dimensionalization of variables as

$$x = \frac{X}{K_S/\gamma},\ s = \frac{S}{K_S} \text{ and } \tau = \lambda t$$

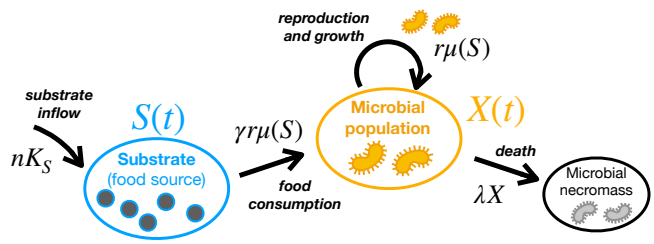

FIG. 2. Schematic of the minimal model in Eqs. (1-2).

such that K_S sets the scale of the substrate concentration, K_S/γ that of the microbial population, and the death rate λ is a natural timescale. The equations become

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}\tau} &= \frac{r}{\lambda}\mu(s)x - x\\ \frac{\mathrm{d}s}{\mathrm{d}\tau} &= \frac{n}{\lambda} - \frac{r}{\lambda}\mu(s)x\end{aligned} \tag{3}$$

The only remaining relevant parameters are thus the non-dimensional reproduction rate r/λ and the substrate supply n/λ. We must thus learn about dynamics within this phase diagram.

C. Fixed points, decay rates, and oscillating behavior

Fixed point (X^*, S^*). The only fixed point of the system is given by searching for $\frac{\mathrm{d}X}{\mathrm{d}t} = \frac{\mathrm{d}S}{\mathrm{d}t} = 0$ and so

$$(x^*, s^*) = \left(\frac{n}{\lambda}, \mu^{-1}\left(\frac{\lambda}{r}\right)\right) \tag{4}$$

where $\mu^{-1}(s)$ is the inverse function of $\mu(s)$, which is also an increasing function of s. Quite naturally, the death rate λ decreases the equilibrium microbial concentration, and increases the equilibrium food concentration. Also naturally, a higher food supply rate n increases the equilibrium microbial population X^*, yet it is surprising that it does not set the equilibrium food concentration. Instead, the equilibrium food concentration is given by a balance of two rates: microbe consumption rate and death rate.

One can note that there also exists a trivial stationary point where the population is extinct $X^* = 0$, and the substrate concentration increases at a constant rate according to the substrate inflow $\frac{\mathrm{d}S}{\mathrm{d}t} = nK_S$.

Decay rates. Around the fixed point, one may evaluate the stability of the system by investigating the Jacobian of the system. Formally if we define $\mathcal{F}_s$ and $\mathcal{F}_x$ as $\frac{\mathrm{d}x}{\mathrm{d}t} = \mathcal{F}_x(x,s)$ and $\frac{\mathrm{d}s}{\mathrm{d}t} = \mathcal{F}_x(x,s)$, then the response of the system near a fixed point $(x,s) = (x^* + \delta x, s^* + \delta s)$ is given by

$$\begin{pmatrix}\frac{\mathrm{d}\delta x}{\mathrm{d}t}\\ \frac{\mathrm{d}\delta s}{\mathrm{d}t}\end{pmatrix} = J\begin{pmatrix}\delta x\\ \delta s\end{pmatrix},\ \text{with } J = \begin{pmatrix}\partial_x\mathcal{F}_x & \partial_s\mathcal{F}_x\\ \partial_x\mathcal{F}_s & \partial_s\mathcal{F}_s\end{pmatrix} \tag{5}$$

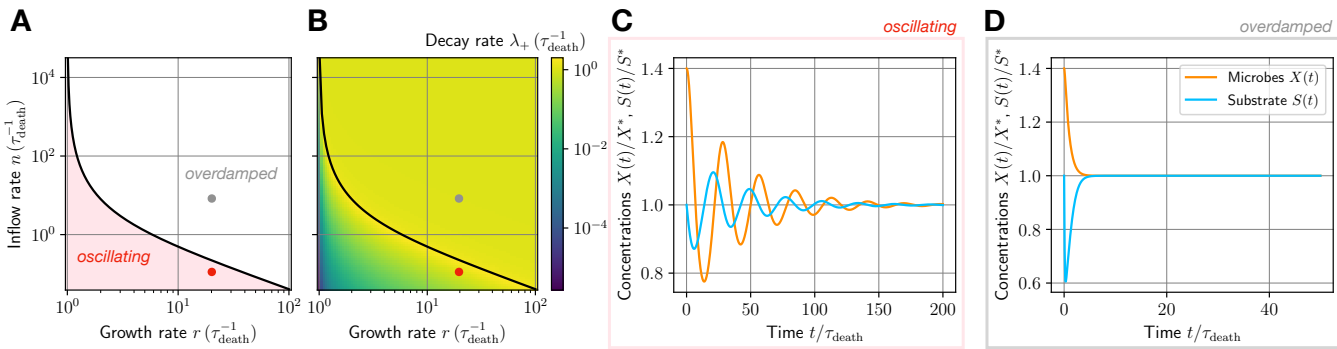

FIG. 3. Behavior of the basic model. (A) phase diagram representing the possible dynamics in the inflow rate versus growth rate space. (B) Same diagram but with colors indicating the magnitude of the damping rate. (C) Typical oscillating solution, using $r = 2\ \tau_{\rm death}^{-1}$ and $n = 0.1\ \tau_{\rm death}^{-1}$. (D) Typical overdamped solution, using $r = 2\ \tau_{\rm death}^{-1}$ and $n = 10\ \tau_{\rm death}^{-1}$. The locations of (C) and (D) are indicated in (A-B) with dots. Notice the change of scale between (D) and (C).

and each function is evaluated at the fixed point. Here,

$$J = \begin{pmatrix} 0 & \frac{r}{\lambda}\mu'(s^*)x^* \\ -\frac{r}{\lambda}\mu(s^*) & -\frac{r}{\lambda}\mu'(s^*)x^* \end{pmatrix} = \begin{pmatrix} 0 & \beta \\ -1 & -\beta \end{pmatrix} \tag{6}$$

where we have defined the non-dimensional parameter

$$\beta = \frac{r\mu'(s^*)x^*}{\lambda} \tag{7}$$

whose interpretation we come back to in the following section. The eigenvalues of this matrix are

$$\frac{\lambda_\pm}{\lambda} = \frac{-\beta \pm \sqrt{\beta^2 - 4\beta}}{2}. \tag{8}$$

The eigenvalues are either (i) real and negative or (ii) complex with a negative real part, corresponding to decaying solutions towards the fixed point either in an (i) overdamped or (ii) oscillating way. The oscillations – in both microbial population and food concentration – occur if $\beta^2 \leq 4\beta$ or equivalently $\beta \leq 4$ which translates into a constraint on n and r. These oscillations occur with frequency

$$\frac{\Omega}{\lambda} = \sqrt{4\beta - \beta^2}. \tag{9}$$

So far, we have simply assumed $\mu(s)$ to be a continuous, increasing function of s. Given the steady state values, we can see that $\beta = rn\mu'(\mu^{-1}(\lambda/r))/\lambda^2$, and hence if n is sufficiently smaller, there will exist a range of values for r where $\beta \leq 4$ and oscillations should arise. It is not necessary to assume more properties of $\mu(s)$ for oscillations to emerge. Oscillations are thus a quite universal feature of our general model.

To illustrate these mathematical results, we take as an example the case of Monod kinetics where $\mu(s) = s/(1+s)$. We reproduce the condition for oscillations or not in Fig. 3-A in a phase diagram depending on the only 2 relevant physical parameters: the non-dimensional reproduction rate r/λ and the substrate supply n/λ. We find that oscillations predominantly occur for sufficiently small inflow rates, as was also seen in a closely related model [33]. In addition, in the oscillating region, the decay rate of the oscillations, $\beta/2$, is, most of the time, much smaller than in the overdamped case, where it is given by the smallest eigenvalue (in amplitude), λ_+, see Fig. 3-B. We present typical examples of an oscillating solution in Fig. 3-C and overdamped one in Fig. 3-D. Clearly, the overdamped solution converges much faster to its stationary state.

D. Mechanism for the emergence of oscillating solutions

Now we interpret these mathematical results in mechanistic terms. Firstly, why do the oscillations appear? To interpret this, we closely follow Ref. [33]. Suppose that as a starting point, the biomass is slightly in excess compared to the fixed point, but the substrate concentration is given by its steady state value S^*. This means that the rate of substrate consumption exceeds the inflow rate: thus the substrate concentration decreases. As a result, the substrate concentration quickly reaches a regime in which it cannot sustain microbial growth, and the biomass concentration decreases. At some point, biomass concentration has decreased sufficiently that again the substrate inflow rate exceeds the consumption rate: substrate concentration increases again but is still too low to allow for biomass growth. Eventually, the substrate concentration is high enough to allow for biomass growth again, until the biomass exceeds a certain threshold, where the substrate concentration decreases again, and the cycle starts again.

In practice, the emergence of oscillations via the above mechanism is only possible if the system is slow enough when it responds to changes in substrate concentration, the "upstream" phenomenon, compared to the "downstream" phenomenon of microbial death, introducing a

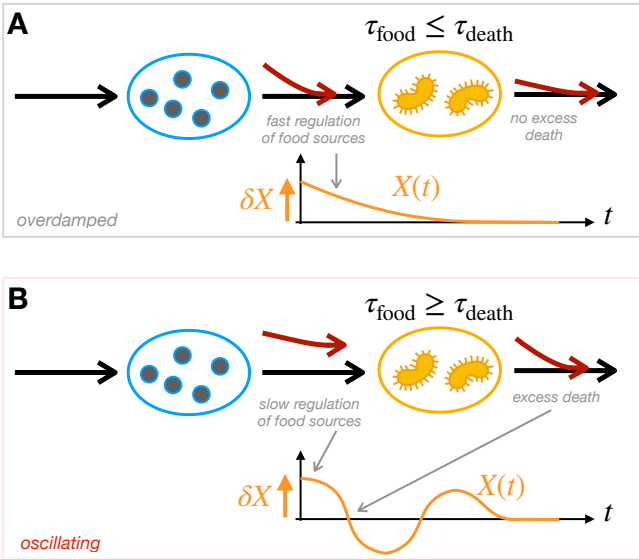

FIG. 4. Schematic interpretation of possible dynamics of the model in Eqs. (1-2). (A) In the overdamped scenario, a fast regulation of food sources prevents excess death, resulting in a stable approach of equilibrium. (B) In the oscillating case, the regulation of food sources is slow, resulting in excess death response and creating oscillatory response towards equilibrium.

delay that causes these oscillatory cycles – see schematic illustration in Fig. 4. This can be translated by a condition on timescales. Clearly, the timescale associated with microbial death corresponds to the inverse of the microbial death rate, $\tau_{\text{death}} = 1/\lambda$. When the concentration changes by a small amount, say $s = s^* + \delta s$, then the timescale of adaptation of say, substrate concentration, is clearly given by $\tau_{\text{food}} = 1/r\mu'(s^*)x^*$. These timescales are compared through the parameter β, since by Eq. (7)

$$\beta = \frac{r\mu'(s^*)x^*}{\lambda} \equiv \frac{\tau_{\text{death}}}{\tau_{\text{food}}} \tag{10}$$

can indeed be interpreted as a ratio of timescales. The condition for the emergence of oscillations, $\beta \leq 4$, translates on a condition on timescales as

$$\text{if } \tau_{\text{food}} \gtrsim \tau_{\text{death}}, \text{oscillations occur.} \tag{11}$$

When the upstream phenomenon is slow compared to the downstream one, we might expect that the system does not respond fast enough to prevent oscillations, and reciprocally. In this paper, we will show how the condition given in Eq. (11) can be used repeatedly to interpret behavior in various scenarios.

Finally, we further interpret the stability around the fixed point. Whether through oscillations or directly damped, solutions reach the fixed point with a decay rate that increases with β: the more responsive the system, the faster the decay, as could have been intuitively expected. In general, the equations are built in a self-regulating way, such that an excess of resources translates in microbial growth which in turn regulates the amount of resources until the system finds a steady state. When $\beta \geq 4$, the system responds quickly, avoiding delays between resource consumption and growth, and is also damped faster. The period of the oscillations is given by $1/\Omega \sim 1/\sqrt{\beta}$ and is consistent with this "time delay" interpretation.

In the canonical case of Monod kinetics, $\mu(s) = s/(1 + s)$, the fixed point is

$$(x^*, s^*) = \left(\frac{n}{\lambda}, \frac{1}{r/\lambda - 1}\right), \tag{12}$$

and the timescales become

$$\tau_{\text{food}} = \frac{\lambda}{rn}\left(1 - \frac{\lambda}{r}\right)^{-2}, \tau_{\text{death}} = \frac{1}{\lambda}. \tag{13}$$

The condition $\beta = \tau_{\text{death}}/\tau_{\text{food}} \leq 4$ for the emergence of oscillations translates into a constraint on n and r. In practice, we can always expect the reproduction and growth rate to be larger than the death rate $r \geq \lambda$, since otherwise a stable population could not be sustained. This simplifies Eq. (13) such that

$$\tau_{\text{food}} \simeq \frac{\lambda}{rn}, \tau_{\text{death}} = \frac{1}{\lambda}. \tag{14}$$

When substrate is flowed in at a higher rate, so when n increases, this increases the stable population size, see Eq. (12). As a result, the population can adapt more quickly to changes in substrate concentration, as indicated via Eq. (14). Higher substrate inflow rates can thus prevent oscillations, and increase the rate at which the population converges to the steady state.

II. PREVENTING OR FACILITATING OSCILLATORY BEHAVIOR.

We now explore various modifications of the model to include common yet more complex bio-physical features. We will show that, mathematically, modifications can easily be captured within the same framework, especially condition Eq. (11) and conclusions on oscillatory behavior drawn without requiring further calculations. This will allow us to identify physical phenomena that prevent or facilitate oscillatory behavior.

A. Recycling via microbial necromass

We first explore behavior when part of the microbial necromass – or deceased microbes – is converted back into food sources, see for example Refs. [31, 41]. To account for such "recycling" we can modify Eq. (2) as

$$\frac{\mathrm{d}S}{\mathrm{d}t} = nK_S - \gamma r\mu(S)X + \alpha\gamma\lambda_D X \tag{15}$$

where $\alpha < 1$ is a nondimensional number characterizing the conversion of necromass into reuseable food sources.

We now non-dimensionalize variables as $\tau = \lambda(1-\alpha)t$, and introduce an effective substrate influx $n_\alpha = n/(1-\alpha)$ as well as $\mu_\alpha(s) = (\mu(s) - \alpha\lambda/r)/(1-\alpha)$ such that we obtain a system of equations exactly similar to Eq. (3), as

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}\tau} &= \frac{r}{\lambda}\mu_\alpha(s)x - x \\ \frac{\mathrm{d}s}{\mathrm{d}\tau} &= \frac{n_\alpha}{\lambda} - \frac{r}{\lambda}\mu_\alpha(s)x. \end{aligned} \tag{16}$$

For simplicity we assume again Monod kinetics. The fixed point only slightly changes and becomes

$$(x^*_\alpha, s^*_\alpha) = \left(\frac{x^*}{1-\alpha}, s^*\right). \tag{17}$$

Recycling contributes to increase the steady-state microbial population, as one would expect, by increasing the effective influx of substrate. Remarkably, the steady state substrate concentration does not change. This again, is due to the fact that internal microbial dynamics set the equilibrium substrate concentration and not other processes. The timescales become

$$\begin{aligned} \tau^{(\alpha)}_{\text{food}} &= \left(\frac{r}{\lambda}\mu'_\alpha(s^*_\alpha)x^*_\alpha\right)^{-1} = \tau_{\text{food}}(1-\alpha)^2 \\ \tau^{(\alpha)}_{\text{death}} &= \frac{1}{\lambda} = \tau_{\text{death}}. \end{aligned} \tag{18}$$

The timescale to adapt to changes in substrate concentration decreases due to recycling, in part because the sustained steady state population is larger and in part because the system is quicker to adapt to changes thanks to the recycling process. This thus reduces the range over which oscillations occur in phase space. In fact $\beta_\alpha = \tau^{(\alpha)}_{\text{death}}/\tau^{(\alpha)}_{\text{food}} = \beta/(1-\alpha)^2$, and the condition $\beta_\alpha \leq 4$ translates into a condition $\beta \leq 4(1-\alpha)^2$: the range over which oscillations occur is narrower. In addition, the oscillations decay with a damping rate as $\exp(-\beta_\alpha\tau) = \exp(-\beta\lambda t/(1-\alpha))$ and thus adaptation is also faster with recycling. One can therefore consider the system is more "stable" in the presence of recycling. A typical example of an oscillatory solution in the recycling case is shown in Fig. 5-A (opaque lines) and compared to the reference case where $\alpha = 0$ (transparent lines), clearly illustrating this behavior.

Why does recycling lead to longer oscillations but faster decay rates? Consider again for interpretation a hypothetical scenario where biomass is in slight excess compared to the fixed point, but substrate concentration is at steady state S^*. The rate of substrate consumption thus exceeds the inflow rate but not as much because recycling helps to sustain the current over-populated state: the substrate concentration decreases more slowly than in the no-recycling case – see Fig. 5-B. Similar reasoning applies to the next steps of the cycle. This essentially demonstrates that the oscillations occur slower than without recycling because the imbalance between substrate/microbial concentrations is slower to establish and invert. However, because the system responds slower, adaptation to the steady state is faster.

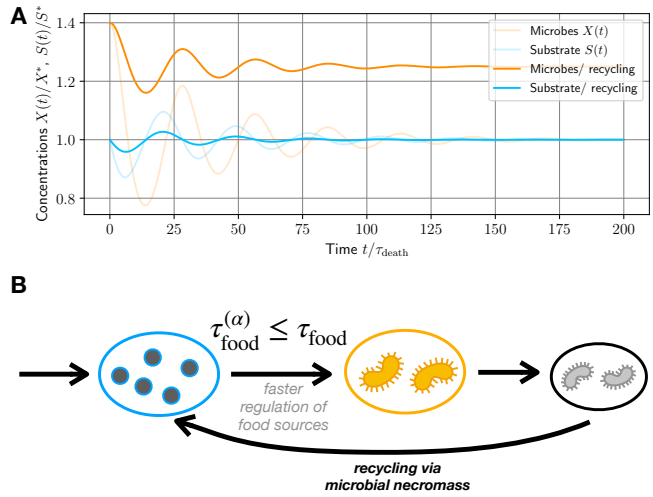

FIG. 5. Impact of recycling on oscillatory solutions. (A) Typical solutions with recycling, comparing to the reference case (lighter color) of Fig. 3-C without recycling. Parameters are the same as in Fig. 3-C and with $\alpha = 0.2$. (B) Schematic impact of recycling: by providing new food sources, recycling speeds up food source regulation.

B. Complementary food sources

We explore now the case where microorganisms can grow on two food sources. Food sources are complementary in the sense that microorganisms can grow on either but do not require both to grow. We can therefore write the following set of equations

$$\begin{aligned} \frac{\mathrm{d}X}{\mathrm{d}t} &= r\mu_S(S)X + r\mu_C(C)X - \lambda X \\ \frac{\mathrm{d}S}{\mathrm{d}t} &= nK_S - \gamma r\mu_S(S)X \\ \frac{\mathrm{d}C}{\mathrm{d}t} &= nK_C - \gamma r\mu_C(C)X \end{aligned} \tag{19}$$

where for simplicity C refers to the concentration of the second food source we considered r, n, and γ to be similar for both substrates and C is the second substrate. Nondimensionalizing $c = C/K_C$ and $s = S/K_S$ it is obvious that s and c satisfy the same dynamics. If initial conditions are the same, all dynamics in time of c and s are equal. We can then rather define $s = 2S/K_S$ the total nondimensional substrate concentration, such that the dynamics are now given by

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}\tau} &= \frac{r}{\lambda}\mu_{\text{comp}}(s)x - x \\ \frac{\mathrm{d}s}{\mathrm{d}\tau} &= \frac{n_{\text{comp}}}{\lambda} - \frac{r}{\lambda}\mu_{\text{comp}}(s)x \end{aligned} \tag{20}$$

where we introduced $\mu_{\text{comp}}(s) = 2\mu(s/2)$ and $n_{\text{comp}} = 2n$.

Using the general framework derived above and Monod kinetics it is then straightforward to show that the steady

state of the system is given by

$$(x^*_{\text{comp}}, s^*_{\text{comp}}) = \left(2x^*, \frac{2}{2r/\lambda - 1}\right). \tag{21}$$

The population sustained by this system is doubled since the substrate influx is doubled. Comparatively, the steady-state substrate concentration for each compound $s^*_{\text{comp}}/2$ is smaller than that in the case of a single food source because the steady state population is larger.

The timescale for adaptation to changes in substrate concentration becomes

$$\begin{aligned} \tau^{(\text{comp})}_{\text{food}} &= \left(\frac{r}{\lambda}\mu'_{\text{comp}}(s^*_{\text{comp}})x^*_{\text{comp}}\right)^{-1} \\ &= \tau_{\text{food}} f\left(\frac{r}{\lambda}\right) \\ \text{where } f(y) &= \frac{2\,(y-1)^2}{(2y-1)^2} \end{aligned} \tag{22}$$

while the timescale for death does not change. One can easily show that for $y = r/\lambda \geq 1$, then $f(y) \leq 1/2$. The time to adapt to substrate concentration changes is thus shorter with multiple food sources. This is due in part to the fact that the total sustained population is larger but also the two food sources act as complementary reservoirs when one food source is missing, enabling faster recovery. As a result the reactivity parameter

$$\beta_{\text{comp}} = \beta/f(r/\lambda) \tag{23}$$

such that $\beta_{\text{comp}} \geq 2\beta$. The oscillations occur if $\beta_{\text{comp}} \leq 4$ which translates into $\beta \leq 2$, which narrows down the range over which oscillations occur, stabilizing the system. The damping factor is given by β_{comp} and hence is always larger than β. For illustrative purpose we again represent these effects in Fig. 6. Complementary food sources thus tend to stabilize the system.

C. Necessary food sources

As a direct parallel to the complementary food sources we explore the case where microorganisms can grow only if two food sources are present, that we name "necessary" food sources. We can therefore write the following set of equations

$$\begin{aligned} \frac{\mathrm{d}X}{\mathrm{d}t} &= r\mu_S(S)\mu_C(C)X - \lambda X \\ \frac{\mathrm{d}S}{\mathrm{d}t} &= nK_S - \gamma r\mu_S(S)\mu_C(C)X \\ \frac{\mathrm{d}C}{\mathrm{d}t} &= nK_C - \gamma r\mu_S(S)\mu_C(C)X \end{aligned} \tag{24}$$

where for simplicity we considered again r, n, and γ to be similar for both substrates. Again, nondimensionalizing $c = C/K_C$ and $s = S/K_S$, and provided both food sources start with similar initial conditions, they satisfy

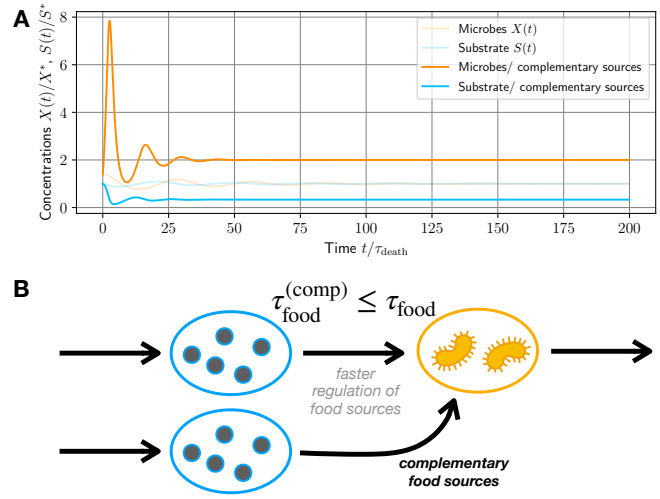

FIG. 6. Impact of adding a complementary food source on oscillatory solutions. (A) Typical solution with complementary food sources, comparing to the reference case (lighter color) of Fig. 3-C. Parameters are the same as in Fig. 3-C and the same for the two complementary food sources. (B) Schematic impact of complementary food sources: by providing more and directly edible food sources, food source regulation is sped up.

the same dynamics. We can then take $s = S/K_S$ the nondimensional substrate concentration, which satisfies

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}\tau} &= \frac{r}{\lambda}\mu_{\text{nec}}(s)x - x \\ \frac{\mathrm{d}s}{\mathrm{d}\tau} &= \frac{n}{\lambda} - \frac{r}{\lambda}\mu_{\text{nec}}(s)x \end{aligned} \tag{25}$$

where we introduced $\mu_{\text{nec}}(s) = \mu(s)^2$. Note that the above system Eq. (25), is equivalent to Eq. (24) only if initial conditions for the food sources are the same, meaning that for the stability analysis below, we explore stability with respect to slight changes in both food concentrations.

Using the general framework derived above and Monod kinetics it is then straightforward to show that the steady state of the system is given by

$$(x^*_{\text{nec}}, s^*_{\text{nec}}) = \left(x^*, \frac{1}{\sqrt{r/\lambda} - 1}\right). \tag{26}$$

The steady-state population sustained by this system is the same as for the reference case. It also appears that the steady-state substrate concentration for each compound is higher than in the reference case, which is a result of the population being maintained by both food sources at once.

The timescale for adaptation to changes in substrate

concentration becomes

$$\tau_{\text{food}}^{(\text{nec})} = \left(\frac{r}{\lambda}\mu'_{\text{nec}}(s^*_{\text{nec}})x^*_{\text{nec}}\right)^{-1} = \tau_{\text{food}} g\left(\frac{r}{\lambda}\right) \quad (27)$$

$$\text{where } g(y) = \frac{(y-1)^2}{2\sqrt{y}\left(\sqrt{y}-1\right)^2}$$

while the timescale for death does not change. One can easily show that for any value of y then $g(y) \geq 2$. The time to adapt to changes in substrate concentration is thus longer than that in the reference case with multiple necessary food sources. As a result the reactivity parameter is larger, and can be written as

$$\beta_{\text{nec}} = \beta/g(r/\lambda). \quad (28)$$

Oscillations occur when $\beta_{\text{nec}} \leq 4$ which translates into $\beta \leq 4g(r/\lambda)$. Since $g(y) \geq 2$, the range over which oscillations occur is necessarily broader than the reference case. The damping factor is given by β_{nec} and hence always smaller than β, such that perturbations to equilibrium take longer to relax. This means necessary food sources tend to destabilize the system.

This behavior is illustrated by Fig. 7. In Fig. 7-A we present a typical oscillatory solution to the dynamics in the "two necessary food sources" case, where the parameters are the same as for the oscillatory solution in the reference case in Fig. 3-C. Clearly, the system undergoes drastic oscillations, where the microbial concentration approaches zero. The mechanism is illustrated in Fig. 7-B, where the face that two food sources are necessary makes for a slower regulation of food sources upon changes of microbial population levels.

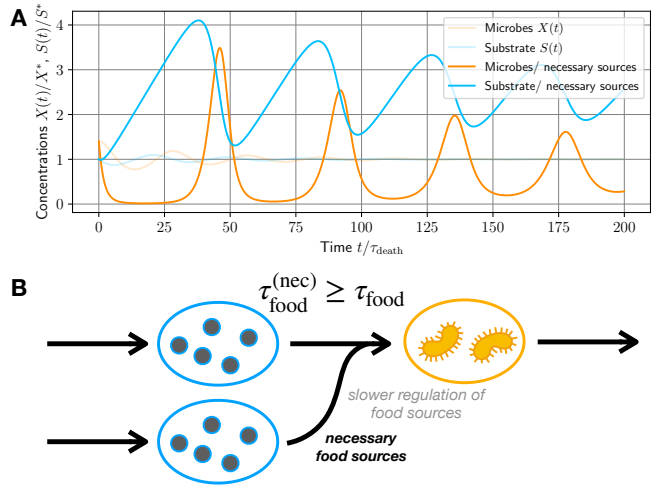

FIG. 7. Impact of adding a necessary food source on oscillatory solutions. (A) Typical solution with necessary food sources, comparing to the reference case (lighter color) of Fig. 3-C. Parameters are the same as in Fig. 3-C and the same for the two necessary food sources. (B) Schematic impact of necessary food sources: by restricting conditions for growth on two necessary food sources, food source regulation is slowed down.

D. Substrate removal

Our starting equations Eq. (2) are very close to that in Ref. [33] but for a substrate removal term which would modify only the equation for the substrate dynamics as

$$\frac{\mathrm{d}S}{\mathrm{d}t} = nK_S - \gamma r\mu(S)X - n_{\text{out}}S \quad (29)$$

where n_{out} is a rate of removal, which could correspond to removal by external flows in the system, as for instance in a chemostat. The additional n_{out} term is not straightforward to include in the general framework, so the stability analysis has to be done from scratch – details are not reported here, but the principle is similar and are detailed in Ref. [33]. Compared to our reference case, the steady state biomass concentration is changed and decreases slightly to

$$(x^*_{\text{out}}, s^*_{\text{out}}) = \left(x^*\left[1 - \frac{n_{\text{out}}}{n}s^*\right], s^*\right). \quad (30)$$

In practice, the amount of available resources for growth is constantly diminished by the substrate outflow, and thus the carrying capacity is lowered. The stability analysis around the fixed point can be performed and yiels slightly more complex results. In the limit of a small outflows, $n_{\text{out}} \ll \lambda$ then one can show oscillations occur for values of $\beta \leq 4 - 2n_{\text{out}}/\lambda$, so over a range that is always smaller than in the absence of substrate removal. We can rewrite this condition in terms of the timescales as diminishing the substrate adaptation timescale

$$\tau_{\text{food}}^{(\text{out})} = \tau_{\text{food}}\left(1 - 2n_{\text{out}}\tau_{\text{food}}\right). \quad (31)$$

In the presence of substrate removal, surprisingly, the smaller microbe population does not slow down the system. In fact, a slightly higher substrate level is more easily adsorbed here by the presence of the substrate removal, and that process speeds up substrate adaptation to fluctuations and thus stabilizes the system.

Note that when $n_{\text{out}} = \lambda$ indeed there are no oscillations, this is the "chemostat" model [42]. The chemostat model though, prevents to account for special – yet probably more realistic – cases where the outflow of different substrates may be different and neglects death or other phenomena that might reduce microbial population.

III. WASTE PRODUCTION IS NOT AFFECTED BY OSCILLATIONS

Given that oscillations might arise on microbial dynamics, one might wonder what the consequences of these oscillations are for abiotic resources, like waste production. Waste production, in the form say of carbon diox-

ide, can be modeled, within our general framework, as

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \zeta\gamma r\mu(S)X \tag{32}$$

where W is the concentration of waste (or carbon dioxide) and $\zeta \leq 1$ is a conversion factor. At steady state, $\frac{\mathrm{d}W}{\mathrm{d}t} = \zeta\gamma r\mu(S^*)X^* = \zeta n K_S \equiv r_W^* K_S$. The waste production rate $r_W^* = \zeta n$ is directly proportional to the inflow of carbon, as one might expect.

More interestingly, we can study how a solution evolves around a fixed point to quantify the total amount of waste produced before reaching steady state. One can notice off Eq. (2) that

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \zeta\left(nK_S - \frac{\mathrm{d}S}{\mathrm{d}t}\right) \tag{33}$$

such that the total waste production at long enough times is given by

$$W(t) \simeq \zeta(S(0) - S^*) + r_W^* t. \tag{34}$$

The initial substrate concentration thus sets the total waste production. If the initial substrate concentration is larger than the steady state value, substrate in excess will be wasted. Reciprocally, if the initial substrate concentration is lower than the steady state value, inflowing substrate will serve to reach the steady state value and avoid waste. All in all, this yields natural results where if food sources are in excess, waste is generated. This is true regardless of the way the steady state solution is reached, whether in an overdamped or oscillatory way. The presence of oscillations thus does not contribute to increase or decrease waste production.

Waste production is thus dominated by steady state parameters. In cases where the dynamics are more complex, waste production will be modified accordingly. For instance, in the case with recycling, waste production is still given by Eq. (32). At steady state though

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \zeta\gamma r\mu(S_\alpha^*)X_\alpha^* = \zeta\frac{n}{1-\alpha}K_S \equiv \frac{r_W^*}{1-\alpha}K_S. \tag{35}$$

Compared to the case without recycling, carbon production is more important at steady state, naturally because the population sustained at steady state is larger and, thus, produces more waste. Similarly, in the case of complementary (respectively necessary) food sources, we would expect the waste production rate to be larger (respectively smaller).

IV. CONCLUSION

Here, we have reported the conditions under which decaying oscillatory dynamics of a single microbial species and of its food source might arise. Our general framework highlights that only light conditions are required to observe oscillatory dynamics. The key point is to have 4 balancing mechanisms to get an imbalance of timescales: microbial growth, microbial death, food consumption, and food inflow. These mechanisms are so universal for microbial systems that the presence of oscillatory dynamics is quite likely even in more complex systems. There are also no strong conditions on the efficiency of reproduction depending on the amount of available food sources S – *i.e.* the shape of $\mu(S)$ – to get oscillations: it should just be a continuous, increasing function of S, which is again something expected and quite universal.

We have rationalized that the oscillations occur if and only if there is an imbalance between the time to adjust to changes in food supply levels τ_{food} and the time to recover from excess microbial population numbers τ_{death}. Since microbes rely on food sources to grow, microbes represent the "downstream" phenomenon. If microbial adaptation is the faster of the two processes, $\tau_{\text{food}} \gtrsim \tau_{\text{death}}$, it will respond too quickly for food sources to follow and oscillations will occur. This principle is generic enough that one can interpret different models with the same lens: recycling food sources, relying on complementary food sources or continuously removing food sources speeds up adaptation to changes in food supply levels, and τ_{food} decreases. In contrast, relying on multiple simultaneous food sources has the opposite effect, τ_{food} increases – see the summary Table I. We can thus conclude that oscillatory dynamics at the single population level are quite generic, yet they may not be so likely to occur in realistic systems given that many environmental factors can stabilize the system and prevent oscillations. Remarkably, effects which tend to facilitate growth, such as recycling food sources or relying on complementary food sources, stabilize the system.

We recall, that unlike Lotka-Volterra dynamics – often relying on logistic growth equations – which investigate only biotic, *i.e.* reproducing species, here, in the consumer-resource (CR) model we investigate both biotic and abiotic, *i.e.* non-reproducing, compounds. CR models can converge to a logistic-growth-like model, assuming a sharp enough separation of timescales between biotic growth and abiotic depletion rate [38]. This allows us to draw further understanding on the Lotka-Volterra models. In particular, the steady state microbial population of the CR model corresponds to the carrying capacity of a logistic growth model, and the decay rate can be viewed as the logistic growth rate. However, a single microbial species described by a logistic growth equation will not undergo oscillations, and so the oscillatory phenomena described here can only be accounted for with CR models.

Beyond the homogeneous, simple situation explored here, many extensions of the model are possible. First, it is expected that oscillations originate at different scales, especially at smaller scales. Even at the level of a single cell, oscillations in the abundance of a given substrate can undergo large fluctuations and oscillations [43, 44]. This suggests to make models with even more layers of scales, and rigorously coarse-grain models to obtain ef-

Case	Substrate adaptation timescale	Comparison
Minimal model	$\tau_{\text{food}} \simeq \lambda/rn$	reference case
Recycling with coefficient α	$\tau_{\text{food}}^{(\alpha)} = \tau_{\text{food}}(1-\alpha)^2$	*more stable*: narrower range of parameters where oscillations arise, faster decay rate of oscillations
Complementary food sources	$\tau_{\text{food}}^{(\text{comp})} = \tau_{\text{food}} \frac{2(r/\lambda-1)^2}{(2r/\lambda-1)^2}$	*more stable*: narrower range of parameters where oscillations arise, faster decay rate of oscillations
Necessary food sources	$\tau_{\text{food}}^{(\text{nec})} = \tau_{\text{food}} \frac{(r/\lambda-1)^2}{2\sqrt{r/\lambda}\left(\sqrt{r/\lambda}-1\right)^2}$	*less stable*: broader range of parameters where oscillations arise, slower decay rate of oscillations.
Substrate removal	$\tau_{\text{food}}^{(\text{out})} = \tau_{\text{food}}\left(1-2n_{\text{out}}\tau_{\text{food}}\right)$	*more stable*: narrower range of parameters where oscillations arise, faster decay rate of oscillations

TABLE I. Summary of the results of the different models investigated in this paper.

fective behavior at larger scales [34, 38], beyond standard Lotka-Volterra or logistic growth models. Second, naturally at these smaller scales fluctuations occur because of the small amount of species involved. Fluctuations are also expected to originate from a changing environment. It would thus be interesting to investigate how such systems respond to fluctuations. This was investigated in the context of the model in Ref. [33] with substrate removal, where oscillations would persist over a range of parameters. However the question remains on how microbial dynamics might respond to external environment fluctuations alone. Finally, most ecosystems reside in highly heterogeneous environments. For instance, the distribution of nutrients in soils is highly heterogeneous starting with oxygen content [12, 45] necessarily shaping microbial communities. There is thus a vast interplay of dynamics to be understood at the nutrient-microbiome level in more realistic systems.

DATA AVAILABILITY

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

AUTHOR DECLARATIONS

Conflict of Interest

The authors have to conflicts to disclose.

Author Contributions

Benedetta Ciarmoli: Investigation (equal); Software (equal); Visualization (equal); Writing - original draft (equal). **Sophie Marbach**: Conceptualization (lead); Investigation (equal); Methodology (lead); Supervision (lead); Visualization (equal); Writing - original draft (equal); Writing - review & editing (lead).

ACKNOWLEDGEMENTS

We wish to acknowledge fruitful discussions with Seppe Kuehn and Nelly Henry. B.C. received funding from the Sorbonne Université Institute for Sustainable Development.

[1] E. Walling, A. Trémier, and C. Vaneeckhaute, A review of mathematical models for composting, Waste Management **113**, 379 (2020).

[2] L. M. de Jesús Astacio, K. H. Prabhakara, Z. Li, H. Mickalide, and S. Kuehn, Closed microbial communities self-organize to persistently cycle carbon, Proceedings of the National Academy of Sciences **118** (2021).

[3] W. Amelung, D. Bossio, W. de Vries, I. Kögel-Knabner, J. Lehmann, R. Amundson, R. Bol, C. Collins, R. Lal, J. Leifeld, *et al.*, Towards a global-scale soil climate mitigation strategy, Nature communications **11**, 1 (2020).

[4] J. Lehmann, C. M. Hansel, C. Kaiser, M. Kleber, K. Maher, S. Manzoni, N. Nunan, M. Reichstein, J. P. Schimel, M. S. Torn, *et al.*, Persistence of soil organic carbon caused by functional complexity, Nature Geoscience **13**, 529 (2020).

[5] M. Schloter, P. Nannipieri, S. J. Sørensen, and J. D. van Elsas, Microbial indicators for soil quality, Biology and

Fertility of Soils **54**, 1 (2018).

[6] P. Nannipieri, J. Ascher, M. Ceccherini, L. Landi, G. Pietramellara, and G. Renella, Microbial diversity and soil functions, European journal of soil science **68**, 12 (2017).

[7] K. Gowda, D. Ping, M. Mani, and S. Kuehn, Genomic structure predicts metabolite dynamics in microbial communities, Cell **185**, 530 (2022).

[8] M. S. Datta, E. Sliwerska, J. Gore, M. F. Polz, and O. X. Cordero, Microbial interactions lead to rapid micro-scale successions on model marine particles, Nature communications **7**, 11965 (2016).

[9] T. T. Nguyen, E. J. Zakem, A. Ebrahimi, J. Schwartzman, T. Caglar, K. Amarnath, U. Alcolombri, F. J. Peaudecerf, T. Hwa, R. Stocker, *et al.*, Microbes contribute to setting the ocean carbon flux by altering the fate of sinking particulates, Nature communications **13**, 1657 (2022).

[10] B. Waclawiková, A. Codutti, K. Alim, and S. El Aidy, Gut microbiota-motility interregulation: insights from in vivo, ex vivo and in silico studies, Gut microbes **14**, 1997296 (2022).

[11] S. Giri, S. Shitut, and C. Kost, Harnessing ecological and evolutionary principles to guide the design of microbial production consortia, Current Opinion in Biotechnology **62**, 228 (2020).

[12] J. C. Angle, T. H. Morin, L. M. Solden, A. B. Narrowe, G. J. Smith, M. A. Borton, C. Rey-Sanchez, R. A. Daly, G. Mirfenderesgi, D. W. Hoyt, *et al.*, Methanogenesis in oxygenated soils is a substantial fraction of wetland methane emissions, Nature communications **8**, 1567 (2017).

[13] S. Shibasaki and S. Mitri, Controlling evolutionary dynamics to optimize microbial bioremediation, Evolutionary applications **13**, 2460 (2020).

[14] R. MacArthur, Species packing and competitive equilibrium for many species, Theoretical population biology **1**, 1 (1970).

[15] I. A. Hatton, O. Mazzarisi, A. Altieri, and M. Smerlak, Diversity begets stability: Sublinear growth and competitive coexistence across ecosystems, Science **383**, eadg8488 (2024).

[16] J. Hu, D. R. Amor, M. Barbier, G. Bunin, and J. Gore, Emergent phases of ecological diversity and dynamics mapped in microcosms, Science **378**, 85 (2022).

[17] G. Bunin, Ecological communities with lotka-volterra dynamics, Physical Review E **95**, 042414 (2017).

[18] A. Altieri, F. Roy, C. Cammarota, and G. Biroli, Properties of equilibria and glassy phases of the random lotka-volterra model with demographic noise, Physical Review Letters **126**, 258301 (2021).

[19] F. Roy, M. Barbier, G. Biroli, and G. Bunin, Complex interactions can create persistent fluctuations in high-diversity ecosystems, PLoS computational biology **16**, e1007827 (2020).

[20] R. May and A. R. McLean, *Theoretical ecology: principles and applications* (OUP Oxford, 2007).

[21] Y. Deng, M. Mauri, M. Vallet, M. Staudinger, R. J. Allen, and G. Pohnert, Dynamic diatom-bacteria consortia in synthetic plankton communities, Applied and Environmental Microbiology **88**, e01619 (2022).

[22] A. Picot, S. Shibasaki, O. J. Meacock, and S. Mitri, Microbial interactions in theory and practice: when are measurements compatible with models?, Current Opinion in Microbiology **75**, 102354 (2023).

[23] J. P. O'Dwyer, Whence lotka-volterra? conservation laws and integrable systems in ecology, Theoretical Ecology **11**, 441 (2018).

[24] N. I. van den Berg, D. Machado, S. Santos, I. Rocha, J. Chacón, W. Harcombe, S. Mitri, and K. R. Patil, Ecological modelling approaches for predicting emergent properties in microbial communities, Nature ecology & evolution **6**, 855 (2022).

[25] A. Dal Co, S. Van Vliet, and M. Ackermann, Emergent microscale gradients give rise to metabolic cross-feeding and antibiotic tolerance in clonal bacterial populations, Philosophical Transactions of the Royal Society B **374**, 20190080 (2019).

[26] P. Chesson, Macarthur's consumer-resource model, Theoretical Population Biology **37**, 26 (1990).

[27] S. Shibasaki, M. Mobilia, and S. Mitri, Exclusion of the fittest predicts microbial community diversity in fluctuating environments, Journal of the Royal Society Interface **18**, 20210613 (2021).

[28] O. J. Meacock and S. Mitri, Environment-organism feedbacks drive changes in ecological interactions, Ecology letters **28**, e70027 (2025).

[29] J. E. Goldford, N. Lu, D. Bajić, S. Estrela, M. Tikhonov, A. Sanchez-Gorostiaga, D. Segrè, P. Mehta, and A. Sanchez, Emergent simplicity in microbial community assembly, Science **361**, 469 (2018).

[30] E. D. Lee, C. P. Kempes, and G. B. West, Growth, death, and resource competition in sessile organisms, Proceedings of the National Academy of Sciences **118**, e2020424118 (2021).

[31] A. Fowler, H. Winstanley, M. McGuinness, and L. Cribbin, Oscillations in soil bacterial redox reactions, Journal of Theoretical Biology **342**, 33 (2014).

[32] A. Fowler, Starvation kinetics of oscillating microbial populations, in *Mathematical Proceedings of the Royal Irish Academy*, Vol. 114 (JSTOR, 2014) pp. 173–189.

[33] B. S. Khatri, A. Free, and R. J. Allen, Oscillating microbial dynamics driven by small populations, limited nutrient supply and high death rates, Journal of Theoretical Biology **314**, 120 (2012).

[34] A. Skichko and E. Kol'tsova, Mathematical model for describing oscillations of bacterial biomass, Theoretical Foundations of Chemical Engineering **40**, 503 (2006).

[35] W. Borzani, R. E. Gregori, and M. L. Vairo, Some observations on oscillatory changes in the growth rate of saccharomyces cerevisiae in aerobic continuous undisturbed culture, Biotechnology and Bioengineering **19**, 1363 (1977).

[36] D. Porro, E. Martegani, B. M. Ranzi, and L. Alberghina, Oscillations in continuous cultures of budding yeast: a segregated parameter analysis, Biotechnology and Bioengineering **32**, 411 (1988).

[37] T. Koffel, T. Daufresne, and C. A. Klausmeier, From competition to facilitation and mutualism: a general theory of the niche, Ecological Monographs **91**, e01458 (2021).

[38] S. A. Reynolds and C. E. Brassil, When can a single-species, density-dependent model capture the dynamics of a consumer-resource system?, Journal of theoretical biology **339**, 70 (2013).

[39] T. Welker and H. Stark, Dividing active and passive particles in nonuniform nutrient environments, New Journal of Physics **26**, 053039 (2024).

[40] J. Monod, The growth of bacterial cultures, Selected Papers in Molecular Biology by Jacques Monod **139**, 606 (2012).

[41] X. Sanchez-Vila, S. Rubol, A. Carles-Brangari, and D. Fernàndez-Garcia, An analytical solution to study substrate-microbial dynamics in soils, Advances in water resources **54**, 181 (2013).

[42] H. L. Smith and P. Waltman, *The theory of the chemostat: dynamics of microbial competition*, Vol. 13 (Cambridge university press, 1995).

[43] S. Bi, M. Kargeti, R. Colin, N. Farke, H. Link, and V. Sourjik, Dynamic fluctuations in a bacterial metabolic network, Nature Communications **14**, 2173 (2023).

[44] U. Schaefer, W. Boos, R. Takors, and D. Weuster-Botz, Automated sampling device for monitoring intracellular metabolite dynamics, Analytical biochemistry **270**, 88 (1999).

[45] T. Fenchel and B. Finlay, Oxygen and the spatial structure of microbial communities, Biological Reviews **83**, 553 (2008).