Collective effects in the population growth of microbials

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We investigate the population growth of microbial species. While traditional approaches rely on the logistic equation, assuming the same growth type for all the community members, we show that the stochastic θ-logistic model (SθLM) for microbial ecosystems captures the diversity of growth patterns through a single parameter, θ. The estimation of this parameter from empirical data unveils a non-trivial distribution across taxa, indicating that population increasing is strictly species-dependent. Remarkably, the logistic scenario is not necessarily the most likely one, and sublinear growth is statistically ruled out. In addition to improving our understanding of how microbial abundance evolves over time, these results engage the field as a whole. From a macroecological perspective, this suggests that the abundance fluctuation distribution follows a generalized pattern, with the Gamma distribution discussed in previous literature being just a special case. Significantly, it contributes to the long-standing stability-diversity debate in the context of microbial ecosystems by discarding recent solutions involving sublinear growth.

Introduction.—In community ecology, the development of theoretical models has often been hindered by the scarcity of datasets and the difficulty of collecting new ones. However, the situation of microbial communities is quite different. The study of these has recently been challenged by the breakthrough of metagenomics [1–3], which, among many other advances, has been distinguished by the production of an astonishing and unprecedented amount of data. It is precisely this empirical richness that, in addition to stimulating formulation of a new class of models, calls for the continuous validation of these.

The state of the art in microbial models reflects a recent and significant effort primarily focused on population dynamics. A large portion of these studies has been aimed at reproducing macroecological patterns that typically refer to populations in steady-state conditions [4–11]. Given this context, the modeling of microbial dynamics has been developed with a focus mainly on what occurs in the steady state, leaving the formalization of the growth process in the background. This indeed has been often treated through convenience choices, almost dictated by habit, which, while they may be more or less suitable for certain purposes, could be extremely limited for others.

Specifically, the growth over time of microbial populations has so far been assumed to follow a logistic profile. This has been, historically, the preferred choice as it provides a simple mechanism for exponential convergence to equilibrium and the concept of carrying capacity captures the competition for a finite resource. Here, different species are distinguished only by their intrinsic growth rates, but they all evolve according to the same functional profile. While this model has catalyzed significant advances in our understanding, in this paper we claim that it is too restrictive to accommodate recent evidence highlighted by the huge amount of data produced in recent years.

The study of microbial dynamics beyond the traditional logistic model is not merely an exercise in generalization for its own sake. On the contrary, there are clear indications that moving beyond this framework is perhaps a natural path and can help us reveal many behaviors that we are currently not seeing. For example, a very recent work by I. A. Hatton *et al.* [12] has demonstrated that sublinear growth, *i.e.* a growth scaling as a sublinear power with biomass, provides important insights into the longstanding conflict between stability and diversity, a result that has sparked a debate that is far from being closed [13]. On the other hand, it is important to note that several decades ago, studies already highlighted the heterogeneity of growth types for communities composed of birds, mammals, fish, and insects [14, 15]. Therefore, it is pertinent to ask whether this also applies to microbes.

In light of all this, we propose the stochastic θ-logistic model (SθLM) in the field of microbial ecology. This comprises a deterministic part and a stochastic one. The former, the θ-logistic model [16], allows for different types of growth —including logistic and sublinear as special cases— through a parameter, θ, which regulates the dependence between the per-capita growth and biomass. The latter instead embodies the environmental random fluctuations observed in real data [4, 6, 17, 18] and is chosen to be in the multiplicative form well discussed in previous literature [4, 19, 20].

In this framework, we aim to characterize the growth profile of several real biomes [22], specifically focusing on gaining insight into the values of the corresponding θ parameter. To achieve this goal, we employ Bayesian

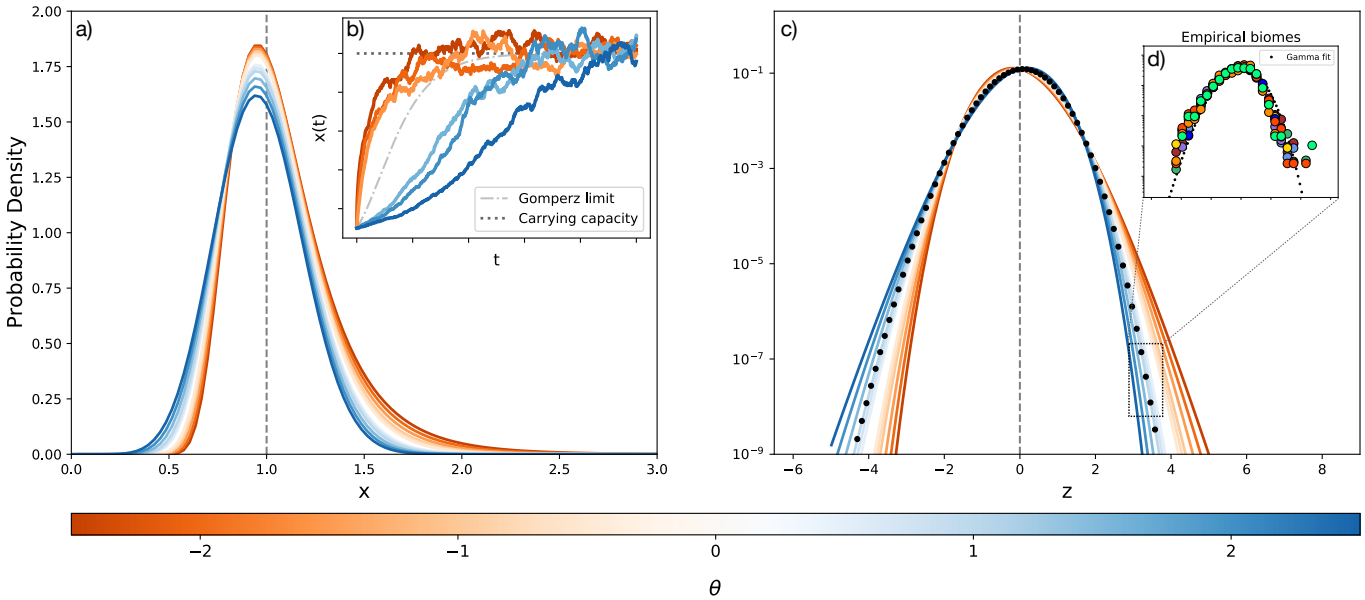

FIG. 1. **a)** Generalized Gamma AFD, $P(x)$, in Eq. (4) for different values of θ indicated in the colorbar. **b)** Solution of the SθLM (3) for $\theta = -2.5, -2, -1.5, 1.5, 2, 2.5$, obtained by means of the *Euler-Maruyama* method [21] with $x(0) = 0.1$ and $dt = 10^{-3}$. The black dotted line depicts the carrying capacity K, while the grey dot-dashed line refers to the solution of the Gomperz limit in Eq. (2). **c)** Graphical representation of $\log(\bar{P}(z))$ in Eq. (7), *i.e.* the logarithm of the Generalized Gamma AFD expressed as a function of the standardized abundance z in Eq. (6), for several values of θ. The black dots portray the Gamma fit of the biomes AFDs presented in the inset **d)**, where we presented the $\log(\bar{P}(z))$ of nine real biomes: Seawater, Soil, Sludge, Oral1, Gut1, Gut2, Glacier, River, Lake [22]. All the plots have been realized with $\tau = 0.1, K = 1, w = 0.5$.

techniques, which allow us to infer the distribution of θ values from empirical datasets. The conclusions drawn from this analysis are twofold: 1) The distributions depict non-trivial configurations that are far from being peaked, suggesting that microbial population growth varies significantly between species, with the logistic case not being the most likely scenario; 2) Importantly, negative values of theta are highly improbable, indicating that microbial growth is never sublinear. Building on these results, we discuss their contributions to the state of the art in microbial ecology, from macroecological patterns to the stability-diversity debate.

The model.—The θ-logistic model [16] is defined by the following equation

$$\dot{x} = \frac{x}{\tau\theta}\left[1 - \left(\frac{x}{K}\right)^{\theta}\right], \tag{1}$$

where x is the species population (also referred to as abundance, or density of individuals), τ is its intrinsic growth time, and K is the carrying capacity. The parameter θ governs the relationship between the *per capita* growth rate $\dot{x}$ and the abundance x, providing information about the curvature of the resulting growth profile, *i.e.* its concave/convex character.

In this way, the model (1) is able to capture a wide range of behaviors according to the value of θ. The situation in which $\theta > 0$ defines a linear growth for small abundances ($\dot{x} \propto x$), with the specific case of $\theta = 1$ referring to the logistic scenario, while $-1 < \theta < 0$ describes a sublinear growth ($\dot{x} \propto x^{1-|\theta|}$). The transition from positive to negative θ values is smooth, since in the limit $\theta \to 0$ the equation matches the well-known Gompertz model [23]

$$\dot{x} = -\frac{x}{\tau}\log\left(\frac{x}{K}\right). \tag{2}$$

The analysis of real biomes reveals the presence of rapid random fluctuations around a stationary value [6, 17], suggesting that microbial population dynamics are inherently stochastic. Consequently, the model (1) is endowed with a noise term accounting for these fluctuations. Such a noise in the model is typically expressed as a product of a random variable and a function of abundance [24, 25], which can take various forms depending on the biological process governing fluctuations. This function may be constant (for immigration), square-rooted (for demographic noise), or linear (for environmental noise). Determining the specific form of this function can be achieved by analyzing the differences between empirical abundances at successive time points [6]. The result, illustrated in Figure SI2, suggests a presence of a linear noise term, arising from random variations in environmental variables such as changes in pH or temperature [4]. This finding is supported by time series analyses in [6] and corroborates claims made in [4].

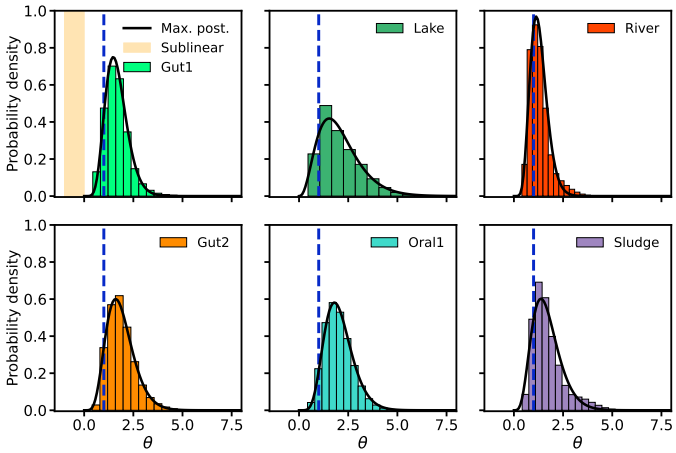

FIG. 2. **Distribution of θ across species for several biomes**. The histograms were generated from the posterior samples of all species, so they already include the uncertainty of each species. The black line represents the prior Gamma distribution of the θ parameter using the modal values of the hyperparameters ν_0 and k_0. The figure demonstrates a strong alignment between the posterior and prior distributions, indicating that the population posterior follows a Gamma distribution. For computational limitations, in making this figure, species appearing in less than 95% of the samples were filtered out.

Thus, the stochastic θ-logistic model (SθLM) is defined by the Langevin-like equation:

$$\dot{x} = \frac{x}{\tau\theta}\left[1 - \left(\frac{x}{K}\right)^{\theta}\right] + x\xi(t), \tag{3}$$

where $\xi(t)$ is a zero-mean Gaussian white noise such that $\langle \xi(t)\xi(t')\rangle = w\delta(t-t')$, with w measuring the variance of growth-rate fluctuations due to environmental stochasticity. In Fig. 1 **b** we depict several numerical realization of the model for different values of θ: the situation in which $\theta = 1$ corresponds to the Stochastic Logistic Model (SLM) introduced in [4]. Equation (3) describes the intrinsic stochastic dynamics in the abundance of different taxa, each expected to have unique parameters. However, for clarity, taxonomic identity is not explicitly included in the equation.

The flexibility of the generalized gamma distribution.— In the context of macroecology [26, 27] —the prominent approach so far to treat microbial communities— a natural way to characterize the aforementioned fluctuations is through their distribution. This is named Abundance Fluctuation Distribution (AFD) and it encodes the variability of stationary abundances across metagenomic samples. In mathematical terms, this is a time-independent probability distribution obtained as the steady-state of the Fokker-Planck equation related to a given Langevin equation. In the specific situation of Eq. (3) this takes the form of a *Generalized Gamma* [25, 28]:

$$\begin{aligned} P(x) &= \frac{1}{Z}\left(\frac{x}{K}\right)^{\alpha-2}\exp\left[-\frac{\alpha}{\theta}\left(\frac{x}{K}\right)^{\theta}\right], \\ Z &= \left(\frac{\theta}{\alpha}\right)^{\beta}\frac{K\Gamma(\beta)}{|\theta|}, \end{aligned} \tag{4}$$

with the mean value and the variance of the distrbution above are respectively given by

$$\begin{aligned} \langle x\rangle &= K\left(\frac{\theta}{\alpha}\right)^{\frac{1}{\theta}}\frac{\Gamma(\beta+\frac{1}{\theta})}{\Gamma(\beta)}, \\ \mathrm{Var}(x) &= \langle x\rangle^2\left[\frac{\Gamma(\beta+\frac{2}{\theta})\Gamma(\beta)}{\Gamma(\beta+\frac{1}{\theta})^2} - 1\right], \end{aligned} \tag{5}$$

where we have set $\alpha \equiv 2/w\tau\theta$, $\beta \equiv (\alpha-1)/\theta$. Notice that $\beta \geq 0$ regardless of the sign of θ. The details of the calculations to obtain Eq. (4) are presented in Sec. SI I.

It is worth highlighting that in the case where $\theta = 1$, corresponding to logistic growth, we recover the results obtained in previous literature, with the equation 4 taking the form of a Gamma distribution. However, this distribution, as well as its moments, can take on various configurations depending on the values of θ —see Fig. 1 **a**— and the other two parameters α and K. For instance, the distribution can be a stretched exponential ($\alpha = 2$), an ordinary exponential ($\alpha = 2$, $\theta = 1$), a (positive) half-normal ($\alpha = \theta = 2$), or a Weibull ($\alpha = \theta$). Furthermore, in the limit $\theta \to 0$ the distribution (4) becomes a lognormal (more details are presented in Sec. SI III).

Nevertheless, such a richness of behaviors, indicative of the possible growth modes that a species can follow, cannot be captured through the representational schemes used in previous works. The AFD is indeed typically analyzed in terms of the standardized variable [4, 9, 11, 29]

$$z = \frac{\log x - \langle \log x\rangle}{\sqrt{\mathrm{Var}(\log x)}}. \tag{6}$$

With this choice, the distribution $\bar{P}(z)$ takes an *Exp-Gamma* form

$$\begin{aligned} \log\bar{P}(z) &= \log\left[\frac{\sqrt{\psi'(\beta)}}{\Gamma(\beta)}\right] + \beta u - e^{u}, \\ u &\equiv \psi(\beta) + \varepsilon\sqrt{\psi'(\beta)}z, \end{aligned} \tag{7}$$

where $\varepsilon \equiv \mathrm{sign}(\theta)$ and $\psi(x) = \Gamma'(x)/\Gamma(x)$ is the Di-Gamma function [30] (see Sec. SI IB for the calculations behind Eq. (7)).

The above quantity is the primary object used to represent abundance variability in many studies. In Fig. 1**c**, we show this for different values of θ, describing various growth types. Notably, all distributions (and thus all growth models) can be categorized into just

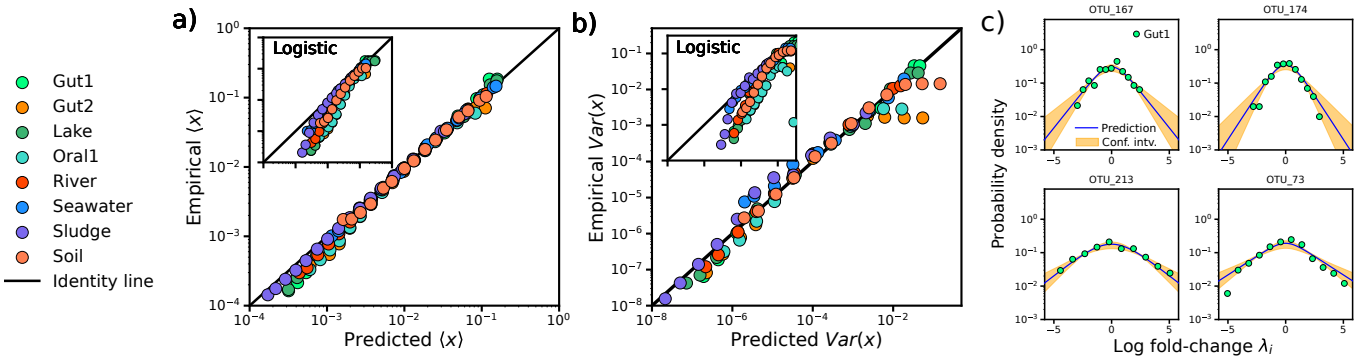

FIG. 3. **Consistency test for the θ inference** Plot of the average **(a)** and variance **(b)** over posterior samples obtained through Eqs. (5) for the biome species against the the empirical ones. Dots provide a coarse-grained visualization of these magnitudes, with error bars intentionally left aside for the sake of clarity (detailed uncertainty information is available in Sec. VIII of the SI). Insets show the same test applied to the SLM, and show its tendency to underestimate both mean and variance across most of the population. **(c)** Log fold-chande distribution, *i.e.* distribution of the of consecutive abundance ratio $\lambda = x_{s+1}/x_s$ for individual species. The panels here depict only four randomly chosen species; for more extensive visualizations, please refer to Sec. VIII of the SI. In cross-sectional data, where the autocorrelation time is effectively infinite, the distribution's insights are already encapsulated by the AFD (derivations can be found in Sec. VII of the SI). This test acts as confirmation that our model accurately reproduces the entire AFD.

two types, labeled by $\varepsilon = \pm 1$. Interestingly, a graphical comparison with empirical data suggests a better agreement with positive values of θ, thereby discarding negative ones, which correspond to sublinear growth patterns. However, despite this initial indication, it is not possible at this level to extract detailed information about how microbial species grow: this information cannot be obtained through an analysis based solely on the standardized AFD.

Inference method and Results.—Estimates of the parameter θ have been obtained in the past through least squares fits of the dynamic equation (1) to time series data [12, 15, 16, 31]. This method has many drawbacks—such as the poor estimation of derivatives produced by a finite-difference scheme applied to noisy data, or the underlying assumption that the noise follows a normal distribution—which lead to not very reliable estimates of the actual values of θ (See Sec. IV of the SI for more details). In our work, however, the estimation of such a parameter is carried out through a Bayesian inference procedure, a method that benefits from the result obtained for the expression of the Generalized Gamma distribution (4), which serves as a likelihood function.

Microbiome data do not consist of lists of species abundances, though. A typical sample is a vector of counts $\mathbf{n}_s = \left(n_{1,s}, n_{2,s}, \ldots, n_{S,s}\right)$, where $n_{i,s}$ is the number of reads attributed to taxon $i = 1, \ldots, S$ in sample s. The total number of reads across all taxa in each sample, $\sum_i n_{i,s} = N_s$, is referred to as the *sampling effort* or *sampling depth*. Thus, to the inherent variability of the abundances induced by the dynamics (captured by the distribution (4)), we must add the variability introduced by the sampling process. We can describe this sampling by a Poisson distribution with mean $x_{i,s}N_s$. Therefore, the probability to observe n_i counts of the ith taxon in the given sample s is obtained by marginalizing over x_i, namely

$$P(n_i|N_s, \Omega) = \frac{N_s^{n_i}}{n_i!} \int_0^\infty dx_i \, P(x_i|\Omega) x_i^{n_i} e^{-x_i N_s}, \qquad (8)$$

with $P(x|\Omega)$ being the generalized Gamma distribution (4), which depends on the set of parameters $\Omega = \{\theta, K, \tau w\}$. This will be the likelihood of our Bayesian analysis. As for the prior distribution for each of the parameters $\zeta = \{K, \tau w\}$, we choose $\delta e^{-\delta\zeta}$, with $\delta > 0$ a small constant. These priors ensure the positiveness of these parameters, while being quite agnostic at the same time (more details are discussed in Sec. VI of the SI).

The first estimates we made of the distribution of θ (using a prior similar to that of the other parameters) suggested that it can be reasonably fitted by a Gamma distribution, so we finally decided to assume this as the prior for θ, and estimate the related "hyper-parameters" (priors for these hyper-parameters are chosen as those of K and τw). This hierarchical Bayesian approach not only refines the estimates, but also allows cross-learning among taxa, enhancing the overall robustness and accuracy of our parameter estimations while reducing overfitting at the same time.

Figure 2 shows the population posterior for theta as obtained from several biomes. The posterior distributions are right-skewed and unimodal (very close to a Gamma distribution), with the logistic case being a plausible scenario, though not necessarily the most likely. For example, the peaks for lake, seawater, and river biomes are quite close to the logistic case, while those for Gut1 and Oral1 biomes are somewhat further away. Remarkably,

the likelihood that θ takes negative values is null, delivering so a compelling result: microbial growth is never sublinear.

To evaluate the quality of our Bayesian approach, we conducted a posterior predictive check. This method endorses the accuracy of our model by demonstrating how well it replicates the full abundance distributions of individual species, as detailed in the Supplementary Information. Along the same line, in Fig. 3, we demonstrate the consistency of our analysis by plotting the resulting average and variance against empirical values and recovering the distribution of the logarithmic fold-change $\log(x_{s+1}/x_s)$ which has been recently studied in several works [5, 8, 32, 33].

Conclusions and Discussion.— The last developments in metagenomic techniques are revolutionizing our understanding of microscopic life, inevitably leading to a race for a theory capable of addressing the new world being revealed to us. Our paper adheres to this recent trend and addresses a previously unexplored issue: how do microbial populations grow? Combining empirical analysis and mathematical modeling, we reveal a remarkable variability in the growth types —embodied in the parameter θ— across different species, demonstrating that the assumptions on which a large part of previous work is based, *i.e.* a logistic growth for all community members, are limited and reductive. Importantly, despite this variability, for none of the biomes we analyzed sublinear patterns represent a plausible scenario, a behavior that differs significantly from that of other types of ecosystems, such as plant and birds [12, 14, 15], and could constitute a "signature" of microbial communities.

In addition to understanding how their populations evolve, these results shed light on the microscopic behavior of microbes. Herein, it deserves to mention the paper of Petroni *et al.* [25] which provides useful insights about the meaning of θ by linking it to the survival energy. The survival energy scales with population as $E_s \sim n^{\theta}$, or equivalently, the energy per bacterium scales as $\sim n^{\theta-1}$. This means that if $\theta < 1$, the population is aiding the survival of the bacteria, whereas if $\theta > 1$, it is hindering it. The first case could arise because a population of bacteria cooperates in some way to exploit a resource. Regarding the second case, consider for example a compact colony of bacteria where the resource comes from the outside. Bacteria on the periphery have access to the resource, while those on the interior are shielded by those on the outside and receive less. As the population increases, less resource reaches the interior, requiring more resource for them to survive.

This kind of conclusions certainly requires an extension of the present analysis, for example from the empirical side, considering a larger dataset involving more biomes and possibly with finer sampling, but also from a modeling perspective, introducing interactions, as well as other microscopic mechanisms, and studying their interplay with the θ parameter. Specifically, one might indeed wonder whether introducing interactions and repeating the same Bayesian analysis would change the results for the population increasing, and if so, how. In any case, regardless of all this, even at this level our results are capable of impacting the state of the art in microbial community research, making progress in various directions.

Modern metagenomic techniques are based on the extraction of information, such as microbial abundances and the total number of species, from different *samples*, which serve as snapshots of the ecosystem. Hence, a natural question that arises in this new scenario is the following: how do the different ecological observables, such as abundances and diversity, vary across our collected samples? An important step forward on this issue was made with the seminal paper by Jacopo Grilli [4], who studied how the abundances of different species are distributed over samples, that is, the Abundance Fluctuation Distribution (AFD). Not only did he manage to determine the analytical form of this distribution—a Gamma—by proposing a microscopic model capable of reproducing it, but more importantly, he showed that this configuration is "universal" i.e., invariant across a number of real biomes, both human and non-human. An important conclusion of our analysis is that this generalized growth went unnoticed as a consequence of the particular statistical analysis performed on the data —the rescaling in Eq. (6)— while the true configuration of the AFD is that of a Generalized Gamma, which shows a clear dependence on θ and therefore changes significantly depending on the species. Specifically, in agreement with the distributions in Fig. 2, the Gamma distribution related to $\theta = 1$ remains a plausible pattern, but it is just one among many others.

Another implication of this result concerns Taylor's law [34], which is the polynomial relationship between the mean value —calculated across samples— of species abundance and its corresponding variance. This is an omnipresent pattern in ecology that, in microbial communities, manifests as a quadratic relationship [4]. Nevertheless, a closer analysis of empirical data shows that this relationship constitutes a first-order approximation characterized by an uncertainty that can extend up to three orders of magnitude. What is the mechanism responsible for this uncertainty? In [11] we showed that this may explained by taking into account interspecies interactions, with the original quadratic law arising as a small interaction limit. In Sec. II of the SI we derived Taylor's law within the framework of the SθLM (3), revealing a distinct dependence on θ. This, together with the variability of the parameter values presented in Fig. 2, suggests that clearly, in addition to interactions, θ can also introduce uncertainty around the relationship between means and variances. Weighing these different

sources of uncertainty constitutes a possible future perspective.

Finally, our analysis directly intervenes in the long-standing conflict between stability and diversity, perhaps the most heated debate in ecology for about fifty years [35, 36]. The paper of Hatton *et al.* [12] is the most recent contribution in this context and indicates that sublinear growth —a behavior more than common in many types of ecosystems according to their data analysis— can reconcile the relationship between the number of species and local asymptotic stability, thus finding agreement with experimental evidence. Although this work has sparked a currently ongoing debate [13], regardless of its resolution, it can be stated that its conclusions are not applicable to microbial communities, as our inference for the values of theta almost entirely rules out sublinear growth. Overall, the debate on stability and diversity is still open with regard to microbes and will require further efforts to align theory with experimental evidence.

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