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Synchrony and idiosyncrasy in the gut microbiome of wild baboons

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Human gut microbial dynamics are highly individualized, making it challenging to link microbiota to health and to design universal microbiome therapies. This individuality is typically attributed to variation in host genetics, diets, environments and medications but it could also emerge from fundamental ecological forces that shape microbiota more generally. Here, we leverage extensive gut microbial time series from wild baboons—hosts who experience little interindividual dietary and environmental heterogeneity—to test whether gut microbial dynamics are synchronized across hosts or largely idiosyncratic. Despite their shared lifestyles, baboon microbiota were only weakly synchronized. The strongest synchrony occurred among baboons living in the same social group, probably because group members range over the same habitat and simultaneously encounter the same sources of food and water. However, this synchrony was modest compared to each host's personalized dynamics. In support, host-specific factors, especially host identity, explained, on average, more than three times the deviance in longitudinal dynamics compared to factors shared with social group members and ten times the deviance of factors shared across the host population. These results contribute to mounting evidence that highly idiosyncratic gut microbiomes are not an artefact of modern human environments and that synchronizing forces in the gut microbiome (for example, shared environments, diets and microbial dispersal) are not strong enough to overwhelm key drivers of microbiome personalization, such as host genetics, priority effects, horizontal gene transfer and functional redundancy.

Mammalian gut microbiotas are highly complex, dynamic ecosystems. From these dynamics emerge a set of life-sustaining services for hosts, which help them digest food, process toxins and resist pathogens. Despite their importance, our understanding of how gut microbial communities change over time within hosts, especially the collective dynamics of microbiotas from hosts in the same population, is poor[1,2]. This gap exists in part because we lack time-series data that track gut microbiotas longitudinally across many hosts living together in the same population. As a result, it has been difficult to answer key questions. For example, when host populations encounter shifting environments and resources, does each host's microbiota respond similarly—that is, in synchrony—or idiosyncratically to these changes? Further, what factors predict synchronized versus idiosyncratic microbiota?

Answering these questions is important because synchronized gut microbial communities, if and when they occur[1], could help explain shared microbiota-associated traits in host populations, such as patterns of disease susceptibility[3,4]. A high degree of synchrony may also suggest that similar ecological principles govern changes in microbial composition across hosts[5]. Further, there is theoretical justification to expect coordinated microbial dynamics, as host populations and their microbiotas can be considered a 'microbiome metacommunity' (for example, refs. [6–9]). Metacommunity theory predicts that synchrony will arise across microbiotas if their hosts experience similar environmental conditions and/or high rates of microbial dispersal between hosts[10,11]. In support, fruit bats living in the same colony exhibit coordinated fur microbiota, due to shared environments and microbial dispersal[1].

However, even in the presence of such synchronizing forces, there are many reasons to expect that hosts in a microbiome metacommunity will exhibit idiosyncratic (individualized) microbial compositions and dynamics. First, idiosyncratic dynamics are expected when the same microbes in different hosts respond in different ways to environmental fluctuations, chance events or interactions with other microbes[12–15]. These forces are probably important in microbiotas where priority effects, functional redundancy and horizontal gene flow can cause the same microbe to play different ecological roles and exhibit different environmental responses in

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different hosts[16–19]. Second, several cross-sectional studies, in both humans and animals, find that individual hosts exhibit distinctive gut microbiotas and host identity explains a large fraction of population-wide microbiome taxonomic variation[1,20–25]. Further, some longitudinal studies in humans and animals find personalized gut microbial dynamics[1,24,26–28]. This personalization is usually attributed to interpersonal differences in diet, medications and lifestyle[27,29–31]. If correct, then idiosyncratic microbiome dynamics may be simply explained by a lack of shared environmental drivers rather than distinct microbiome responses to shared environments (but see ref. [27]). In contrast, if personalized dynamics persist even when hosts share the same environment, then (1) host-specific dynamics may not be solely attributable to interpersonal differences in lifestyles; (2) predicting the dynamics of microbial taxa in individual hosts may prove difficult; and (3) microbiome interventions that rely on manipulating taxa may face challenges beyond heterogeneity in lifestyles and instead may be related to conserved ecological principles across microbiomes.

Results and discussion

Baboon gut microbiota show seasonal and annual cycles. We tested for gut microbial synchrony using 17,265 16S ribosomal RNA gene sequencing-based microbiome profiles from 600 baboons living in 12 social groups over a 14-yr span[32] (Fig. 1a and Supplementary Fig. 1). The baboons were members of the well-studied Amboseli baboon population[33], who experience shared diets, environments and opportunities for between-host microbial dispersal. All groups used an overlapping ~60 km^2 range (Fig. 1b and Supplementary Video 1; ref. [32]) and all baboons experienced the same seasonal changes in rainfall and temperature. Seasonal weather patterns drive a rotating set of baboon foods, including grass corms in the dry season and growing grass blades and grass seed heads in the wet season[32,34,35] (Fig. 1c,d).

We began by visualizing annual and interannual fluctuations across all 17,265 samples over the 14-yr span of the data. Consistent with prior research on primates[36–38], we found population-wide, cyclical shifts in microbiome community composition across seasons and years (Fig. 2). This wet–dry seasonal cyclicity was primarily observable in the first principal component (PC1) of a principal component analysis (PCA) of centred log-ratio (clr)-transformed amplicon sequence variant (ASV) read counts (Fig. 2a,b and Supplementary Figs. 2–4; PC1 explains 16.5% of the variance in microbiome composition). PC1 exhibited its lowest values during the dry season and highest values during the wet season, mirroring monthly rainfall (Fig. 2b and Supplementary Fig. 4). PC1 was also linked to annual rainfall across years, exhibiting especially low values throughout 2008 and 2009, corresponding to the worst drought in the Amboseli ecosystem in 50 yr (Fig. 2a,b). We also observed small but statistically significant seasonal differences in PC2 and PC3 (8.4% and 3.7% of variation in community composition; Fig. 2c and Supplementary Figs. 2–4) and in measures of alpha diversity (Fig. 2c and Supplementary Figs. 4 and 5), as has been reported in other ecosystems[39]. Together, these seasonal changes are probably caused by seasonal shifts in plant phenology and its effects on diet (Fig. 1d), as well as the effects of rainfall and other weather variables on bacterial exposures from the environment (for example, soil communities and sources of drinking water).

In terms of individual microbiome taxa, 17% of phyla (2 of 12) and 38% of families (13 of 34) exhibited significant changes in abundance between the wet and dry seasons (Fig. 2c and Supplementary Table 1; linear models with false discovery rate (FDR) threshold = 0.05). These changes were significant for the phyla Firmicutes and Tenericutes (Fig. 2c,d and Supplementary Fig. 6) and were especially pronounced for the families Helicobacteraceae, Coriobacteriaceae, Burkholderaceae, Bacteroidales RF16 group, vadinBE97, Spirochaetaceae and Campylobacteraceae (Fig. 2c and Supplementary Fig. 7). Of the ASVs, 28% also exhibited significant changes in abundance across seasons (97 of 341 ASVs; linear models with FDR threshold = 0.05 for $n = 393$ models; Supplementary Fig. 8 and Supplementary Tables 2 and 3). However, most ASVs, families and phyla did not change in abundance, suggesting that many taxa play consistent roles in the gut throughout the year, including Kiritimatiellaeota, Elusomicrobia, Ruminococcaceae, Clostridiaceae 1 and Rikenellaceae (Fig. 2c, Supplementary Figs. 6 and 7 and Supplementary Table 1).

Baboon gut microbial dynamics are individualized. While the microbiome metacommunity exhibited cyclical, seasonal shifts in composition, microbiome dynamics across different baboons were only weakly synchronized. Instead, consistent with prior observations of microbiome personalization[1,20–25], patterns of temporal autocorrelation indicated that each baboon exhibited largely individualized gut microbiome compositions and dynamics (Fig. 3). In support, ASV-level Aitchison similarity was much higher for samples collected from the same baboon within a few days of each other than for samples from different baboons over the same time span, regardless of whether those animals lived in the same or a different social group (Fig. 3a,b; Kruskal–Wallis: $P < 2.2 \times 10^{-16}$ for all comparisons). Likewise, a PERMANOVA of Aitchison similarities between 4,277 samples from the 56 best-sampled baboons (Supplementary Fig. 9) revealed that host identity explained 8.6% ($P < 0.001$) of the variation in community composition, much larger than the variation explained by sampling day or month ($R^2 = 2.5\%$ and 1.4%), group membership (2.2%) or the first three PCs of diet (0.04–2.4%; Supplementary Table 4 and Supplementary Fig. 10).

Aitchison similarity among samples from the same baboon fell steeply for samples collected a few days to a few months apart, indicating that individualized dynamics are strongest for samples collected close in time (Fig. 3a–c). At longer time scales (for example, months and years), self-similarity was modest but samples from the same baboon were significantly more similar to each other than they were to samples from different baboons, even for samples collected several years apart (Fig. 3a,c and Supplementary Figs. 11 and 12). Following the initial steep decline in self-similarity, community similarity rose again at 12-month intervals, both within and between hosts, reflecting synchronized, seasonal microbial dynamics across the host population. These small, 12-month peaks in similarity were visible even for samples collected >5 yr apart, indicating that individual hosts and the population at large return to similar microbiome community states on 12-month cycles over several years (Fig. 3c). Hence, the patterns in Fig. 3a,c show both idiosyncratic and synchronized microbial dynamics: over short time scales, hosts are much more similar to themselves than they are to others but, on annual scales, all hosts are weakly synchronized across seasons.

The greater influence of individualized dynamics compared to synchronized dynamics can also be captured by comparing microbiome dynamics for deeply sampled hosts sharing the same habitat at the same time (Fig. 3d and Supplementary Fig. 13). For instance, during the 2008–2009 hydrological year, we collected nearly one sample per month from 17 baboons. When we aligned these time series, we observed little convergence to similar values within any given month and little evidence of shared changes in the top three PCs of ASV-level microbiome composition over time (Fig. 3d). Consequently, the microbiome of each baboon took a different path over the ordination space over the same 1-yr span (Supplementary Fig. 13 and see Supplementary Fig. 14 for similar results during 2007–2008).

Microbiome taxa varied in their contributions to individualized gut microbiome compositions (Fig. 3e and Supplementary Fig. 15). For the 56 best-sampled hosts (Supplementary Fig. 9), several phyla and families exhibited substantial variation in host mean clr-transformed abundance (across repeated samples for that host) compared to

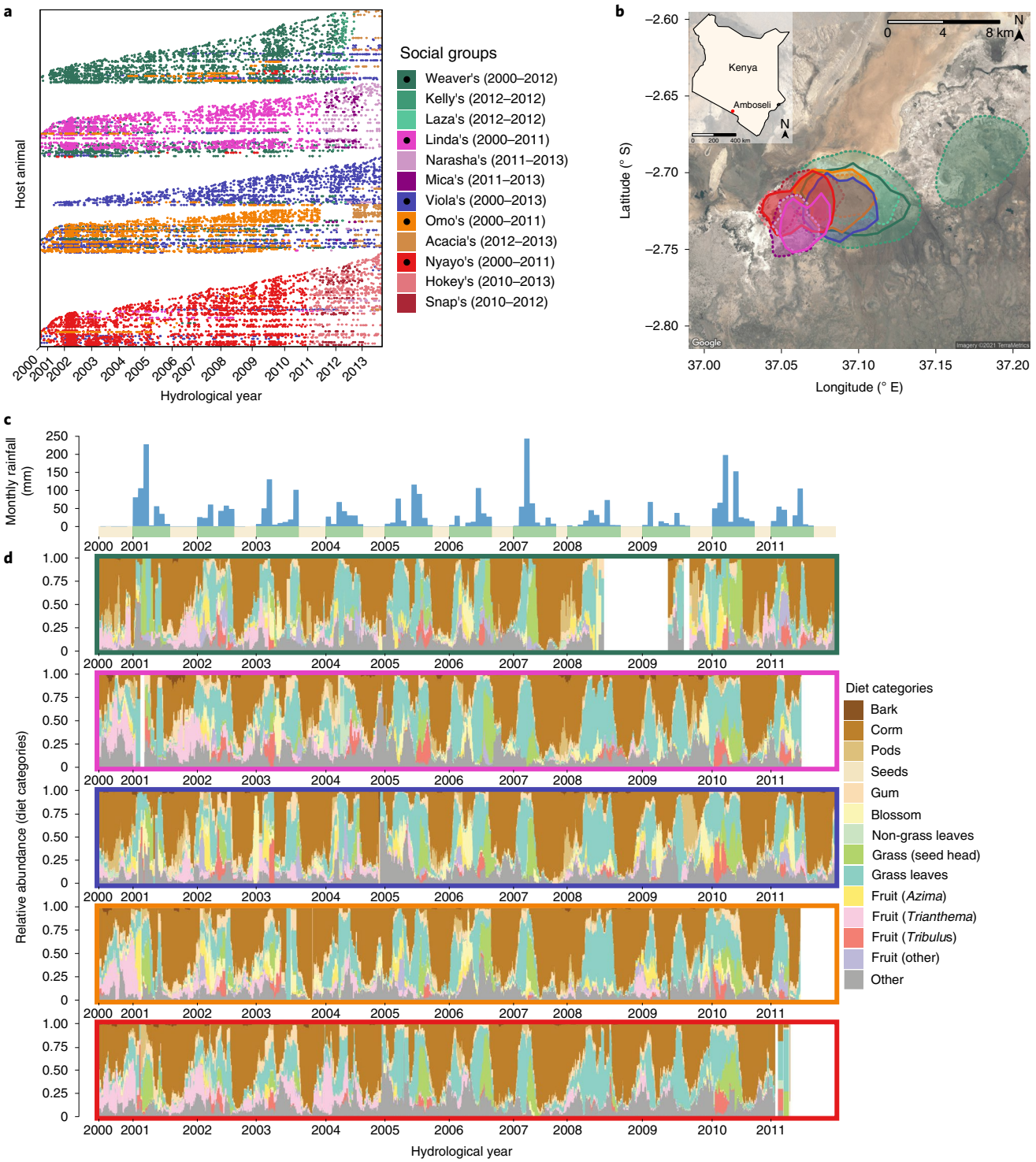

Fig. 1 | Baboons in Amboseli experience shared environments at multiple scales. a, Our microbiota time series consisted of 17,265 16S rRNA gene sequencing gut microbial profiles. Each point represents a microbiota sample, plotted by the date it was collected (*x* axis). Each row (*y* axis) corresponds to a unique individual host. Samples were collected from 600 wild baboons living in five original social groups (indicated by dark colours marked with black dots in the legend) and seven groups that fissioned/fused from these original groups (no black dots). **b**, All baboon groups ranged over a shared ~60 km^2 area and the social groups had largely overlapping home ranges. Ranges are shown as 90% kernel densities over the sampling period specific to each group; five original social groups are shown with solid borders, fission and fusion products with dashed borders. **c**, Monthly rainfall amounts (blue bars, in mm) with yellow and green stripes along the *x* axis representing dry and wet seasons, respectively, with the width of the green stripes reflecting the number of months within the focal year that had at least 1 mm of rainfall. **d**, Temporal shifts in diet from the years 2000 to 2013, shown as the relative abundance of diet components in the five original social groups over 30-d sliding windows before each sample collection date. Colours correspond to the 13 most common food types, while the grey bars correspond to other or unknown food types. Coloured boxes around each panel in **d** reflect each of the five original, most extensively sampled social groups (colours as in **a** and **b**). The white bars indicate time periods where no diet data were collected. Credit for base map in **b**: Google, TerraMetrics.

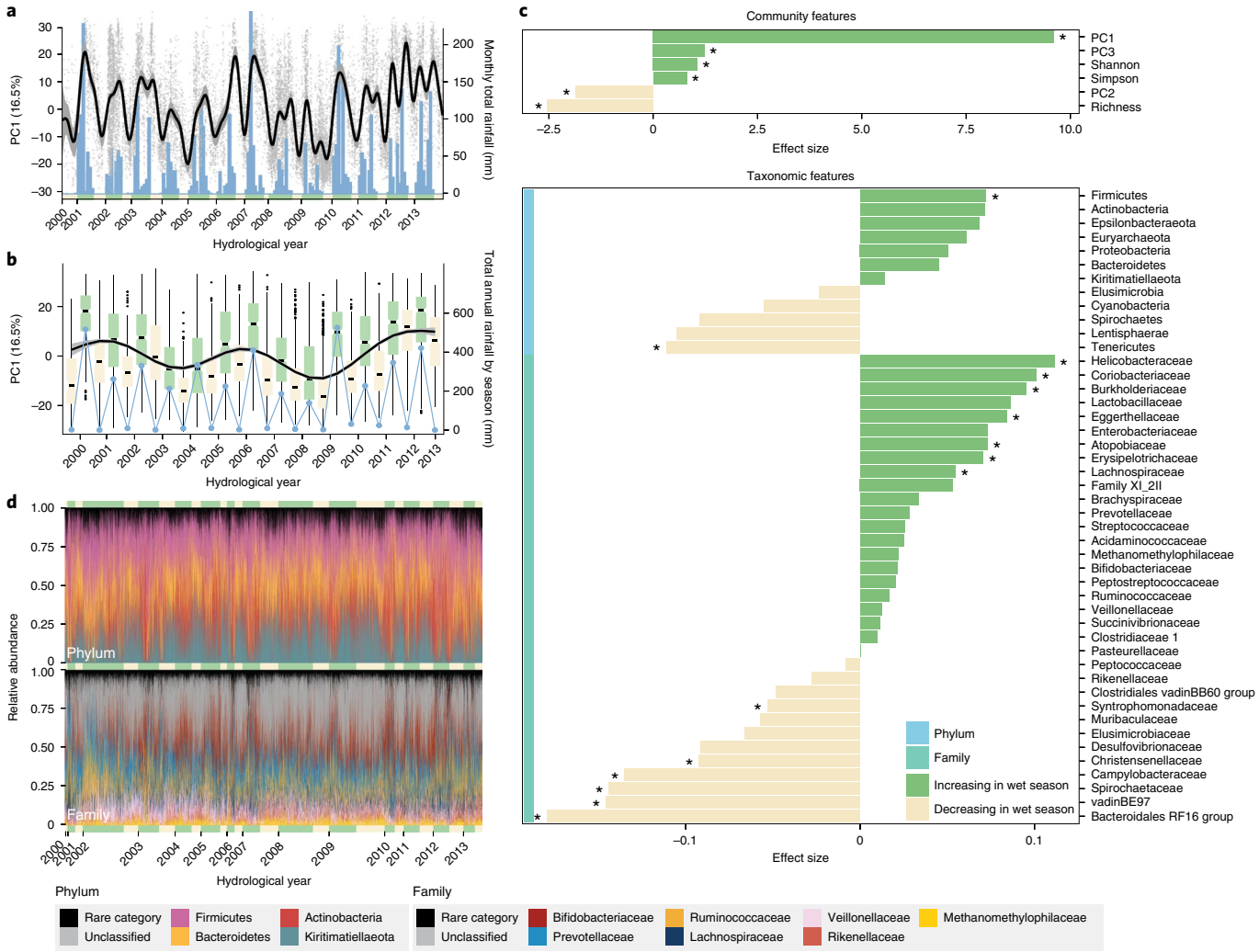

Fig. 2 | Baboons show population-wide, cyclical shifts in microbiome community composition across seasons and years. a, Changes in microbiome PC1 mirror monthly rainfall across all 14 yr. The grey points show values of PC1 for each of the 17,265 samples (*y* axis) on the dates they were collected (*x* axis). The black line and grey band are a plate regression spline and 95% simultaneous confidence interval for daily changes in microbiome PC1. Blue bars show monthly rainfall (right-hand *y* axis) and the yellow and green bars along the *x* axis represent dry and wet seasons, respectively, with the width reflecting the number of months within the focal year with at least 1 mm of rainfall. **b**, Changes in microbiome PC1 on an annual scale across all 14 yr ($n = 17{,}265$ samples). The box plots (box and whiskers indicate the median, 25th/75th percentile and 1.5× interquartile range (IQR)) show the distribution of PC1 in wet (green) and dry (yellow) seasons. The black line and grey band are a plate regression spline and 95% simultaneous confidence interval for annual changes in microbiome PC1. Blue points show total annual rainfall (right-hand *y* axis). **c**, The effect of season varies across 52 features of the microbiome, including six community features (top panel) and 46 taxa (bottom panel; 12 phyla, light blue vertical bar; 34 families, turquoise vertical bar; for 341 ASVs, Supplementary Fig. 13). Each horizontal bar shows the effect of season from linear mixed models for each feature. Asterisks indicate features that changed significantly between the wet and dry seasons ($n = 17{,}265$ samples; FDR threshold = 0.05). See Supplementary Figs. 6 and 7 for feature-specific smooths and Supplementary Fig. 8 and Supplementary Table 3 for results for ASVs. **d**, Bar plots showing the relative abundance of ASVs coloured by the four most common microbial phyla (above) and the seven most common families (below) across all 17,265 samples. Green and yellow bars along the *x* axes represent wet and dry seasons, respectively, with the width corresponding to the number of samples in the focal hydrological year and season. Of the ASVs, 22.9% (78 of 341) could not be assigned to a known family ('unclassified', shown in grey). The abundance of ASVs unclassified to family in the lower plot is ~35% because one unclassified ASV was the second most abundant ASV in the dataset, with a mean abundance of 16.9% across all samples (ASV no. 2, phylum Kiritimatiellaeota, order WCHB1-41; Supplementary Table 2).

their mean clr-transformed abundance across all hosts. These taxa included the phyla Cyanobacteria, Spirochaetes, Lentisphaerae and Elusimicrobia and the families Spirochaetaceae, vadinBE97, Elusimicrobaceae and Muribaculaceae (Fig. 3e and Supplementary Fig. 15). These highly variable taxa exhibited below-average abundances compared to less variable taxa (Supplementary Fig. 16). Hence, idiosyncratic dynamics may be more often linked to uncommon than common taxa, perhaps because uncommon taxa have greater functional variability across hosts.

To test whether individualized gut microbial dynamics could be explained by microbial dispersal limitation between hosts, we used the Sloan Neutral Community Model for Prokaryotes to estimate metacommunity-wide migration probabilities, *m*, for ASVs in each season and hydrological year[40,41]. Parameter *m* provides a measure of dispersal limitation because it represents the probability that 'vacancies' in a local community (a host's microbiome) will be replaced by dispersal from the microbiome metacommunity (other hosts), as opposed to reproduction within a focal host's community[40,41].

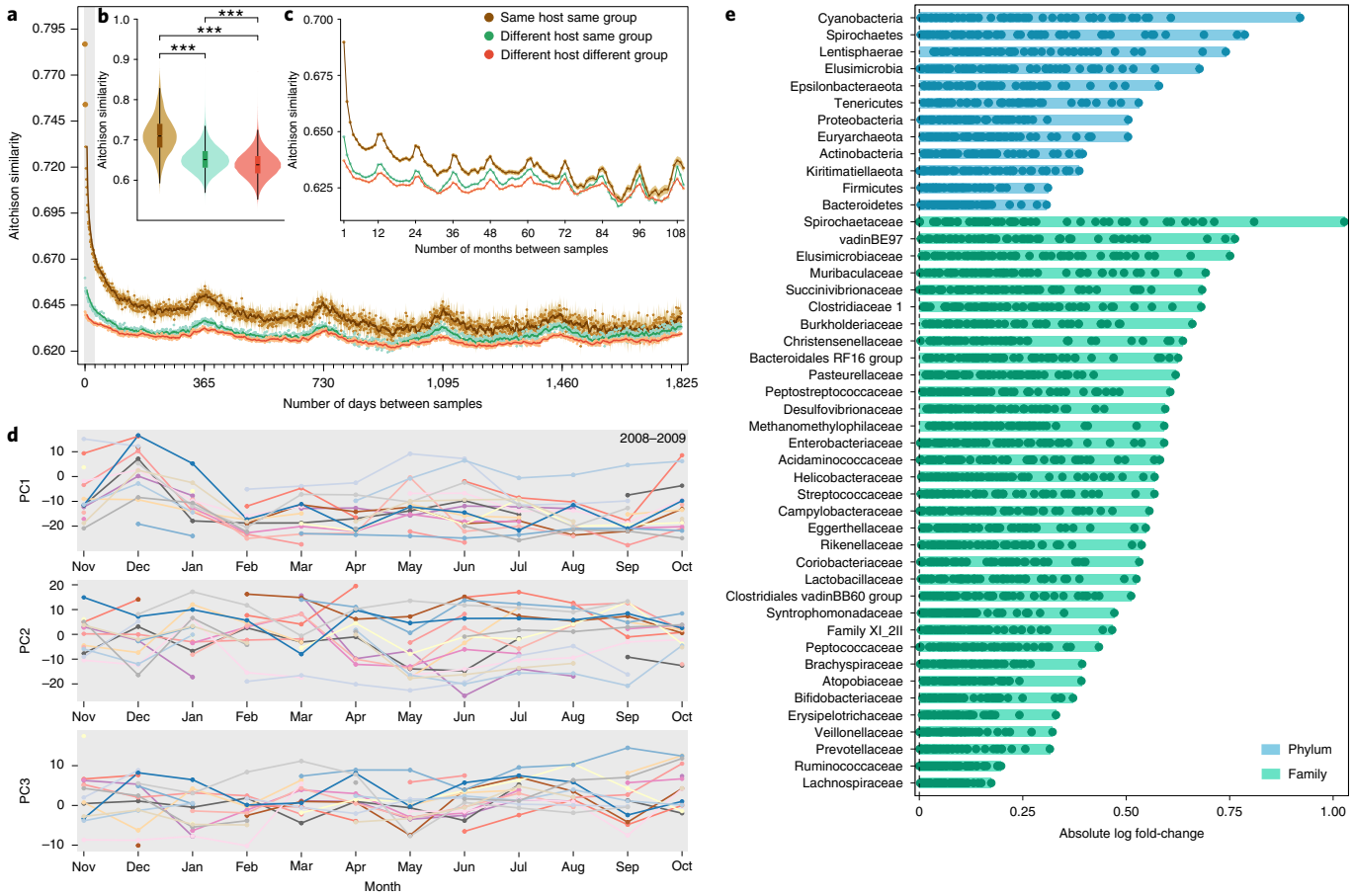

Fig. 3 | Baboons exhibit largely idiosyncratic gut microbial compositions and dynamics. a, Temporal autocorrelation in baboon gut microbiome communities for samples collected on the same day and up to 5 yr (1,825 d) apart. Points show mean ASV-level Aitchison similarity (*y* axis) between samples as a function of the number of days between sample collection (*x* axis; small tick marks correspond to months). Lines depict moving averages (window size = 7 d) and their ribbons show 95% confidence intervals. The grey region on the left indicates samples collected within 1 month of each other. Brown points show average Aitchison similarity between samples collected from the same baboon ($n = 392{,}817$ distinct sample pairs from 547 hosts with two or more samples); green points show similarity between samples from different baboons living in the same social group ($n = 16{,}391{,}761$ distinct sample pairs); orange points show similarity between samples from different baboons living in different social groups ($n = 77{,}520{,}289$ distinct sample pairs). **b**, Average Aitchison similarity between pairs of samples collected within 10 d of each other. Samples from the same baboon are significantly more similar than samples collected from different baboons in the same or different social groups (Kruskal–Wallis; $P = 2.22 \times 10^{-16}$; *n* distinct sample pairs = 5,791 for within-host comparisons; 218,340 for different host same group; 779,054 for different host different group). Box and whiskers indicate the median, 25th/75th percentile and 1.5× IQR. ***$P < 0.0001$. **c**, Temporal autocorrelation in Aitchison similarity on monthly scales for samples collected up to 10 yr apart (*n* distinct sample pairs = 496,057 for within-host comparisons; 23,433,667 for different host same group; 114,170,919 for different host different group). **d**, Microbiome dynamics for 174 samples from 17 baboons for which we had at least one sample from 10 months or more during the 2008–2009 hydrological year (November 2008 to October 2009). Panels show each individual's mean values for microbiome PC1, PC2 and PC3; each coloured line represents a distinct host. See Supplementary Fig. 14 for similar results during another densely sampled time period. Gaps indicate that the focal host did not have a sample in a given month. **e**, Some taxa have more idiosyncratic abundances than others. Each horizontal bar shows a given taxon's minimum and maximum absolute log fold-change in abundance across the 56 best-sampled hosts (hosts are represented as points within the bars; see Supplementary Fig. 9 for information on the 4,277 samples from the 56 best-sampled hosts). Absolute fold-changes were calculated, for a given taxon in a given host, as the taxon's average clr-transformed abundance across all samples from that host, relative to the taxon's grand mean in all hosts in the population. Hosts with large absolute fold-changes for a given taxon therefore have abundances of that taxon that are either well above or below average compared to its abundance in the host population at large (hosts with points close to zero exhibited taxonomic abundances typical of the population at large). For many taxa, hosts varied in their absolute log-ratio values, indicating that they also deviated substantially from each other in the abundance of those taxa. Taxa (*y* axis) are ordered (from top to bottom) by their highest absolute log-ratio value across the 56 best-sampled hosts. Blue bars represent microbial phyla; green bars represent families. See Supplementary Fig. 15 for a longitudinal version of this analysis for the most and least idiosyncratic phyla and families.

We found little evidence that dispersal limitation contributed to idiosyncratic compositions and dynamics. The probability that a given ASV lost from a host's microbiota would be replaced by an ASV from another host in the population was nearly 40% (average host population-wide *m* across seasons and years was 0.373 with range 0.332–0.416; Supplementary Fig. 17). These migration probabilities are generally lower than those others[9] found for marine sponges sampled from the same location (*m* across sponge species: minimum, 0.36; median, 0.78; maximum, 0.86) but much higher than for mice and nematodes, both in natural and laboratory populations (mice, $m_{wild} = 0.11$ and $m_{lab} = 0.18$; nematode, $m_{wild} = 0.03$ and $m_{lab} = 0.01$). Hence, dispersal limitation is low for baboon microbiota in Amboseli.

Interestingly, when we redefined the microbiome metacommunity to be the host's social group, instead of the whole host population, migration probabilities were similar (average m across groups was 0.355 with range 0.347 to 0.365; coloured points on Supplementary Fig. 17). Hence, despite several studies that find microbiome compositional differences between hosts living in different social groups, including in the Amboseli baboons[1,42–46], social groups are not major barriers to microbial colonization between baboons, perhaps because of their overlapping home ranges, similar diets and network connections via male dispersal (Fig. 1).

Shared environments lead to modest synchrony across hosts. To quantify the relative magnitude of idiosyncratic versus synchronized dynamics across the host population, social groups and hosts and to test whether synchrony varies for a set of common microbial taxa, we used generalized additive models (GAMs) to capture the nonlinear, longitudinal changes in 52 microbiome features (three PCs of ASV-level community variation, three metrics of ASV-level alpha diversity and clr-transformed relative abundances of 12 phyla and 34 families). For each feature, we ran three GAMs to measure the deviance explained in gut microbial dynamics by successive sets of parameters, reflecting the nested nature of our variables (Fig. 4a, x axis of Fig. 4c and Supplementary Table 5). The population-level model (model P) captured factors experienced by the whole host population, including average rainfall and maximum daily temperature in the 30 d before sample collection and random-effect splines to capture monthly and annual cyclicity in microbiome features (for example, Fig. 2a,b; see Supplementary Fig. 18 for effects of time of day, which was not included). The group-level model (model P + G) included all the predictor variables in model P and added a random-effect spline for each social group and variables to capture temporal changes in each group's diet, home range use and group size (Fig. 4a,c). The host-level model (model P + G + H) included all of the predictor variables in model P + G and added a random-effect spline for each host and variables for host traits, including sex, age and social dominance rank (Fig. 4a,c).

Consistent with our autocorrelation analyses (Fig. 3), comparing the deviance explained for each microbiome feature across the three models revealed stronger idiosyncratic than synchronized dynamics for most microbiome features (Fig. 4b,c). Host-specific factors, especially host identity, explained, on average, ten times the deviance in the longitudinal dynamics of microbiome features, compared to factors shared across all hosts and more than three times the deviance by factors shared with group members. Specifically, model P only explained on average 3.3% (range 0.46–14.0%) of the deviance across all 52 microbiome features (pink bars in Fig. 4b and Supplementary Table 6), compared to 8.1% on average after adding group-level factors to the population-level model (increase from model P to model P + G; range 2–25%; green bars in Fig. 4b and Supplementary Table 6) and 30.1% of the deviance after including host-level dynamics (model P + G + H; range 11.0–62.2%) for the same set of features (yellow bars in Fig. 4b and Supplementary Table 6). Importantly, the added deviance for model P + G + H compared to model P or model P + G was not caused by including more parameters. Randomizing host identity and host-level traits across samples, while keeping each sample's annual, seasonal and group identity intact, led to a substantial drop in deviance explained compared to the real data (Supplementary Fig. 19).

Of the 52 microbiome features, 44 exhibited greater gains in deviance by adding host-level factors to model P + G, compared to adding group-level factors to model P. Of these 44 features, 22 features gained >20% deviance explained between model P + G and model P + G + H (Fig. 4b and Supplementary Table 6). Three of the most common phyla, Actinobacteria, Bacteroidetes and Firmicutes all gained >20% deviance explained between model P + G and model P + G + H (Actinobacteria, 27.1%; Bacteroidetes, 24.6%; Firmicutes, 25.2%; Fig. 4b and Supplementary Table 6). The most idiosyncratic features (those that gained >30% deviance explained by adding host-level factors), were microbiome PC2, the phylum Euryarchaeota and the families Campylobacteraceae, Methanomethylophilaceae and Desulfovibrionaceae (Fig. 4b and Supplementary Table 6). Even the most synchronous feature, microbiome PC1 (14% deviance explained by the P model), gained 23.2% deviance explained when adding host-level factors to the P + G model.

Removing covariates from model P + G + H one at a time, while keeping all other covariates intact, revealed that host identity explained nearly all of the deviance in our models (Fig. 4c and Supplementary Table 6; average loss in deviance explained by removing host identity was 17.3% versus 0.2% deviance for all other factors). Beyond host identity, the next most important factor was the geographic area where the group travelled in the 30 d before sample collection, which explained 1% of the deviance, on average, across all 52 features (Supplementary Fig. 20 and Supplementary Table 6). All other individual predictor variables had only minor effects on deviance explained (Supplementary Fig. 20 and Supplementary Table 6).

To investigate whether some of the idiosyncrasy we observed was due to host genetic effects, we tested for a relationship between the deviance explained by each GAM and the narrow-sense heritability (h^2) of microbiome taxon abundance as estimated previously[32]. We found that higher levels of deviance explained by model P + G + H were predicted by higher taxon heritability (Pearson's correlation $R = 0.37$, $P = 0.016$; Fig. 5a). In contrast, we found no such effect at the population or group level, as expected since genotype is a property of individual hosts, not groups or populations (model P + G, $R = 0.047$, $P = 0.76$; model P, $R = 0.0085$, $P = 0.96$; Fig. 5b). We explained substantially more deviance by adding the host level to model P + G for microbiome taxa with $h^2 > 0.05$ than we did for taxa with very low h^2 values (model P + G + H, minimum 16.0, median 32.6, maximum 53.4 versus model P + G, minimum 4.6, median 11.1, maximum 26.8; Fig. 5b). Hence, some idiosyncrasy in gut microbiome dynamics is probably a consequence of differences in host genotype. However, because h^2 estimates cannot be mapped directly onto estimates of deviance explained in GAMs, direct estimates of genetic versus environmental effects on host dynamics remain an important topic for future work.

The strongest synchrony is among social group members. Previous research finds that hosts in the same social group have more similar gut microbiota than hosts in different groups[1,42–44,47]. Likewise, in our current dataset, several taxa exhibited abundances that were, on average, higher or lower within a given group compared to their average abundance in the host population at large (Supplementary Figs. 21 and 22). Hence, we tested whether shared social group membership is linked to greater microbiome synchrony than hosts in different groups. In support, the patterns of temporal autocorrelation in Fig. 3a showed that hosts in the same group have more similar microbiomes than those in different groups, especially for samples collected within 10 d of each other (Fig. 3b; Kruskal–Wallis, $P < 2.2 \times 10^{-16}$). Likewise, samples from the same group occupy similar ordination space over time (Supplementary Video 2). While small, these group-level similarities were detectable, even for samples collected >2 yr apart (Fig. 3c and Supplementary Fig. 11a). The addition of group-level splines to our GAMs led to gains in deviance that explained >10% for 15 of 52 microbiome features, including all three microbiome PCs, five phyla and seven families (Fig. 4b,c and Supplementary Table 6).

Gut microbial congruence among group members could also be linked to shared behaviours and environments: baboons in the same group eat the same foods at the same time, travel as a unit across the landscape and may be grooming partners that are frequently in physical contact[32,48–52] (Fig. 1b,d). Indeed, after host identity, the next most important variable in model P + G + H was the group's home

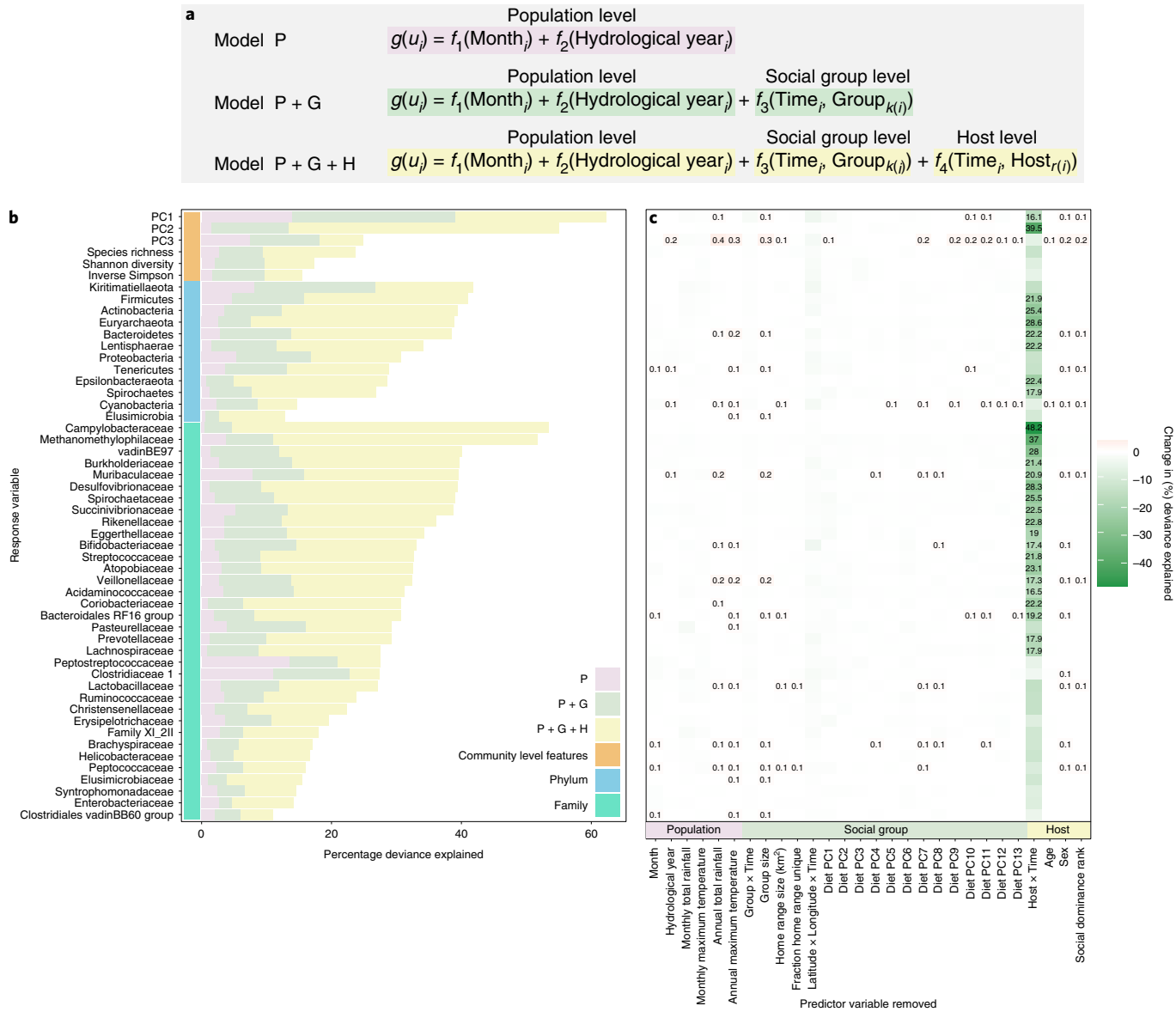

Fig. 4 | Multilevel modelling identifies idiosyncratic microbial dynamics. a, We fit three hierarchical GAMs to 52 microbiome features measured in 4,277 samples from the 56 best-sampled baboons, all of whom lived in the five social groups sampled the longest (between 2002 and 2010; median, 72.5 samples per host; minimum, 48 samples; maximum, 164 samples; Supplementary Fig. 9). Each model contained successive sets of predictor variables reflecting population-level factors (pink), group-level factors (green) and host-level factors (yellow). The factors at each level are listed at the bottom of **c** and defined in Supplementary Table 5). **b**, Illustration, for each microbiome feature (response variable), of the deviance explained by model P and the successive sets of predictor variables added in model P + G and model P + G + H, respectively (Supplementary Table 6; percentage deviance is a measure of goodness-of-fit for nonlinear models and is analogous to the unadjusted R^2 for linear models). **c**, The loss in deviance explained is shown for model P + G + H as we successively removed each predictor variable in turn from model P + G + H, keeping the model otherwise intact (Supplementary Table 7). Losses in deviance are shown in green and we only provide numeric values for losses in deviance >15%. Gains in deviance are shown in pink; we only show numeric values for gains >0.1%.

range in the 30 d before sample collection (Supplementary Fig. 20 and Supplementary Table 7). Despite previous evidence that grooming partners have similar microbiota[42], we did not find evidence for this pattern in our data (Supplementary Fig. 23). Samples collected from individuals with strong grooming bonds were not more similar than samples from animals with weak or no grooming relationships (Supplementary Fig. 24). However, the lack of a grooming effect in this dataset should be interpreted with caution. Our prior research on this topic[42] characterized microbial communities using shotgun metagenomic sequencing from >90% of social network members, all within 30 d of each other. Such data provide higher taxonomic resolution and more accurate estimates of abundance than 16S data and may more accurately capture transmission between hosts.

Conclusions

We find that gut microbial dynamics are both weakly synchronized across hosts and strongly idiosyncratic to individual hosts. Like members of a poorly coordinated microbial orchestra, microbial communities in different baboons are only weakly 'in concert' across the host population. Instead, gut microbial dynamics are idiosyncratic at the level of individual hosts and each baboon 'player' approaches the gut microbial 'song' differently. Our results contribute to mounting

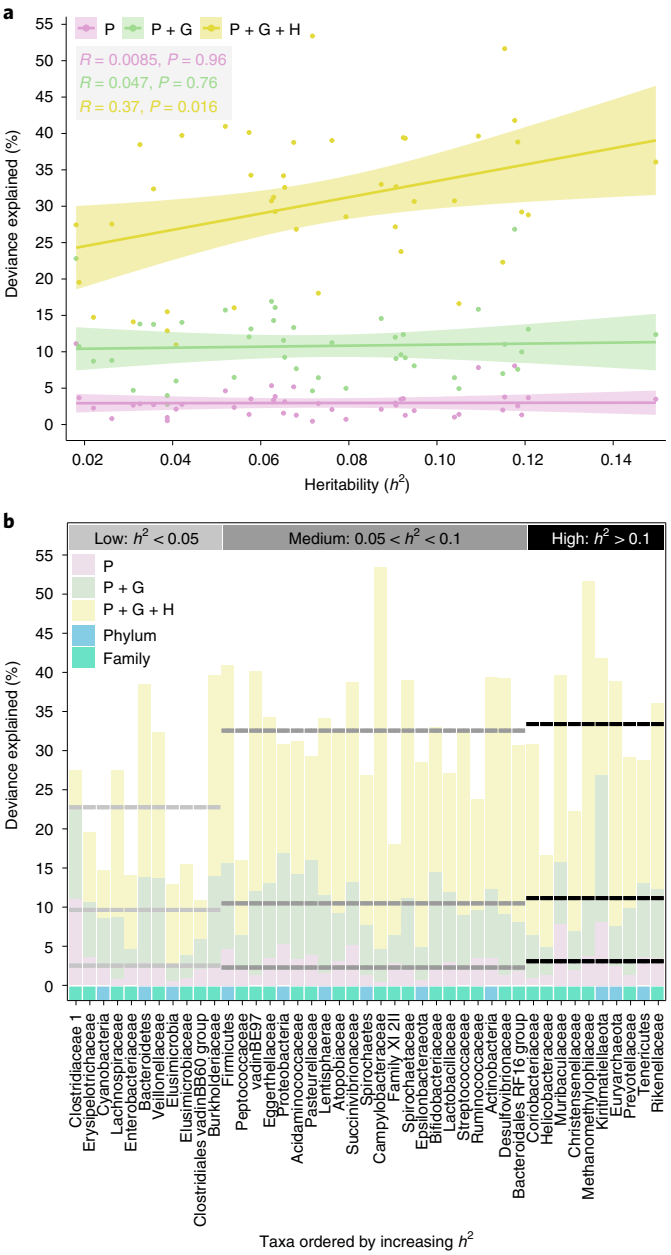

Fig. 5 | Microbiome taxon heritability is associated with idiosyncratic dynamics. a, Deviance explained (*y* axis) by the phylum and family level GAMs (from Fig. 4) plotted against the focal taxon's heritability estimate (h^2; *x* axis). Pink, green and yellow denote model P, model P + G and model P + G + H, respectively. Each regression line is plotted with its 95% confidence interval. **b**, Deviance explained (*y* axis) across the model hierarchy (pink, model P; green, model P + G; yellow, model P + G + H) for each taxonomic feature (at the phylum and family level; *x* axis). The *x* axis is ordered by increasing heritability with light blue and turquoise squares representing phyla and families, respectively. Horizontal dashed lines show the average deviance explained per model for taxa with low heritability estimates ($h^2 < 0.05$; light grey); medium heritability estimates ($0.05 < h^2 < 0.1$; dark grey); and high heritability estimates ($h^2 \geq 0.1$; black).

evidence that forces proposed to synchronize gut microbial metacommunities—shared environments, diets and between-host microbial dispersal—can create modest synchrony among hosts, especially for hosts living in the same social unit. However, these forces are typically not strong enough to overwhelm powerful and well-known drivers of microbiome personalization, including host genetic effects, individual-level priority effects, horizontal gene transfer and functional redundancy[16–19]. Interestingly, these idiosyncratic dynamics were strong even for microbial phyla and families, whose dynamics reflect multiple microbial functions and interactions that potentially buffer them against large fluctuations in abundance. We expect that the personalized dynamics we observed will be even stronger for finer taxonomic levels, especially bacterial species or strains that exhibit a high degree of functional variability across hosts.

Understanding if hosts in the same social group or population exhibit shared microbiome dynamics may be useful to researchers interested in predicting individual microbiome changes, linking microbiome dynamics to health outcomes and designing broadly effective microbiome interventions. These objectives have already been difficult to achieve, in part because of gut microbial personalization in humans and animals. For instance, predictive models of gut microbiome dynamics from one person fail when they are applied to other people[27]. Our results support the idea that microbiome predictions and interventions focused on specific taxa will require personalized approaches. Even then, 'universal' microbiome therapies that work the same way for all hosts may be unattainable. Instead, interventions will probably work best when they are designed for host groups or populations that have shared compositions and dynamics. Functional redundancy and horizontal gene flow may also mean that functions will be more predictable than taxa and prediction and intervention efforts that focus on microbiome functional traits (for example, metabolite levels; the presence of specific pathways) will probably be less affected by gut microbiome personalization. Together, our results provide insights about the extent and ecological causes of microbiome personalization and they indicate that personalized compositions and dynamics are not an artefact of modern human lifestyles.

Methods

All data collection procedures adhere to the regulations of the Institutional Animal Care and Use Committees of Duke and Notre Dame universities and to the laws of Kenya. A complete description of our methods is in the Supplementary Methods 1A–C.

Study subjects. Our subjects were individual wild baboons studied by the Amboseli Baboon Research Project (ABRP) in Kenya[33]. Baboons are terrestrial primates that live in stable social groups, typically with 20 to 130 members. The 600 baboons in our dataset lived in 12 social groups between April 2000 and September 2013 (5 original groups and 7 groups that were fission/fusion products from these original groups; Fig. 1a). ABRP collects detailed longitudinal data on rainfall and temperature; social group membership, ranging patterns and diet; and host traits such as age, sex, social relationships and dominance rank (Supplementary Methods 1A). The Amboseli ecosystem is a semi-arid savanna with a 5-month-long dry season spanning June to October, during which very little rain falls. The remaining 7 months (November to May) constitute the wet season, which has highly variable rainfall (mean annual rainfall between 2000 and 2013 was 319 mm; range 140–559 mm).

Sample collection. Most of the microbiota data we use here were published previously[32] but we include data from 1,031 additional samples that were generated at the same time using the same methods (they were not included in the heritability analysis of ref. [32] because we lack pedigree information for these hosts). The addition of these 1,031 samples led to a total of 17,265 samples in our study. These samples were collected from baboons who ranged in age from 7.4 months to 27.7 years, spanning these animals' natural lifespans (Supplementary Fig. 1a). Each baboon was sampled a median of 19 times and 124 baboons were sampled at least 50 times (Supplementary Fig. 1b). On average, these samples spanned 4.3 yr of a baboon's life (range 4 d to 13.2 yr; Supplementary Fig. 1c), with a median of 35 d between consecutive samples (Supplementary Fig. 1d).

DNA extraction and sequencing. DNA was extracted from each sample using MoBio and QIAGEN PowerSoil kits and subjected to 16S rRNA sequencing on the Illumina HiSeq 2500 platform (896,911,162 total sequencing reads; mean was 51,913.6 reads per sample; range 1,021–477,241; Supplementary Fig. 1e). We used DADA2 (ref. [53]) for sequence quality processing following the default protocol for large datasets. To allow us to compare the dynamics of individual taxa in different hosts, we filtered to taxa found in at least 20% of samples, resulting in 341 ASVs

(mean 162 ASVs per sample; range 19–311 ASVs; Supplementary Fig. 1f and Supplementary Table 2). This filtering captured 92% of the reads and many of the same compositional properties of the dataset when filtered to 5% prevalence (Supplementary Fig. 25). DNA concentration and ASV diversity were not predicted by time since sample collection (Supplementary Fig. 1g,h). As is typical for wild microbiota, 22.9% of the 341 ASVs could not be assigned to a known family (78 of 341) and 5.5% of ASVs could not be assigned to a known phylum (19 of 341; Supplementary Table 2). To address the compositional nature of our data, read counts were clr-transformed independently in each sample (including independent transforms for samples from the same individual), before all analyses[54,55].

Statistical analyses. To test whether shared environmental conditions and host traits lead to similar gut microbial compositions and synchronized dynamics across the microbiome metacommunity, we first characterized patterns of temporal autocorrelation in ASV-level Aitchison similarity within and between hosts over time. Our expectation was that, if hosts or social groups exhibit idiosyncratic composition and dynamics, then samples collected close in time from the same baboon or from baboons in the same group, should be more similar than they are to samples collected from different baboons living in different groups. Alternatively, if gut microbial dynamics are strongly synchronized, then samples collected close in time across the metacommunity should be compositionally similar and samples collected from the same host should not be substantially more similar than samples from different baboons. These analyses were run in R (v.4.0.2; ref. [56]) using custom-written functions (code and analysed data are available on Open Science Framework/GitHub as noted in Code availability).

To test whether dispersal limitation could explain microbiome idiosyncrasy, we estimated metacommunity-wide microbial migration probabilities in each season and year using the Sloan Neutral Community Model for Prokaryotes[40,41]. This model assumes that each local community, defined as the ASV-level microbial composition of a single host in a given season-year, is the outcome of stochastic population dynamics and microbial immigration from other hosts in the microbiome metacommunity (other local communities). Briefly, local communities have a constant size n and individual microbes within each local community die at a constant rate. These deaths create vacancies that can be occupied, either by individuals immigrating from the microbiome metacommunity (with probability m) or by daughter cells from any taxon within the local community (from reproduction within the same host, with probability $1-m$). Taxa that are common in the metacommunity have a higher chance of occupying vacancies than do rare taxa. Without immigration from the microbiome metacommunity, ecological drift leads each host's microbial diversity to reduce to a single taxon. Thus, the migration probability, m, represents the metacommunity-wide probability that any taxon, randomly lost from a given host/local community, will be replaced by dispersal from the microbiome metacommunity, as opposed to reproduction within hosts[40,41]. Following ref. [57], m can be interpreted as a measure of dispersal limitation, such that low migration probabilities signify high dispersal limitation. We estimated season and hydrological year-specific values for m by defining the microbiome metacommunity as either the hosts' social group or the whole host population. We fit neutral models using nonlinear least-squares regression as implemented in the R package tyRa[58].

To quantify the relative magnitude of idiosyncratic versus synchronized dynamics for community metrics and common families and phyla, we used GAMs to capture the nonlinear, longitudinal dynamics of 52 features, including the first three PCs of ASV-level composition, three indices of alpha diversity (ASV richness, the exponent of ASV-level Shannon's H and the inverse Simpson index for ASVs, as computed by the function reyni from the R package vegan[59]) and the clr-transformed abundances of 12 phyla and 34 families present in >20% of samples. We analysed phyla and families (as opposed to genera or ASVs) because phyla and families are highly prevalent across samples (mean prevalence is 85.6% for the 12 phyla and 73.7% for the 34 families), offering excellent power to compare their dynamics between different baboons. However, phyla and families might exhibit stronger synchrony than lower-level taxa because, compared to species or strains, the dynamics of families and phyla reflect multiple microbial processes and interactions, which are expected to buffer them against large fluctuations in abundance. Further, the processes and interactions that a given phylum or family collectively encompasses may be more consistent across hosts than those carried out by an individual species or strain (although this consistency will vary depending on the phylum, family or process in question[18,60]).

Our GAMs allowed us to calculate the percentage deviance in each feature's dynamics attributable to factors that could contribute to synchronized dynamics at different scales (percentage deviance is a measure of goodness-of-fit for nonlinear models and is analogous to the unadjusted R^2 for linear models). We considered deviance explained by factors at three scales: those experienced by the whole host population (for example, rainfall and temperature), those differentiated by social groups (for example, group identity, group home range location and diet) and those differentiated at the level of individual hosts (for example, host identity, sex, age and social dominance rank; see later for complete model structures). If microbiome community dynamics are largely idiosyncratic, then population- and group-level factors will not explain considerable deviance in microbiota change over time and, instead, a large fraction of the deviance will be attributable to host identity, controlling for shared environments, behaviours and traits. Alternatively, if shared environments and behaviours across the population and within social groups synchronize gut microbiota, then population- and group-level factors should explain substantial deviance in community dynamics. To ensure sufficiently dense sampling for identifying host- and group-level dynamics, all three GAMs were run on a subset of the full dataset, consisting of 4,277 16S rRNA gene sequencing profiles from the 56 best-sampled baboons living in the five social groups sampled the longest (between 2002 and 2010; median, 72.5 samples per host; minimum, 48 samples; maximum, 164 samples; Supplementary Fig. 9). GAMs were fit using the R package mgcv[61–63].

To test whether host genetic effects contribute to gut microbial idiosyncrasy, we performed a post hoc analysis of the relationship between the deviance explained in the GAMs for each microbial taxon and the heritability of that taxon's relative abundance[32]. If host effects on microbiome dynamics are in part explained by host genotype, we predicted that taxon heritability should be positively correlated with deviance explained at the host level (model P + G + H) but not at the group or population level (model P and model P + G).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The 16S rRNA gene sequences are deposited on EBI-ENA (project ERP119849) and Qiita (study 12949; ref. [64]). Note that our research permission from Kenya Wildlife Service prohibits third-party sharing of the biological samples themselves.

Code availability

Analysed data and code are available on the JRB's Open Science Framework/GitHub repository at https://doi.org/10.17605/OSF.IO/ERDXA

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Author contributions

E.A.A., J.R.B., L.B.B., R.B., J.A.G., S.M. and J.T. designed the research. E.A.A., S.C.A., R.B., M.R.D., L.G., J.B.G., L.R.G., N.G., S.M., V.Y., N.H.L., T.L.W., R.S.M., J.K.W., L.S., L.B.B. and J.T. produced the data. J.R.B., T.J.G., D.J., L.G. and J.-C.G. performed the bioinformatics. J.R.B., K.R. and S.M. performed the statistical analyses. E.A.A. and J.R.B. wrote the manuscript with important contributions from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data for this study
Data analysis	OSF/Github repository at: https://doi.org/10.17605/OSF.IO/ERDXA

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

16S rRNA gene sequences are deposited on EBI-ENA (project ERP119849) and Qiita [study 12949]. Analyzed data and code is available on the first author's Open Science Framework / GitHub repository: https://doi.org/10.17605/OSF.IO/ERDXA

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☒ Life sciences ☐ Behavioural & social sciences ☐ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	The primary sample size for this study was 17,265 16S rRNA gene sequencing-based microbiome profiles from 600 baboons living in 12 social groups over a 14-year span
Data exclusions	To allow us to compare the dynamics of individual taxa in different hosts, we filtered the microbiome profile in each sample to taxa found in at least 20% of samples, resulting in representatives from 341 amplicon sequence variants (ASVs), 34 families, and 12 phyla.
Replication	This is an observational study of a single, natural host population, not an experiment. The natural population cannot be replicated.
Randomization	Biological samples were collected opportunistically across subjects. While subjects vary in the number of samples available, sample collection was not biased with respect to particular aspects of identity (e.g. age, sex, group membership etc.)
Blinding	The study did not involve an experimental treatment. No individuals were blinded with respect to variables of interest.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	Not applicable.
Wild animals	This was an observational study of a natural population of wild baboons in the Amboseli ecosystem in Kenya. All data collection was non-invasive and involved collecting fecal samples from the ground or observing baboon behavior from a few meters distance.
Field-collected samples	Fecal samples were collected non-invasively in the field from the ground, within 15 minutes of defecation and were preserved in 95% ethanol in the field. Samples were stored at approximately 25°C until transport to the University of Nairobi, where they were freeze-dried, sifted to remove larger pieces of vegetation, and stored at -20°C. Upon arrival in the United States, samples were stored at -20°C. Samples were freeze dried because they were originally collected to measure steroid hormone levels. Previous work has shown that microbiome samples stored in ethanol and freeze-dried yield comparable results to other preservation methods.
Ethics oversight	All data collection procedures adhere to the regulations of the Institutional Animal Care and Use Committees of Duke, Princeton, and Notre Dame universities, and to the laws of Kenya.

Note that full information on the approval of the study protocol must also be provided in the manuscript.