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Special feature paper: Application of ecological and evolutionary theory to microbiome community dynamics across systems.

Application of ecological and evolutionary theory to microbiome community dynamics across systems

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A fundamental aim of microbiome research is to understand the factors that influence the assembly and stability of host-associated microbiomes, and their impact on host phenotype, ecology and evolution. However, ecological and evolutionary theories applied to predict microbiome community dynamics are largely based on macroorganisms and lack microbiome-centric hypotheses that account for unique features of the microbiome. This special feature sets out to drive advancements in the application of eco-evolutionary theory to microbiome community dynamics through the development of microbiome-specific theoretical and conceptual frameworks across plant, human and non-human animal systems. The feature comprises 11 research and review articles that address: (i) the effects of the microbiome on host phenotype, ecology and evolution; (ii) the application and development of ecological and evolutionary theories to investigate microbiome assembly, diversity and stability across broad taxonomic scales; and (iii) general principles that underlie microbiome diversity and dynamics. This cross-disciplinary synthesis of theoretical, conceptual, methodological and analytical approaches to characterizing host-microbiome ecology and evolution across systems addresses key research gaps in the field of microbiome research and highlights future research priorities.

1. Introduction

Host-associated microbiomes play fundamental roles in host phenotype, ecology and evolution. Understanding the factors that influence microbiome assembly, diversity and stability in plant and animal hosts is therefore a major avenue of microbiome research. However, the application of ecological and evolutionary theory to microbiome community dynamics is complicated by features of the microbiome, including horizontal gene transfer, rapid evolution and the production of public goods and antimicrobial compounds [1].

Microbiome research, made possible by recent advances in technological and analytical tools to characterize the diverse assemblages of host-associated microbiota, has transformed our understanding of the role of host-associated microbiota in health and disease, and, ultimately, their ecology and evolutionary trajectory [2–5]. Given the significant influence of the microbiome on host health and disease susceptibility, these microbial communities offer promising targets for the diagnosis, prevention and treatment of disease in agricultural, veterinary and medical practice. Engineering host microbiomes is a tantalizing challenge, with potential for disease suppression and treatment in plant and animal hosts. However, given the complexity and dynamic nature of these systems, success in predicting, managing and ultimately engineering the microbiome will need to incorporate both ecological and evolutionary principles [2].

Further advances in this field require researchers to develop and compare different model systems to deconstruct the microbiome and to develop new theories and models to encompass the complexity and dynamics of the microbiome (e.g. rapid evolution, public goods, horizontal gene transfer). Comparison across diverse systems enables collective progress in such endeavours and overcomes organism-specific challenges, such as (i) challenges in isolating and cultivating microbiota [6], (ii) an ability to manipulate microbiomes and test infectivity in model systems that are not possible in human microbiome studies due to ethical considerations and (iii) the relative focus of funding/analytical effort on human microbiomes, providing highly informative high-resolution longitudinal and cohort studies. Consequently, comparisons across different model biomes and scales are necessary in order to better understand the ecology of host-associated microbiomes. To this end, we sought to organize a special issue that highlights: (i) the effects of the microbiome on phenotype, ecology and evolution; (ii) the application and development of ecological and evolutionary theories to investigate microbiome assembly, diversity and stability in plant and animal hosts across broad taxonomic scales; (iii) the general principles that underlie microbiome diversity and dynamics, using dynamical systems thinking; and (iv) presents a cross-disciplinary synthesis of theoretical, conceptual, methodological and analytical approaches to characterizing host–microbiome ecology and evolution.

This special feature in *Proceedings of the Royal Society B* contains 11 articles (six research articles and five review articles) that address the ecology and evolution of plant, human and non-human animal microbiomes, to provide a cross-disciplinary synthesis of theoretical, conceptual, methodological and analytical approaches to characterizing host microbiomes and their influence on host health, ecology and evolution.

2. Effects of the microbiome on phenotype, ecology and evolution

The main driver of microbiome research is the growing evidence that host-associated microbiomes can and do shape phenotypic, ecological and evolutionary adaptation in the host. Among the functions of the microbiome is the effect that microbial communities can have on pathogen colonization and disease. Ossowicki *et al.* [7] exemplify this idea in their exploration of disease suppression in wheat (*Triticum aestivum*) by soil-associated microbiota. They find that suppression of the pathogen *Fusarium culmorum* is only conferred by 14% of soils, but that this protection cannot simply be ascribed to presence/absence of particular microbiota or function. Ascribing functions, such as disease suppression, to particular microbiomes requires the ability to manipulate the interaction and can be relatively easily done for soils. However, manipulating host–microbiota interactions in animal hosts is arguably a more challenging endeavour. Greyson-Gaito *et al.* [8] explore the power of microbiota transplants for testing the impact of gut microbiota on host health and phenotype, cautioning about the importance of considering the ecological realism of the transplant when interpreting the results.

Leftwich *et al.* [9] explore the evolutionary potential of mixed modes of microbiota transmission in animal hosts, simulating the impact of vertical transmission, environmental acquisition and mixed modes of transmission and their evolutionary significance to host gut–microbiome relationships. The impact of transmission mode on microbiome composition and function has obvious relevance to host evolution and phenotype, with implications for reproductive isolation and speciation. Links between the microbiome and host phenotype influence how hosts might respond to environmental change and stress, especially in terms of how quickly the host can alter its physiology. Stothart *et al.* [10] tested this idea by comparing the gut microbiomes of eastern grey squirrels in urban versus forest environments. They find that, although environment itself is important, variation in the microbiome is more strongly explained by measures of the hypothalamic–pituitary–adrenal hormonal system, which is indicative of recent stress in the host.

Given the short generation time of microbial species relative to their hosts, there is a clear reason to expect evolutionary processes to be occurring within the microbiome over the course of a single host lifetime. Scanlan [11] explores this idea by focusing on the mouse and human studies, arguing that these processes are not only common but also critical to understanding and predicting host–microbiome interactions. Over longer time scales, exploring phylogenetic patterns of associations between hosts and their microbiota has proven an exciting way to infer their evolutionary relationships. Recent interest in ‘phylosymbiosis’, as elegantly introduced by Lim & Bordenstein [12], has led to numerous comparisons of host-associated microbiomes across host phylogenies [13]. When detected, these patterns have been used to suggest both a level of specificity in host–microbiome interactions and the potential role for microbiomes in shaping speciation and vice versa. In this issue Trevelline *et al.* [14] explore the potential for phylosymbiosis across 15 species of cranes, all of which had been kept in the same environment and under the same diet. They observed a pattern of phylosymbiosis, but only after incorporating absolute microbial densities and removing male birds, suggesting interesting differences between birds and mammals (where patterns of phylosymbiosis seem more robust).

3. Developing theoretical and conceptual frameworks for microbiome community dynamics

Ecological and evolutionary theories developed for macroecology are increasingly applied to explain phenomena connected with host-associated microbiomes, but are ultimately constrained by the unique features of the microbiome, the complexity of host–microbiota–environment interactions across space and time, and a lack of microbiome-specific hypotheses and predictions. In recent decades, methodological and analytical advances have led to an explosion in the generation of empirical data, but the development of microbiome-focussed hypotheses, predictions and conceptual frameworks lags behind the generation of these data [1,15]. However, genotypic and phenotypic properties of microorganisms are tractable to laboratory manipulation, and consequently, combinations of

computational modelling and empirical studies offer opportunities to test new hypotheses on the eco-evolutionary properties of the microbiome. Several of the articles within this special feature develop and apply theoretical and conceptual frameworks that test hypotheses regarding the eco-evolutionary drivers of host–microbiome interactions.

Angell & Rudi [16] describe a combinatorial game theory model that assessed the impact of nutrient utilization strategies of microbiota on the composition of the infant gut microbiome. Their computational model predicted initial mother–child transmission of specialists, followed by a shift to generalist microbiota after three months of age in the immature expanding gut microbiome. The model predicted that generalists are replaced by specialists after 12 months, during maturation of the human gut microbiota. While the model simulations represent a simplified model of the system *in vivo*, it generates important predictions of microbiome assembly and dynamics in the infant gut microbiome that can subsequently be tested empirically to explain known patterns of alpha and beta diversity with age.

Biotic interactions are fundamental to microbiome stability, and Herren [17] further develops the idea of cross-feeding and competition between microbiota by generating metabolite-explicit models to assess the impact of microbial invasion on cross-feeding and competition. The model predicted that microbiomes with stronger cross-feeding and competition exhibited lower invasion risk, but when the invasion was successful, diversity and productivity decreased and cross-feeding was disrupted. Scanlan [11] reviews the role of rapid microbial evolution in the human gut, addressing key knowledge gaps surrounding the mode, tempo and functional impacts of drift and selection, and their impact on microbial evolution in the gut microbiome. This analysis is framed in the context of ‘ecological opportunity’, where environmental change can alter niche availability, to ultimately affect persistence or displacement of members of the gut microbiota. Leftwich *et al.* [9] address a lack of theoretical models to explore the transmission mode of symbiotic microbiota in animal hosts using deterministic discrete generation mathematical models to simulate population-level associations between host animals and symbionts. In particular, the model assessed vertical transmission, environmental acquisition and mixed modes of transmission, in establishing a conceptual framework which suggests that mixed modes of microbial transmission lead to the highest frequencies of host–microbe associations and ultimately transmission mode is important in establishing host–microbiome stability. These theoretical models lay the foundation for future empirical studies to test and verify these theories.

Disease suppressiveness in soils confers resistance against root pathogens of plants and is typically mediated by poorly characterized chemical interactions between bacterial microbiota. Consequently, invasion success and ecological opportunity are important determinants of health and disease in plant pathosystems. Ossowicki *et al.* [7] describe an extensive study of field soils for suppression of the fungal pathogen *Fusarium culmorum*, using wheat as a model system. Gamma irradiation of soils and a lack of correlation of physico-chemical parameters with suppression confirmed that disease suppressive phenotypes have a microbiological basis, but there was a lack of correlation of taxonomic diversity across suppressive soils. As microbiota diversity and composition could not explain disease suppressive

phenotypes, the authors propose that several independent mechanisms may impart disease suppressive phenotypes on different soils, including microbial volatile production in some and co-occurrence of specific taxa (e.g. *Acidobacteria*) in others.

Microbiomes play fundamental roles in health and disease. In the context of plant health, Doonan *et al.* [18] investigated the role of host–microbiota–insect interactions in the acute oak decline (AOD) pathosystem. AOD is a complex decline disease where the cumulative effects of several abiotic (environmental) and biotic (bacterial pathogens and bark boring beetles) factors result in stem tissue necrosis and disruption of nutrient and water flow, often leading to rapid decline and death of the tree. Virulence has been described as an emergent property [19]. Emergent properties cannot be explained by their individual components, and the outcome of these interactions is greater than the sum of its individual parts and not irreducible to their individual components [19]. Using emergent virulence as a conceptual framework to assess the interactions between the host, microbiota and insects in AOD, Doonan *et al.* [18] combined reductionist (RNAseq analysis of single and dual cultures of bacterial species) and emergentist approaches (log infection tests inoculated with insect larvae and bacterial cultures) to demonstrate the emergent properties of microbe–microbe and host–microbiota–insect interactions. These experiments revealed cooperation between key bacteria associated with tissue necrosis in affected trees, and in the presence of beetle larvae, gene expression of bacterial virulence genes and symptom severity (tissue necrosis) were amplified, demonstrating the emergent properties of microbiota–host–insect interactions in AOD symptomology.

Lim & Bordenstein [12] review the concept of phylosymbiosis, ‘microbial community relationships that recapitulate the phylogeny of their host’ [20]. Such relationships between microbiota composition and related host species are detectable in many plant and animal hosts, and are regulated by mechanisms that are ripe for future investigations, and reliant upon appropriate conceptual, empirical and analytical approaches that are reviewed here [12]. Trevelline *et al.* [14] present an empirical study of the gut microbiota of 15 captive crane species, detecting weak signatures of phylosymbiosis. Interestingly, incorporation of absolute microbial cell density data obtained by flow cytometry with 16S rRNA gene profiles of microbiota composition improved the strength of the signal of phylosymbiosis. The concept of phylosymbiosis, combined with the methodological roadmaps presented in this special feature, provides a hypothesis-driven framework for future studies of microbiota composition across host systems, and to understand eco-evolutionary processes that shape host–microbiota interactions. Knowledge of the composition of the microbiota in relation to host phylogeny and the eco-evolutionary processes that shape these interactions are important considerations in microbiome transplant experiments, and in the production of precision microbiome treatments that are at the forefront of the field of microbiome research.

To guide future developments in microbiota transplant research, Greyson-Gaito *et al.* [8] propose the concept of ecological reality (or ‘EcoReality’). They review studies that report microbiota transplants in non-human animals and identify experimental factors that impact the ecological reality of the experiment. The authors use this to generate a

conceptual framework to guide improvements in the EcoReality of future empirical research studies where microbiota are transplanted. Such approaches are critical to enhance our prospects of leveraging host microbiomes, for example, in the sustainable development of teleost aquaculture where microbiome manipulation has the potential to influence host diet, immunity, welfare and selection to support this burgeoning industry of fisheries and aquaculture [21].

Collectively, these studies advance micro-ecological theory through consideration of the role of game theory, ecological opportunity, microbial invasion, rapid evolution, cross-feeding, diseases suppression, emergent virulence and phylosymbiosis in microbiome assembly, stability and dynamics. Moving forward, these theoretical and conceptual frameworks will facilitate the generation of specific hypotheses that allow us to predict and test microbiome composition and function, with potential to inform the manipulation and transplantation of microbiota for precision treatment, guided by knowledge of the factors that drive microbiome assembly and enhanced ecological reality in empirical studies.

4. Methodological and analytical approaches for characterizing host microbiomes

The development and testing of ecological and evolutionary theories that incorporate the microbiome is important to enhance knowledge and understanding of host–microbiota interactions and their effects on eco-evolutionary processes [1], and to move beyond descriptive accounts of microbiome composition [22]. Such advances require the development of theoretical and conceptual frameworks such as those discussed in §3 to drive hypothesis generation and predictions that can be tested through the careful design of empirical studies. The field of microbiome research therefore transcends disciplines, as exemplified by the diversity of methodological and analytical approaches described in the contributions to the special feature, including mathematical modelling [9,16–18], DNA and RNA sequencing [7,10,14,18], flow cytometry [14], infection tests in model and non-model pathosystems [7,18], physico-chemical and volatile analysis [7], and measures of hormone activity to assess host physiological responses to its environment [10].

A major theme pervading this special feature is the link between mathematical model simulations and empirical studies [9,11,16,17]. Angell & Rudi [16] compared probabilistic model simulations with empirical observations to test whether a game theory model of generalist or specialist nutrient utilization strategies could explain the assembly and dynamics of the infant gut microbiome. In this study, development of a generalist-specialist model that extends the host selection model to incorporate combinatorial game theory with nutrient utilization best described the observed patterns of microbial diversity and function in the empirical data. Leftwich *et al.* [9] developed deterministic discrete generation mathematical models to assess the potential role of mixed modes of microbiota transmission on the evolutionary potential in animal systems. Such modelling approaches are valuable, as they facilitate the development of theoretical frameworks on which future empirical studies can be designed to test and validate model predictions.

Lim & Bordenstein [12] reviewed recent data on signals of phylosymbiosis in microbiomes and present an analytical

framework for the quantitative analysis of phylosymbiosis across host taxa. They suggest that the adoption and expansion of this workflow could lead to improved identification of patterns of phylosymbiosis and enhance opportunities to understand the role of ecological and evolutionary processes in host–microbiome associations. Microbiome transplant studies represent an important and increasingly applied approach to characterize host–microbiota interactions. While stating that although there is a clear need for highly controlled microbiome transplant experiments, Greyson-Gaito *et al.* [8] reviewed the breadth of ecological reality in microbiome transplant studies and identified nine experimental conditions that affect EcoReality. Their analysis suggests that the ‘EcoReality’ of microbiota transplant studies has increased over time, and they present a roadmap for enhancing EcoReality in future transplantation experiments. Following this theme, Doonan *et al.* [18] describe the emergent properties of host–microbiota–insect interactions that drive AOD, a complex decline disease of oak trees. They combined *in vitro* transcriptome experiments comprising single and poly-species bacterial cultures growing on oak tissue, with more complex infection tests combining bacterial inoculations with the addition of beetle larvae in a novel oak log infection model, to demonstrate the cumulative impact of these interactions on the pathology of AOD. Ossowicki *et al.* [7] used soil transplantation experiments to demonstrate the microbiological basis of disease suppression in wheat (*Triticum aestivum*) to the soil pathogen *Fusarium culmorum*, providing fascinating insights into the mechanistic diversity of disease suppression in soils.

5. Factors that shape microbiome assembly, diversity and stability in hosts across broad taxonomic scales

In testing hypotheses derived from theoretical and conceptual frameworks discussed above, this special feature explores several different factors that shape the assembly and stability of host-associated microbiomes, integrating knowledge from across systems that include plants, humans, insects, birds, rodents and teleost fish. The human gut microbiome has arguably received greater research focus than other host systems, but comparing microbiome assembly and dynamics across broad systems provides fertile ground for hypothesis design and empirical testing. Combinations of reductionist approaches and more complex experiments *in vivo* for model systems where they are more amenable, for example, where ethical considerations are less restrictive compared to human microbiome studies (e.g. infection tests and microbiota transplants in plants), provide excellent opportunities to explore such hypotheses [18].

Angell & Rudi [16] investigated factors that shape the assembly, dynamics and diversity of the infant gut microbiota within the first 12 months of age. Combining game theory simulations that encompassed generalists and specialists, their models matched empirical data and predicted increased alpha and reduced beta diversity with age, highlighting the initial competitive advantage of generalists with a transition to more specialized bacteria during maturation. Metabolic

cross-feeding is ubiquitous across microbial communities, with implications for community assembly and stability in terms of biotic interactions and invasion. Herren [17] developed a metabolite-explicit model which predicted that stronger cross-feeding between microbiota reduced invasion risk, but when the invasion was successful (under intermediate levels of cross-feeding), cross-feeding, productivity and diversity was reduced, which increased the risk of secondary invasion. Microbiota may be vertically transmitted with their hosts, acquired environmentally, or through mixed modes of transmission (vertical and horizontal), and can lead to stable co-associations. Leftwich *et al.* [9] developed deterministic mathematical models to simulate conditions which promoted stable co-associations between hosts and their microbiota. They observed that transmission mode was an important criterion for host–microbiota stability, with mixed modes of transmission resulting in greatest host–microbiota associations.

Rapid evolution of microorganisms across time and space, and their functional consequences, is an important yet poorly studied phenomenon in the context of host-associated microbiomes. Scanlan [11] discusses the impact of rapid evolution and ecological opportunity on bacterial adaptation, colonization and persistence in the gut microbiome, and suggests combined experimental evolution and genomic approaches to identify drivers of evolution in the microbiome. Niche availability and niche discordance are key factors that govern the capacity for a lineage with a certain phenotype to persist in an environment. Two relevant empirical studies in this special feature also address the functional interactions between plant hosts, microbiota and the environment in the context of plant disease [7,18].

Host phylogeny and physiology may also shape the composition of host microbiomes. Phylosymbiosis describes higher microbiome diversity between species than within host species and is observed by comparing host phylogenies and microbiome dendrograms and observing relationships between microbiome beta diversity and host genetic relationships (discussed by Lim & Bordenstein [12]). Treveline and colleagues detected weak phylosymbiotic signals in 15 species of cranes when male individuals were removed from the analysis and microbial cell density counts were included, leading to a suggestion that transmission route and host filtering impact the strength of phylosymbiotic signals. Changes in a host's environment may also influence its microbiome; however, a key question in microbiome research is whether microbiome restructuring is driven predominantly by the external environment changes, or the host's physiological response to this change. Stothart *et al.* [10] test this hypothesis in by analysing the impact of urbanization on grey squirrel populations, suggesting that impacts of environmental change on the microbiome occur indirectly through altered effects on host physiology. Perry *et al.* [21] provide an insightful discussion of the deterministic forces that drive microbiome dynamics and function in sustainable teleost aquaculture and highlight research gaps and future opportunities for microbiome manipulation.

6. Conclusion and future research priorities

This special feature addresses key research gaps in microbiome research by developing theoretical and conceptual

frameworks to describe factors that influence microbiome assembly and stability, including a generalist-specialist game theory model of infant gut microbiome maturation [16], a metabolite-explicit model of microbial cross-feeding and invasion [17] and theoretical models on the role of mixed modes of transmission on stable host–microbiota associations [9]. Additional advances include conceptual and methodological frameworks for detection of host phylogeny and microbiome relationships [12,14], rapid microbial evolution and ecological opportunity in gut microbiomes [11], and approaches to enhance the ecological reality of microbiome transplant studies [8]. The deterministic assembly of teleost fish microbiomes and possibilities for microbiome manipulation for sustainable aquaculture are also discussed [21]. Empirical studies applied the theory of emergent virulence to demonstrate the emergent properties of complex host–microbiota interactions in the context of plant disease [18], the impact of host physiology on the microbiome [10] and the role of soil microbiota in disease suppressive phenotypes of plants and soil transplantation to confer pathogen resistance [7].

Moving forward, it is important the field of microbiome research continues to develop ecological and evolutionary theories that incorporate the microbiome and its unique features, and that they are subsequently tested empirically using complementary, transdisciplinary approaches. A key theme emanating from this feature is the power of combining complementary approaches from different disciplines to address such questions. In addition to providing new theoretical and conceptual models to assess the ecology and evolution of host-associated microbiomes, the articles presented in this special feature also highlight ongoing research gaps and future research priorities for the field, including: (i) the validity of highly controlled microbiome transplant experiments, but guidelines for broadening Eco-Reality in future experiments [8], as appropriate, (ii) greater consideration of host physiology and its impacts on microbiome assembly and dynamics [10], (iii) the need for applied experimental evolution studies to characterize rapid evolution within microbiomes [11], and (iv) integrated theoretical, conceptual and empirical approaches are required to address complex host–microbiome–environment interactions. This may include combinations of experimental evolution and genomics approaches to study rapid evolution and functional consequences [11], host physiology [10], applying conceptual frameworks for statistical analysis of quantitative signals of phylosymbiosis across taxa [12,14], microbiota transplants [7,8], or the combination of reductionist and emergentist approaches to disentangle complex host–microbiota–insect interactions associated with disease [18].

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