The macroecological dynamics of sojourn trajectories in the human gut microbiome

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Abstract

The human gut microbiome is a dynamic ecosystem. Host behaviors (e.g., diet) provide a regular source of environmental variation that induce fluctuations in the abundances of resident microbiota. Despite these displacements, microbial community members are highly resilient in that they tend to fluctuate around characteristic steady-state abundances in healthy human hosts rather than suffering extinction or dominating the community. These temporary excursions from steady-state abundances, known as *sojourn trajectories*, have the potential to inform our understanding of the fundamental dynamics of the microbiome, as well as how often-reported measures (e.g., mean and variance of abundance) relate to temporal dynamics and, ultimately, the timescale of growth. However, to our knowledge, the macroecology of sojourn trajectories has yet to be systematically examined in any ecological system. In this study we leverage theoretical tools from the study of random walks to characterize the duration of sojourn trajectories, their shape, and the degree that diverse community members exhibit similar qualitative and quantitative dynamics. After ruling out the contribution of stationarity, we leveraged the Stochastic Logistic Model as a theoretical lens for interpreting our empirical observations. We find that the typical timescale of a sojourn trajectory does not depend on the mean abundance of a community member (i.e., its carrying capacity), though it is strongly related to its coefficient of variation. This work provides fundamental insight into the dynamics, timescales, and fluctuations exhibited by diverse microbial communities.

Main

While microbial communities in the human gut consistently maintain steady-state abundances over extended timescales, individual community members can deviate for periods of time. These excursions away from and subsequent returns to said steady-state values, known as *sojourn trajectories*, have been systematically studied for various stochastic models [1, 2] and quantitatively examined in neurological [3] geophysical systems [4]. However, to our knowledge, sojourn trajectories have yet to be investigated in any ecological system, much less understood through the lens of ecological models.

Here we provide the first characterization of the sojourn dynamics of microbial communities in the human gut, investigating the timescales of sojourn trajectories ($\mathcal{T}$) and their relationship with the typical deviation. We both interpret our findings and generate quantitative predictions using the Stochastic Logistic Model of growth (SLM;

Supporting Information), a minimal ecological model where species dynamics are governed by self-limiting growth and environmental noise. This model has provided insight into the macroecology of microbial communities both within and across hosts [5, 6], in experimental communities [7], and across phylogenetic scales ranging from strains to phyla [8–10], justifying its selection.

We first identified and re-processed highly time-resolved human gut microbiome 16S rRNA datasets from healthy hosts with daily or near-daily sampling ([11–14]; Table S1; SI). Leveraging the observation that the distribution of abundances of individual community members tends to follow a gamma distribution, the mean and CV of each ASV were inferred using sampling-aware maximum likelihood (Fig. S1; SI). As typical abundances can vary by orders of magnitude in microbial communities, abundances were rescaled by their time-averaged mean and log transformed, $y(t) \equiv \ln\left(\frac{x(t)}{\bar{x}}\right)$ (Fig. S2). This new variable has the added convenience of allowing us to obtain mathematical predictions of sojourn properties using the SLM (SI).

We first investigated sojourn trajectories as consecutive observations where a community member deviated from and then returned to its steady-state abundance (Fig. 1a). By calculating sojourn times for all ASVs in all datasets, we were able to obtain an empirical probability distribution (Fig. 1b). This empirical distribution could not be captured by assuming observations were independently drawn from a stationary distribution (i.e., gamma; Fig. S3; SI), nor by a null distribution generated by permuting time labels (Fig. S4). Rather, a time-dependent solution of the SLM was required to capture the shape of the empirical distribution, the shape of which depended on the timescale of growth (τ).

With the distribution of sojourn times identified it was necessary to investigate how sojourn trajectories of different length $\mathcal{T}$ relate to one another. This dependency has been characterized as the scaling relationship between $\mathcal{T}$ and the area under a given sojourn trajectory, $\mathcal{A}(\mathcal{T})$, the result of which tells us how different trajectories need to be rescaled to have the same shape (Fig. 1a; SI) [1, 2]. We found the absence of a relationship between the two quantities, meaning that the area of a sojourn trajectory is effectively independent of its sojourn time ($\mathcal{A}(\mathcal{T}) \equiv \mathcal{A}$), a result that is predicted by the SLM when the timescale of growth is much less than the typical sojourn time ($\tau \ll \mathcal{T}$; Fig. 1c; SI). Motivated by this success, we tested the prediction that $\mathcal{A}$ scaled with the inverse environmental noise of an ASV (a function of their CV), finding that the exponent predicted by the SLM sufficiently captured the empirical trend (inset of Fig. 1c).

The fact that $\mathcal{A}$ was independent of $\mathcal{T}$ informs our understanding of the typical deviation from the steady-state *within* a sojourn trajectory, $\langle y(t) - \bar{y} \rangle_{\mathcal{T}}$. Prior theoretical efforts have found that a wide range of stochastic dynamics can be captured by a scaling relationship that depends on $\mathcal{T}^{\alpha}$ for a given exponent (see SI for additional details). The absence of a relationship in Fig. 1c tell us that $\alpha = 0$, meaning that sojourn deviations should exhibit similar trajectories for different values of $\mathcal{T}$ *without* additional rescaling. This prediction held, as empirical trajectories $\langle y(t) - \bar{y} \rangle$ did not systematically change with increasing $\mathcal{T}$ (Fig. 1d; S5).

Up to this point we have investigated the similarities in the sojourn dynamics of microbial community members but have neglected how quantitative differences can shape typical sojourn times. Therefore, we examined the relationship between the mean sojourn time (i.e., $\langle \mathcal{T} \rangle$) and the strength of environmental noise (i.e., σ), comparing our observation to the relationship predicted by the SLM (Fig. 2a). Focusing on the dataset with the highest temporal resolution, permitting the lowest possible values of $\mathcal{T}$ to be estimated (Table S1; [12]), we both confirmed the existence of the relationship as well as the validity of our predictions (Fig. 2b). Our derivation of $P(\mathcal{T})$ does not explicitly contain the carrying capacity as a parameter (Eq. S26), meaning that the model

predicts the *absence* of a relationship between the mean relative abundance of an ASV and $\langle \mathcal{T} \rangle$, a prediction that also held in the data (Fig. S6). Together, these results indicate that sojourn times within the gut are independent of the carrying capacity but depend heavily on the strength of environmental noise that a community member experiences.

Building on prior investigations into the temporal dynamics of microbial communities [6, 15–18], this study centered the macroecology of excursions from steady-state abundances by leveraging a theoretical framework from statistical physics [1, 2]. We found that while the timescale of growth was necessary to recapitulate the distribution of sojourn timescales, sojourn trajectories were effectively scale-free. These results could be interpreted under the SLM as excursions from the steady-state, largely reflecting the strength of environmental noise. Due to the available data, this study focused on healthy hosts, though it would be of interest to extend our analyses to the scenario where microbiomes are effectively out of steady-state as such perturbations have the potential to impact stability [19]. We note that the length of time between observations is a crucial experimental parameter that determines the dynamics that can be observed. Traditional fecal sample collection effectively limits our temporal resolution to $\delta t \sim 1$ day and alternative dynamics will likely be observed in systems where $\tau \gg \delta t$, though ecological models such as the SLM may continue to provide useful interpretations.

Data and code availability

Public raw sequence data used in this study were obtained from previous studies (Table S1). Data processed for this study are available on Zenodo DOI: `10.5281/zenodo.15754231`. All code is available on GitHub under a GNU General Public License: `sojourn_macroeco`

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Author contributions

W.R.S. and J.G. conceptualized the project, performed the derivations, and wrote the manuscript. W.R.S. performed all analyses.

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Figures

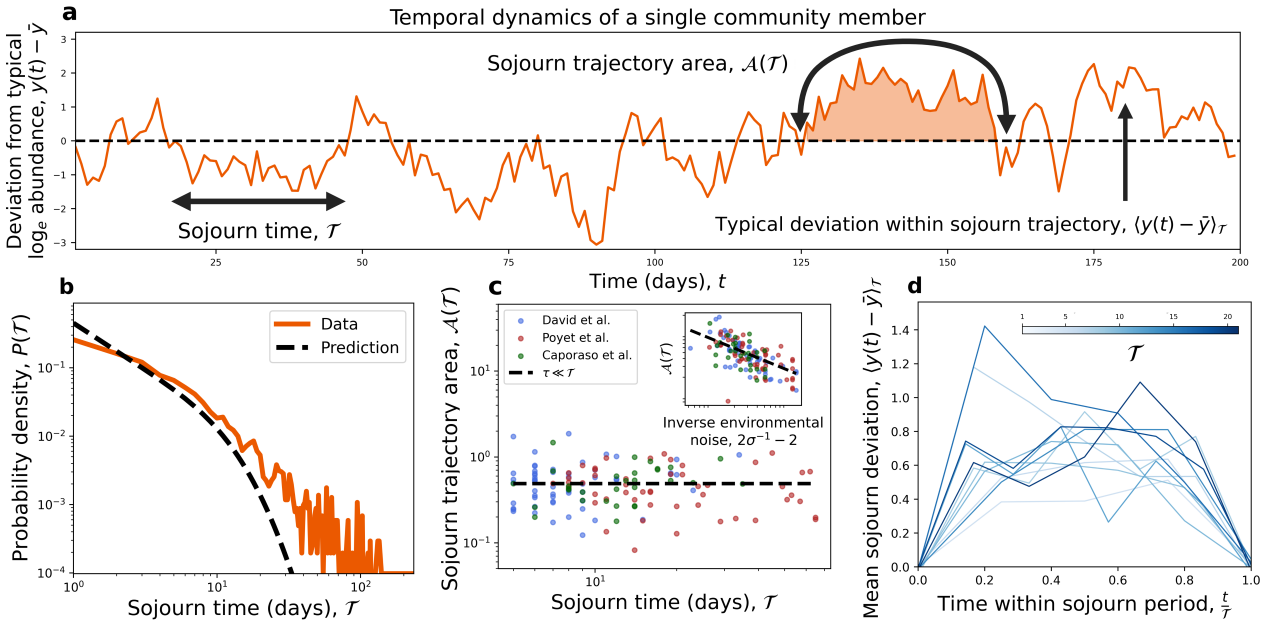

Figure 1. Patterns of sojourn trajectories inform our understanding of microbial community dynamics. a) We investigated the macroecology of sojourn trajectories using log-transformed relative abundances that have been rescaled by their mean ($y(t) \equiv \ln\left(\frac{x(t)}{\bar{x}}\right)$). Consecutive fluctuations of $y(t)$ either above or below the time-averaged mean were investigated, focusing on three previously identified patterns [1, 2]: 1) the distribution of sojourn times $P(\mathcal{T})$, 2) the area under a sojourn trajectory and its relationship with $\mathcal{T}$, and 3) how the mean deviation within a sojourn trajectory depends on $\mathcal{T}$. **b)** The empirical $P(\mathcal{T})$ could only be captured using a form of the SLM where the growth rate resulted in abundances at future observations being conditioned on the current abundance. **c)** We find a lack of dependency between $\mathcal{T}$ and $\mathcal{A}$ across datasets but a consistent relationship between the inverse strength of environmental noise and $\mathcal{A}$, results that are predicted by the SLM under the parameter limit where the growth rate is typically much smaller than $\mathcal{T}$. **d)** Given that $\mathcal{A}$ is a constant, we predict that that the mean sojourn deviation should *not* vary with $\mathcal{T}$, a result that holds when we investigate the data.

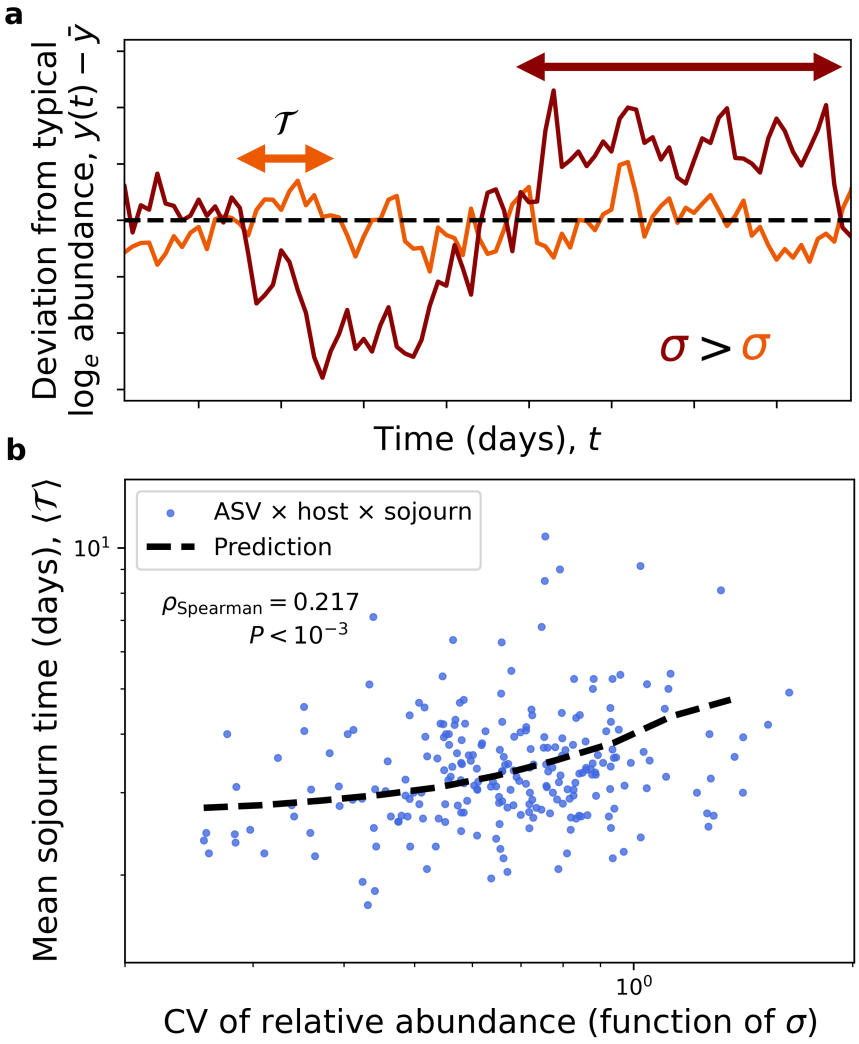

Figure 2. Increase in mean sojourn times across ASVs can be interpreted as an increase in the strength of environmental noise. a) Under the SLM we predict that community members subjected to stronger sources of environmental noise (higher σ) will have larger sojourn times. **b)** This prediction holds in the data, as $\langle \mathcal{T} \rangle$ tended to increase with the CV of relative abundance, which can be interpreted as a function of the strength of environmental noise under the SLM. This empirical relationship could be captured using the SLM with σ inferred from the timeseries of each ASV. As an additional source of validation, we confirmed the existence of a significant positive relationship using Spearman's rank correlation coefficient.