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Forum

Microbial contributions to host life history trade-offs

Lauren Petrullo [1,2,*], Gregory F. Albery[3], Aura Raulo[4,5], and Amy R. Sweeny[6]

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

The ubiquity of trade-offs

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 towards one process will occur at the expense of others, leading to **trade-offs** (see Glossary) that can constrain organismal adaptation and evolution. Host microbiomes can play multiple roles in these trade-offs because **mutualistic**, **commensal**, and **pathogenic** bacteria can themselves provide resources for their hosts (e.g., by releasing energy from ingested food or preventing resource loss to parasites). Compositional microbiome changes can also influence behaviour, altering the intake of resources and other microbes [1]. As such, host microbiomes can compensate for or govern life history trade-offs [2]. They can also be costly to maintain [3], prompting hosts to optimise across microbiome maintenance and other competing phenotypic traits.

Microbiomes can reallocate host resources

Much of vertebrate immune function occurs in the gastrointestinal tract, serving as a key interface between the host and its complex gut microbiome. Among other functions, **mucosal immunity** maintains the capacity of the gut microbiome to respond to dietary and environmental changes [4]. This requires a delicate balance between **immune vigilance** and tolerance of beneficial microbes. However, because immunity is energetically costly, host activities or environmental pressures that alter resource allocation to immunity can affect the efficacy of microbial moderation, possibly inhibiting gut microbiome function and stability.

Such trade-offs are likely common but, as yet, unexplored. During periods of nutritional stress, infection, or increased energetic demand (e.g., reproduction and migration), resources may be reallocated from microbiome homeostasis, increasing susceptibility to the invasion of pathogenic microbes and **dysbiosis** [5]. Reciprocally, gut microbiota influence immune function by modulating immune cell development, calibrating inflammatory responses, and conferring colonisation resistance against pathogens [6]. Alterations to gut microbiome composition are thus likely to have cascading effects on host immunity and pathogen defence.

Because pathogens are generally a **resource sink**, there exists an optimal investment in immune regulation of the microbiome that minimises subsequent resource loss to parasites, either via microbiome-associated immune resistance or by parasite colonisation prevention by the microbes themselves. The gut microbiome is therefore a complex intermediary between multiple costs that must be minimised. Understanding these trade-offs is crucial for understanding how organisms manage the competing demands of vigilance against pathogens and changing intrinsic metabolic requirements.

Microbiomes can expand host resource pools

Gut microbes can directly supplement host metabolism and expand host resource pools by liberating energy and

Glossary

The Anna Karenina principle: the notion that healthy and stable microbiome communities tend to be relatively similar or constrained, while disrupted microbiome communities become dissimilar and more variable.
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 suboptimal microbiome function and/or composition, sometimes termed an 'imbalance'.
Environmental microbial transmission: acquisition of microbes from the external environment (e.g., soil, plants, and dietary items).
Functional redundancy: a microbiome containing coexisting 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.
Mucosal immunity: immune defences at the mucosal surface in the gastrointestinal tract that protect against pathogens while tolerating and even nourishing commensal or beneficial microbes.
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.
Social microbial transmission: acquisition of microbes from conspecifics; can occur directly (e.g., through physical contact) or indirectly (e.g., through contact with faecal material via coprophagy or other behaviours).
Trade-offs: 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 microbial transmission: the direct transfer of microbes from parent to offspring, which typically occurs via birth, nursing, or through parental care.

nutrients from otherwise inaccessible sources. Through microbial fermentation of indigestible plant components, hosts gain access to short-chain fatty acids (SCFAs) that serve as energy substrates and metabolic signalling molecules. Similarly, microbial detoxification of dietary components allows hosts to exploit otherwise harmful plant secondary compounds, broadening their dietary niche [7]. Gut microbiota also underpin host thermal tolerance, regulating energy homoeostasis and heat production [8]. These functions can aid host adaptation to novel environments, reduce interspecific competition, and stabilise or optimise host performance.

Through these pathways, microbiomes may exacerbate host trade-offs. For example, compositional homogeneity in the gut during mammalian development may favour fermentative pathways essential for nutrient extraction from milk, promoting growth but compromising immune priming if microbial alpha diversity is reduced. Likewise, gut microbes can both produce and metabolise amino acids [9], which can bias investment in host reproduction at the expense of somatic maintenance or growth.

Such functions may also ameliorate trade-offs. Enhanced SCFA production during periods of resource limitation can help hosts maintain energy balance [10]. Some gut microbes, particularly those crucial to host development, may provide dual benefits by supporting both growth and immune priming [11], leading to shallower trade-offs. These pathways could extend the scope of host energy budgets by creating novel pools of usable resources that change the economics of host resource allocation decisions.

Behaviour as a microbiome-associated trade-off mediator

If host investment in life history traits functions as a lever system, the gut microbiome may act as a force on the beam by reallocating host resources, producing directional effects that create or shift trade-offs. It can also act as a fulcrum, balancing trade-offs by expanding the pool of host resources to allocate. Behaviour, which fulfils a unique function by allowing animals to rapidly and flexibly respond to internal and external cues, can further modify these effects (Figure 1). Social behaviours (e.g., grooming [12]) can shape microbiome variation by facilitating **social microbial transmission**, while spatial behaviours (e.g., foraging and environmental exposure) can shape microbiome variation by promoting **environmental microbial transmission** [13]. Gut microbes acquired from conspecifics can affect host energy homoeostasis by transferring metabolic capabilities and supporting immune development and resistance to pathogens. Social behaviour can also recalibrate microbiomes to meet changing host energy demands [14]. Because social contact spreads both beneficial microbes and potential pathogens, the relationship between sociality and immune resilience remains complex.

Critically, behaviours influence and are influenced by microbiota and resources, which creates the potential for behaviour to mediate and impose trade-offs. For example, a socially isolated individual may experience an impoverished or homogeneous microbiome, which reduces metabolic efficiency. However, social isolation may also reduce exposure to pathogens transmitted by conspecifics, providing a potential fitness benefit. This benefit may be particularly important if the microbial homogeneity associated with social isolation reduces immune resistance. That same social isolation could shift allocation from reproduction towards maintenance

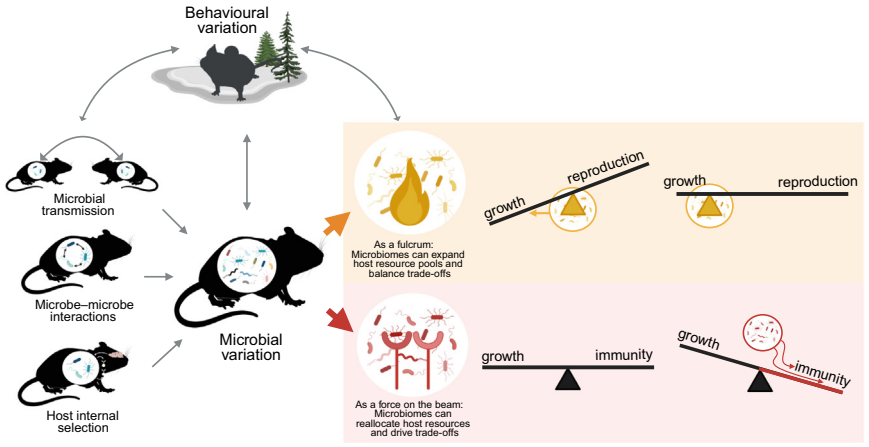

Figure 1. Eco-evolutionary dimensions of microbiome-mediated host life history trade-offs. Microbial variation arises through three primary processes: within-community host internal selection (e.g., selective forces imposed by the host immune system or diet), within-community microbe–microbe interactions (e.g., competition and mutualism among microbes of the same microbiome), and between-community dispersal through transmission (e.g., microbial transmission between hosts). These processes necessarily shape the microbial functions that can influence host life history trade-offs. As a fulcrum, microbiomes may mitigate host costs of reproduction when growth is prioritised by liberating energy through fermentation or detoxification to balance reproductive demands. As a force on the beam, host internal selection for microbes with immune-modulating capacity following pathogen exposure may divert microbial function away from processes such as somatic growth. Such shifts could lead to the competitive exclusion of existing or socially acquired microbes that occupy similar niches, modifying microbial capacity for trade-off optimisation. These complex feedbacks are further modified by host behaviour, which governs microbial acquisition from social and environmental sources, and influences—the processes that shape variation in microbial mediation of host trade-offs. Figure created with BioRender (https://BioRender.com).

and growth, placing different pressures on the microbiome and the generation of other metabolic resources.

Microbiome studies can make progress towards situating these dynamics into host life histories with thoughtful sampling regimes, natural or experimental perturbations, and targeted statistical metrics (Box 1). These approaches offer an imminently feasible advance towards understanding the role of microbial communities in host life history and can better inform ecological and evolutionary dynamics in nature.

Microbiomes as components of host life history evolution

The marked individuality of host microbiomes suggests that detectable trade-offs among host life history traits may be eclipsed by individual differences in microbiome quality. Hosts with optimally responsive microbial communities ('microbial silver spoons') may better integrate cues to reallocate resources adaptively, and these benefits could be passed across generations through **vertical microbial transmission**. For instance, they may harbour greater microbial alpha diversity and thus be able to minimise trade-offs through **functional redundancy.** Microbiomes could also be more flexible, shifting adaptively under host control to match changing internal or external demands and conditions. By contrast, microbially mediated trade-offs may be amplified under environmental stress in hosts whose microbiomes have been compromised by developmental hardship or environmental instability. Such differences in the capacity for microbial mediation of host trade-offs could reflect within-individual plasticity in, for instance, immune responses to the microbiota; or it could instead be genetically encoded, driving selection among individuals.

At higher levels, these processes may generate population-level variation in the costs and benefits of microbially mediated life histories. Populations experiencing ecological disruption (e.g., drought and epidemics) may suffer steeper trade-offs if these disruptions increase microbial beta diversity (i.e., **the Anna Karenina principle** [15]). Trade-offs could alternatively be minimised if increased microbial variation increases the likelihood of microbiome–environment matches across the population, similar to bet-hedging. Populations with a higher frequency of microbial silver spoons may show dampened trade-offs and greater demographic stability. Microbiomes may therefore influence not only individual life histories but also population variance in resource allocation strategies.

Box 1. Integrating microbiomes into host trade-offs: 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 trade-offs (Figure I). 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. Relationships between the microbiome and life history can be elucidated in both observational (via longitudinal, repeated sampling across relevant host groups, and social/spatial scales) and experimental (via perturbation experiments) contexts. In either case, careful selection of statistical approaches can help characterise relevant microbial dynamics and their relationships to simultaneous life history dynamics. For instance, indicators of a dysregulated microbiome (e.g., decreased alpha diversity and high rate of community turnover) may indicate a period of stress and constrained resource availability within the host that impacts regulation of the microbiota. 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 trade-offs. Exploration of these approaches and workflows over time will help isolate the precise microbial pathways that regulate and metrics that signify the emergence of host life history trade-offs.

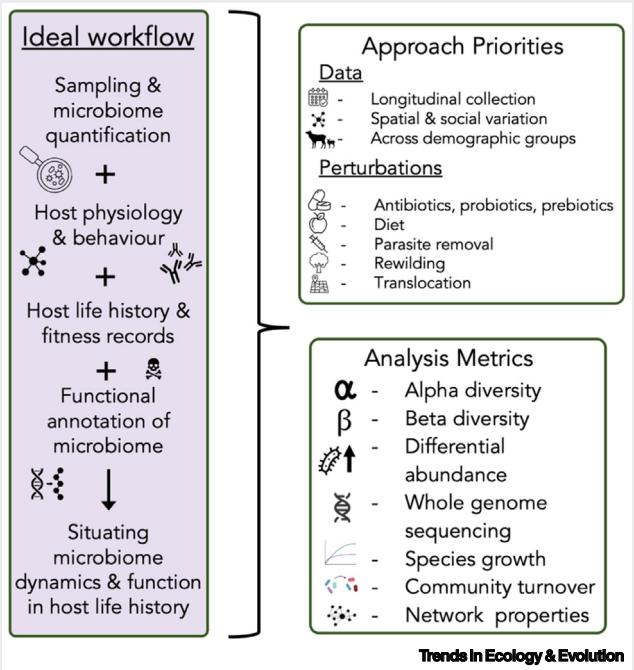

Figure I. Opportunities to integrate microbiomes into life history. Figure created using PowerPoint and Flaticon.

Over longer timescales, we expect these effects to be bounded by the fidelity of host–microbe associations. Microbes acquired through vertical or social transmission may become trapped within host lineages or social networks, limiting how flexibly they can shape patterns of host growth, reproduction, and somatic maintenance over evolutionary time. Nevertheless, these dynamics suggest that microbiomes are embedded within host life histories, emerging as mediators of the trade-offs that shape their evolution.

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Declaration of interests

The authors declare no competing interests.

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA
[2]Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA
[3]School of Natural Sciences, Trinity College Dublin, Dublin, Ireland
[4]Department of Computing, University of Turku, Turku, Finland
[5]Department of Biology, University of Oxford, Oxford, UK
[6]Institute of Ecology and Evolution, University of Edinburgh, Edinburgh, UK

*Correspondence:
petrullo@unc.edu (L. Petrullo).

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