

# A unified conceptual framework for prediction and control of microbiomes

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Microbiomes impact nearly all systems on Earth, and despite vast differences among systems, we contend that it is possible and highly beneficial to develop a unified conceptual framework for understanding microbiome dynamics that is applicable across systems. The ability to robustly predict and control environmental and human microbiomes would provide impactful opportunities to sustain and improve the health of ecosystems and humans alike. Doing so requires understanding the processes governing microbiome temporal dynamics, which currently presents an enormous challenge. We contend, however, that new opportunities can emerge by placing studies of both environmental and human microbiome temporal dynamics in the context of a unified conceptual framework. Our conceptual framework poses that factors influencing the temporal dynamics of microbiomes can be grouped into three broad categories: biotic and abiotic history, internal dynamics, and external forcing factors. Both environmental and human microbiome science study these factors, but not in a coordinated or consistent way. Here we discuss opportunities for greater crosstalk across these domains, such as leveraging specific ecological concepts from environmental microbiome science to guide optimization of strategies to manipulate human microbiomes towards improved health. To achieve unified understanding, it is necessary to have a common body of theory developed from explicit iteration between models and molecular-based characterization of microbiome dynamics across systems. Only through such model-experiment iteration will we eventually achieve prediction and control across microbiomes that impact ecosystem sustainability and human health.

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## Introduction

An intrinsic property of natural biological systems is that they are dynamic and microbiomes are no exception [1]. Understanding the factors that govern microbiome dynamics presents an enormous challenge [2], but new opportunities can emerge by placing studies of temporal dynamics in the context of a *unified conceptual framework* (Box 1; Figure 1). A unified conceptual framework can help guide the application of developing technologies (e.g. multi-omics) beyond discovery-based exploration towards hypothesis driven investigations [3]. This is essential for maximizing the scientific insights provided by developing technologies, and ultimately enabling knowledge of processes that govern microbiome temporal dynamics.

To predict the function of environmental or human microbiomes under future states and to harness them to achieve beneficial ends requires understanding the processes governing microbiome temporal dynamics [4,5]. For example, environmental microbiomes provide important ecosystem services [6–8]; a key question is whether they can provision those services in the face of environmental perturbations such as storms, fires, droughts, and contaminant releases. On the human side, microbiomes play essential roles in health and there is significant interest in manipulating microbiomes towards improved health [9] by maintaining beneficial characteristics of microbiomes while suppressing harmful ones. In both systems, predictable outcomes must ultimately be rooted in knowledge of temporal dynamics of the microbiome with respect to community composition, gene expression, and metabolic function [2,10].

While there is a need to ultimately control environmental and human microbiomes for beneficial outcomes to society, there is significant uncertainty regarding the factors governing the temporal dynamics of microbiomes. By advancing a unifying conceptual framework we intend to organize collective thinking [11,12] and investigation of microbiome temporal dynamics. Doing so across environmental and human microbiomes further provides an opportunity to identify major gaps within each of these fields and to promote crosstalk between them. Our goal is to stimulate purposefully coordinated efforts between environmental and human microbiome research targeting a shared conceptual framework focused on transferable knowledge of the processes governing microbiome temporal dynamics.

**Box 1 A unified conceptual framework for microbiome research.**

Our conceptual framework is grounded in ecological theory that is applicable across systems and is based on the individual and combined influences of three overarching factors: historical contingencies, internal dynamics, and external forcing factors. These three factors can be conceptualized as having deterministic influences over microbiomes in that they can systematically increase the fitness of some taxa while suppressing others. All three are also influenced by stochasticity, however, wherein random birth and death events can erode an otherwise deterministic trajectory. The three forcing factors are defined as follows:

*Historical contingencies:* The historical conditions, including abiotic and biotic history, that lead to the present characteristics of a microbiome and that may influence how the system responds to future perturbations.

*Internal dynamics:* Factors within the microbiome that lead to its changes over time, including evolutionary dynamics, organismal and species interactions, and microbe-driven changes to the environment that feedback on the microbiome; also termed autogenic succession.

*External forcing factors:* Extrinsic factors that influence microbiome temporal dynamics, including abiotic drivers as well as biotic drivers that arise from immigration or invasion of new organisms entering a community; also termed allogenic succession.

We propose that separating these overarching factors into three categories provides a useful heuristic for organizing conceptual thought and theory development. A key point, however, is that these factors operate simultaneously and continually feedback on each other (Figure 1). We therefore assert that to enable robust prediction and control, new theoretical and experimental paradigms are needed that explicitly account for these factors and their feedbacks.

**Conceptual foundations**

Our conceptual framework is based on the idea that factors influencing the temporal dynamics of microbiomes can be broken into three broad categories: biotic and abiotic history, internal dynamics, and external forcing factors (Box 1; Figure 1). These three factors are each multifaceted, interact with each other, and feedback with microbiomes. This makes predicting and controlling microbiome dynamics and function an enormous challenge.

There is increasing recognition that biotic and abiotic history strongly influence microbiome responses to perturbation [13–15]. This dependence of future dynamics on historical conditions is referred to as ‘historical contingency’. Historical contingency has both biotic and abiotic aspects. On the biotic side, there are ecological and evolutionary processes that govern the assembly of microbiomes through time, thereby governing the microbiome found at any given point in time and space [16]. This history provides the initial conditions for how a microbiome will respond to perturbation, driven through either internal or external factors [17].

History sets the stage, but microbiome dynamics play out due, in part, to processes internal to the microbiome. Such processes include evolutionary dynamics, organismal and

species interactions, and microbe-driven changes to the environment that in turn influence the microbiome [16,18,19]. Collectively, this suite of processes is classically referred to as autogenic succession, whereby changes in the biological community through time are driven by dynamics within the community. This concept has a long history in plant ecology (e.g. [20]), but has received much less explicit attention within the microbial ecology of environmental and human systems.

In addition to internal dynamics, external forcing factors can strongly govern microbiome temporal dynamics. Classically this is referred to as allogenic succession, which is often focused on abiotic drivers. This concept is rooted in the idea that the environment deterministically selects for some taxa and against others. It is important to consider biotic aspects of external forcing factors as well, in terms of the impacts of dispersal or immigration [21]. The input of new individuals or species coming from outside the local community can strongly influence the community temporal dynamics, as in the case of invasive species [22]. This blurs the line between autogenic succession and allogenic succession, and in some ways connects these concepts.

The connection between autogenic and allogenic succession highlights that history, internal dynamics, and external forcing are interrelated and there are no clear boundaries distinguishing them. Separating these concepts into three categories provides a useful heuristic to organize thinking, but it is important to recognize the connections and interactions among these conceptual domains. For example, the historical assembly of microbiomes is directly related to future autogenic and allogenic succession [17]. In our conceptual framework, the past influences the future, thereby providing an integrated view of the factors driving microbiome temporal dynamics (also see [13]).

To advance a unified conceptual framework, the following sections examine a sampling of recent literature studying the influences of history, internal dynamics, or external factors on temporal dynamics in environmental or human microbiomes. In turn, we identify commonalities and differences across environmental and human microbiomes in terms of how these factors work and have been studied/conceptualized, which points to outstanding challenges and opportunities.

**Historical contingencies**

Historical contingencies are mechanistically influenced by both environmental and biological history. Historical environmental conditions result in physicochemical conditions representing the initial conditions that, in turn, influence how features such as resource availability respond to environmental change. For example, a history of low precipitation may change the physical structure of

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