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Review Article

Shift of The Neutral-Niche Dynamics in The Human Microbiome Under Disturbances Associated with Lifestyle Changes

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Abstract

Background: It is well recognized by now that human micro biome has far reaching influences on our healthy and diseases. One venue to investigate the influences can be through the study of the mechanisms of microbial community assembly and diversity maintenance. In this article, we apply a hybrid model of neutral-niche dynamics by Ofiteru et al. to reanalyze the dataset from David et al.'s study on the effects of life style to the micro biome of two individuals, aiming to explore the shift of the neutral-niche dynamics in the human micro biota.

Results: We obtained two major findings. First, in gut, Faecali bacterium prausnitzii, an anti-inflammatory bacterium, exhibited high neutral dynamics, and few other species showed similar level of neutral dynamics. In contrast, in the oral micro biome, more species demonstrated high neutral dynamics. Second, we detected some bacterial species whose neutral-niche dynamics are strongly associated with the occurrences of disturbances such as change of diets and infection.

Conclusions: We postulate that the difference between gut and oral micro biota could be due to the open gateway nature of oral habitat, which makes it difficult for niche-selected species to maintain. The balance shift in the neutral-niche dynamics may play an important role in dysbiosis and possess broad health implication.

Background

The great significance of human microbiota on our health and diseases been recognized increasingly thanks to the human micro biome projects [1,2]. For examples, microbiota offer critical services such as protecting against diseases [3,4] stimulation of intestinal angiogenesis [5] and regulation of host fat storage [6], which are critical for our health. In the mean time, micro biota is thought to relate to a number of diseases, such as inflammatory bowel disease [7,8], colon cancer [8,9], obesity Le et al. [10] and type-2 diabetes Qin et al. [11]. Though human microbiota are relatively stable in the long-term scale [12,13], factors such as use of antibiotics [14-16], unhealthy diets [17,18] and diseases [19,20] and other disturbances are likely to break the balance and may cause the so-termed dysbiosis-state of micro biome associated with diseases.

Theoretically, the mechanism of community assembly and diversity maintenance should have far reaching influence on the services of human micro biome on its host, but our understanding of the mechanism per se has been very limited. Traditionally, there have been two diametrically opposite opinions on this issue, i.e., deterministic niche theory and stochastic neutral theory [21-26] and extensive investigations have been conducted, including reconciling both theories in various frameworks of hybrid models in macro ecology of plants and animals. The forces that govern the formation of micro biota is supposed to be controlled by a number of deterministic factors, such as host species, genotype, diet, health and interactions between microbes [27], which seem to support the niche theory. The fundamental assumption of niche theory is that the ecological traits vary among different species [28]. The alternative neutral theory that is proposed by Hubbell [23] and has been applied in ecology area for years brings a novel idea that micro biota assembly may be driven by stochastic process of dispersal and ecological drift, of which the assumption is that all species are ecologically equivalent (i.e. all species have equal birth, death, dispersal and speciation rates) [29].

In this study, we apply one of the hybrid frameworks originally developed by Ofiţeru et al. [31] to further investigation the possibly combined niche and neutral effects in the human gut micro biota. Ofiteru et al. [31] argued that neutral dynamics should play an important role in the community assembly if the same neutral models could explain the dynamics of populations in a community. Specifically, they recalibrated and validated a purely neutral model and an extended parsimonious model including environmental factors to fit time-series of populations in a microbial wastewater treatment community. Another factor motivated Ofiteru et al. (2010) 'recalibration' is their critic to the most common method for testing the neutral theory. They argue that (i) the commonly used methods are not robust enough because different parameters pairs could result in similar species abundance distribution (SAD); (ii) the relative importance of niche and neutral forces are difficult to differentiate, since the niche process and neutral process are probably jointly responsible for the community assembly Dumbrell et al. [32], Stegen et al. [33]; (iii) neutral models may fail to identify the effects of environmental factors when neutral process exert partly.

The dataset Ofiteru et al. [31] originally used to validate their calibrated model was from Wells et al.'s [34] study on the micro biota in a carefully managed wastewater treatment plant with well-controlled environment, which appears to be a relatively stable habitat for microbes and the neutral dynamics model is likely to perform better. However, it has not be tested that in a relatively unstable ecosystem such as the human gut where sudden disturbances such as diseases or change of lifestyle may occur relatively frequently. Therefore, we set two objectives in this study. The first objective is to investigate the neutral-niche dynamics for the most common species in the micro biota of human body that is a less stable environment where niche effect could be more strongly dominant. Second, we would like to explore the environment-driven alterations of neutral-niche dynamics for the most common species. To implement our study, we choose to reanalyze the dataset from David et al. [35] study aiming at exploring the effects of disturbance and lifestyle on the dynamics of human-associated micro biota, in which they recruited two individuals and followed and sampled them daily for a period of about one year. The study was rather comprehensive and offered an ideal dataset for conducting our investigation. Their original analysis was focused on whole community level analysis and did not involve any analysis of neutral dynamics at either community or population (individual taxon) level.

Environmental effects and corresponding niche-neutral dynamics affecting individual species may vary according to the specific attributions of species. It is still possible that neutral dynamics, at least partly, influence the time-series of populations when observed samples failed to pass the neutrality test using traditional methods. Hence, under our first objective, with Ofiteru et al.'s method [31], we may identify the portion of variance of the time-series of taxon populations driven by neutral dynamics. Although the gut may be a relatively stable environment in our daily life, both of the two individuals recruited in David et al. study [35] had experienced dramatic environment disturbance during the research period. One individual had traveled from a major American metropolitan area to the capital of a developing nation in Southeast Asia between days 71 and 122, exposed to new diet and environment and got diarrhea twice during the traveling. Another individual suffered from an infection caused by food poisoning between days 151 to 159. By applying Ofiteru et al. [31] method, we hope to explore whether the neutral dynamics would change during or after the dramatic disturbances.

Methods

Dataset description and preprocessing

The dataset we reanalyzed was originated from David et al. [35] study. In their study, 2 individuals were recruited, individual A and B. For individual A, stool samples were collected daily between days 0 and 346, named A-Gut group, and saliva samples were collected daily between days 26 and 364, named A-Saliva group. For individual B, stool samples were collected daily between days 0 and 252, named B-Gut group. For each sample, the V4 regions of 16S rRNA genes were amplified and sequenced with Illumina GAIIx. The time-series OTU tables of 3 groups were picked at 97% similarity via QIIME analysis pipeline (v1.3). The data analysis, including the calculation of OTU tables should refer to David et al. [35].

To make our analysis more informative biologically, we excluded the species without confirmed names. The Ofiteru et al. [31] model adopts a weighted least-squares regression to estimate the parameters, where the weight of independent variable is [X(1-X)]-1 (X represents the independent variable), requiring the independent variable (i.e., abundance of each OTU at every time point) to be a non-zero value. To adapt to such requirement, we filtered out OTUs with more than 5% zero occurrences in the time-series and for OUT containing zero values (less than 5% zero occurrences), we added 1 to the abundance of time-series at all time potions.

Computational procedures of the neutral and hybrid models

We used a calibrated neural model by Ofiţeru et al. [31], derived from Hubbell neutral model and extended for time-series data of OTUs in the micro biota, where environmental effects can be added when necessary. The model assumes that the species in a local community originated from a source community (meta community), where the species abundance distribution (SAD) obeys a log-series distribution with a single shape-deciding parameter θ. The difference between SAD in local community and that in metacommunity could be described with a function of a pair of parameters, NT and m, where NT is the number of individuals in the hypothetic neutral local community and m is the probability that an individual in the local community would be replaced by an individual from the meta community rather than from local reproduction when it died. An advantage factor (α’) representing the effect of external environment factors on birth rate is added, therefore the neutral assumption would be broken if α’ was not 0. In other words, the model would represent a pure neutral dynamic when α’ was 0; when α’ was not 0, the model would be hybrid dynamics as it combined neutral dynamic and environmental effects. A stochastic differential equation (SDE) could be used to describe the dynamics of observed relative abundance of the i-th specie at time t, X(t), which is controlled by the parameters NTm and p, the relative abundance of the specie in the metacommunity. That is,

$$dX(t)=\{N_T m[p-X(t)]+2\alpha' X(t)[1-X(t)]\}\frac{1}{a}dt+\frac{1}{\sqrt{a}}\sqrt{2X(t)[1-X(t)]}dW_t, \qquad (1)$$

where Wt is a Wiener process (standard Brownian motion) and a is an unknown constant that is related to the time between birth and death. For each of the dataset we tested, X(t) is known at successive 365 time points (one year) and dX(t) could be calculated as the longitudinal change in the relative abundance of a certain specie during the period. Eq. (1) could be approximated with a linear model, i.e.,

$$dX=m_0+m_1Y_1+m_2Y_2+\varepsilon \qquad (2)$$

where

$$m_0=\frac{N_T mp}{a},\quad m_1=-\frac{N_T m}{a},\quad m_2=\frac{2\alpha'}{a},\quad Y_1=X,\quad Y_2=X(1-X)$$

And Error $\varepsilon=\frac{1}{\sqrt{a}}\sqrt{2X(t)[1-X(t)]}dW_t$

When α›=0, the weighted least-squares regression analysis can be utilized to estimate the parameters m0 and m1, where the dependent variable is dX and the weight of independent variable is [X(1-X)]-1 Ofiteru et al. [31].

A fundamental piece of information the above listed questions should reveal is: to what degree the neutral model could explain the dynamics of common species? For each species in the three groups we designated previously, the purely neutral model (α’=0) was fitted across the entire period of sampling, respectively. The R-squared was used to measure the variability (portion of variance) that can be explained by the neutral dynamics for each species.

With the aim to study whether or not and how the environmental disturbances would influence the dynamics of species in micro biota, we selected and reanalyzed a set of subsets. For individual A (A-Gut group and A-Saliva group) who traveled abroad during the day 71 to 122, when he moved from a major American metropolitan area to the capital of a developing nation in Southeast Asia, where he had rather different diet and had diarrhea during days 80 to 85 and 104 to 113. We divide the whole time period into pre-travel, mid-travel and post-travel periods and reanalyzed A-Gut and A-Saliva groups in 3 time periods respectively using purely neutral model. For individual B (B-Gut group) who had an enteric infection resulted from food poisoning induced by Salmonella sp. during the days 151 to 159, we fitted the neutral model to the data in pre-infection and post infection respectively.

Results

Neutral dynamics of common species

After preprocessing based on the description in the Materials and Methods section, we obtained 14 species in A-Gut, 62 species in A-Saliva and 4 species in B-Gut for our analysis. To the complete time-series data of each species in 3 groups, a purely neutral model was fitted, and the results were displayed in (Tables 1, 2 & 3), respectively. The results for A-Saliva were displayed only partially in (Table 2), and the remaining was listed in the online Supplementary (Table S1). The portion of variance that can be explained by neutral model was measured by the R-squared values (R2). First, for the most common species in the two gut datasets, the portion of variance that could be explained by the neutral model is low and ranged from 0.2% to 8.1%, with the exception of Faecalibacterium prausnitzii that exhibited high neutral dynamics (R2 of model is 0.384 in A-Gut and 0.142 in B-Gut) and the most fitted models had R-squared values lower than 0.1, suggesting that neutral dynamics exerted limited effects on the gut microbial species, apart from Faecalibacterium prausnitzii. However in the saliva dataset, the R-squared values of most species were relatively high, where 25.81% (16/62) fitted models for the most common species had R-squared values higher than 0.2 and 12.9% (8/62) had R-squared values higher than 0.3, indicating that neutral dynamics may play a significant role in the saliva micro biota.

Table 1: The parameter values of the purely neutral model for the most common species in A-Gut group.

Species Name	ARDA	m_0	m_1	Std Err	R^2	p-value
Bifidobacterium gallicum	0.03	0.004	-0.13	0.259	0.008	0.109
Bacteroides uniformis	0.016	0.01	-0.658	0.341	0.05	0
Bifidobacterium longum	0.013	0.002	-0.128	0.139	0.01	0.062

Eubacterium rectale	0.012	0.001	-0.056	0.136	0.002	0.42
Ruminococcus gnavus	0.008	0.002	-0.201	0.116	0.022	0.007
Bifidobacterium adolescentis	0.008	0.001	-0.134	0.168	0.005	0.187
Bacteroides caccae	0.006	0.002	-0.375	0.131	0.043	0
Faecalibacterium prausnitzii	0.006	0.004	-0.663	0.047	0.348	0
Streptococcus thermophilus	0.004	0.002	-0.583	0.098	0.081	0
Bifidobacterium dentium	0.002	0	-0.222	0.058	0.027	0.002
Clostridium orbiscindens	0.001	0.001	-0.541	0.061	0.068	0
Blautia producta	0.001	0	-0.414	0.041	0.053	0
Collinsella aerofaciens	0.001	0	-0.25	0.036	0.03	0.001
Clostridium hylemonae	0	0	-0.761	0.034	0.059	0

Table 2: The parameter values of the purely neutral model for the 10 most abundant most common species in A-Saliva group.

Species Name	ARDA	m_0	m_1	Std Err	R^2	p-value
Streptococcus pneumoniae	0.012	0.012	-0.965	0.029	0.509	0
Streptococcus sinensis	0.021	0.017	-0.813	0.036	0.493	0
Granulicatella adiacens	0.02	0.015	-0.781	0.048	0.374	0
Rothia aeria	0.006	0.005	-0.856	0.032	0.355	0
Streptococcus gordonii	0.008	0.006	-0.764	0.039	0.345	0
Actinobacillus porcinus	0.052	0.031	-0.597	0.086	0.344	0
Leptotrichia buccalis	0.002	0.001	-0.688	0.017	0.317	0
Streptococcus porcinus	0.008	0.005	-0.71	0.049	0.307	0
Streptococcu sphocae	0	0	-0.731	0.014	0.294	0
Capnocytophaga sputigena	0.001	0	-0.729	0.013	0.283	0

Table 3: The parameter values of the purely neutral model for the most common species in B-Gut group.

Species Name	ARDA	m_0	m_1	Std Err	R^2	p-value
Bacteroides plebeius	0.207	0.022	-0.135	2.592	0.001	0.702
Bacteroides uniformis	0.045	0.015	-0.341	0.295	0.055	0.001
Faecalibacterium prausnitzii	0.003	0.001	-0.394	0.042	0.142	0
Bacteroides acidifaciens	0	0	-0.228	0.011	0.075	0

The effects of travel and infection on the neutral dynamics of common species

Individual A was exposed to new diet and had diarrhea twice during the period of traveling, days from 71 to 122, and individual B got infection days from 151 to 156, both of which could be considered as dramatic environmental disturbance on internal physiological environment. Despite the global view, our results demonstrated that the neutral dynamics of some species were reduced significantly by such disturbances while some others remain stable or slightly increased. In A-Gut group, for examples, the R-squared value, which represented the effect of neutral dynamics, for Bifid bacterium gallium dropped from 0.670 in the per-travel to 0.005 in the mid-travel and then increased slightly to 0.100 in the post-travel, the R-squared value for Eubacterium rectal dropped from 0.617 in the pre-travel to 0.002 in the mid-travel and then increased slightly to 0.101 in the post-travel, and the R-squared value for Bifid bacterium longum changed from 0.269 to 0.008 and to 0.109 finally, while the R-squared values for the other species showed relatively very small variances.

In B-Gut group, the neutral dynamics for Bactericides plebeians and Bactericides uniforms almost disappeared after the infection, given that the R-squared value changed from more than 0.2 to near 0, whereas the R-squared value for Faecalibacterium prausnitzii increased from 0.084 to 0.410, suggesting that environmental disturbance would not always result in the loss of neutral dynamic for some species. In the oral samples, i.e. the A-Saliva group, though the change of variance was much more complex, the majority of species, especially those abundant ones, stayed in the relative high R-squared values, even after exposing to the environmental disturbance. The curves of R-squared values for each species in different periods in 3 groups were displayed in (Figure 1) (A-Gut), (Figure S1) (A-Saliva) and (Figure S2) (B-Gut) and the parameters were listed in (Table S2), (Table S3) and (Table S4) respectively.

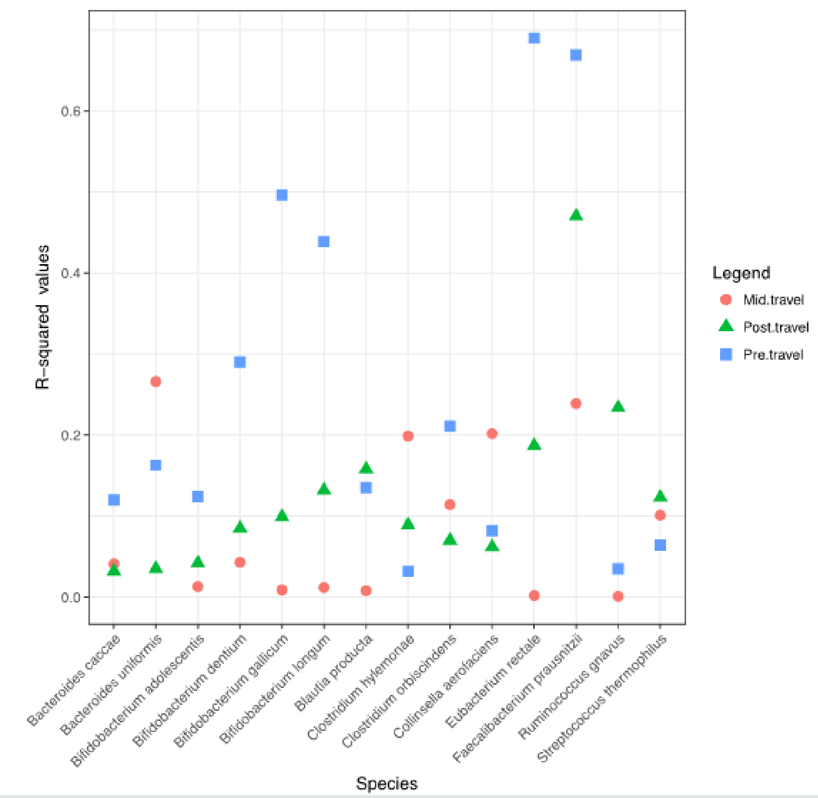

Figure 1: The R-squared (R^2) values for the most common species in A-Gut in different periods.

Discussion

The relatively stable temporal dynamics of microbiota could be a key to prevent us from the pathological disorders. However, as mentioned in the introduction, a great deal of external and internal factors would affect the normal microbiota and finally lead to more susceptibility to pathogens, obesity and auto-inflammatory diseases David et al. [35] The first step to study the long-term dynamics is to conduct longitudinally observations on both the host and micro biota at regular time intervals. Wet is not only the immense cost of labor power and material resources, but also the enforcement of individual compliance that make following the individuals for a long time strictly a non-trivial task. Hence, the high-resolution time-series with good quality and coupled metadata are scarce. In David et al. [35] study, they followed two individuals daily for a year for both micro biota and host and found micro biota can be quickly and profoundly altered via common actions and experiences, which made us wonder the underlying mechanism for such alteration.

From an ecological perspective, niche theory emphasizing the deterministic factors and neutral theory underlining the stochastic factors could be used to describe the opposite forces that shape the micro biota. In fact, they are probably jointly responsible for the micro biota assembly Dumbrell et al. ; Stegen et al. [32,33] From the stationary ranked abundance distribution testing neutrality solely, ignoring the name of taxa, the information about the dynamics of individual taxa will be lost. However, the longitudinal dynamics of individual taxa can be very significant in shaping the micro biota due to specific attributions and interactions. We maintained that it is equally important to reveal such differences.

In Ofiteru et al. [31] study, they recalibrated a neutral model to test the neutral dynamics of individual taxa through time-series. In Ofiteru et al. [31] study, they revealed that it is possible to explain relative high portion of the variance in the time series of abundance for the top two ranked taxa in two functional groups. However they could not test all taxa due to the limitation from the T-RFLP (Terminal Restriction Fragment Length Polymorphism) method in failing to detect the rare taxa. We are able to test more species using their model, thanks to the high throughput next generation sequencing technology harnessed in David et al. study [35].

We found that relatively small portion of temporal variances of the most common species in the gut samples could be explained by neutral dynamics, suggesting that they have low resistances to environmental effects. However, there are also certain species that could exhibit high neutral dynamics in gut, such as Faecalibacterium prausnitzii in this study. In contrast, in the saliva samples, the neutral model could explain even higher portion of variance for amount of common species than those taxa tested in Ofiteru et al.[31] study, in which a well-controlled artificial environment for microbes were sampled. One of possible reasons might be that the oral is an open gateway linking external environment and our body, where the environmental disturbance occurred routinely via materials exchange and foods/drinks intake, resulting in eliminations for the species that had low resistances to disturbances and consequently the stayed taxa could maintain high neutral dynamics.

Another merit of our study is revealing the change of neutral dynamics for species caused by observed environmental disturbances, which provided us a better understanding on the underlying mechanism of the changes of individual populations in the micro biota and a guide to better manage the important species as well. (Table S2, S3 and S4) in the supplementary information showed evident differences during/after the periods of disturbances for some species. For example, in A-Gut group, lactic acid-producing bacterium Bifid bacterium (*B. gallicum and B. longum*) was found of the highest neutral dynamics, but during the period of traveling, they lost neutral dynamics (R-squared for neutral models dropped to near zero), which meant they would be influenced by environmental factors more easily. Bifid bacterium is thought to be able to inhibit the growth of pathogens and protect human from diarrhea [36-40], and to enhance the immune function via increase in anti-inflammatory cytokines Ouwehand et al. [41]. To some extent, for microbes, the property of neutral dynamics may be considered as a protective factor against environmental disturbances, hence it is possible to be associated with the dysbiosis of certain beneficial species that the loss of neutral dynamics, such as the example of Bifid bacterium in A-Gut, resulting from loss such protective factor, which may be a significant reason for individual A to get diarrhea twice during his travel period.

In the B-Gut group, two Bactericides (Bactericides plebeians and Bactericides uniforms) were also found to loss their neutral dynamics after the infection, though another Bactericides (Bactericides acidifaciens) did not vary obviously in the neutral dynamics and Faecalibacterium prausnitzii even increased drastically. David et al. [35] found that, for individual B, more than half of gut taxa persistently declined and did not recovery to the pre-infect state during the remaining sampling dates. Their hypothesis that competitors replaced the lost taxa made great sense, but the underlying ecological force was not explored. We believed that, for some species, the loss of neutral dynamics property could increase the possibility that they were influenced by environmental factors and replaced by competitors, which could be one of the possible explanations for the competitive displacement hypothesized by David et al. [35]. In the A-Saliva samples, the condition was more complex and most species did not experience an obvious decrease in neutral dynamics, which is understandable given that oral has been exposed to frequently environmental disturbances, so the left species maintain higher resistance to environmental effects. Though it may be too assertive to conclude that dysbiosis would occur due to the change of neutral dynamics of some species, such influence should not be ignored. In a big picture, such alterations probably made the whole micro biota more fragile to environmental impacts and pathologic dysbiosis may occur ultimately due to accumulative effects.

Author Contributions

Y.X and Y.C conceived the study, Y.X, G.Y and Q.H analyzed the data, prepared the tables and figure and interpreter the results. Y.X wrote the paper, G.Y and Y.C reviewed the paper. All authors have read and approved the manuscript.

Competing interest

The authors declare no competing interest.

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