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Review

Why Does the Gut Have So Many Species? The Paradox of the Plankton in Human Microbial Ecology

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Abstract: The human gut nurtures an exceptionally diverse microbial community, with over a thousand species coexisting despite apparent competition for limited resources. This phenomenon challenges the classical principle of competitive exclusion, drawing parallels with Hutchinson's 'Paradox of the Plankton'. Through an ecological lens, this paper examines mechanisms that sustain such high species richness, categorising them into niche-based and neutral processes. Niche differentiation, environmental heterogeneity, evolutionary trade-offs, and microbial interactions create conditions for stable coexistence, while stochastic forces such as ecological drift, migration, and speciation also shape community structure. Furthermore, higher-level selection, influenced by host-microbiome interactions, may play a role in maintaining diversity. A deeper understanding of these processes is crucial, not only for theoretical ecology but also for advancing microbiome-based therapeutic interventions.

Keywords: species diversity; niche theory; microbial ecology; ecological drift; host-microbe interactions; neutral theory

1. Introduction

The average, healthy human gut is home to more than one thousand species of bacteria and archaea [1,2]. This mega-diverse microbial assemblage has been shown to contribute to human health in numerous ways: fermentation in the large intestine produces a suite of short-chain fatty acids which contribute to energy acquisition and regulation of the gut epithelium [3]; both the adaptive and innate immune systems may be initially trained, and subsequently calibrated, by interactions with commensal bacteria in the gut [2]; and a healthy microbiome also appears to protect the host from certain infections, notably *Clostridium difficile* [4]. A number of studies have correlated the level of species diversity in the gut with disease states, including obesity [5,6], inflammatory bowel diseases [7,8], and recurrent *C. difficile* infections [9].

Based on intuition, theoretical treatment[10–12], and empirical observation [13,14], the coexistence of two species which occupy exactly the same niche should be untenable in the long term. This is perhaps the only rule in ecology to be elevated to the status of a natural law. Gause's Law, named for the Russian biologist who contributed heavily to its experimental description, is also called the principle of competitive exclusion, since it is based on the reciprocally negative interactions between two species which depend on the same limiting resource. It has been further refined to the statement: n species cannot coexist on fewer than n resources, niches, or limiting factors[15]. The growth of one population necessarily leads to the decline of the other, ultimately leading to its extinction, and at equilibrium, only the better competitor is able to persist. Examples of strong, negative correlations, or even co-exclusionary relationships, between some species [16] in the human microbiome suggest that competitive exclusion is a relevant process.

While exceptions to this principle are frequently suggested[17,18], and many cases of stable coexistence have been robustly described, none have served to overthrow Gause's Law [19]. Instead, discovery of general mechanisms of coexistence, the most important of which are described below, have served to refine the definition of 'niche', and improved the theoretical understanding of competition. Thanks to this policy of modifying definitions and theory rather than lowering its status, Gause's Law has been widely described, as a tautology [20,21]. This may be the case, although it has nonetheless served as a rallying point for ecological discovery [15]. How, given a finite number of limiting resources

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and an apparently homogeneous environment, can more than 1000 species of bacteria co-occur in the human gut?

The perceived contradiction between this central tenant of community ecology and the observation of high diversity in nature led G. Evelyn Hutchinson to write 'The Paradox of the Plankton' [20]. In that classic paper, Hutchinson asked why, given the apparently homogeneous environment and small number of limiting resources, freshwater phytoplankton communities are so incredibly diverse.

Given the parallels between Hutchinson's question and our own, it does not seem so far fetched that community ecology literature would have answers relevant to human microbiology. Along with Hutchinson's earlier treatise, 'Homage to Santa Rosalia' [22], which has a similar theme, 'The Paradox' has inspired much of the last half century of community ecology. Numerous mechanisms allowing for stable coexistence have been hypothesized and tested, expanding our understanding of niche processes. What's more, challenges to a number of assumptions implicit in our surprised reaction to this high species richness have yielded alternative models of community assembly which may improve our holistic understanding. Here, I'll review this literature in order to identify processes which may contribute to the high diversity of the human gut microbiome.

2. Explanations for Diversity

Through a combination of theoretical and empirical study, a number of processes which oppose competitive exclusion have been identified, and may contribute to the maintenance of species richness in nature. These, and perhaps some not yet described, must ultimately explain the extreme diversity of the human gut. By understanding the underlying mechanisms, more detailed explanations for the relationships between microbiome diversity and human health may be elucidated.

Mechanisms which serve to maintain species richness can be conceptually partitioned into two categories [23]. 'Niche processes' increase the strength of intraspecific competition relative to interspecific. Resource specialization, predator mediated coexistence, and temporal niches represent just a few; these and others will be described below. 'Neutral processes', encompass everything that is not dependent on the fundamental differences between species. Ecological drift, speciation, and migration are the major neutral processes and their role in gut diversity will also be explored.

2.1. Niche Processes

Competitive exclusion is dependent on the mutual, negative interaction between two species competing for the same limiting resources. While these resources are frequently trophic, they need not be: physical space [24,25], inhibitory or toxic byproducts—especially in microbes [26] and other density dependent constraints on growth can also be limiting resources. Intriguingly, one or more aspects of host immune response may play the role of a resource in the microbial community. For instance, cross-reactivity of the immune system to two members of the microbiome may lead to mutually negative effects of each species on the other, analogous to a limiting trophic resource [2].

Simple, non-mechanistic models of multi-species growth, such as Competitive Lotka-Volterra [10,11], incorporate these limitations as a single term for each species, the carrying capacity of the environment, while a separate interaction terms define the effect of the other species on that carrying capacity. The carrying capacity terms are therefore a description of the strength of self-regulation for each species—i.e. intraspecific competition—and the ratios of the interaction terms to carrying capacities can be interpreted as the strength of interspecific competition.

2.1.1. Ecological Niches

When species consume the same limiting resource interspecific interactions are relatively strong, whereas without overlap in consumed resources, interactions may be non-existent Along with our intuition, analysis of this model shows that two species can stably coexist when intraspecific effects are stronger than interspecific for both[27]. Resource niches, which decrease the magnitude of interaction terms, therefore promote coexistence.

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As an intriguing side-effect of this model, when interspecific effects are stronger than intraspecific for both species, a potential result of allelopathic interactions and interference competition, the outcome is dependent on the starting state of the system[28]; whichever species is initially dominant outcompetes the other. In the gut microbiome, similar 'priority effects' could explain the temporally stable differences between individuals[29,30], or the high recurrence rate of antibiotic associated diarrhea[31]. Additional study of alternative stable states in the human microbiome could lead to improved treatments for various ailments.

Based on this model of niche mediated coexistence, it is reasonable to ask if there are enough niches to explain the thousand or more OTUs co-occurring in the human gut. Resource niches in heterotrophic macrobes are largely determined by the size and resistance of prey items; it's easy to see how a species of finch might specialize on seeds of particular size and shell thickness. Heterotrophic bacteria, by contrast, are only capable of absorbing small molecules, no larger than several hundred daltons. Is it possible that there are sufficiently many *different* substrates with high enough abundance and stability to sustain each of these microbial populations? Just like Hutchinson's plankton, at first glance, it would appear unlikely that the diversity of limiting resources could match the observed species diversity. Nonetheless, this is an empirical question worth pursuing, and tallying the array of trophic options available in the gut should yield interesting results. One first-pass approach would be to identify the number of ATP generating metabolic modules in a gut shotgun metagenome[31]. Even if there are a multitude of carbon sources, nitrogen compounds may be more broadly limiting [32]. If this is true, the case for a niche based explanation for gut species richness would appear tenuous as the diversity of nitrogen sources is relatively low.

While Competitive Lotka-Volterra is able to model the persistence of species which occupy sufficiently different niches, perhaps more satisfyingly, Tilman's explicitly mechanistic competition model [33], also yields stable coexistence between species. By describing not only the growth of multiple populations but also the depletion of multiple resources, this model was able to demonstrate that species dependent on the exact same substrates may coexist when each is growth limited by a different one. For instance, two bacteria which both grow on glucose and ammonium may persist indefinitely if glucose concentrations are low enough to check the growth of one, and ammonium concentrations are low enough for the other.

As a result of this mechanism, supplementation of a limiting resource may remove the constraint on one species' growth, allowing it to exclude the other in competition for the remaining limiting resource. This effect was harnessed by Tilman to show that increasing resource availability can result in reduced diversity of plant communities[34]. A similar test in mice could asses the importance of limiting resources in maintaining gut biodiversity.

2.1.2. Environmental Heterogeneity

Of course, the entire length of the human digestive system can hardly be considered a single environment. Fecal samples, the source of most richness estimates, are the summation of microbial populations which persist in food, oral, gastric, small intestinal, and colonal habitats, and maybe other ecologically relevant subdivisions. Perhaps the total number of resource niches contributing to the diversity of microbes in feces, is better estimated as the sum of limiting resources within each environment along the digestive tract. Environmental factors, such as temperature, pH, oxygen availability, and the host immune system, all affect—and in many cases invert—the outcome of competition [35].

Oxygen partial pressure is a particularly interesting component of the host environment, with the potential to substantially influence both the niches available, and the outcome of competition in the gut [36]. At the oral end of the gastrointestinal tract, bacterial communities have access to high concentrations of oxygen, resulting in selection for those species which are able to reap the benefits of aerobic respiration and resist the toxic effects of the oxygen molecule itself [37]. Respiration by the microbial community quickly depletes oxygen concentrations until, after a short distance into the small intestine, the gut lumen is largely anaerobic. Host absorption removes simple molecules in the small intestine, leaving bacteria in the colon with a rich array of polysaccharides to be broken into glucose or other monomeric sugars and fermented [3]. Ultimately, this process provides the host with large quantities of short-chain fatty acidsn, contributing as much as 10% of total caloric intake in humans[38].

Despite the anaerobic nature of the intestinal lumen, the gut epithelium is richly perfused with blood, resulting in diffusion of oxygen through the mucous layer into the internal environment. This proximodistal oxygen gradient suggests that some gut bacteria, especially those occupying the mucosa, may be able to respire the abundant sugars and short-chain fatty acids, a significantly more profitable metabolism. Clearly, oxygen dynamics alone create a number of divergent 'climates' in the gut, potentially supplying new niches, and maintaining the long-term viability of additional species.

This environmental differentiation between body sites may be paired with microenvironmental variation at the centimeter scale or smaller[37]. Temporal fluctuations, as well, are probably a ubiquitous experience for microbes in the human gut due to behavioral and physiological cycles of the host and directional flow of lumen contents. One study suggests that the gut microbiome may have its own circadian rhythm[39]. Both temporal and spatial heterogeneity have been studied as mechanisms of coexistence [40]. When environmental changes invert the direction of selection, the frequency of these fluctuations, whether in space or time, is expected to have an important effect on the outcome of competition[20].

For many species of microbes—as in most plants and some animals—dormant or resistant life-stages can persist in the environment for long periods of time [41]. These 'seed banks' have important implications for local diversity, since they integrate species richness over past environmental conditions[42]. Microbial seed banks have been shown to contribute to the diversity found in soil [41]. While dormant stages are probably quickly washed out of the linear reaches of the human gut, the appendix and other branched portions may provide for the long-term persistence of slower growing comunity members [43].

2.1.3. Evolutionary Trade-Offs

The observation that the outcome of competition is context dependent reflects another central theme of community ecology. No species is ecologically superior in all environments, demonstrating the universality of physiological trade-offs. Negative pleiotropy between the ability to grow on different substrates directly explains resource specialization[44]. Besides those based on environmental and trophic trade-offs[45], an entire suite of coexistence mechanisms depend on more abstract correlations between species traits.

One such mechanism is the competitor-colonizer trade-off ([46]; for a brief review see [47]), which results in coexistence through the partitioning of space between species. Given a trade-off between dispersal or colonization ability and competitive ability, a superior colonizer can quickly occupy habitat space which has become open due to local catastrophe or chance extinction. While the superior competitor will eventually reach the same locality and outcompete the first species, with sufficient density of unoccupied space the colonizer may be able to disperse quickly enough to maintain a stable population. Depending on the particular parameters, these 'fugitive' species can coexist indefinitely with the superior competitor. It is possible that a similar model describes successional processes on food particles in the gut [48].

2.1.4. Network Effects

While negative frequency dependent effects, such as resource limitation, serve to stabilize two-species interactions, third species can also contribute to these negative feedbacks, sometimes promoting stable coexistence. Predator and parasite mediated coexistence have been described theoretically [49] and empirically [50]. The result of a new exploitative interaction on the initial competition is partially dependent on the exact structure of the trophic network; either a generalist predator or one which specializes on the weaker competitor serves to quicken the rate of ecological selection. Conversely, independent predators of each species or a predator which specializes on the stronger competitor can lead to stable coexistence. In part due to the popularity of 16S based surveys of the microbiome which often ignore both eukaryotic and viral members of the community, studies of predators and parasites of bacteria and archaea in the human gut are lacking. Incorporating these factors may help to explain some of the remarkable biodiversity. Undoubtedly, portions of the species richness observed in macroscopic organisms can be explained not through exploitative, but rather mutualistic interactions. Pollinator species in the tropics, for instance, frequently have highly specific mutualisms with flowering plants which provide trophic resources [51]. The specificity of this relationship provides tailored niches for individual pollinators, potentially contributing substantially to the total species capacity of these ecosystems[52,53]. Analogous mutualisms in microbes, for instance between bacteria which produce auto-inhibitory hydrogen and methanogenic archaea [54], could similarly support increased diversity. High specificity mutualisms are likely responsible for some of the species richness found in the gut, but exactly how much is unclear. Further research into these types of species interactions may inform not only our understanding of biodiversity, but also provide a predictive framework for the impact of perturbations on community composition.

2.2. Neutral Processes

The search for mechanisms of coexistence has been a near obsession for community ecologists. This is partially a byproduct of the popular analytic approaches, especially stability analysis, many of which were brought to the field from mathematics in the middle of the 20th century [55,56]. More recent influences have come from thermodynamics, statistical mechanics, and evolutionary biology, inspiring a new wave of non-equilibrium theories of biodiversity. Here we will refer to these collectively as ‘non-niche’ or ‘neutral’ processes, although this means grouping a diverse array of forces by only their distinction from niche mechanisms. Three general processes fall into this category: drift, fluctuations in the abundance of finite populations due to the stochasticity of survival and reproduction; migration, the movement of individuals into or out of the system; and speciation, the in situ generation of diversity through evolutionary change. Along with the niche process of ecological selection, these perfectly parallel the four processes considered in population genetics[23]: selection, drift, mutation, and migration. Neutral processes have major implications for the maintenance of biodiversity in the human gut.

2.2.1. Ecological Drift

Ecological drift, like its evolutionary counterpart, is the result of the inherently statistical nature of births and deaths in natural populations, and results in a random walk of relative abundances through time. Like competitive exclusion, acting in isolation for sufficient time, ecological drift results in the loss of diversity. This is because the random walk ultimately leads to extinction, a non-reversible event. Whereas niche processes are deterministic and standard mathematical models describe dynamics in infinitely large communities, ecological drift is strongest in small populations, where stochastic births, deaths, and disasters can result in large percent changes in abundance. Microbes of detectable abundance in the human gut are necessarily large populations. With on the order of 10^{14} microbial cells in the human GI tract[57], any species at even 0.01% abundance in community surveys has a population size akin to the number of people on the planet. Nonetheless, even large populations are subject to drift, especially in this case, since the physical locations of a particular species in the gut lumen is likely clumpy [58], and therefore death and washout may not be statistically independent events. Any finite size community is therefore not in equilibrium, and consideration of long-term stability is superseded by analysis of statistical expectations over time. This perspective is a reminder that community composition, and therefore species richness, is constantly in flux.

The stochasticity of ecological drift is tempered, however, by the determinism of niche processes, which in some cases buffer species from extinction through negative density or frequency dependent

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selection, and in others quickens the pace through unmitigated competition. Besides small population sizes, the relative importance of drift is increased when species are of more similar fitness. Mechanisms which decrease fitness differences can therefore increase the time to competitive exclusion [40,59].

One such equalizing mechanism is environmental variability. When climatic variables fluctuate at a frequency similar to the rate of competitive exclusion, such that the relative fitness of two competitors is continually inverted, fitness difference are effectively brought closer to zero[20,60] Short term diversity can therefore be increased by environmental fluctuations at the right time scale. In the human gut, this mechanism may be highly important, since temporal fluctuations are ubiquitous and occur at a variety of time scales [39]. Alternatively, even in static environments, fitness equivalency may be the norm, a hypothesis supported by the prevalence of physiological trade-offs[59].

Whether the diversity of the human gut is the result of deterministic, stabilizing mechanisms, or processes which equalize fitness between species is a key question [59], and may have implications for the management of microbiome related dysbiosis.

2.2.2. Migration and Speciation

With competition and drift actively removing diversity from local communities, migration and speciation serve to as a counterbalance, introducing new species either *de novo*, in the case of speciation, or by immigration from outside the local system. By conceptually partitioning local and regional communities, speciation within the relatively small, local community can be effectively ignored and replaced with migration, though speciation at the regional scale is the ultimate source of global biodiversity. The Theory of Island Biogeography [61] was an early model describing the effect of migration rates on local diversity, specifically the balance of two rate processes: migration from a external species pool and local extinction. Surprisingly, this simple, equilibrium model of species richness fits well patterns of diversity on island archipelagos without invoking niches or competitive differences [62]. Island Biogeography, as a model of community assembly in the human gut, predicts a constantly changing species composition, despite an equilibrium species diversity. This is not held up by the empirical observation that the gross composition of the human gut microbiome is relatively constant. Regardless, a portion of the members of the gut community may be determined by migration from the external environment. Searching 16S time series for these kinds of dynamics may be an important line of research.

Stephen Hubbel's Unified Neutral Theory of Biodiversity[63] attempted to replicate this success, but with a more explicit treatment of mechanism and several controversial assumptions which limit applicability. Hubbel's model has been reformulated for microbial populations [64], and may serve as a valuable null hypothesis in identifying community compositions which cannot be explained by purely neutral processes [65]. It is possible that a significant fraction of the species in the human gut are transients from the external environment. If this hypothesis is correct then community composition should reflect primarily neutral processes.

2.3. Emergent Properties and Higher Level Selection

As a result of the immense importance of the gut microbiome to host health, the global prevalence of any single species is not only determined by its relative fitness in competition with other community members, but also its effect on fitness of the host. This is a classic example of an extended phenotype [66], and may help to explain the evolution of host-microbe mutualisms [67]. Some of the benefits conferred by microbial communities are likely to be not just the sum of its parts, but irreducible properties of the community structure as a whole. Community stability and invasion resistance [68], for instance, may protect the host from pathogens [69], and is not yet been shown to be a property of any individual symbiont[70]. Diversity itself may be causally related to both community function and stability [71]. Selection for emergent properties which are most advantageous to the host, combined with high fidelity transmission of communities between hosts, sets the stage for evolution to act not at the level of microbial populations, but instead on full communities [72,73]. Higher level selection

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could result in the evolution of a highly diverse communities [56]. Alternatively, host genotypes which promote community diversity may be selected for, a reversed example of an extended phenotype.

Hypotheses which depend on higher level selection are open to several common criticisms [74]. Foremost among these is the necessary fidelity of transmission. If communities are assembled from a largely random assortment of environmental microbes, then selection acting on emergent properties does not affect the prevalence of these community level traits over time. Alternative explanations, such as monotonic effects of symbionts on host fitness and host genotype control are often more parsimonious.

3. Conclusion

With little previous research, the source of extreme species richness in the human gut is a standing question. The relative importance of stabilizing mechanisms which promote long term coexistence, versus non-equilibrium processes, such as drift, migration, and *in situ* diversification remains to be tested, and all four processes are likely to take part. For community ecology, Hutchinson's 'Paradox of the Plankton' has served as a focus for theoretical study, ultimately leading to a diverse mathematical basis for empirical study. With the advent of culture-free methods in microbiology, human microbiome research has quickly assumed the task of describing our symbiotic community. As the field begins the process of developing predictive capabilities and tools for community management, a similarly robust theoretical foundation will be of paramount importance. A central question, such as explaining the observed diversity of the gut community, will serve to motivate and focus theory and experimentation, with positive repercussions for applications as well. Human microbiome research *is* community ecology. While there are undoubtedly qualitative differences between microbial and macroscopic communities, the literature of traditional ecology is a valuable resource in the transition to a predictive and applied science.

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