Integrative and Comparative Biology

Integrative and Comparative Biology, volume 0, number 0, pp. 1–16
doi:10.1093/icb/icx046

Society for Integrative and Comparative Biology

SYMPOSIUM

Group Living and Male Dispersal Predict the Core Gut Microbiome in Wild Baboons

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From the symposium "With a Little Help from My Friends: Microbial Partners in Integrative and Comparative Biology (SICB wide)" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

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Synopsis The mammalian gut microbiome plays a profound role in the physiology, metabolism, and overall health of its host. However, biologists have only a nascent understanding of the forces that drive inter-individual heterogeneity in gut microbial composition, especially the role of host social environment. Here we used 178 samples from 78 wild yellow baboons (*Papio cynocephalus*) living in two social groups to test how host social context, including group living, social interactions within groups, and transfer between social groups (e.g., dispersal) predict inter-individual variation in gut microbial alpha and beta diversity. We also tested whether social effects differed for prevalent "core" gut microbial taxa, which are thought to provide primary functions to hosts, versus rare "non-core" microbes, which may represent relatively transient environmental acquisitions. Confirming prior studies, we found that each social group harbored a distinct gut microbial community. These differences included both non-core and core gut microbial taxa, suggesting that these effects are not solely driven by recent gut microbial exposures. Within social groups, close grooming partners had more similar core microbiomes, but not non-core microbiomes, than individuals who rarely groomed each other, even controlling for kinship and diet similarity between grooming partners. Finally, in support of the idea that the gut microbiome can be altered by current social context, we found that the longer an immigrant male had lived in a given social group, the more closely his gut microbiome resembled the gut microbiomes of the group's long-term residents. Together, these results reveal the importance of a host's social context in shaping the gut microbiome and shed new light onto the microbiome-related consequences of male dispersal.

Introduction

Social animals are thought to acquire many of their resident bacteria from conspecifics, both through direct transmission from social partners and indirect transmission from shared environments (Lax et al. 2014; Powell et al. 2014; Tung et al. 2015). In support, several studies have shown that social organization and behavior shape an individual's microbiome composition (e.g., White et al. 2010; Koch and Schmid-Hempel 2011; Meadow et al. 2013). These effects may be important to the evolution of animal social behavior because inter-individual variation in gut microbial composition is increasingly linked to variation in host health and fitness (Turnbaugh et al. 2009a; Huffnagle 2010; Heijtz et al. 2011; Koch and Schmid-Hempel 2011; Ezenwa et al. 2012; Forsythe and Kunze 2013; Bordenstein and Theis 2015). However, we still

have only a limited understanding of how social organization and behavior affect patterns of microbial transmission between individuals in wild systems, and ultimately the composition and function of animal microbiomes.

To date, social organization and behavior are thought to influence two primary dimensions of microbiome composition: microbial alpha diversity, i.e., the number and distribution of bacterial taxa in an individual host, and beta diversity, i.e., differences in microbial community composition between hosts. In terms of alpha diversity, social partners have been proposed to serve as bacterial reservoirs, promoting microbial diversity within hosts and maintaining microbiome stability in the face of gains and losses of individual taxa (Lombardo 2008; Moeller et al. 2016a). In support, some studies have found that animals with high levels of social contact harbor more diverse gut microbiomes than animals who are less socially connected (Levin et al. 2016; Li et al. 2016b; Moeller et al. 2016b, although Levin et al. 2016 also found evidence of the opposite effect). Further, in bees, experimentally reducing an individual's social contacts decreases their gut microbial diversity (Billiet et al. 2016). These effects may have important consequences for hosts: in free-living non-microbiome communities, high biodiversity is associated with greater community stability and productivity (e.g., Lehman et al. 2000; Tilman et al. 2006; Hooper et al. 2012a). In the microbiome, high alpha diversity is likewise proposed to promote long-term compositional and functional stability and resistance to invading pathogens (Dillon et al. 2005; Lozupone et al. 2012b). However, additional gut microbial taxa may also be largely functionally redundant, and the functional consequences of alpha diversity in animal microbiomes are the topic of considerable debate (Shade and Handelsman 2012; Moeller et al. 2016b).

In terms of beta diversity, socially mediated patterns of transmission are thought to promote microbiome community similarity among group members and social partners. Social group-specific microbiomes have been reported for several body sites and in a wide variety of taxonomic groups, including humans, non-human primates, carnivores, frogs, birds, and insects (Koch and Schmid-Hempel 2011; Degnan et al. 2012; McKenzie et al. 2012; Theis et al. 2012; Dunn et al. 2013; McCord et al. 2013; Song et al. 2013; Leclaire et al. 2014; Schloss et al. 2014; Gomez et al. 2015; Tung et al. 2015; Aivelo et al. 2016; Bennett et al. 2016; Levin et al. 2016; Whittaker et al. 2016). Such effects could be important because more similar microbial communities are presumed to have similar functional capacities and may provide similar "ecosystem services" to their hosts, including effects on digestion, immune responses, vitamin synthesis, or handling of plant secondary compounds (Costello et al. 2012; Delsuc et al. 2013; Ainsworth et al. 2015).

We tested the relationships between social behavior and gut microbial alpha and beta diversity in both "core" and "non-core" members of the gut microbiome. The presence and abundance of core and non-core gut microbial taxa are thought be shaped by different host and environmental factors. Core taxa are, by definition, found in the majority of hosts of a given species (Hamady and Knight 2009) and are thought to make major contributions to the gut microbiome's normal functions (e.g., digestion and vitamin synthesis; Savage 1977; Walter and Ley 2011; Shade and Handelsman 2012; Zhang et al. 2016). The high prevalence of core taxa suggests that these microbes may be actively curated and retained by the host's immune system (Hansen et al. 2010; Hooper et al. 2012b). Further, their abundance may be driven by interactions with other common microbial taxa (Stecher et al. 2010). In contrast, less prevalent, non-core taxa are proposed to often be transient, as they typically occur in a minority of hosts and are not consistently present in the same host over time (Martínez et al. 2013; Tinker and Ottesen 2016). Their dynamics may be shaped by patterns of microbial colonization from the environment, including conspecific hosts (Hanson et al. 2012). Hence, non-core microbes might be more likely to reflect recent social or external exposures.

To investigate this possibility, and to clarify the role of different social factors in gut microbiome composition, we performed 16S rRNA gene sequencing on 178 fecal samples (78 individuals) collected from baboons living in two social groups in a well-studied wild baboon (*Papio cynocephalus*) population living in the Amboseli ecosystem in Kenya. To do so, we took advantage of detailed data on the baboons' demography, social relationships, and habitats collected by the Amboseli Baboon Research Project since 1971 (Alberts and Altmann 2012). Prior research on this population indicated that each social group harbored distinct gut microbiomes and that close grooming partners have more similar gut microbiomes than those who rarely groom each other (Tung et al. 2015).

Here, we expanded both the sample size and scope of our analyses to test three main hypotheses for both the core and non-core microbiome: (1) that sociality is linked to elevated gut microbial alpha diversity; (2) that increased social interaction

promotes increased gut microbial similarity (beta diversity) between individuals; and (3) that the length of an immigrant male's membership in his current social group predicts his microbiome similarity to long-term group residents. In all cases, we expected social effects on microbiome composition to be stronger in non-core than core gut microbial taxa. We predicted that baboons living in the larger social group and/or those who engaged in more grooming would have higher gut microbial diversity than individuals living in the smaller group or who were socially isolated. We also predicted that adult males, who disperse between social groups and encounter more diverse environments and social partners in the process, would exhibit higher gut microbial alpha diversity than adult females, who do not disperse. With respect to beta diversity, we expected that gut microbial similarity between individuals would be highest for members of the same social group and close grooming partners. Finally, we predicted that immigrant males that were members of their social group for a longer period of time would be more similar to other group residents than recent immigrants. Taken as a whole, our study improves our understanding of which aspects of microbiome community composition are most sensitive to a host's social environment.

Methods

Study subjects and sample collection

Since 1971, the Amboseli Baboon Research Project (ABRP) has collected continuous data on the demography, social interactions, and ranging patterns of hundreds of individual baboons in the Amboseli ecosystem in Kenya (Alberts and Altmann 2012). These data are collected by experienced field observers who visit each baboon social group 3–4 times per week, alternating between morning and afternoon sessions, year-round. All individuals are known and recognized by morphological characteristics.

Study subjects and fecal sampling

From 7 July to 8 August 2012, we collected fecal samples from the members of two baboon social groups, called "Mica's" ($n = 67$ samples from 27 individuals) and "Viola's" ($n = 111$ samples from 51 individuals) groups. These two groups occupied adjacent home ranges, with no home range overlap during the period of sample collection (Supplementary Fig. S1; Tung et al. 2015). Fecal samples from all group members were collected opportunistically within a few minutes of defecation. Samples were preserved in 95% ethanol and stored in the field in an evaporative cooling structure (approximate daily maximum temperature of 25 °C) until shipment to the US, where they were stored at −80 °C (Alberts and Altmann 2011). A total of 179 samples were collected from 79 individuals; 1 sample was removed during quality filtering of our sequencing data, yielding a final dataset of 178 samples from 78 individuals (Table 1; range = 1–5 samples per individual; median = 2 samples per individual).

Profiling gut microbial composition

DNA extraction and 16S rRNA gene sequencing

DNA was extracted from each fecal sample using the Powersoil DNA Isolation kit (MO BIO Laboratories, Inc., Carlsbad, CA) (Turnbaugh et al. 2007; McInnes and Cutting 2010). Illumina libraries were prepared following Davenport et al. (2014). Specifically, we amplified a hypervariable section of the V4 region of the bacterial 16S rRNA gene via polymerase chain reaction using barcoded primers 515F and 806R (Caporaso et al. 2011; Degnan et al. 2012; Yatsunenko et al. 2012). Multiplexed libraries were single-end sequenced (102 bp per sequence) on the Illumina HiSeq 2000 platform at the University of California-Los Angeles Neuroscience Genomics Core, yielding 315,821,753 total raw sequencing reads.

Quality filtering and taxonomic assignment

Quality filtering and taxonomic assignments were conducted using the QIIME-based pipeline detailed in Supplementary Figure S2 (Caporaso et al. 2010). We rarefied the dataset to the sample with the lowest number of reads using the QIIME command single_rarefaction.py, yielding a rarefied OTU table of 151,166 reads per sample (26,907,548 reads total) and 16,583 OTUs (Supplementary Table S1). To differentiate the core and non-core gut microbiome, we split the rarefied OTU table into two tables following definitions used in previous studies: core OTUs were those present in ≥90% of samples, and non-core OTUs were present in <90% of samples (Ugland and Gray 1982; Qin et al. 2010; Li et al. 2013; Ainsworth et al. 2015). In addition to a non-core definition of <90% of samples, we re-ran the analyses with a non-core definition of taxa found in <50% of samples and found qualitatively similar results to those obtained using a 90% non-core cutoff, except where noted below (see Supplementary Results). We additionally repeated the analyses on the whole dataset without differentiating the core and non-core microbiomes, and found the results to be qualitatively similar to the core dataset (see

Table 1 Sample sizes for each social group and baboon age/sex classes

Dataset	Number of samples	Number of samples in Mica's group	Number of samples in Viola's group	Number of individual hosts	Number of individual hosts in Mica's group	Number of individual hosts in Viola's group
All samples	178	67	111	78	27	51
Adult females	57	22	35	30	11	19
Adult males	61	28	33	19	9	10
Juveniles	60	17	43	29	7	22

Supplementary Results). Alpha and beta diversity metrics were calculated in QIIME.

Statistical analyses

Unless noted, all statistical tests were run in R (R Development Core Team 2014) and performed separately for the core and non-core datasets.

Testing H1: Sociality promotes gut microbial alpha diversity

We constructed linear mixed models using the *lmekin* function in the *coxme* package with the following fixed effects: the individual's current social group, sex, grooming partner diversity, and age (Supplementary Table S2; see Supplementary Methods for information on how each of these were collected; Therneau 2015). We note that we did not test direct effects of group size (as opposed to group identity) because we only tested samples from two social groups. Kinship was incorporated in the random effect estimate to control for repeated sampling from some individuals and for relatedness in our study population (Supplementary Table S3). We used three measures of OTU alpha diversity as response variables to capture different aspects of diversity: OTU richness (i.e., the number of distinct OTUs in a sample), Shannon's H (to account for evenness of OTU distribution), and Faith's phylogenetic diversity (to test for a phylogenetic signature; Bates et al. 2015). The best-fitting models were identified using the log likelihood criterion.

Testing H2: Group living and social relationships within groups promote gut microbial community similarity

Gut microbial dissimilarity between individuals was estimated using weighted UniFrac (Lozupone and Knight 2005). Weighted UniFrac was chosen because it accounts for both differences in microbial abundance and evolutionary relationships between taxa (Lozupone and Knight 2005), although we found similar results when we repeated the analyses using unweighted UniFrac and Bray-Curtis beta diversity metrics (see Supplementary Results). To test whether members of the same social group had more similar gut microbiomes than members of different social groups, we performed PERMANOVA in the *vegan* package (Oksanen et al. 2012). Because some individuals were sampled more than others, and because samples from the same individual had similar community compositions (PERMANOVA; $r^2 = 0.64$, $P < 0.001$; Supplementary Fig. S3), all analyses were conducted with one, randomly chosen sample per individual. We ran 1000 iterations of random subsampling to one sample per individual to check the robustness of the resulting r^2 value to the samples included in our analysis. Because the r^2 values varied little across random subsamples, we report the mean r^2 value and associated permutation-based P values in the main text.

Baboon social groups contain maternal and paternal kin (Van Horn et al. 2007), so we ran partial Mantel tests to rule out kinship as a potential explanation for group level microbiome differences. We randomly subset the dataset to one sample per individual and ran 1000 iterations to produce a pseudo Mantel r and permutation-based P value for social effects on beta diversity, controlling for kinship.

To identify OTUs that differed significantly in abundance between social groups, we used linear discriminant effect size analysis (LEfSe; v.1) (Segata et al. 2011). We set the Kruskal–Wallis alpha level to 0.01 and the threshold on the logarithmic LDA scale to 3.0.

To test whether close grooming partners had more similar core and non-core microbiomes than individuals who rarely groomed each other, we ran partial Mantel tests on matrices of within-group beta diversity and grooming bond strength, controlling for kinship or diet for each social group using the *vegan* package in R (Supplementary Tables S4–S7; Oksanen et al. 2012).

Testing H3: Immigrant males who join a social group acquire their new group's gut microbiome

We averaged the weighted UniFrac values between a sample from an immigrant male and samples from all other adult residents of the group who had been members of the social group for ≥ 1 year. We then

ran linear mixed models with mean weighted UniFrac distance as the response variable, length of the immigrant male's group membership as a fixed effect, and individual identity as a random effect.

Results

Defining the core and non-core gut microbiome

We identified 16,583 gut microbial OTUs in the 178 samples in our dataset. These OTUs exhibited a right-skewed distribution across samples such that the vast majority of OTUs (98.7%) were found in <10% of samples (Fig. 1A). Therefore, following previous studies (Ugland and Gray 1982; Qin et al. 2010; Li et al. 2013; Ainsworth et al. 2015), we defined "core" OTUs as those present in ≥90% of samples. The 219 OTUs that comprised this core occurred in 97.8% ± 3.0% (median ± SD) of samples and 98.7% of individuals (±1.9%; accounting for repeat sampling), and they comprised the majority of the sequencing reads in each sample (median ± SD = 62.0% ± 14.7%). The remaining 16,364 OTUs were classified as "non-core" OTUs. Each non-core taxon occurred in 2.8% ± 14.5% (median ± SD) of samples and 5.1% ± 18.3% of individual subjects. Only six phyla occurred in the core microbiome: Bacteroidetes (mean per sample abundance = 39.7%), Firmicutes (36.0%), Actinobacteria (15.6%), Verrucomicrobia (8.2%), Proteobacteria (0.4%), and Cyanobacteria (0.08%). In contrast, 29 phyla were represented in the non-core microbiome, including the six phyla also found in the core microbiome (Fig. 1C). Nineteen bacterial families were found in the core microbiome and 216 families in the non-core (Fig. 1D).

Group living, but not grooming partner diversity, predicted gut microbial alpha diversity

We expected gut microbial alpha diversity to be positively correlated with social group size and grooming partner diversity. With only two social groups, our ability to infer effects of group size is limited. However, we found that, for both the core and non-core microbiome, individuals living in the larger social group (Viola's) exhibited higher gut microbial OTU richness than individuals in the smaller social group (Table 2 and Fig. 2A and B). Further, contrary to our expectations, the difference between the groups was more evident in the core gut microbiome than the non-core microbiome (Table 2 and Fig. 2A and B). Members of Viola's group had 1448 ± 302 (median ± SD) non-core OTUs per sample, compared to 1238 ± 221 non-core OTUs in Mica's group. This pattern was also apparent among the 219 core OTUs (Table 2; Viola's group had 215 ± 8.5 (median ± SD) core OTUs per sample compared to 212 ± 7.1 in Mica's group; Fig. 1B). Because core OTUs defined for the entire study population, by definition, minimize differences between the two social groups, we also repeated our analyses of between-group differences in the size of the core microbiome by defining group-specific core microbiomes (i.e., based on presence in ≥90% of members of each group, rather than the entire study population). We found that Viola's group had a larger group-specific core microbiome than Mica's group (Fig. 2B), with 270 group-specific core OTUs in Viola's group, while Mica's group only had 218 group-specific core OTUs (Fig. 1B).

Contrary to our predictions, we found no evidence that individuals with more diverse grooming relationships had higher gut microbial alpha diversity. Indeed, there was no relationship between an individual's grooming partner diversity and microbiome diversity for any measure of alpha diversity in either the core microbiome or the non-core microbiome ($P > 0.28$ for all linear mixed models).

Social effects on gut microbial beta diversity include the core microbiome

As in previous work in this population (Tung et al. 2015), we found that members of the same social group harbored more similar gut microbiomes than members of different social groups. Here, we observed that this effect extended to both the core and non-core microbiome. Social group membership explained 13.9% of the variance in gut microbial composition for the non-core microbiome (PERMANOVA of weighted UniFrac distances: non-core microbiome permuted $r^2 = 0.139$, permuted $P = 0.001$; Fig. 2C), and 4.7% for the core microbiome (PERMANOVA of weighted UniFrac distances: core microbiome permuted $r^2 = 0.0477$, permuted $P = 0.007$; Fig. 2D), even though core microbiome taxa, by definition, occurred in subjects from both groups. These group-level differences were not driven by kinship between members of the same social group. Gut microbial beta diversity between hosts was still correlated with group membership, even controlling for kinship (partial Mantel; core microbiome permuted $r = 0.099$, permuted $P = 0.014$; non-core microbiome permuted $r = 0.396$, permuted $P = 0.001$). Further, microbiome beta diversity between hosts was not correlated with kinship, controlling for group membership (partial Mantel; core microbiome permuted $r = 0.004$,

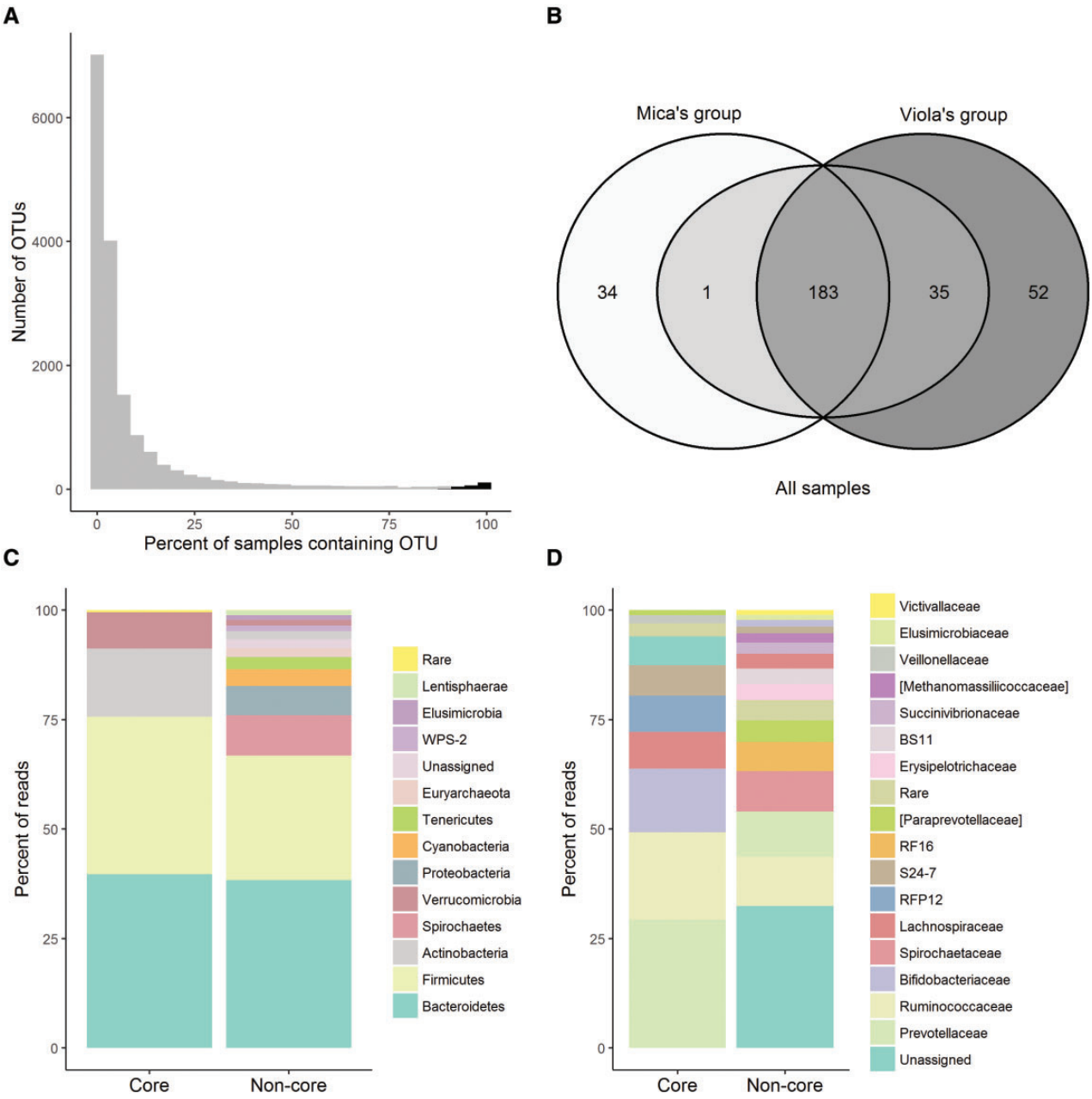

Fig. 1 (**A**) Histogram of OTU prevalence in the 178 microbiome samples in this study. Core OTUs, shown in black ($n = 218$), were found in ≥90% of samples; the remaining OTUs were considered non-core OTUs ($n = 16{,}364$). (**B**) Venn diagram showing overlap in the number of core OTUs across the whole dataset (light gray), core OTUs in Mica's group (white), and core OTUs in Viola's group (dark gray). Numbers indicate overlap counts between datasets; e.g., 183 OTUs are found in ≥90% of the samples in the whole dataset, ≥90% of the samples in Mica's group, and ≥90% of the samples in Viola's group. The 219 core OTUs used in many of our analyses include 183 OTUs that are part of the core microbiome in both social groups, 1 OTU that is part of Mica's core, but not Viola's, and 35 OTUs that are part of Viola's core, but not Mica's. (**C**) Mean relative abundance of bacterial phyla represented by core and non-core OTUs across all samples. Rare phyla were those that comprised, on average, <1% of reads per sample. (**D**) Mean relative abundance of bacterial families represented by core and non-core OTUs across all samples. Rare families were those that comprised, on average, <1% of reads per sample. Bracketed taxa indicate taxon names proposed by the greengenes curators (DeSantis et al. 2006).

permuted $P = 0.55$; non-core microbiome permuted $r = 0.026$, permuted $P = 0.216$).

Linear discriminant effect analysis (LEfSe) revealed several taxa that differed significantly in relative abundance between the two social groups. In the core microbiome, these differences were largely driven by OTUs from two genera (*Bifidobacterium* and *Faecalibacterium*) and two families (Coriobacteriaceae and RFP12) (Supplementary Fig. S4). *Bifidobacterium* also differed in relative

Table 2 Linear mixed models predicting variation in gut microbial alpha diversity in baboons ($n = 178$ samples from 78 individuals)

	Fixed Effects	Estimate	Standard Error	z	*P*	Direction of Effect
Core						
OTU richness	Social group	0.556	0.169	3.29	0.001	Viola's > Mica's
	Age	0.0226	0.0167	1.36	0.18	—
Shannon's H	Social group	0.221	0.0769	2.87	0.004	Viola's > Mica's
	Age	0.0334	0.0077	4.34	<0.001	older > younger
Faith's PD	Social group	0.224	0.062	3.62	<0.001	Viola's > Mica's
	Age	0.014	0.006	2.28	0.022	older > younger
Non-core						
OTU richness	Social group	227.8	48.86	4.66	<0.001	Viola's > Mica's
	Age	14.8	4.84	3.05	0.002	older > younger
Shannon's H	Social group	0.0911	0.127	0.72	0.47	—
	Age	0.0326	0.0125	2.60	0.009	older > younger
Faith's PD	Social group	0.864	1.019	0.85	0.4	—
	Age	0.344	0.101	3.39	<0.001	older > younger

Note: Models show fixed effects that were significant in at least one model. We also tested sex and grooming partner diversity as fixed effects, but these factors were never significant. Kinship between baboons was modeled as a random effect.

abundance between social groups in the non-core microbiome, along with the genera *Prevotella*, *YRC22*, *Coprococcus*, *Succinivibrio*, and *Treponema* (Supplementary Fig. S5). When the non-core microbiome was defined more stringently, however, (50% instead of 90% threshold), non-core OTUs in *Bifidobacterium* did not differ in relative abundance between social groups (Supplementary Results).

In Viola's group, but not Mica's, we found that close grooming partners had more similar core microbiomes than individuals who rarely groomed each other (Fig. 3). In Viola's group, close grooming partners had more similar core gut microbiota and trended toward significance for non-core microbiota (partial Mantel tests controlling for kinship: core microbiome, $r = 0.071$, $P = 0.009$; non-core microbiome, $r = 0.051$, $P = 0.0549$; partial Mantel tests controlling for diet: core microbiome, $r = 0.064$, $P = 0.047$; non-core microbiome, $r = 0.0597$, $P = 0.06$). We did not find that grooming partners had more similar microbiomes in Mica's group (partial Mantel tests controlling for kinship: core microbiome, $r = 0.085$, $P = 0.11$; non-core microbiome, $r = 0.083$, $P = 0.12$; partial Mantel tests controlling for diet: core microbiome, $r = 0.0725$, $P = 0.18$; non-core microbiome, $r = 0.1298$, $P = 0.065$). However, when we re-defined the non-core microbiome as taxa present in <50% of samples, grooming relationship strength significantly predicted gut microbial similarity for Mica's group (Supplementary Results; partial Mantel tests controlling for kinship: $r = 0.143$, $P = 0.024$; partial Mantel tests controlling for diet: $r = 0.154$, $P = 0.034$). Further, the similar core microbiome effect sizes in both groups suggests that the lack of a significant relationship in Mica's group may be due to lower statistical power (smaller sample size) than in Viola's group. Subsetting Viola's group to the same number of samples as Mica's group no longer yielded significant grooming effects in Viola's group (partial Mantel tests controlling for kinship on 1000 random subsets: core microbiome permuted $r = 0.068$, permuted $P = 0.18$). However, additional samples (e.g., repeated samples over time) would be needed to definitively distinguish between lack of power and lack of a true effect in Mica's group.

Longer male residency increases gut microbiome similarity to other group members

Immigrant males who had lived in their current social group longer had core and non-core microbiota that were more similar to other long-term adult group residents than males with shorter group residency times (Table 3 and Fig. 4). If these effects were solely due to dietary shifts when males moved between groups, we would expect microbiome convergence to occur relatively quickly, over a period of a few days (David et al. 2014). Instead, our results suggest that this process occurs over a more extended time period (months to years). Immigrant males may acquire some microbes from group members via physical contact. Consistent with this hypothesis, we found that immigrant males who had been in the group longer engaged in more frequent

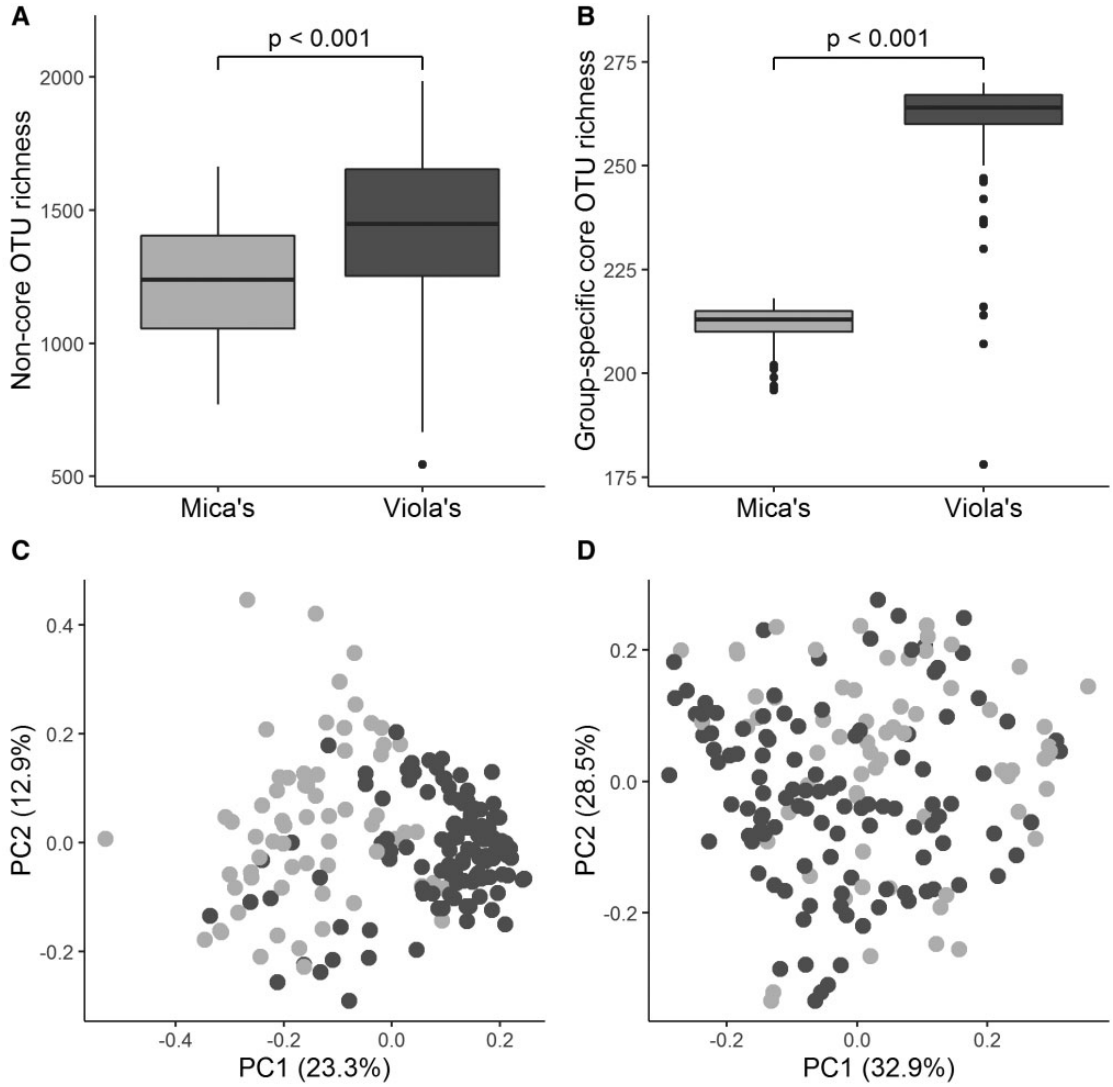

Fig. 2 Boxplots showing differences in gut microbial OTU richness for (**A**) non-core and (**B**) the group-specific core gut microbial communities in each social group. Plots C and D show principal coordinates analyses of weighted UniFrac dissimilarities for (**C**) non-core and (**D**) core gut microbial communities. Mica's group is shown in light gray and Viola's group is shown in dark gray for each panel.

grooming interactions than males who had recently immigrated to the group (linear model; $\beta = 0.05063$, $P = 0.001$). Figure 4 appears to show that males who had been group members for less than a year had greater variance in similarity to long-term residents than adult males who had been members for over year. However, we found no statistical evidence for this pattern (Bartlett's Test for differences in variance; $P > 0.5$ for both the core and non-core microbiome), and, when we subset the data to immigrant males who had been group members for <1 year, we did not find that individuals with greater social integration had more similar microbiomes to the rest of the group than those who were less socially integrated. Future work that uses a longitudinal study design would have more power to detect such a relationship.

Finally, we also found that, compared to females, males had more diverse core gut microbiomes based on Shannon's H (linear mixed model; $z = 2.07$, $P = 0.039$), and more diverse non-core gut microbiomes based on Faith's PD (linear mixed model; $z = 2.97$, $P = 0.003$). While there are many physiological and behavioral differences between male and female baboons, these results are consistent with the idea that sex-differences in dispersal lead to higher gut microbial alpha diversity in males than in females. However, this result should be treated with caution as we did not observe sex differences in all three measures of alpha diversity; we found no differences in gut microbial richness between males and females (linear mixed models; $z = -0.30$, $P = 0.7$ for core OTU richness and $z = 1.66$, $P = 0.096$ for non-core OTU richness). Further, we did not find

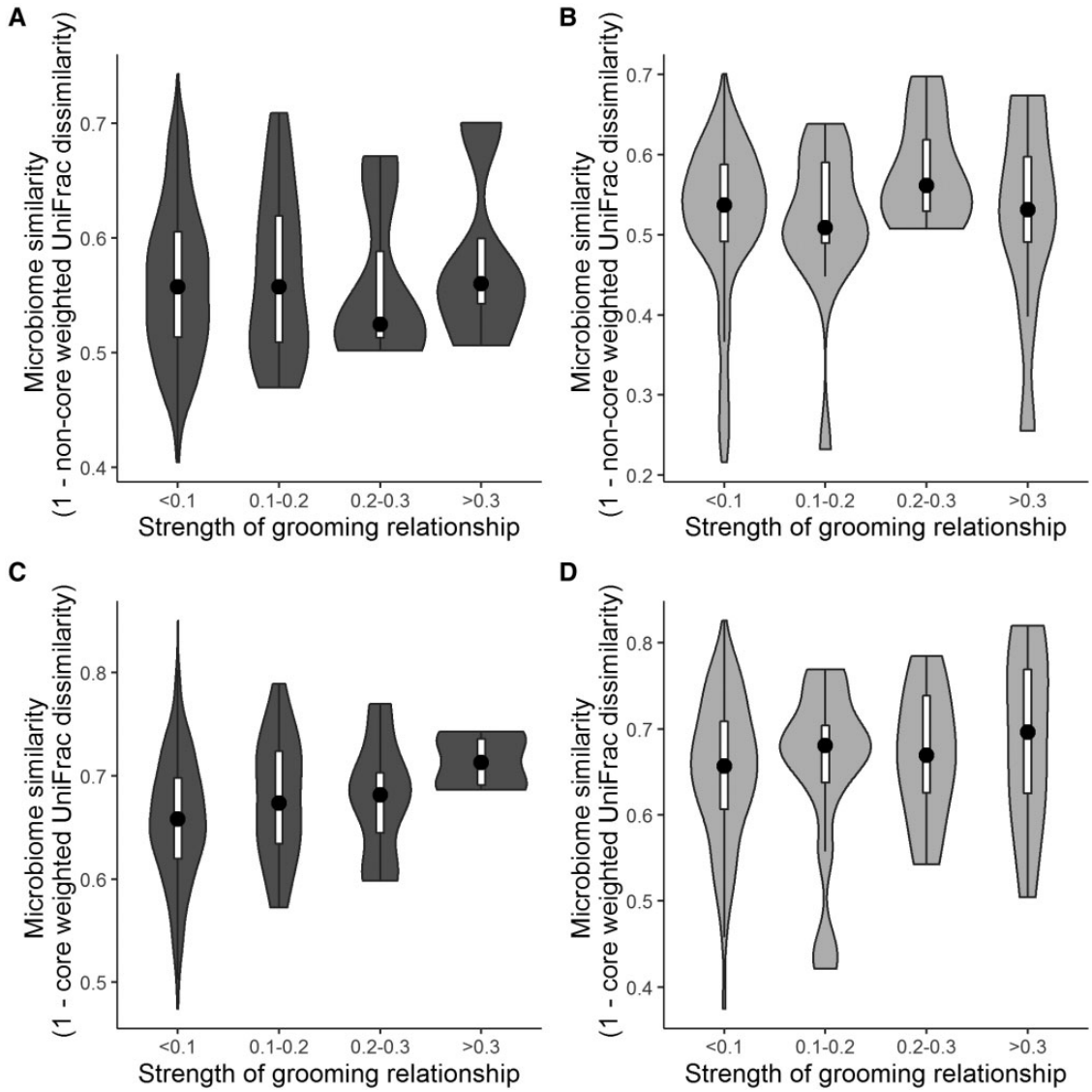

Fig. 3 Violin plots showing the relationship between the strength of grooming relationships and the gut microbial communities. Black dots represent median values and white rectangles represent the first and third quartiles of the data. Rotated kernel density plots representing the underlying data are shown on each side. Stronger bonds predict more similar gut microbiotas in (**C**) the core microbiome in Viola's group but not in (**A**) the non-core microbiome in Viola's group, (**B**) the non-core microbiome in Mica's group, or (**D**) the core microbiome in Mica's group.

statistically significant sex differences in microbial alpha diversity in either the non-core 50% analysis or the whole microbiome (Supplementary Results).

Discussion

Social effects occur in both core and non-core gut microbial taxa

The processes that shape gut microbial presence and abundance are thought to differ for core and non-core gut microbial taxa. Core taxa may be acquired early in life and, because they make substantial contributions to basic gut microbial functions (Walter and Ley 2011; Shade and Handelsman 2012; Zhang et al. 2016), they may be actively retained and managed by hosts (Hansen et al. 2010; Franzosa et al. 2015; Hooper et al. 2012b). In contrast, non-core taxa do not occur consistently between hosts, or even in the same host over time, and their dynamics are thought to reflect recent environmental and social transmission events (Martínez et al. 2013; Tinker and Ottesen 2016). If true, social signatures on the gut microbiome should be stronger in non-core versus core taxa. However, we found that social interactions predict microbiome composition for both core and non-core taxa, and we detected stronger effects in the core microbiome than the non-core microbiome in some cases.

Table 3 Best supported linear mixed models (based on the log likelihood criterion) predicting gut microbial similarity between immigrant males ($n = 61$ samples from 19 individuals) and long-term, adult group residents ($n = 78$ samples from 38 individuals)

	Fixed effects	Estimate	Standard error	DF	*t*	*P*	Direction of effect
Core							
Weighted UniFrac	consecutive years in group	−0.0281	0.0106	59	−2.64	0.0106	↑ time ↓dissimilarity
Non-core							
Weighted UniFrac	consecutive years in group	−0.0126	0.00306	9.39	−4.12	0.0024	↑ time ↓dissimilarity

Note: Subject identity was modeled as a random effect

There are several possible explanations for this finding. First, group-living and social interactions may predict gut microbial composition for both core and non-core taxa because of microbe-microbe interactions. Specifically, because microbes within a community interact, they likely promote or decrease each other's relative abundances in ways that are independent of microbial transmission. Hence even if transmission exerts stronger effects on non-core than core taxa, there may be ripple effects that influence the abundance of core microbiome taxa. Such ripple effects might be caused by competitive and mutualistic interactions between resident taxa (Ley et al. 2006; Coyte et al. 2015), as well as indirect interactions, such as when microbes alter the gut environment to make it more conducive for related taxa to thrive (Stecher et al. 2010). For instance, using a mouse infection model, Stecher et al. (2010) found that closely related bacterial phylotypes were more likely to co-occur in the same host than less related phylotypes. Mice with high levels of Lactobacilli were more likely to be successfully colonized by experimentally introduced *Lactobacillus reuteri* than mice with low abundances of Lactobacilli. This "like will to like" phenomenon, in which closely related taxa co-occur and promote related taxa, has been found in environmental microbes (Chaffron et al. 2010) and in human gut microbes including *Bifidobacterium* spp. and Proteobacteria, both of which occur in our dataset (Lozupone et al. 2012a).

A second explanation is that socially mediated transmission is likely not restricted to non-core taxa, but also exerts strong effects on the abundance of core microbes. It is well known that physical contact between individuals shapes the core microbiome early in life (e.g., Ley et al. 2005; Walke et al. 2011; Sanders et al. 2014); hence individuals may continue to acquire core microbes from conspecifics throughout life. In support, Billiet et al. (2016) found that limiting contact with nestmates or colony material in adult bumblebees led to a significant drop in the abundance of certain core taxa. Further, Li et al. (2016a) suggest that pikas acquire core gut microbial taxa in adulthood via coprophagy. Although the baboons in our study are not coprophagic, physical contact between group members may lead to the transmission of core gut microbes (Song et al. 2013), and future work should explore if mechanisms of social transmission differ between terrestrial hosts, who presumably have more contact with fecal material, and their closely related arboreal relatives. Indeed group members are proposed to serve as reservoirs for core microbes, and it may be advantageous for a host to access a social reservoir of core microbes to recover after an illness or to adapt to local circumstances (Lombardo 2008; Moeller et al. 2016a).

Finally, other aspects of group living, besides social transmission, may influence the abundance of core and non-core gut microbial taxa—at least at the social group level. Specifically, Mica's and Viola's groups had only nominal home range overlap in the year prior to sampling (Supplementary Fig. S1; Tung et al. 2015). Hence, the members of each social group may have been colonized by distinct sources of environmentally transmitted microbes. Other studies have found group- or site-specific microbes in species with geographically close but non-overlapping territories (Leclaire et al. 2014; Maurice et al. 2015; Bennett et al. 2016). For instance, in one study of wild pikas, a substantial portion of the core gut microbes harbored by individuals were also common in local environmental samples (Li et al. 2016a). However, this mechanism cannot explain within social group effects, such as those linked to grooming relationships, because members of the same social group experience very similar environmental exposures, and controlling for habitat use does not remove the effects of grooming on gut microbial similarity (Tung et al. 2015).

Regardless of the underlying explanation for why social effects extend to both the core and non-core microbiome, social structuring in the core microbiome could have functional consequences for hosts. For example, the genus *Bifidobacterium*, which was

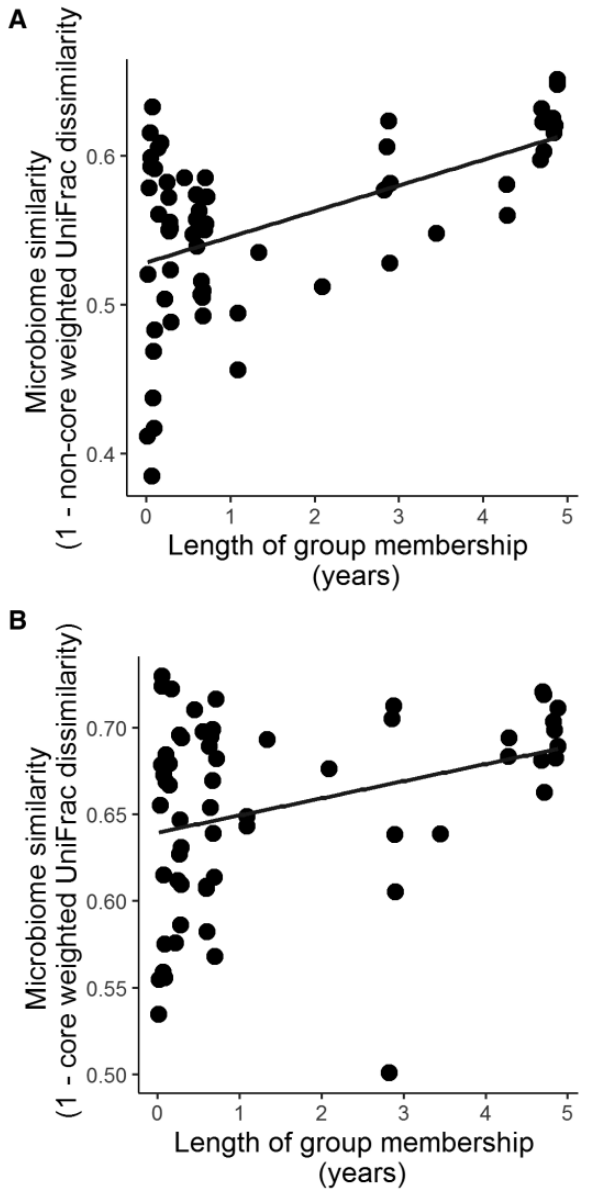

Fig. 4 The longer an immigrant male has lived in his new social group, the more similar his gut microbiome composition is to those of his new group members for both (**A**) the non-core microbiome and (**B**) the core microbiome. The *Y*-axis represents the average pairwise gut microbial similarity (1—weighted UniFrac dissimilarity) between a given sample from an immigrant male and the adult members of his current social group.

socially structured in baboon core and non-core microbiomes, colonizes the gut early in life and plays an important role in processing complex carbohydrates and producing vitamins (Pokusaeva et al. 2011; Turroni et al. 2014). *Faecalibacterium*, which was socially structured in the core microbiome, is one of the most common genera in the human microbiome and can indicate a disease state when present at low levels (Sokol et al. 2008; Miquel et al. 2013). Finally, the genera *Prevotella*, *Succinivibrio*, and *Treponema*, which were structured in the non-core microbiome, are associated with high-fiber human diets (Schnorr et al. 2014). *Treponema*, which was more abundant in the larger, more diverse baboon social group, has been proposed to be an indicator of high gut microbial diversity, perhaps indicating a healthy gut community (Schnorr et al. 2014). As these genera differ in abundance between social groups, future work in this study system could test if differences in individual health between social groups are correlated with the relative abundance of certain taxa.

Host social behavior and gut microbial alpha diversity

A growing number of studies propose that social partners serve as reservoirs of gut microbial diversity, and individuals with more social partners should exhibit higher gut microbial diversity than socially isolated animals (Lombardo 2008; Levin et al. 2016; Li et al. 2016b; Moeller et al. 2016b). In the baboons in our study, we found that the members of the larger social group exhibited higher gut microbial alpha diversity; however, individuals with the highest grooming partner diversity did not have the most diverse gut microbiomes. Although we cannot draw strong conclusions based on only two social groups, a possible explanation for our results is that indirect transmission of microbes from environmental sources may be more important in shaping baboon gut microbial alpha diversity than direct transmission via physical contact between hosts. For instance, the social group with more members (Viola's) also occupied a larger home range than the group with fewer members (Supplementary Fig. S1; Tung et al. 2015). Larger home ranges may put baboons into contact with more diverse microbes, especially if microbial populations are spatially heterogeneous, and if larger home ranges contain more diverse resources, substrates, and microbial communities. However, testing this hypothesis would require repeating these analyses with three or more social groups. To date, no studies have tested the relationship between home range area and gut microbial alpha diversity; but, previous research has shown that home range size predicts intestinal parasite diversity and abundance (Nunn and Dokey 2006; Bordes et al. 2009).

Regardless of the mechanism, social effects on gut microbial alpha diversity may have functional consequences for mammalian hosts. Some papers have proposed that diverse microbiomes are more stable and "healthier" than less diverse microbiomes (Dillon et al. 2005; Lozupone et al. 2012b). In free-living communities, biodiversity stabilizes ecosystems

such that more diverse communities experience less stochasticity (Tilman et al. 2006; de Mazancourt et al. 2013), greater stability against perturbations (Eisenhauer et al. 2012), and increased productivity (Lehman et al. 2000; Venail and Vives 2013). Alternatively, alpha diversity may be functionally redundant, such that multiple unrelated taxa can fulfill the same role (Shade and Handelsman 2012), or have potentially negative consequences, such as Chiyo and colleagues' finding that elephants that had greater gut *Escherichia coli* haplotype diversity also were more likely to harbor pathogenic strains (Chiyo et al. 2014). Further studies are necessary to demonstrate if differences in gut microbial communities have functional consequences for their hosts. Taken together, our results suggest that, if greater core microbial diversity is both biologically significant and beneficial, higher gut microbial alpha diversity may constitute a benefit of living in a large social group with a large home range

Dispersal and the local microbiome

In baboons and many other animals, the consequences of dispersal can range from higher risk of predation and difficulty finding food in unfamiliar habitats, to new reproductive opportunities and improved social status (Alberts and Altmann 1995; Bonte et al. 2012). Our results suggest a novel consequence of dispersal: changes in gut microbial composition. To our knowledge, ours is the first study to show that residence time in a social group predicts similarity of an immigrant animal's microbiome to those of other long-term group residents. There are several potential routes by which dispersing males may acquire a local microbiome, including changes in diet, microbial exposures from the environment, and microbial colonization from the members of their new social group. In our population, dietary shifts are unlikely to be the sole mechanism by which dispersal alters the gut microbiome. Dietary shifts in gut microbiome composition tend to occur rapidly, over hours or days (Turnbaugh et al. 2009b; Fernando et al. 2010; David et al. 2014), whereas our data suggest that males' microbiomes continue to converge with their new social group years after emigration. Thus, direct and indirect transmission are probably important in explaining our results, especially since males who have been resident in a social group longer groom more with others. These interactions create potential routes for direct transmission. In addition, we found that, by some metrics, immigrant males had more diverse microbiomes than adult females, who do not leave their natal groups. While hormonal or dietary differences between males and females may also contribute to male-female differences, the hypothesis that dispersal contributes to diversity in the gut microbiome will be important to test in the future, by comparing males with different dispersal histories over a similar time frame.

As yet, we do not know whether changes in the gut microbiome during dispersal have consequences for hosts, although it may be advantageous for immigrants to develop a "local microbiome" (i.e., one specific to the geographic region). Alberdi et al. (2016) proposed that a plastic gut microbiome may help vertebrate hosts adjust more quickly to changing environmental conditions. Research on humans shows that gut microbial composition correlates with the likelihood of developing gut-related illnesses when traveling (Youmans et al. 2015), which suggests that developing a local microbiome may help hosts adjust to local diets. Finally, some have proposed that a local microbiome can modulate susceptibility to local parasites (Koch and Schmid-Hempel 2012).

Prior research on the disease-related consequences of dispersal have tended to consider effects on the group itself, rather than the individuals who themselves transfer. For instance, social groups may minimize disease risk by excluding immigrants that display signs of illness or refusing to accept immigrants until after a "waiting period" that would reveal whether the immigrant was sick (Freeland 1976). However, because group members greatly outnumber dispersers, the social group should arguably have stronger effects on the microbiomes of immigrants than vice versa. Previous work on chimpanzees suggests that individuals who move between social groups maintain gut microbiome signatures from both groups (Degnan et al. 2012), consistent with our finding that dispersers acquire the local microbiome. One way to test this question in future studies would be to use longitudinal data to track a single disperser's microbiome, along with the microbiomes of individuals in the group that he immigrates into. Leveraging longitudinal data in species that disperse between social groups repeatedly throughout their adult lives, such as baboons, translates to a series of natural experiments that can provide insight into long-term social structuring of the microbiome. Understanding how social context modulates the gut microbiome over time, and the consequences of such effects, is a key area to pursue in future behavioral ecology research.

Acknowledgments

We thank D. Jansen and E. Miller for help with statistical analyses. We thank the Kenya Wildlife

Services, Institute of Primate Research, National Museums of Kenya, National Council for Science and Technology, members of the Amboseli-Longido pastoralist communities, Tortilis Camp, Ker and Downey Safaris, Air Kenya, and Safarilink for their cooperation and assistance in Kenya. A number of people contributed to the long-term data collection over the years, and we are grateful to all of them for their dedication and contributions. Particular thanks go to the Amboseli Baboon Project long-term field team (R.S. Mututua, S. Sayialel, and J.K. Warutere), and to V. Somen and T. Wango for their assistance in Nairobi. We are grateful to Karl Pinc for his contributions to the development of Babase, the Baboon Project database. We also thank the database technicians, particularly D. Onderdonk, C. Markham, T. Fenn, N. Learn, L. Maryott, P. Onyango and J. Gordon. This research was approved by the IACUC at Princeton University, the University of Notre Dame, and Duke University and adhered to all the laws and guidelines of Kenya.

Funding

This work was supported by the National Science Foundation and the National Institutes of Health, especially the National Institutes of Aging; in the past decade, in particular, the Amboseli Baboon Project acknowledges support from IOS 1053461, IBN 9985910, IBN 0322613, IBN 0322781, BCS 0323553, BCS 0323596, DEB 0846286, DEB 0846532, IOS 0919200, R01 AG034513, R21 AG049936, and P01 AG031719. This paper was also directly supported by IOS 1638630. We also thank Duke University, Princeton University, the University of Notre Dame, the Chicago Zoological Society, the Max Planck Institute for Demography, the L.S.B. Leakey Foundation, and the National Geographic Society for support at various times over the years.

Supplementary data

Supplementary data available at *ICB* online.

Data archiving

Sample metadata and supplements are available in the Dryad Data Repository (doi:10.5061/dryad.nh044). Raw sequencing data are deposited in NCBI's Short Read Archive (BioProject PRJNA388566).

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