Title: Microbial contributions to host life history tradeoffs

Authors: *[1]Lauren Petrullo, [2]Gregory F. Albery, [3,4]Aura Raulo, [5]Amy R. Sweeny

Affiliations:

1 Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ, USA

2 School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

3 Department of Computing, University of Turku, Turku, Finland

4 Department of Biology, University of Oxford, Oxford, UK

5 Institute of Ecology & Evolution, University of Edinburgh, Edinburgh, UK

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***Corresponding author**: Lauren Petrullo, laurenpetrullo@arizona.edu

Abstract

All organisms must allocate finite resources among growth, maintenance, and reproduction, generating trade-offs that constrain adaptation. Here, we argue that host microbiomes are dynamic resource engines capable of reallocating and generating energy and resources for their hosts. In doing so, they may recalibrate the tradeoffs fundamental to life history evolution.

The ubiquity of tradeoffs

The problem of how to invest a finite amount of energy into competing processes of growth, somatic maintenance, and reproduction is universal in nature. Life history theory predicts that energy allocation toward one process will occur at the expense of others, leading to **tradeoffs** (see Glossary) that can constrain organismal adaptation and evolution. Host microbiomes can play multiple roles in these tradeoffs. First, microbiomes take host resources to regulate and maintain, and also produce resources themselves (e.g., by releasing energy from ingested food or preventing resource loss to parasites). Second, microbiome composition is determined in part through transmission of **mutualistic**, **commensal** and **pathogenic** microbes. Reciprocally, changes in microbiome composition can influence behaviour, altering the intake of resources and other microbes. As such, the microbiome can act as both a mediator and a driver of tradeoffs by compensating for costly changes, or by forcing hosts to preferentially optimise among phenotypic traits. Here, we present “stand-in” pathways by which microbiota can reroute host resources from one process to another, as well as “generative” pathways that create energy for hosts to invest in other processes.

Microbiomes can reallocate host resources through stand-in pathways

Approximately 70% of vertebrate immune function occurs in the gastrointestinal tract, and is a main interface between the host and its complex gut microbiome [1]. Among other functions, gut immunity ensures the gut microbiome is maximally functional and adaptable to dietary and environmental change [2]. This requires a delicate balance between **immune vigilance** and tolerance of beneficial microbes. However, because immunity is energetically and nutritionally costly, host activities or environmental pressures that alter resource allocation to immunity will affect the efficacy of microbial moderation, possibly inhibiting gut microbiome function and stability [3] .

Such tradeoffs are likely common, but have yet to be explored. During periods of nutritional stress, infection, or increased energetic demand (e.g., reproduction or migration), resources may be reallocated from microbiome homeostasis, increasing susceptibility to invasion of pathogenic microbes and **dysbiosis** [4]. Reciprocally, gut

54 microbiota influence immune function by modulating immune cell development,
55 calibrating inflammatory responses, and providing colonisation resistance against
56 pathogens [5]. Alterations to gut microbiome composition are thus likely to have
57 cascading effects on host immunity and pathogen defense.
58
59 Because pathogens are generally a **resource sink**, there exists an optimal investment
60 in immune regulation of the microbiome that minimises subsequent resource loss to
61 parasites via microbiome-associated immune resistance and colonisation prevention.
62 The gut microbiome is therefore a complex intermediary between multiple resource
63 costs that must be minimised. Understanding these tradeoffs is crucial for
64 understanding how organisms manage competing demands of vigilance against
65 pathogens and metabolic economy under environmental change.
66
67 **Microbiomes can expand host resource pools through generative pathways**
68 Gut microbes can directly supplement host metabolism and expand host resource pools
69 by producing energy and nutrients from otherwise inaccessible sources. Through
70 microbial **fermentation** of indigestible plant components, hosts gain access to **short-**
71 **chain fatty acids** (SCFAs) that serve as energy substrates and metabolic signalling
72 molecules. Similarly, microbial detoxification of dietary components allows hosts to
73 exploit otherwise harmful plant secondary compounds, broadening their dietary niche
74 [6]. Gut microbiota are also critically important to host thermal tolerance, regulating
75 energy homeostasis and heat production [7]. These functions can aid host adaptation to
76 novel environments, reduce interspecific competition, and stabilise or optimise host
77 performance.
78
79 Through these generative pathways, microbiomes can both exacerbate and ameliorate
80 host tradeoffs. Compositional homogeneity in the gut during mammalian development
81 may favor fermentative pathways essential for nutrient extraction from milk, promoting
82 growth but compromising immune priming if microbial **alpha diversity** is reduced.
83 Likewise, gut microbes can both produce and metabolise amino acids [8,9], which can
84 bias investment in host reproduction at the expense of somatic maintenance or growth.

Generative functions may also mitigate tradeoffs. Enhanced SCFA production during periods of resource limitation can help hosts maintain energy balance [10]. Some gut microbes, particularly those crucial to development, may provide dual benefits by supporting both growth and immune priming [11], leading to shallower or minimal tradeoffs for their hosts. These pathways could extend the scope of host energy budgets by creating novel pools of usable resources that change the expected magnitude of some host tradeoffs.

Behaviour as a microbiome-associated tradeoff mediator

Behaviour fulfils a unique function in allowing animals to rapidly and flexibly respond to internal and external cues. Exposure to microbes shapes microbial variation through **social transmission,** via agonistic [12] and affiliative social behaviours (e.g., grooming, [13]), and **environmental transmission,** via spatial behaviours (e.g., foraging and environmental exposure, [14], **Figure 1**). Gut microbes acquired from conspecifics can affect host energy homeostasis by transferring metabolic capabilities and supporting development of healthy immune function and resistance to pathogens. Social behavior can also recalibrate microbiomes to meet changing host energy demands [15]. Yet, since social contact spreads both beneficial microbes and potential pathogens, the relationship between sociality and immune resilience remains complex.

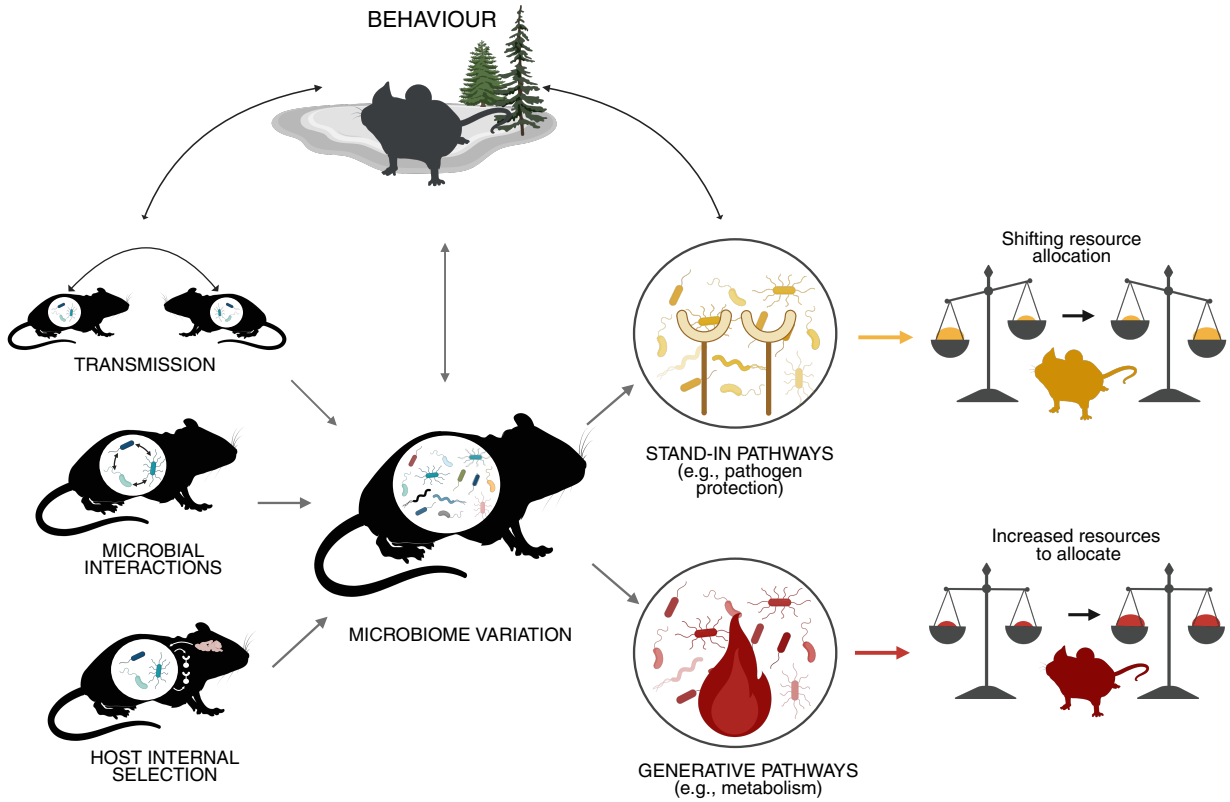


Figure 1. Eco-evolutionary dimensions of microbiome-mediated host life history tradeoffs. Microbial variation arises through three primary processes: within-community local selection (e.g., selective forces imposed by host immune system or diet), within-community local interactions (e.g., competition and mutualism among microbes of the same microbiome), and between-community dispersal (e.g., microbial transmission between hosts). These processes necessarily shape microbial stand-in and generative pathways that can influence host life history tradeoffs. For example, pathogen exposure may induce host internal selection for microbes with immune modulating capacity, diverting microbiome function away from processes like metabolism or dietary detoxification. Such shifts could lead to the competitive exclusion of existing or socially-acquired microbes that occupy similar niches, further modifying microbial capacity for tradeoff optimisation. These complex feedbacks are further modified by host behavior, which governs microbial acquisition from social and environmental sources, and influences–across multiple scales–the processes that shape variation in microbial mediation of host tradeoffs.

Critically, behaviours influence and are influenced by both microbiota and resource availability, which creates the potential for behavior to mediate and impose tradeoffs. A socially isolated individual may experience an impoverished microbiome, which reduces metabolic efficiency and has a fitness cost. However, social isolation may reduce exposure to conspecifics' pathogens, which provides a fitness benefit, particularly if the individual's non-diverse microbiome leads to reduced immune resistance. That same social isolation could shift allocation from reproduction towards maintenance and growth, which puts different pressures on the microbiome and other metabolic resource generation processes.

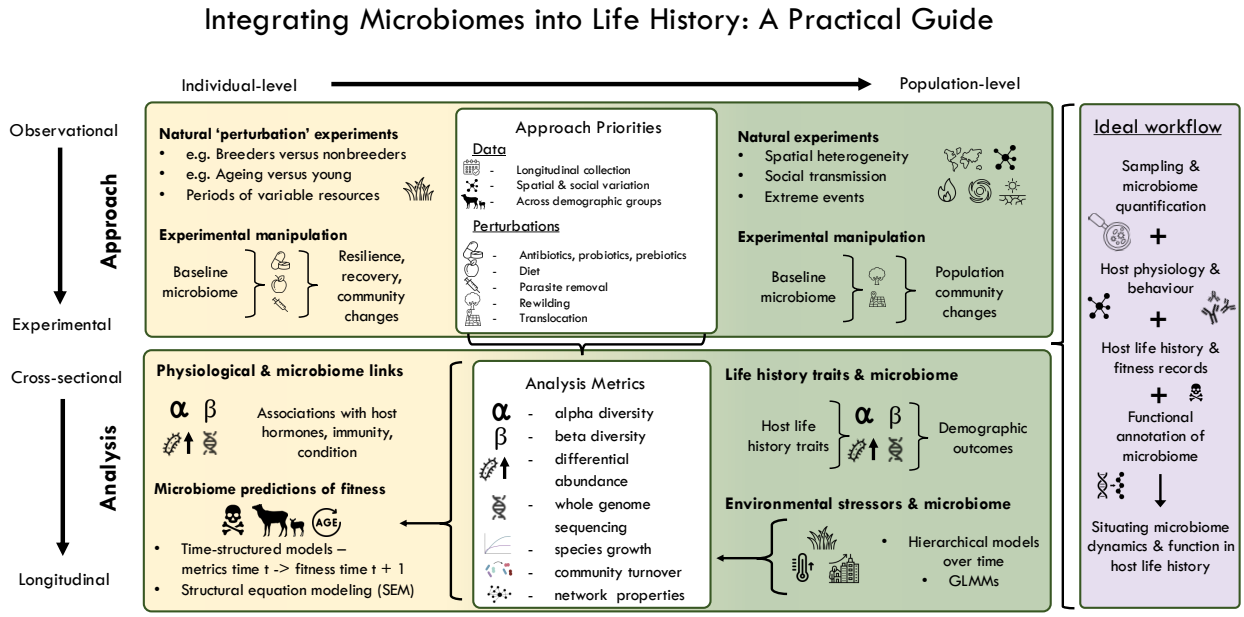
Microbiomes as levers and fulcrums of host life history evolution

The marked individuality of host microbiomes suggests that detectable tradeoffs may be eclipsed by individual differences in microbiome quality. Hosts with optimal or optimally-responsive microbial communities ("microbial silver spoons") may better integrate cues to reallocate resources adaptively. For instance, they may harbor greater microbial alpha diversity, minimising trade-offs when they occur through **functional redundancy.** Microbiomes could also be more flexible, shifting adaptively under host control to match changing demands and conditions. By contrast, microbially-mediated tradeoffs may be amplified under environmental stress in hosts whose gut microbiota have been compromised by developmental hardship or environmental instability (e.g., Caesarean section, food scarcity).

Differences in the capacity for microbial mediation of host tradeoffs could be genetically encoded, driving selection among individuals, or could instead reflect within-individual plasticity. Such differences can generate population-level variation in the costs and benefits of microbially-mediated life histories. Populations experiencing ecological disruption (e.g., drought, epidemics) may suffer steeper tradeoffs if disruption causes microbial scatter, increasing **beta diversity**. Populations with a higher frequency of microbial silver spoons may show dampened tradeoffs and greater demographic stability. Microbiomes may therefore influence not only individual life histories, but also population-level variance in resource allocation strategies. Studies of vertebrate life

histories should thus consider microbiomes as dynamic and transmissible engines of resource optimisation and phenotypic spread that can influence host resource allocation decisions (**Box 1**).

Box 1. Integrating microbiomes into host tradeoffs: a practical guide. As new methodological approaches for characterising host-microbe interactions continue to emerge, so do opportunities to incorporate microbiomes into studies of host life histories and associated tradeoffs. Key recommendations include aligning microbial and demographic data across comparable temporal scales, accounting for both ecological and host-intrinsic sources of variation, and distinguishing causal from correlative pathways (**Box 1 Figure**).



Observational studies could leverage natural fluctuations (e.g., reproductive rhythms, patterns of senescence) or extreme events (e.g., resource pulses, introduction of novel pathogens, natural disasters) to investigate the rate and nature of microbial change associated with behavioral and life history responses. Investigations into the microbial changes that accompany transitions into and out of different reproductive states could consider simultaneous data collection on immune markers, as microbial recalibration toward host reproductive success may lead to immune deficits.

When feasible, observational studies should consider higher resolution genomic approaches (e.g., shotgun, long-read, and/or whole genome sequencing) to improve functional interpretations of host-microbe interactions. Experimental approaches that incorporate controlled quantification of microbial resilience and recovery will have maximal power to capture microbial mediation of host tradeoffs. As an example, quantifying the proportion of host energy expended during and after a controlled disturbance (e.g., following antibiotic exposure or rewilding) to minimise dysbiosis or a microbial state-change can reveal the metabolic cost of microbial resilience and associated mitigation of any tradeoffs. Quantification of host energy expended to return the gut microbiome to a pre-disturbed state following a disturbance (i.e., recovery) can likewise reveal the cost of preserving microbiome community stability and associated disinvestment in other processes. Layered within food/energy supplementation and concomitant collection of biomarkers associated with key life history processes (e.g., immune, reproductive, and/or metabolic markers), such approaches will help isolate the precise microbial pathways that regulate the emergence of host life history tradeoffs.

Over longer timescales, the gut microbiome can act as a lever by recalibrating host investment in life history processes, producing directional effects. It can also act as a fulcrum, balancing resources when environmental stress would otherwise force tradeoffs. We expect these roles to be bounded by the fidelity of host–microbe associations: microbes acquired through social or **vertical transmission** may become trapped within host lineages or social networks, constraining their influence on host strategies over evolutionary time. Ultimately, these dynamics suggest that microbiomes are inevitably embedded within host life histories, emerging as both mediators and modulators of the tradeoffs that shape their evolution.

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Declaration of Interests

The authors declare no competing interests.

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Glossary

- **Alpha diversity** – A measure of within-sample microbial diversity, often quantified as species richness or by indices that incorporate evenness and spread (e.g., Shannon Index).
- **Beta diversity** – A measure of between-sample microbial diversity or dissimilarity that quantifies how different microbial communities are from one another (e.g., Jaccard, Bray-Curtis).
- **Commensal –** A type of symbiotic relationship in which one partner benefits while the other is unaffected.
- **Dysbiosis** – A microbial shift caused by a disturbance that results in a sub-optimal microbiome function and/or composition, sometimes termed an “imbalance”.
- **Environmental transmission** – Acquisition of microbes from the external environment (e.g., soil, plants, dietary items).
- **Fermentation** – The anaerobic breakdown of organic substrates by microbes that yields energy and produces by-products such as short-chain fatty acids, alcohols, or gases.
- **Functional redundancy** – A microbiome containing co-existing microbes that possess similar traits and play similar functional roles within the microbial community.
- **Immune vigilance** – A process by which the immune system continuously monitors the body for the presence of pathogens and abnormal cells/processes.
- **Mutualistic** – A type of symbiotic relationship in which both partners benefit.

- **Pathogenic –** A type of symbiotic relationship in which the microbe benefits at the expense of its host, for example by causing host disease, illness, and/or infection.
- **Resource sink** – Any process or trait that requires a large proportion of an organism's limited energy or resources, thus reducing what remains available for other functions.
- **Short-chain fatty acids (SCFAs)** – Metabolic end-products of microbial fermentation (e.g. acetate, propionate, butyrate) that can serve as energy sources and signaling molecules for hosts.
- **Social transmission** – Acquisition of microbes from conspecifics; can occur directly, for instance through physical contact, or indirectly, for instance through contact with fecal material.
- **Tradeoffs** – Constraints that force organisms to allocate limited resources among competing functions such as growth, reproduction, and survival, such that investment in one reduces investment in another.
- **Vertical transmission** – The direct transfer of microbes from parent to offspring, which typically occurs via birth, nursing, or parental care.