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# Genes, geology and germs: gut microbiota across a primate hybrid zone are explained by site soil properties, not host species

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Gut microbiota in geographically isolated host populations are often distinct. These differences have been attributed to between-population differences in host behaviours, environments, genetics and geographical distance. However, which factors are most important remains unknown. Here, we fill this gap for baboons by leveraging information on 13 environmental variables from 14 baboon populations spanning a natural hybrid zone. Sampling across a hybrid zone allowed us to additionally test whether phylosymbiosis (codiversification between hosts and their microbiota) is detectable in admixed, closely related primates. We found little evidence of genetic effects: none of host genetic ancestry, host genetic relatedness nor genetic distance between host populations were strong predictors of baboon gut microbiota. Instead, gut microbiota were best explained by the baboons' environments, especially the soil's geologic history and exchangeable sodium. Indeed, soil effects were 15 times stronger than those of host–population $F_{ST}$, perhaps because soil predicts which foods are present, or because baboons are terrestrial and consume soil microbes incidentally with their food. Our results support an emerging picture in which environmental variation is the dominant predictor of host-associated microbiomes. We are the first to show that such effects overshadow host species identity among members of the same primate genus.

## 1. Introduction

The mammalian gut microbiome plays a central role in host physical functioning by helping hosts digest complex carbohydrates, synthesize vitamins, metabolize toxins and resist pathogens [1]. The last decade of research on mammalian gut microbiota has uncovered considerable heterogeneity between conspecific hosts, especially when those hosts live in geographically distinct populations [2–5]. However, we do not yet understand which processes create between-population differences in gut microbiota. Several factors may be important, including host behaviours and environments, biogeography and host genetic effects (e.g. host genotype effects on feeding behaviour, gut motility or immunity). Disentangling these factors is important for understanding the processes that govern gut microbiome assembly and how mammals respond to environmental variation.

To date, three broad factors are commonly linked to between-population heterogeneity in gut microbiota: (i) host behaviours, diets and environments; (ii) biogeography; and (iii) host genetic effects. Each factor reflects one or more microbiome assembly processes [2,3,5–8]. First, between-population differences in host behaviours, diets and environments can lead to microbial species sorting, both inside and outside of hosts, with consequences for microbiome composition [1,9]. Species sorting is an ecological process in which local environmental conditions shape which species survive in a given habitat [10]. For instance, different host populations may consume distinct diets, leading to differences in gut contents and different microbes inside the gut [4]. Outside the host, the microbes that hosts encounter on food or on conspecifics are shaped by other environmental forces, including climate, soil and water [8,11–13].

Second, gut microbial differences between host populations could be driven by isolation by distance (IBD), a nearly universal biogeographic pattern in which community dissimilarity increases with geographical distance between host populations [14]. IBD is driven by microbial demographic stochasticity (i.e. ecological drift) and between-population dispersal of microbes or their hosts. This balance between drift and dispersal determines the degree of microbiome community differentiation between populations.

Third, between-population differences in gut microbiota have been linked to a range of host genetic factors, including host genotype, genetic ancestry and population genetic structure. These factors likely reflect several underlying processes, including genetic contributions to host control of the microbiome (e.g. genes involved in immune responses against microbes), genetic effects on host feeding behaviour and diet (e.g. dietary preferences, lactose tolerance in adulthood) or gut physiology (e.g. gut motility, insulin secretion), and vertical transmission from parents to offspring [15,16].

Disentangling the relative influence of host behaviours and environments, IBD and genetics in shaping mammalian gut microbiota is challenging. Doing so requires complementary information on host behavioural and environmental factors, geographical distance and genetic differences between several populations. To date, most such studies include information on just two of these data types [2,5,6,17]. Only a few have information on three, and the environmental data tend to be coarse-grained, with habitat differences binned into broad categories such as forest type [7,18], salt versus fresh water [8], season [19] or climate zone [3]. Hence, we still do not understand how host environments, geography and genetics work together to shape population- and species-specific microbiotas.

Here, we test the contributions of host genetic ancestry, host environments and geographical distance to shaping gut microbiota in 191 baboons from 14 populations across a baboon hybrid zone (figure 1) [20]. We leverage detailed data on between-population environmental differences, including 13 measures of the physical environment, such as vegetation, soil traits and elevation. All of these variables could influence microbial species sorting, either via the composition of the baboons' diets or via microbial exposures from the environment. Baboons are omnivores that consume a variety of fruits, leaves, seeds, insects, roots and, more rarely, small vertebrates; such dietary items are often directly eaten from the ground and dusted with soil, providing a potential transmission route for soil microbes to colonize baboon gut microbiota [21]. The 14 study populations are spread over a 375 km transect across a natural hybrid zone between yellow and anubis baboons (*Papio cynocephalus*; *Papio anubis*) in Kenya [20]. Hybrid zones offer a key advantage in understanding the drivers of microbiome variation: because hosts with distinct genetic ancestry co-reside at the same site, hybrid zones help break up the correlation between host genetics and host environments. In the hybrid zone studied here, genetic ancestry (measured as a 'hybrid score' for each individual) is uncorrelated with major sources of host ecological variation, including the environmental traits we consider [20,22,23]. Further, there is an emerging paradigm of host species-typic microbiomes, including primates, such that each host species harbours a distinctive gut microbiota, and between-species gut microbial similarity often recapitulates host phylogenies [5,7,24]. These species-specific microbiota have recently been implicated in hybrid lethality and speciation [17,25]. However, whether species-specific microbiota occur in closely related primate species—especially species that are ecologically similar, sometimes sympatric, and hybridize—is unknown. To disentangle genetic, environmental and geographical predictors, we use a recently developed Bayesian method for differentiating ecological and geographical effects called BEDASSLE (Bayesian estimation of differentiation in alleles by spatial structure and local ecology), applying this method for the first time to microbiome data [26,27]. BEDASSLE allows us to simultaneously disentangle the relative predictive power of geographical distance, host genetic distance and multiple environmental variables while avoiding the statistical problems to which Mantel tests are prone, such as increased risk of type 1 error when variables are spatially autocorrelated [28]. Together, our results reveal the processes that shape primate gut microbiota across a landscape by simultaneously testing multiple explanations for between-species and between-population differences.

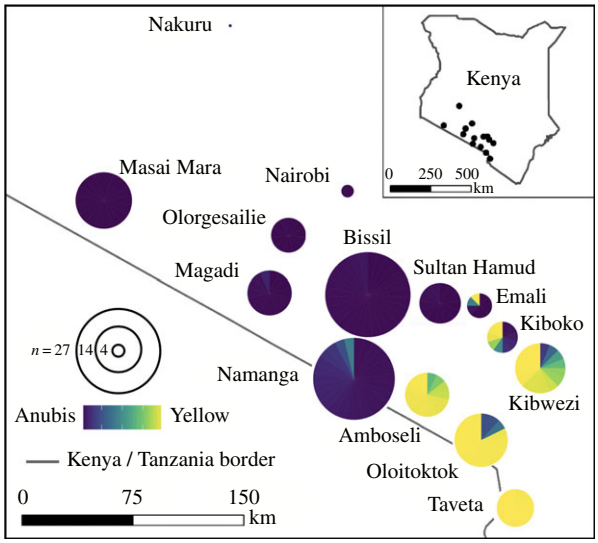


**Figure 1.** Locations of 14 populations in Kenya, indicated by pie charts; pie chart diameter represents the relative sample size at each population (electronic supplementary material, table S1). Colours indicate genetic ancestry of baboons sampled at each population.

## 2. Methods

### (a) Study populations and sample collection

Faecal samples were collected from 14 geographically distinct sites (or 'populations') in Kenya (figure 1). Samples were collected in

June–July 2008 as part of a previous study on the population genetics of this hybrid zone (electronic supplementary material, table S1) [20]. For 13 populations ($n = 177$ samples), samples were collected from the ground within a few hours of defaecation [20]. Occasionally, samples were collected from locations frequented by the baboons when they were not currently present; in these cases, samples were up to a few days old, although the precise time until collection for individual samples is not known. For the 14th population (Amboseli, $n = 14$ samples; electronic supplementary material, table S1), samples were collected from known individuals during the same date range as the other 13 populations, within a few minutes of defaecation. All samples were collected using a single-use spatula to scoop 2–5 g of faecal material from the leading edge of the sample (if possible), placed into 15–20 ml of 95% ethanol, homogenized to permeate the sample with ethanol, and stored at ambient temperature until export, when they were stored at −80°C [29].

Our sampling protocols raise two potential confounds. First, we did not avoid portions of the sample in contact with the ground; hence, some samples could have been contaminated with soil microbes from the environment. However, the quantity of soil microbes relative to gut microbes would be very small in these cases because mammalian faeces contains 1000 times the number of microbial cells in a typical soil sample [30,31]. See the electronic supplementary material, §1 for a full discussion of the effects of soil contamination; we find our results are robust to the removal of rare taxa and/or the addition of small numbers of contaminating reads. Second, samples varied in the amount of time they were exposed to the environment before preservation. To test the effects of time to ethanol preservation on the gut microbiome, we performed a time-series experiment in Amboseli to test whether exposing faeces to the environment for 15 min–48 h after defaecation altered observed microbiota (see electronic supplementary material, §2). Consistent with previous studies [32,33], time to preservation had minor effects on microbial α- and β-diversity and could not explain between-population differences (see Results; electronic supplementary material, figure S1A,B).

## (b) Measuring genetic variation between baboon hosts and populations

All baboon faecal samples ($n = 191$; mean ± s.d. = 14 ± 7 per population) were genotyped at 12 highly polymorphic microsatellite loci [20]. All microsatellite genotypes were distinct, indicating that each sample was from a different baboon. We used these genotype data to calculate three summary statistics: (i) pairwise genetic relatedness between baboons (Coancestry v. 1.0.1.8; Lynch & Ritland method [34]); (ii) hybrid ($q$) scores for each baboon (TESS v. 2.3.1 [35] via the settings in [20]); and (iii) between-population $F_{ST}$ (*hierfstat*; Weir & Cockerham 1984 method [36]).

## (c) Measuring environmental differences between populations

We characterized environmental differences between all 14 populations using 13 environmental variables extracted from high-resolution maps (electronic supplementary material, tables S2 and S3 and figure S2; [37–39]). Full methods for quantifying environmental differences between populations are in electronic supplementary material, §3. These variables included vegetation type, 10 soil traits, geological history and elevation. All of these variables are potential predictors of baboon foods and/or microbial exposures from the environment. Most were uncorrelated with each other (electronic supplementary material, table S3; mean Mantel $R$ (±s.d.) = 0.089 (±0.207); range = −0.241–0.882). For each population, we measured each environmental variable based on a 28 km$^2$ circle (6 km diameter) surrounding the sampling location (electronic supplementary material, figure S2) using ArcMap 10.2.2 [40]. Six kilometre corresponds to the largest observed core home range diameter (i.e. 75% of usage time) of baboons in Amboseli (L.E.G. *et al*. 2014, unpublished data), making 28 km$^2$ a generous estimate of range size.

## (d) Measuring geographical distance between populations

*Geographical distance*. We calculated the distance in kilometres between the GPS coordinates collected for each population [20] (*geosphere*; Haversine method [41]).

## (e) Characterizing gut microbiota in each sample

DNA was extracted from faecal samples using MoBio's Powersoil DNA Isolation kit. We amplified the 16S rRNA gene V4 region and ran paired-end sequencing on the Illumina HiSeq 2000 platform. Sequences were processed using the pipeline detailed in electronic supplementary material, figure S3 and §4. We retained 26 458 080 reads after quality filtering (range = 30 700–430 465 per sample), which clustered into 2711 operational taxonomic units (OTUs; range = 133–1152 per sample).

## (f) Statistical analyses

Unless noted, all statistical tests were run in R [42].

### (i) Between-population differences in gut microbiota

We tested whether host populations differed in microbial composition using PERMANOVA (*vegan* [43]). To investigate between-population differences in OTU richness, we ran linear models with population and read count as fixed effects and corrected for multiple comparisons with Tukey's HSD test (*multcomp* [44]).

### (ii) Host genetic effects on gut microbial composition

To test whether baboon hybrid scores predicted microbial dissimilarity, we ran PERMANOVAs with weighted UniFrac dissimilarity as the response variable. We also used Mantel tests to correlate pairwise genetic relatedness between baboons with weighted UniFrac dissimilarities. Finally, we constructed phylogenetic trees for genera with 10 or more OTUs in our dataset to visualize microbial phylogenetic clustering by host species identity. For this analysis, anubis, yellow and hybrid baboons were defined using the cut-offs in [20]; hybrid score less than 0.02 was anubis, 0.02–0.98 was hybrid and greater than 0.98 was yellow (elsewhere, we model ancestry using continuous estimates).

### (iii) Testing the relative contributions of host environments, geographical distance and genetic ancestry to between-population differences in gut microbiota

We first ran exploratory, bivariate Mantel tests to identify variables to include in a spatially explicit multivariate Bayesian model (BEDASSLE) [27]. For each Mantel test, we correlated a matrix of the mean weighted UniFrac dissimilarity between microbiome samples from each pair of populations with matrices of between-population differences in geographical distance; genetic distance ($F_{ST}$); and each of the 13 environmental variables (table 1). We then incorporated significant predictors ($p < 0.05$) of population-wise weighted UniFrac dissimilarity into BEDASSLE [26]. We discuss the assumptions of the BEDASSLE model and its applicability to microbiome data in electronic supplementary material, §5, figures S4–S9 and table S4.

BEDASSLE fits effect sizes for each environmental predictor and geographical distance; the ratio between these effect size

**Table 1.** Mantel tests correlating between-population differences in environmental, genetic and geographical variables with microbiome community dissimilarity (weighted UniFrac). Variables are listed in order of decreasing effect size in the full dataset. Italicized text indicates significant correlations.

| environmental variable | Mantel *r* | *p*-value | *r* (Amboseli excluded) | *p* (Amboseli excluded) |
|---|---|---|---|---|
| *soil exchangeable sodium (%)* | *0.77* | *0.004* | *0.62* | *0.027* |
| *soil pH* | *0.60* | *0.043* | −0.11 | 0.656 |
| *geological composition (Bray–Curtis)* | *0.42* | *0.008* | *0.40* | *0.019* |
| *soil total nitrogen (g/kg)* | *0.37* | *0.046* | 0.03 | 0.395 |
| soil clay cation exchange capacity | 0.32 | 0.051 | 0.00 | 0.389 |
| *geography (km)* | 0.25 | 0.136 | *0.52* | *0.008* |
| soil drainage | 0.19 | 0.198 | −0.05 | 0.514 |
| vegetation composition (Bray–Curtis) | 0.13 | 0.222 | −0.07 | 0.575 |
| soil SOTER (Bray–Curtis) | 0.12 | 0.232 | −0.05 | 0.609 |
| elevation (m) | 0.08 | 0.27 | 0.24 | 0.069 |
| soil bulk density | 0.06 | 0.265 | 0.19 | 0.175 |
| host genetic distance ($F_{ST}$) | 0.04 | 0.464 | 0.17 | 0.243 |
| soil cation exchange capacity | −0.01 | 0.423 | −0.04 | 0.538 |
| soil sand (%) | −0.01 | 0.454 | −0.07 | 0.622 |
| soil total carbon | −0.08 | 0.644 | 0.04 | 0.356 |

estimates is interpretable as the between-population geographical distance (km) required to alter OTU distributions the same amount as a single unit of the environmental predictor. For example, for $F_{ST}$, the model translates the effect of a change from $F_{ST} = 0$ to $F_{ST} = 1$ between baboon populations on microbial community similarity into an equivalent geographical distance. We modelled three predictors in addition to geographical distance: (i) between-population $F_{ST}$, (ii) geological Bray–Curtis distance, and (iii) distance on the first principal component (PC1) of the three soil traits that significantly predicted weighted UniFrac dissimilarity in bivariate Mantel tests (exchangeable sodium, pH and total nitrogen [45]). PC1 explained 98.6% of the variance in these soil traits. We calculated the relative contribution of each soil trait—sodium, pH and total nitrogen—to the soil PC1 score based on each trait's loading score (electronic supplementary material, table S5), following [46].

### (iv) Predictors of gut microbial α-diversity

To test if host environments or genetics predicted OTU richness, we ran a linear mixed model (*coxme* [47]). Fixed effects included environmental variables that predicted weighted UniFrac dissimilarity in bivariate Mantels, host hybrid score and read count. Random effects were population membership and geographical distance between populations.

### (v) Microbial lifestyle traits

We tested whether OTU prevalence was predicted by microbial lifestyle traits consistent with environmental transmission. We predicted that OTUs found in every population would be essential to baboon gut microbial functioning, specific to baboons and less likely to occur in the physical environment. By contrast, less prevalent OTUs should represent environmentally acquired taxa whose dynamics might be shaped primarily by environmental species sorting [9,48]. These taxa should be associated with lifestyle traits that would make them more easily acquired from the environment: the ability to form spores and tolerate oxygen.

To test these predictions, we divided OTUs into those found in 'all populations' ($n = 457$ OTUs) versus those that were not ('some populations'; $n = 2254$ OTUs). For OTUs assigned to genera in the Genomes OnLine Database [49], we pulled oxygen requirement and sporulation information. We then ran hypergeometric tests to test if OTUs found in some populations were enriched for environmental acquisition traits compared to OTUs found in all populations.

## 3. Results

### (a) Gut microbiota differ between host populations

Each baboon population exhibited a distinct gut microbiota. The abundance of common microbial phyla varied across populations (figure 2*a*), and population membership explained 31% of the variation in microbial β-diversity across samples (PERMANOVA; $R^2 = 0.31$, $p < 0.001$). Most population pairs (69%) differed significantly in microbial composition after correcting for multiple testing (pairwise PERMANOVAs; figure 2*b*). α-diversity also differed between populations (figure 2*c*); the median OTU richness ranged from $414 \pm 142$ (median ± s.d.) OTUs per sample in the population with the lowest α-diversity (Amboseli) to $912 \pm 94$ OTUs per sample in the population with the highest diversity (Bissil).

Baboons from Amboseli had particularly distinctive gut microbiota (figure 2). This distinctiveness was not due to differences in sample preservation time, which had no significant effects on microbial α- or β-diversity (α-diversity: $p = 0.85$; electronic supplementary material, figure S1A; PERMANOVA controlling for individual identity: $R^2 = 0.046$, $p = 0.069$; electronic supplementary material, figure S1B). When excluding Amboseli from our analyses, population still explained 23% of the variance in baboon gut microbiota (PERMANOVA; $R^2 = 0.23$, $p < 0.001$) and significantly predicted OTU richness ($p < 0.001$). We include Amboseli in subsequent analyses, but if its inclusion changed the results, we also report results excluding Amboseli. We also tested the effect of excluding populations with $n < 10$ samples to confirm that small sample sizes were not unduly influencing our results. These

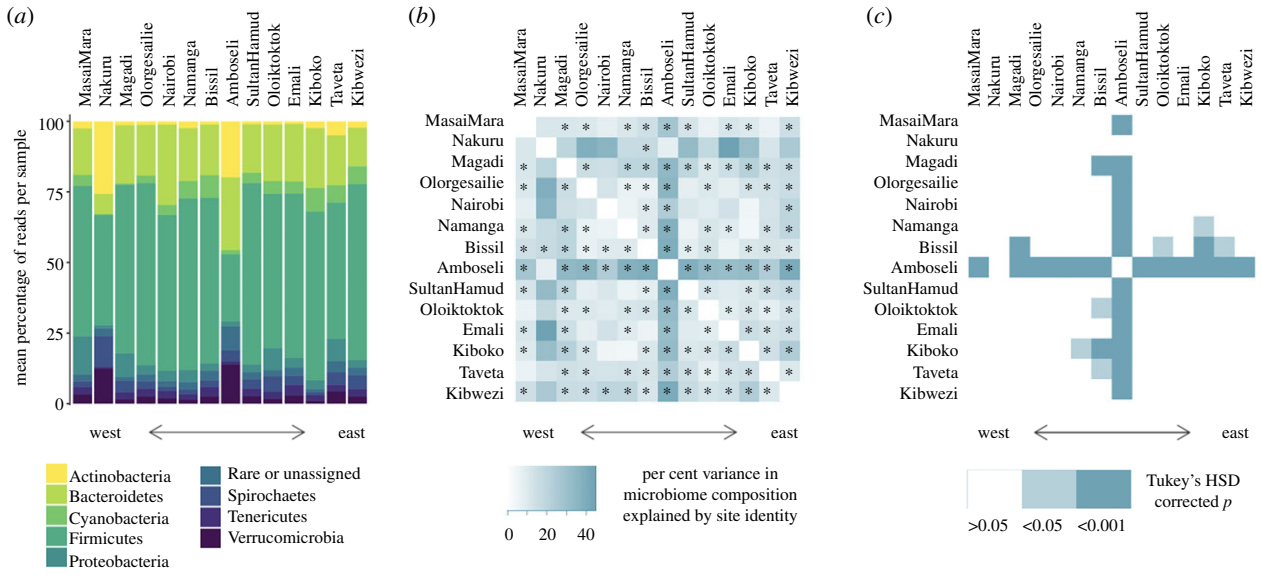


**Figure 2.** Gut microbiota differ between baboon populations. Populations are ordered from west to east (figure 1). (*a*) Relative abundance of microbial phyla across the 14 populations. (*b*) Sixty-nine per cent of populations differed significantly in microbiota composition (pairwise PERMANOVAs with a 10% false discovery rate; '*' indicates significance at $p < 0.05$). Population identity explained up to 40% of variation in β-diversity. (*c*) OTU richness varied by population. *p*-values ranged from $p > 0.05$ (white) to $p < 0.001$ (dark), after controlling for multiple comparisons.

analyses consistently produced qualitatively similar results (electronic supplementary material, tables S6 and S7).

## (b) Host genetic ancestry and genetic relatedness were not strong predictors of baboon gut microbiota

Host hybrid score did not predict microbial α-diversity, nor did hosts cluster as a function of hybrid score in an ordination (electronic supplementary material, table S8 and figure S10A, B). Hybrid score also did not predict UniFrac dissimilarity, either within populations after correcting for multiple testing (electronic supplementary material, table S9) or across all baboons when populations were pooled (PERMANOVA; $R^2 = 0.002$; $p = 0.8$). Finally, pairwise genetic relatedness between baboons also did not predict microbial dissimilarity within populations after correcting for multiple testing (electronic supplementary material, table S9). When we pooled all samples together and controlled for population membership in a partial Mantel framework, there was a non-significant trend such that closer relatives had more similar microbiota (partial Mantel; $R = -0.016$, $p = 0.069$; electronic supplementary material, figure S10C).

In taxon-specific analyses, we did not find any microbes that varied in abundance based on host genetic ancestry, controlling for differences in the environment and geographical distance between populations (electronic supplementary material, table S10). For bacterial genera with 10 or more OTUs, there was no clear host species signature on OTU phylogenetic relationships (electronic supplementary material, figure S11).

## (c) Host environments predict between-population differences in baboon gut microbiota

In contrast with host genetic factors, host environments were strongly associated with between-population differences in baboon gut microbiota. In bivariate Mantels, UniFrac dissimilarity was best predicted by four environmental variables: the per cent of exchangeable sodium in the soil, soil pH, soil total nitrogen and site geology (table 1 and figure 3*a–d*). The *r*-values associated with these Mantel correlations indicated large effect sizes when each variable was tested individually: 77% of the variation was explained by sodium, 60% by pH, 42% by total nitrogen and 37% by site geology. Geographical distance between populations only predicted microbiota if samples from Amboseli were excluded (table 1 and figure 3*e*). Genetic distance between host populations ($F_{ST}$) did not explain between-population differences in β-diversity (table 1 and figure 3*f*). Importantly, after correcting for multiple testing, there were no significant correlations between host–population genetic distance, geographical distance or any of the significant environmental variables (although sodium and pH were correlated at 0.882; $p = 0.16$; electronic supplementary material, table S3).

To disentangle the relative contributions of host environments, geography and genetic distance to between-population differences in baboon microbiota, we used the Bayesian spatial modelling approach in BEDASSLE [27]. We found that between-population differences were largely driven by the sites' geological histories, soil traits and geographical distance (table 2). When normalizing the effect sizes of our predictors to the middle 50% of each variable, the effects of geological history were three times stronger than for geographical distance (i.e. the effect of geological history normalized to the middle 50% of our data was equivalent to travelling 341 km, while the median geographical distance between populations in our dataset was 112 km; table 2) and more than 15 times stronger than host genetic distance (341 versus 22 km; table 2). The effect of PC1 of dominant soil traits (sodium, pH, total nitrogen) was similar to geographical distance (122 versus 112 km; table 2) and more than five times stronger than genetic distance (122 versus 22 km). Unpacking this effect size in the light of the variable loadings on PC1, the majority of this effect size was driven by sodium, with minimal contributions from soil pH and nitrogen (electronic supplementary material, table S5).

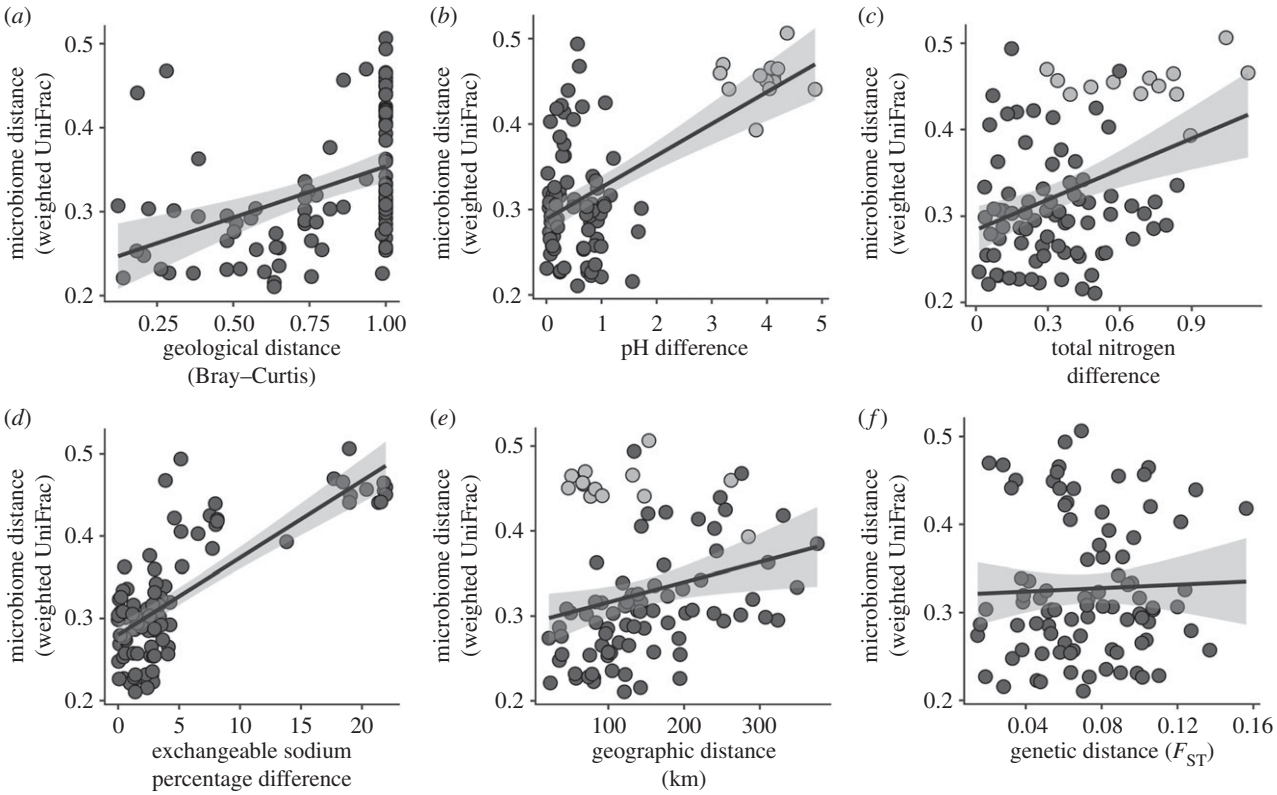


**Figure 3.** Baboons from populations with less similar (*a*) geology, (*b*) soil pH, (*c*) soil nitrogen and (*d*) soil sodium had less similar gut microbiota. (*e*) Geographical distance and (*f*) between-population $F_{ST}$ did not predict gut microbiota between host populations (table 1). Each point represents a pair of populations. Excluding Amboseli changed the significance of three environmental effects: (*b*) soil pH and (*c*) soil nitrogen no longer predicted microbiome dissimilarity, but (*e*) geographically distant populations had significantly less similar microbiomes (table 1). In (*b,c,e*) points, comparing samples from Amboseli to other populations are in grey.

**Table 2.** BEDASSLE effect sizes for each predictor variable presented as both (i) the mean geographical distance in km between hypothetical populations necessary to observe a 1-unit change in the predictor variable, and (ii) these effect sizes normalized to reflect the middle 50% of the data for each variable. For example, a 1-unit change in $F_{ST}$ is equivalent to travelling approximately 518 km. However, the middle 50% of $F_{ST}$ estimates in our study fell between 0.052 and 0.095, much less than a change of 1 unit of $F_{ST}$. The difference between $F_{ST}$ 0.095 and 0.052 (0.043) is equivalent to travelling only 22.3 km.

| predictor variables | mean geographical distance equivalent (km) per 1 unit predictor variable (95% CI) | effect size for each predictor (in km) normalized to reflect the difference between the 25th and 75th percentile in our data |
|---|---|---|
| geology Bray–Curtis | 894 (673–1,126) | 341 |
| soil PC1 | 34 (25–43) | 122 |
| genetic $F_{ST}$ | 518 (390–653) | 22 |

Consistent with BEDASSLE, soil sodium and geological history predicted OTU richness, controlling for geographical distance between populations: pH, nitrogen and host hybrid score did not (electronic supplementary material, table S6). Populations with high sodium had much lower OTU richness than populations with low sodium, such that a shift from the most to least salty soils (23–1% sodium) led to a loss of 323 OTUs—a striking effect size, given that the median OTU richness in our samples was 414 OTUs.

## (d) Environmental differences between sites predict the distribution of microbes and life-history traits

In support of environmental effects, the 2254 OTUs not present in every population (some populations) were enriched for an aerobic lifestyle compared to the 457 OTUs found in all populations (hypergeometric test; adjusted $p < 0.001$; electronic supplementary material, figure S12A,B). OTUs found in 'some populations' were depleted for an anaerobic lifestyle (hypergeometric test; adjusted $p < 0.001$; electronic supplementary material, figure S12B) and tended to be enriched for sporulation, although this latter effect was not significant ($p = 0.099$; electronic supplementary material, figure S12C). Hence, OTUs found in some populations may be spatially inconsistent across the landscape and environmentally acquired. In support, OTUs found in 'some populations' had lower prevalence when they were present (mean = 34% of hosts) compared to OTUs present in all populations (mean > 90% of hosts).

Finally, we tested for environmental effects in microbial genera and phyla. We found that 7% of taxa significantly differed in abundance as a function of environmental traits, controlling for geographical distance (electronic supplementary material, table S10). Soil pH, exchangeable sodium and total nitrogen predicted the per-sample abundance of a broad array of taxa, while geological composition predicted the abundance of Proteobacteria.

## 4. Discussion

Gut microbiota are often strikingly different across populations of taxonomically similar host species [4,5,7]. However, because host environments, genetics and geographical distance often covary, the processes driving population-specific gut microbiota are difficult to disentangle. Across a baboon hybrid zone, the primary drivers of population-specific gut microbiota were host environments and, to a lesser extent, IBD. Contrary to patterns deeper in the primate evolutionary tree [5,7,24,50], we found no evidence for phylosymbiosis between the two closely related, hybridizing baboon species in our study. Instead, and somewhat surprisingly, between-population differences in baboon gut microbiota were strongly predicted by local geology and soil chemical properties. These results support the emerging scientific consensus that, in closely related host species, a host's environment is a dominant driver of gut microbial variation [12,51]. If such effects are widespread, they have implications for how host environments affect host physical functioning and health: A host's external ecology shapes their internal ecology with consequences for the 'ecosystem services' microbiomes provide to hosts.

### (a) Environmental heterogeneities shape microbiota

Host behaviours and environments can have profound effects on gut microbiota. These effects include hosts' social and mating partners [13,51,52], prey [8] and physical environments [8,13]. For instance, source tracking between sticklebacks, their environments and food revealed that 13% of stickleback intestinal OTUs are derived from surrounding water, and 73% are from their prey [8]. In humans, microbiotas are similar among people living in the same house [13,51]; in one recent study, relatives only exhibited similar microbiota if they had a history of sharing a household [51].

These environmental effects are important for two reasons. First, they represent an underappreciated mechanism by which environments influence an organism's physical functioning. Environmentally, acquired microbes can have long-term effects on human health [53], short-term effects on metabolism [54] and influence normal development [55]. Second, environmental effects on microbiome composition call into question arguments that hosts and their microbiotas represent holobionts that act as coherent units of selection [25]. If gut microbes are able to survive in both animal intestines and the external environment—a question future studies should seek to answer—focusing solely on the holobiont may miss an important part of these microbes' selective environments [56].

In our study, the dominant environmental drivers of baboon gut microbiota were a site's geological and soil properties. There are at least four explanations for this finding. First, soil may predict the availability of baboon foods, and thus diet composition. However, we included site vegetation as a variable, which is probably a more direct measure of the baboons' diets than soil; yet vegetation did not explain gut microbial differences. Second, contaminating soil microbes could explain our results. We think this explanation is unlikely because mammalian faeces is one of the densest microbial communities on Earth [30]. Hence, sequencing reads from contaminating soil microbes should be rare compared with those from gut microbiota (less than 0.005% of total reads; see electronic supplementary material) and should not have an appreciable effect on microbial abundance estimates for any OTU. Notably, if soil contaminants introduced new OTUs otherwise absent in baboon gut microbiota, our results would be sensitive to removal of rare OTUs: they are not (see electronic supplementary material). Third, microbes may have colonized baboon faecal samples from soil or air after it was deposited on the ground. However, in our time-series experiment, samples exposed to the environment for up to 2 days did not differ substantially in microbial composition compared to samples collected minutes after defaecation.

Fourth, and perhaps most interestingly, soil properties may shape soil microbial communities, which in turn directly colonize baboon intestines. Baboons are terrestrial primates that spend the majority of their waking hours on the ground, and their hands, feet and fur are often coated with soil. They consume plants that lie close to the ground, especially grass corms, which are covered in soil because baboons must uproot the plant to access the corm. Baboons also groom conspecifics, often licking the fur of other individuals who have been in contact with soil. However, if soil microbes colonize baboon guts, we do not know if they are dead or dormant, or if instead they establish and become living members of the microbiome. In other mammals, soil microbes may contribute to microbiome function. In pikas, environmentally acquired gut microbes are enriched for carbohydrate metabolism; it is unknown if these microbes perform these functions for hosts [57]. Piglets experimentally exposed to topsoil during lactation had more diverse gut microbiomes, and improved growth and digestion [58]. If soil microbes colonize primate intestines, terrestrial primates may be more exposed than arboreal primates. Reduced contact with the soil may explain low macroparasite burdens in arboreal primates [59], and new research suggests that the same may be true for primate gut microbiota obtained from soil [60]. In support, past work has found that sympatric terrestrial primates, gorillas and chimpanzees share more bacterial taxa than gorillas and chimps from disparate regions [5].

Amboseli had a particularly divergent local environment and gut microbiota. Amboseli is a dry Pleistocene lake bed with high levels of sodium in the soil (23.0%) and high soil pH (10.6). High soil pH and sodium are associated with less diverse and stable soil microbial communities [11,61]. This low soil microbial diversity may, in turn, explain why baboons from Amboseli had the lowest α-diversity in our study. In support, the population with the next saltiest soil, Nakuru (9.1%), also had low α-diversity, and β-diversity similar to Amboseli, although Nakuru was only represented by one sample. Such effects could have consequences for Amboseli baboons; high gut microbial α-diversity may promote microbiome stability and resistance to invading pathogens [62,63], but whether these effects occur in Amboseli is unknown.

### (b) No evidence for species-typic microbiota across a primate hybrid zone

Across primates, host species identity is a stronger predictor of microbiota than sampling location, a pattern that has been replicated in gorillas, chimpanzees and howler monkeys [5,7,64]. Further, primate gut bacteria exhibit strong phylosymbiosis: bacterial phylogenies diverge with hominid phylogenies across gorillas, humans, chimpanzees and bonobos [24]. These results are commonly assumed to reflect host/microbe coevolution, strong vertical transmission and/or host genetic effects on microbiome composition. If true, then we should also expect to see species-typic microbiomes in recently diverged sister taxa and their hybrids. However, in our study, neither host genetic

ancestry nor pairwise genetic relatedness between hosts explained baboon gut microbiota. Our study is the first to test the effects of host genetics on gut microbiomes in a natural primate hybrid zone, and among the first to do so in any animal. Our results contrast with previous studies, which found that hybrids demonstrate altered microbiota from their progenitor species [65], or that hybridized microbiomes lead to deleterious health effects in mice [17], and death in wasps [25]. Because we did not detect ancestry effects, gut microbial differentiation does not contribute to speciation in baboons.

Data accessibility. Genetic sequencing data have been deposited in NCBI's Short Read Archive under accession number PRJNA517796 [66]. Datasets are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2ts8094 [67]. Code is available from the Archie Lab github at https://github.com/ArchieLab/grieneisen_etal_2019_PRSB.

Authors' contributions. E.A.A., L.E.G. and J.T. conceived and designed the research. L.E.G. performed the laboratory work. G.B. provided guidance on BEDASSLE. M.J.E.C., E.A.A., J.T., S.C.A. and R.B. provided sampling data, reagents, sequencing facilities, host genotype data and provided input on the manuscript. L.E.G. and E.A.A. analysed the data. L.E.G. and E.A.A. wrote the manuscript with input from all authors. All authors read and approved the final manuscript.

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