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Supplementation With Human Foods Affects the Gut Microbiota of Wild Howler Monkeys

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ABSTRACT

Wild primates face a wide range of anthropogenic influences globally that impact their health, fitness, and survival. One area of potential impact that has been particularly understudied is the supplementation of wild primate diets with human foods. Although the consumption of human foods represents a substantial dietary change for wild primates, knowledge of how it impacts their physiology and behavior is limited. Here we explore how human food supplementation impacts wild primates by comparing the gut microbiomes of free-ranging brown howler monkeys (*Alouatta guariba*) in periurban Brazil that do or do not have access to human foods. We found that howler monkeys consuming human foods had reduced gut microbial diversity and reduced relative abundances of fiber degrading microbial taxa, which has been associated with negative health consequences in other animals, including humans. However, the effect size of these differences was relatively small and varied over time. Additionally, the composition of the gut microbiome varied significantly across months, regardless of the access to human foods. We suggest that the biology of this howler monkey population is minimally impacted by human foods. Further empirical research will help clarify the relationship between human food supplementation and health across primate populations, facilitating conservation applications.

Wild primates face a wide range of anthropogenic influences globally that impact their health, fitness, and survival. As a result, it is estimated that ca. 68% of extant primate species are currently threatened with extinction (Estrada and Garber 2022). To support the welfare and conservation of these species, there has been a strong movement over the past several decades to generate empirical data identifying the ecological and health consequences of anthropogenic activity on wild primates. This study has created a strong foundation for understanding how primates are affected by different types of disturbances. For example, loss of habitat can lead to altered diets and social interactions that affect nutritional status and stress levels (Martínez-Mota et al. 2007; Ramsay et al. 2023; Rothman and Bryer 2019). Increased contact with humans and domestic animals in periurban and urban landscapes can lead to pathogen transfer and physical injury (Bicca-Marques 2017; Bicca-Marques et al. 2020; Chaves et al. 2022). However, despite these important advances, key knowledge gaps remain.

One area of potential impact that would benefit from additional study is the supplementation of wild primate diets with human foods (Back and Bicca-Marques 2019; Boug et al. 2017; Hansen et al. 2020; Li et al. 2023; Saj et al. 1999). There are several ways in which supplementation can occur, making it relatively common. Wild primates that live in habitats adjacent to human settlements often have increased access to human foods in the form of crop-feeding and/or trash-feeding (Bempah et al. 2021; Cancelliere et al. 2018; Chaves and Bicca-Marques 2017). While

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Summary

- Howler monkeys consuming human foods have reduced gut microbial diversity and reduced relative abundances of fiber degrading microbial taxa, which has been associated with negative health consequences in other animals, including humans.
- The magnitude of effect of human food supplementation on howler monkey gut microbiomes in this population is small, and gut microbiome composition varies significantly across months, likely due to high proportions of natural food items in the diet.
- There is likely a threshold of human food supplementation past which wild primate microbiomes and physiology are heavily impacted. This howler monkey population does not appear to meet that threshold, but data from more primate populations are necessary to better quantify the threshold.

these foraging activities are often actively discouraged by the associated human communities concerned about the effects on human economic and physical well-being, they are difficult to control and often happen regardless. In contrast, for wild primate populations occupying areas where tourism is popular, supplementation with human foods by guides and visitors can be accepted or even encouraged (Alfonso et al. 2021). Similar dynamics can also occur when human communities neighboring wild primate populations do not view the primates as pests and instead try to care for them by providing them with food from their houses (Back and Bicca-Marques 2019), a condition also observed in urban settings (Lima and Bicca-Marques 2024). Historically, at many field sites, researchers themselves also provisioned primates as part of the habituation process, although this practice has become less common (Asquith 1989; Fedigan 2010).

Regardless of how supplementation happens, it represents a substantial foraging and dietary change for wild primates. Human foods tend to be lower in fiber and plant secondary metabolites and higher in fat, protein, and simple sugars compared to wild primate foods (Milton 1999). As a result, they also tend to be more energetically dense (McLennan and Ganzhorn 2017; Saj et al. 1999). Wild primates may benefit from human food supplementation because of the increased caloric intake (Boug et al. 2017), particularly in environments with chronic or seasonal constraints in food availability. A range of studies have reported increased reproductive success and decreased mortality in provisioned populations (Asquith 1989; Fedigan 2010). However, there may be other health risks such as metabolic dysregulation that these diets introduce (Maréchal et al. 2016; Murray et al. 2016). Current understanding of the magnitude of these risks is limited.

Most studies of human food supplementation in wild primates have focused on social interactions and activity budgets (Asquith 1989; Sugiyama 2015). Vervets, baboons, Assamese macaques, and Lowe's monkeys that consume human foods spend more time resting and less time feeding (Adhikari et al. 2018; Badiella-Giménez et al. 2021; Saj et al. 1999). These behavioral alterations can put primates at risk of metabolic disease, but physiological data that empirically evaluates this risk is difficult to collect non-invasively. Baboons feeding on garbage have increased body weight and subcutaneous fat thickness, as well as elevated leptin levels and insulin resistance, all of which are associated with metabolic disease in humans (Altmann et al. 1993; Banks et al. 2003; Eley et al. 1989). However, it is unclear if these physiological traits carry similar health risks in baboons. Similar data do not exist for other populations and primate species.

Given these challenges, gut microbiome analysis represents a potentially useful tool for non-invasively evaluating the health risks of human food supplementation in populations of wild primates. Data describing the taxonomic composition and function of the gut microbiota can be generated from fecal samples, and variation in these gut microbiome parameters has been associated with variation in metabolism, immune function, and even brain development and behavior in mammals (Al Nabhani and Eberl 2020; Bailey and Coe 1999; Leshem et al. 2020; Hong-Zhe et al. 2020; Newman et al. 2021; Oliphant and Allen-Vercoe 2019; Pronovost and Hsiao 2019; Sylvia and Demas 2018; Visconti et al. 2019; Vuong et al. 2020; Zheng et al. 2021).

Furthermore, within a given primate species, diet is a major driver of gut microbiome variation. For example, in wild black howler monkeys (*Alouatta pigra*), seasonal variation in diet is strongly associated with variation in gut microbiome composition and function (Amato et al. 2015), and similar patterns have been reported in other wild primate populations (Baniel et al. 2021; Beeby and Baden 2021; Hicks et al. 2018; Orkin et al. 2019; Springer et al. 2017). Differences in long-term dietary patterns are also associated with differences in gut microbiome composition across populations of humans and nonhuman primates (Amato et al. 2013; Arumugam et al. 2011; Bueno de Mesquita et al. 2021; Sharma et al. 2020; Wu et al. 2011; Yu et al. 2021). Therefore, the gut microbiome of wild primates is likely to be affected by human food supplementation. Evaluating patterns in gut microbiome composition under these circumstances can provide insight into potential health risks.

This approach has recently been used to explore the effect of trash consumption on wild baboons in Akagera National Park, Ethiopia (Moy et al. 2023). Baboons with unlimited access to trash had reduced gut microbial diversity and reduced relative abundances of fiber-degrading taxa such as Ruminococcaceae, Prevotellaceae, and Lachnospiraceae compared with baboons in the same park with no access to trash. These microbial traits have been associated with increased risk for metabolic disease in humans and animal model studies (Bisanz et al. 2019; Ley et al. 2006; Sonnenburg and Sonnenburg 2019b; Turnbaugh and Gordon 2009), including in primates (Jiang et al. 2022; Koo et al. 2019; Newman et al. 2021). Additionally, the baboons with limited access to trash also had a gut microbiome composition that was more similar to that of baboons with no access to trash, suggesting that a threshold of diet change might be passed in order for the microbiome, and presumably other aspects of health, to be impacted (Moy et al. 2023). As a result, it is possible that not all human food supplementation impacts negatively wild primates.

Here we further explore how human food supplementation impacts wild primate health by describing the gut microbiome of free-ranging brown howler monkeys (*Alouatta guariba*) in periurban Brazil that do or do not have access to human foods. In this population, some groups of howler monkeys receive food items--primarily fruits--from local inhabitants. A previous study of this population found that the consumption of these food supplements reduced the ingestion of native fruits by howler monkeys but did not change the ingestion of native leaves (Back and Bicca-Marques 2019). Additionally, the activity budgets of the howler monkeys remained the same. Given that leaves generally contain high amounts of fiber, we hypothesized that supplemented howler monkeys would have reduced gut microbial diversity but similar relative abundances of fiber degrading taxa compared to non-supplemented howler monkeys. We also hypothesized that these patterns would be consistent across time despite temporal changes in the availability of wild foods being consumed by the howler monkeys.

1 | Methods

1.1 | Study Region and Study Subjects

We conducted this study in six areas (SAR: 8.9 ha, SJA: 6.5 ha, SRO: 1.2 ha, WAN: 11.0 ha, WQR: 8.5 ha, WBD: 6.4 ha) of periurban Atlantic Forest in the Itapuã District, Viamão, state of Rio Grande do Sul, Brazil (Figure 1) from August 2021 to

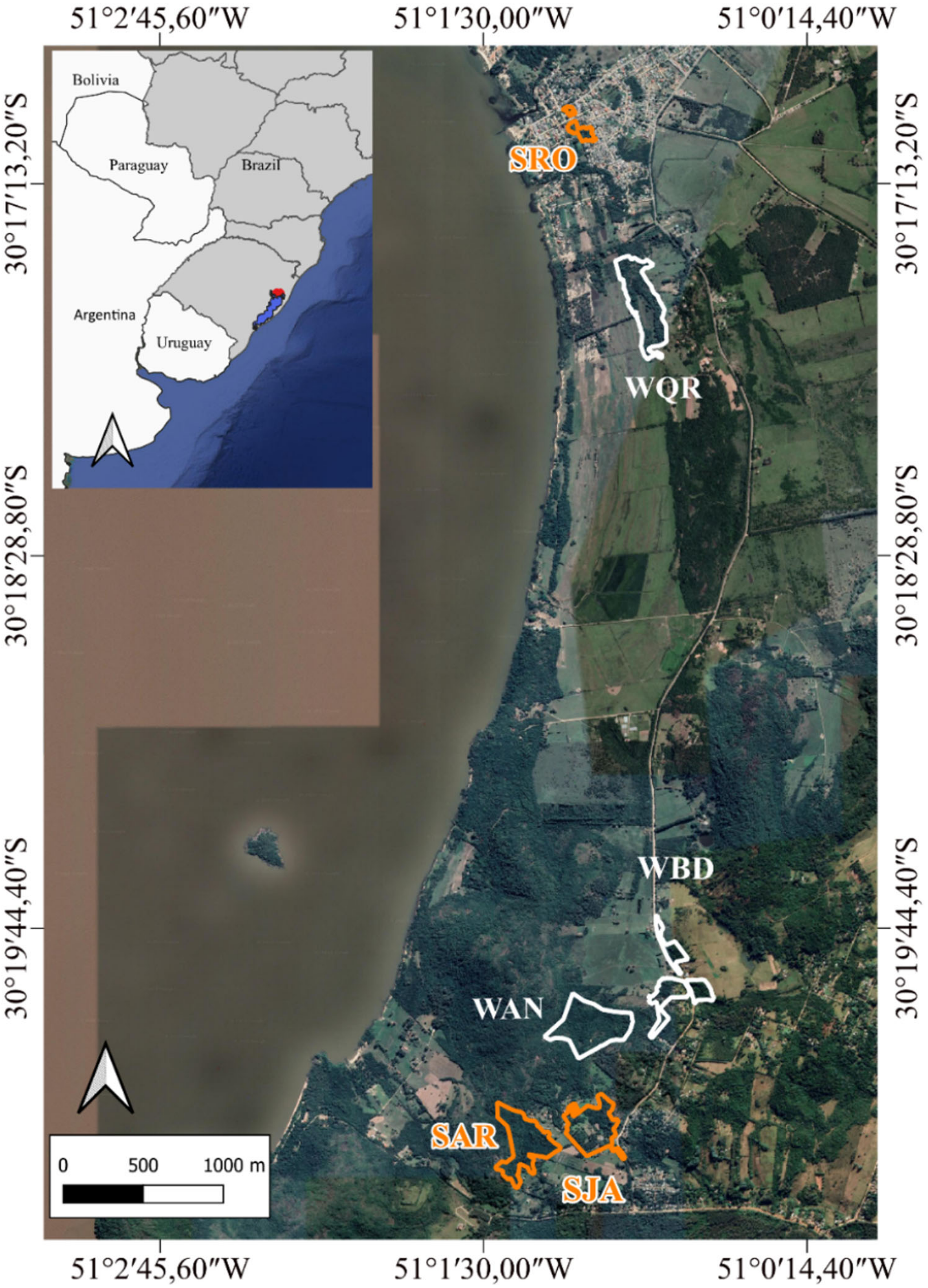

FIGURE 1 | Location of the six study areas in Itapuã, Viamão, Rio Grande do Sul, Brazil. The orange and white colors delimit the home ranges of the supplemented (S) and non-supplemented (W) howler monkey groups, respectively. *Source:* QGIS©.

August 2022. We studied a social group of brown howler monkeys in each area. The WAN, WQR, and WBD groups had no exposure to human settlements or foods and occupied habitats with similar ecology. The SRO, SAR, and SJA groups had access to both human settlements and foods, and each group occupied a slightly different habitat. Considering a 500-m buffer from the centroid of each forest fragment inhabited by the groups, urban infrastructure covered 4.2% of the area inhabited by the SRO group and its surroundings, 2.8% of the SJA's area and 0% of the SAR's area. The area inhabited by SRO is part of the urban matrix of the Itapuã District. The group lived in a forest remnant that includes the backyards of houses. Within this forest, there was an intermittent stream used by the howler monkeys to drink water. The stream was affected by irregular disposal of garbage, such as bottles and other plastic containers, old furniture, branches, and leaves from pruning and backyard cleaning. SRO howler monkeys move around on the roofs and walls of houses.

The forest areas inhabited by the SJA and SAR groups were located in a less urbanized area, approximately 6 km from the Itapuã District. The howler monkeys in these groups used the orchards surrounding houses. They had no contact with household waste but used the ground where domestic animals also passed through. The SJA group used a feeding platform, which was also used for feeding by various birds. The home range of the SAR group was adjacent to the Mantenedor de Fauna Silvestre Rincão do Araticum, which houses brown howler monkeys, capuchin monkeys (*Sapajus nigritus*), and birds rescued from conflicts with the anthropogenic environment by environmental authorities. The SAR howler monkeys roamed over the enclosures and the kitchen roof of the Rincão do Araticum. They also interacted in an affiliative, agonistic, and sexual way with the captive howler monkeys and stole food offered to the capuchin monkeys.

Group size varied from 4 to 9 individuals in the supplemented groups (SAR: 5–6, SJA: 8–9, SRO: 4–5) and from 3 to 11 individuals in the non-supplemented ones (WAN: 7–8, WQR: 10–11, WBD: 4–3; Table 1) due to births, deaths, emigrations, and disappearances.

The WAN, WQR, and WBD groups consumed only plant parts from the native and exotic plant species found in their home ranges. The SAR, SJA, and SRO groups consumed both wild food resources of the native and exotic plant species present in their home ranges and the supplemented resources provided by local inhabitants. Ingestion of human foods was assessed previously using all occurrence focal sampling of the SAR, SJA, and SRO groups for 20–21 days each (Back and Bicca-Marques 2019; Back and Bicca-Marques 2024). The SAR howlers ingested supplements on 12 of the 20 days that they were observed (mean ± sd: 5 ± 2 supplementation events/day). The supplements represented 28% of the total fresh mass ingested during this time (= 15,312 g consumed by one adult group member over the 20-day period, or a mean individual intake of 766 g per day) and involved 79% fruit (*Musa* x *paradisiaca*, *Psidium guajava* and *Solanum lycopersicum*), 11% leaves (*Brassica oleracea* var. *acephala*), 6% stems (*B. oleracea*) and 4% tuberous roots (*Cucurbita pepo*, *Daucus carota* and *Ipomoea batatas*). The SJA howlers ingested supplements on 10 of the 20 days of observation (mean ± sd: 3 ± 2 supplementation events/day). The supplements represented 12% of the total fresh mass ingested (= 17,167 g) and involved 96% fruit (*M.* x *paradisiaca*, *P. guajava*, *Butia* spp., *Citrus reticulata*, *Citrullus lanatus*, *Rhaphiolepis bibas* and *Inga sessilis*), 3% bark (*M.* x *paradisiaca* and *Carica* spp.) and 1% leaves (*Annona sylvatica* and *Morus nigra*). Finally, the SRO howlers ingested supplements on 10 of the 21 days of observation (mean ± SD: 4 ± 2 supplementation events/day). The supplements accounted for 14% of the total fresh mass ingested (= 11,716 g) and involved 68% *M.* x *paradisiaca* fruit and 32% bread. All supplements were offered raw, except for the boiled sweet potato (*I. batatas*) eaten by the SAR howlers and the baked bread eaten by the SRO howlers.

1.2 | Behavioral Sampling and Fecal Sample Collection

JPB monitored the adult individuals of each study group for three to five, often consecutive, sunrise to sunset days during five campaigns. In total, she spent 61 days and 730 h with the supplemented groups (SRO = 21 days, SAR and SJA = 20 each) and 66 days and 780 h with the non-supplemented groups (WBD = 23 days, WQR = 22, WAN = 21).

JPB collected 53 fresh fecal samples from adult and 25 from immature supplemented howlers and 47 samples from adult and 31 from immature non-supplemented howlers immediately

TABLE 1 | Age-sex composition of the study groups during the study.

		Age-sex composition				
Group	**Group size**	**AF**	**AM**	**SB**	**JV**	**IN**
Supplemented						
SAR	5–6	2	1	1–0	1	2
SJA	9–8	3	1	1	1	3–2
SRO	4–5	2	1	0	1	0–1
Non-supplemented						
WAN	7–8	3	1	0	2	0–1
WQR	10–11	3	1	3	3	0–1
WBD	4–3	1	1–0	1–0	1	0–1

Note: AF, adult female; AM, adult male; SB, subadult; JV, juvenile; IN, infant.

TABLE 2 | Number of fecal samples collected from each age-sex class of supplemented and non-supplemented howler monkeys. Four were not included in the analysis because of low DNA quality.

	Supplemented			Total supplemented	Non-supplemented			Total non-supplemented
Age-sex class	**SAR**	**SJA**	**SRO**		**WAN**	**WBD**	**WQR**	
Adult	17	17	19	53	16	15	16	47
Female	11	12	12	35	10	8	10	28
Male	6	5	7	18	6	7	6	19
Subadult	—	6	—	6	4	3	6	13
Female	—	—	—	—	—	3	1	4
Male	—	6	—	6	4	—	5	9
Juvenile	8	3	5	16	5	7	3	15
Female	5	—	5	10	—	—	—	—
Male	—	1	—	1	—	7	1	8
Sex not identified	3	2	—	5	5	—	2	7
Infant	—	2	1	3	—	—	3	3
Total	25	28	25	78	25	25	28	78

after defecation (total = 156 samples; Table 2). Samples were generally collected from different members of a single social group on a single day. The number of samples per adult per season differed because of deaths and dispersals. If a group was composed of less than five individuals during a given sampling season, we collected two stools from the same adult individual on different days. This happened nine times. If the group was composed of five or more individuals, including immature ones, we collected one sample per adult and included samples from immatures. We used a disposable wooden spatula to select fecal material free of urine, soil, and other environmental debris. Each sample was stored in a sterile 15 mL Falcon tube containing 96% ethyl alcohol and identified it with the identity and sex of the individual, the group's name, and the date and time of collection. Samples were preserved in the field in a thermal container containing ice at a temperature < 25°C, as recommended (Hale et al. 2015), for 117 to 825 min. (mean = 483). At the end of each group's data collection, we stored the fecal samples in a refrigerator at a temperature of ca. 5°C at the Laboratory of Primatology of the Pontifical Catholic University of Rio Grande do Sul (Porto Alegre, RS, Brazil). The samples were shipped to the Department of Anthropology of Northwestern University at room temperature (Evanston, IL, USA) for microbiome analysis between 53 and 273 days later (mean = 150). Samples stored in ethanol are not substantially affected by storage temperature (Song et al. 2016).

1.3 | Microbiome Data Generation

We extracted DNA from fecal samples using the Qiagen DNEasy PowerSoil kit with modifications as previously described (Moy et al. 2023). Four samples (two from the WAN group, one from the SJA group, and one from the SRO group) did not have high enough DNA quality to include in further analyses. We used a two-step polymerase chain reaction (PCR) to amplify the V4-5 region of the 16S rRNA gene using the 515 F/926 R primers with Fluidigm linker sequences as previously described (Mallott and Amato 2018). We controlled for contamination by using extraction and PCR negatives. We used a SequalPrep Normalization Plate to purify and normalize PCR products. We sequenced on the Illumina MiSeq V4 platform at the Rush University Microbiome and Genomics Core. Raw DNA sequences are available upon request.

Sequencing yielded 6,718,777 raw sequence reads. All controls had fewer sequence reads than the actual samples and were therefore discarded from subsequent analyses. Excluding controls, we had an average of 43,883 sequences per sample before quality filtering (range of 13,350 to 59,162 sequences per sample). We trimmed, quality-filtered, and dereplicated raw sequence data, inferred amplicon sequence variants (ASVs), and merged paired reads using the DADA2 plug-in (Callahan et al. 2016) for QIIME2 (v2023.2) (Bolyen et al. 2018). We assigned taxonomy in QIIME2 using a Naive Bayes classifier trained on the GreenGenes2 database using the full 16S rRNA gene sequence lengths. We filtered mitochondria and chloroplast ASVs from the data set. After quality filtering, there was an average of 22,076 sequences per sample (range: 8,580 to 39,851 sequences per sample) and a total of 12,230 ASVs.

We generated alpha rarefaction curves using the QIIME2 alpha-rarefaction command. Based on the output, we decided to rarefy our data to 8,000 reads per sample, which resulted in no sample being lost out of our total of 152 samples. We calculated the Shannon alpha diversity and the weighted and unweighted UniFrac distances between samples using the core diversity plug-in in QIIME2. Analysis code is available on GitHub (https://github.com/Kramato-lab/guariba_food_supplementation).

1.4 | Statistical Analysis

We compared the overall gut microbiome community composition of age and sex classes using a permutational analysis of variance (PERMANOVA) using the adonis2 function in the package, vegan (Oksanen et al. 2018) with R software (v4.2.2), for both the unweighted and weighted UniFrac distance matrices. We removed one outlier (a juvenile female from the SRO-supplemented group) from the weighted UniFrac model. We used a linear regression (car package) to test for the relationship between these variables and microbial alpha diversity. Because we detected an effect of age on overall microbial community composition, we controlled for this factor in subsequent PERMANOVAs by including it as the first factor in a "by = 'terms'" model. We were unable to control for the effect of individual because it was completely confounded with diet and therefore absorbed all of the variance associated with diet, precluding us from testing the effect of specific diet differences effectively. We tested the extent to which overall gut microbiome composition differed between social groups within each diet type and across seasons with PERMANOVA. We included human food access and season as interaction factors. We also used a linear regression to test for the relationship between human food access, season, and microbial alpha diversity. We included social group in all models to determine the extent to which microbiome composition and diversity varied among social groups after accounting for differences in diet. Because we had significant interactions between diet and season in our PERMANOVA models, we also ran PERMANOVAs testing for the effect of season and social group for each diet type separately. Finally, we used the ANCOM-BC package (Lin and Peddada 2020) to test for significant differences in the relative abundances of individual GM taxa between age classes, diet types, and over time using the ancombc2 function. Analysis code is available on GitHub (https://github.com/Kramato-lab/guariba_food_supplementation). The ASV table, metadata, and taxonomy assignments are included in the Supporting Information (Tables S1–S3).

2 | Results

Overall microbiome composition differed weakly among howler monkey age classes (PERMANOVA unweighted UniFrac: $F_{3,\ 148} = 2.2$, $r^2 = 0.04$, $p < 0.001$; weighted UniFrac: $F_{3,\ 147} = 2.0$, $r^2 = 0.04$, $p = 0.002$), whereas alpha diversity did not differ ($F_{3,\ 148} = 0.5$, $p < 0.7$). Four taxa varied in relative abundance between infants and adults, and six between juveniles and adults (Table S4). No taxon showed differential relative abundances between subadults and adults. There were very small differences in microbiome composition between sexes only when accounting for the presence and absence of microbial taxa (unweighted UniFrac: $F_{1,\ 133} = 1.5$, $r^2 = 0.01$, $p = 0.04$; weighted UniFrac: $F_{1,\ 132} = 1.2$, $r^2 = 0.01$, $p = 0.27$). Alpha diversity did not differ between sexes ($F_{1,\ 79} = 2.3$, $p = 0.13$). No taxon showed differential relative abundances between sexes.

Controlling for age, variation in overall microbiome composition was significantly but weakly associated with human supplementation (unweighted UniFrac: $F_{1,\ 151} = 3.1$, $r^2 = 0.02$, $p < 0.001$; weighted UniFrac: $F_{1,\ 150} = 3.0$, $r^2 = 0.02$, $p = 0.002$) and season (unweighted UniFrac: $F_{4,\ 151} = 2.3$, $r^2 = 0.05$, $p < 0.001$; weighted UniFrac: $F_{4,\ 150} = 3.6$, $r^2 = 0.08$, $p < 0.001$; Figure 2). There was also a small, but significant interaction between the effects of human supplementation and season on overall microbiome composition (unweighted UniFrac: $F_{4,\ 151} = 1.4$, $r^2 = 0.03$, $p = 0.003$; weighted UniFrac: $F_{4,\ 150} = 1.7$, $r^2 = 0.04$, $p = 0.005$). However, when we tested for the effects of season for supplemented and non-supplemented howlers separately, the individuals consuming a diet restricted to wild foods showed a similar relationship (unweighted UniFrac: $F_{4,\ 75} = 2.1$, $r^2 = 0.10$, $p < 0.001$; weighted UniFrac: $F_{4,\ 75} = 2.9$, $r^2 = 0.13$, $p < 0.001$) compared to howler monkeys consuming a human supplemented diet (unweighted UniFrac: $F_{4,\ 75} = 1.7$, $r^2 = 0.08$, $p < 0.001$; weighted UniFrac: $F_{4,\ 75} = 2.5$, $r^2 = 0.11$, $p < 0.001$). The relative abundances of 44 microbial ASVs also varied between supplemented and non-supplemented individuals, the majority of which belonged to the genus *Prevotella* and the families Lachnospiraceae, Oscillospiraceae, and Ruminococcaceae, which are key taxa in fiber and other carbohydrate degradation. Of the most abundant taxa, ASVs from *Prevotella*, *Ruminococcus*, and *Borkfalkia* exhibited the highest relative

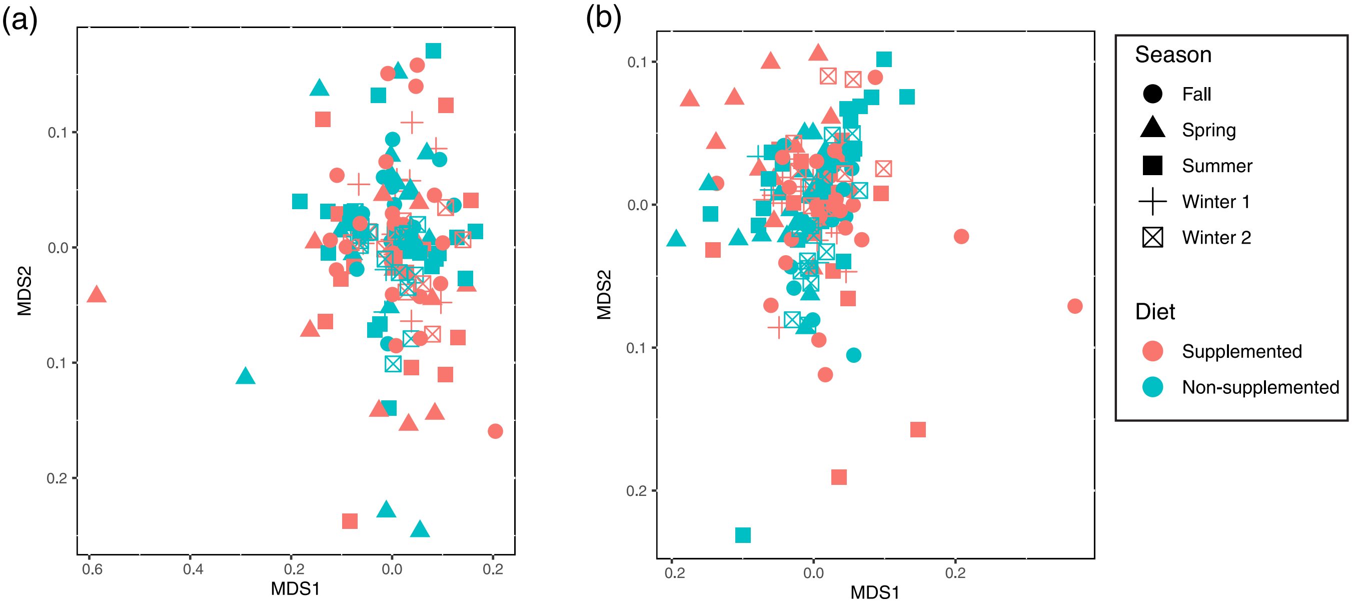

FIGURE 2 | Nonmetric multidimensional scaling (NMDS) plots using (a) unweighted UniFrac and (b) weighted UniFrac distances demonstrate weak clustering of brown howler monkey gut microbiome samples by diet type and season.

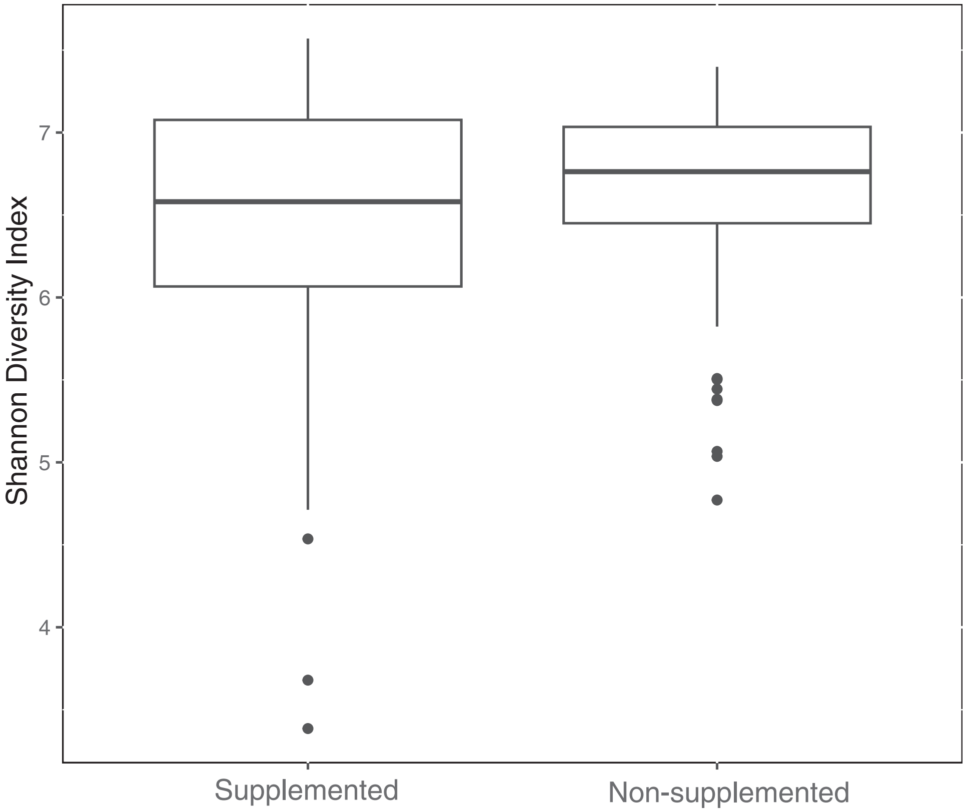

FIGURE 3 | Small but significant differences in gut microbial diversity (Shannon index) between supplemented and non-supplemented brown howler monkeys.

abundances in non-supplemented individuals (Table S5). These taxa are associated with fiber and other carbohydrate degradation. An *Enteromonas* ASV exhibited much higher relative abundance in supplemented individuals, given that it was essentially absent in non-supplemented individuals (Table S5). The relative abundances of 43 microbial ASVs varied across seasons (Table S6), the majority of which belonged to the fiber and other carbohydrate-degrading class Clostridia.

In contrast to microbiome composition, microbial diversity was significantly associated with the access to food supplements ($F_{1,\ 142} = 4.4$, $p = 0.04$; Figure 3), but not season ($F_{4,\ 142} = 1.5$, $p = 0.2$). There was no significant interaction between diet and season ($F_{4,\ 142} = 1.2$, $p = 0.3$).

Additionally, after accounting for diet and season, social groups exhibited significant differences in overall microbiome composition (unweighted UniFrac: $F_{4,\ 151} = 3.8$, $r^2 = 0.09$, $p < 0.001$; weighted UniFrac: $F_{4,\ 150} = 3.8$, $r^2 = 0.08$, $p < 0.001$; Figure S1). There was no effect of social group on microbial diversity for wild howler monkeys ($F_{2,\ 73} = 0.06$, $p = 0.9$), but there was an effect for supplemented howler monkeys ($F_{2,\ 73} = 5.7$, $p = 0.005$; Figure 4).

3 | Discussion

In this study, we aimed to explore the extent to which human food supplementation is associated with changes in the gut microbiome composition of wild brown howler monkeys. As hypothesized, we found that howler monkeys consuming human foods had reduced gut microbial diversity and reduced relative abundances of fiber degrading microbial taxa. However, the effect size of these differences was relatively small and varied over time. In contrast, the composition of the gut microbiome varied significantly across months, regardless of the access to food supplements, reinforcing previous reports of important temporal dynamics in the howler monkey gut microbiome that are likely associated with temporal changes in diet (Amato et al. 2015).

To begin with, we found that food supplementation was associated with significant differences in the gut microbiome composition. As reported in baboons with unlimited access to human trash (Moy et al. 2023), the howler monkeys in this study that had access to supplements had reduced microbial diversity and decreased relative abundances of common fiber-degrading taxa. However, the effects of supplements on the gut microbiome of our study subjects were much smaller than those detected in baboons with unlimited access to trash and more similar to those reported for baboons with limited, occasional access to human foods (Moy et al. 2023). These similarities make sense given that the howler monkeys in our study did not have unlimited access to food supplements and consumed a large proportion of wild foods as part of their diet. In addition, we found both in a previous study (Back and Bicca-Marques 2019) and in the current one that food supplements in our population have no effect on the consumption of native leaves. If the diet were to shift to include almost entirely human foods, we might expect to see even bigger changes in the gut microbiome.

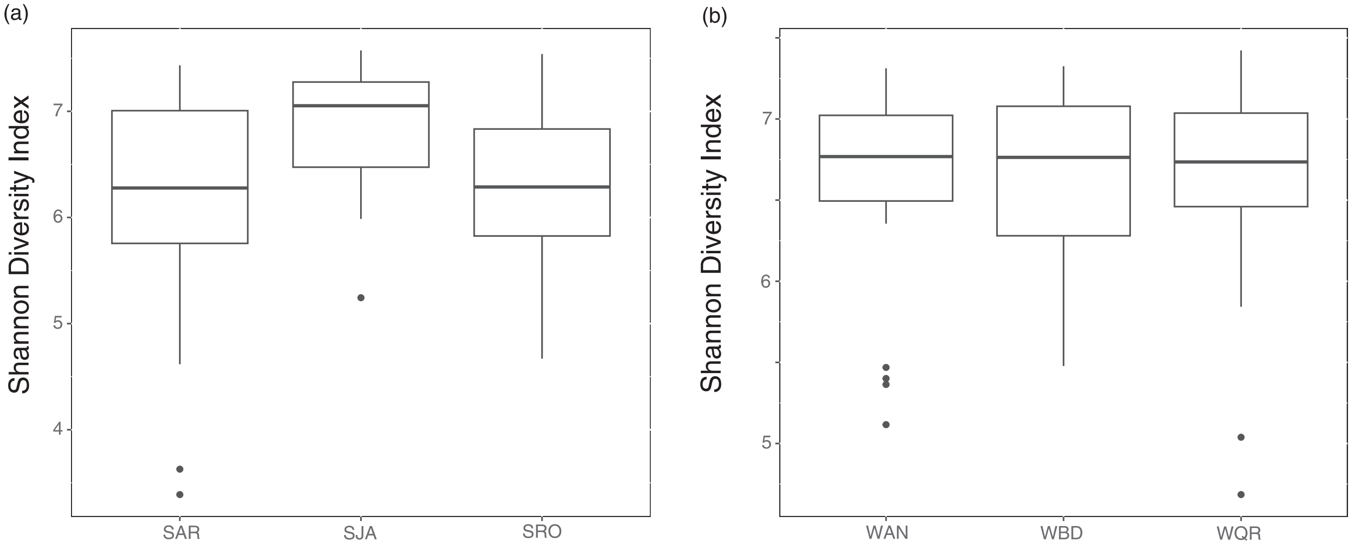

FIGURE 4 | Differences in microbial diversity (Shannon index) across social groups for (a) supplemented and (b) non-supplemented howler monkeys. Only supplemented howler monkeys exhibit significant differences in gut microbial diversity across social groups.

A limited number of nutritional studies suggest that human-derived foods are higher in fat and lower in fiber than wild primate foods (Johnson et al. 2013). We do not have quantitative nutritional data for this study, but the supplemented foods consumed by the howler monkeys were generally fruit and made up only between 12% and 28% of the ingested biomass in the previous study (Back and Bicca-Marques 2019) and, on average, between 8% and 25% of the ingested biomass by each supplemented howlers in the current study (Back 2024). Despite likely differences in fiber content between cultivated and wild fruits, we do not have enough data to assess whether the diets of supplemented howlers were significantly lower in fiber than those of the groups feeding exclusively on native and nonnative fruits and leaves present in their home ranges. The reduced microbial diversity and reduced relative abundances of fiber degrading taxa, such as Prevotellaceae, Ruminococcaceae, and Lachnospiraceae, of the microbiome of supplemented howlers resemble the changes reported in studies of humans consuming high-fat, low-fiber industrialized diets (Clemente et al. 2015; De Filippo et al. 2010; Schnorr et al. 2014; Sonnenburg and Sonnenburg 2019a; Yatsunenko et al. 2012), and may be related to the importance of bananas and boiled sweet potato in the diet of some supplemented groups. For example, bananas are rich in carbohydrates and low in fiber (Oyeyinka and Afolayan 2019). Sweet potatoes are rich in carbohydrates and high in fiber (Mei et al. 2010), but the process of boiling breaks down the fiber. We suggest that some of the same microbial extinctions hypothesized to occur in industrialized human populations consuming a diet high in simple carbohydrates and fats, and low in fiber (Sonnenburg and Sonnenburg 2014; Sonnenburg and Sonnenburg 2019a) may also occur in other primates consuming diets higher in simple carbohydrates and lower in fiber. Nutritional analyses of food items in future studies can help test this hypothesis.

It is possible that the altered relative abundances of multiple microbial taxa that we observed in howler monkeys consuming a human supplemented diet are linked to negative health outcomes, although we have no evidence based on urinalysis of the study subjects (Back and Bicca-Marques 2024). Although we do not have empirical data describing howler monkey physiology in this study, some of the patterns we observed have associated with diseases such as obesity and depression in humans (Kelly et al. 2016; Ridaura et al. 2013). However, it has also been shown in multiple wild primate populations that gut microbiome composition shifts with diet, and are not necessarily associated with negative health impacts (Amato et al. 2015; Baniel et al. 2021; Springer et al. 2017; Sun et al. 2016). Therefore, the differences we detected may also simply be a consequence of distinct diets. Moving forward, biomarkers of howler monkey immune, metabolic, and endocrine function should be generated in conjunction with microbiome data to more directly test the relationship between the howler monkey microbiome and health. These data will increase the utility of the gut microbiome as a biomarker for health and welfare and will further facilitate its use in conservation efforts.

Importantly, one of the strongest effects on gut microbiome composition that we detected in this study were those of season and group. The effects of season are consistent with previous reports that the gut microbiome of other howler monkey species varies markedly over time (Amato et al. 2015; Amato et al. 2016). For example, the black howler monkey (*Alouatta pigra*) gut microbiome shifts in association with diet across seasons, and it appears to generate more host-accessible energy from fiber degradation when easily metabolizable energy intake decreases (Amato et al. 2015). These dynamics appear to help black howlers compensate for temporally reduced food availability and quality. Although we do not have nutritional data of the diet composition of the supplemented and non-supplemented study groups or data describing microbial fiber degradation activity, it is likely that a similar relationship exists in the brown howler monkey. *Alouatta* species are ecologically similar despite species-specific variation in aspects of diet composition in their mostly exclusive geographic ranges (Agostini et al. 2010; Bicca-Marques 2003; Dias and Rangel-Negrin 2015). Therefore, gut microbial activity may benefit all members of the genus in a similar way. Data are currently being collected to further explore this possibility.

Finally, as has been reported in a range of other primate species (Amato et al. 2014; Bennett et al. 2016; Gogarten et al. 2018; Grieneisen et al. 2017; Janiak et al. 2021; Perofsky et al. 2021; Reese et al. 2021), we detected effects of age and, in particular, social group on gut microbiome composition. The microbial differences associated with these factors did not have clear biological implications. However, it is important to consider the potential effects of these variables when testing for the effects of others.

In conclusion, we found that human food supplementation affects the howler monkey gut microbiome in ways that have been linked to negative consequences for health. This finding is an important step towards advancing the use of microbiome analysis as a noninvasive tool for evaluating nonhuman primate welfare and conservation status. However, the relationship between food supplementation and health are likely to vary based on the type and frequency of supplementation and the primate species of interest. Further empirical research in this area will be critical for clarifying these differences and facilitating effective conservation applications.

4 | Management Implications

Supplementation of wild animals with human foods is a globally common occurrence with potentially negative impacts on animal health, and ultimately, conservation. However, it can also be difficult to avoid some level of supplementation in the context of eco-tourism and coexistence of local human and wildlife populations. The gut microbiome is sensitive to variation in host diet and affects various aspects of host biology, making it useful as a biomarker for assessing the impacts of human foods on wildlife. Here, we find that when supplementation is limited to a small percentage of the overall diet, differences in the gut microbiome of wild primates consuming human foods are small. Therefore, potential effects on health are also likely to be small. Future studies should quantify diet thresholds past which the incorporation of human foods into wildlife diets have substantial effects on the gut microbiome and test the extent to which microbiome changes are simply a reflection of diet shifts or also affect host biology and health. Importantly, food types and the animal species consuming them may alter these thresholds.

Author Contributions

Katherine R. Amato: formal analysis (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), supervision (equal), visualization (equal), writing – original draft (equal). **Janaína P. Back:** conceptualization (equal), investigation (equal), methodology (equal), project administration (equal), writing – review and editing (equal). **Maria Luisa Savo Sardaro:** data curation (equal), investigation (equal), methodology (equal), writing – review and editing (equal). **Júlio César Bicca-Marques:** conceptualization (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), supervision (equal), writing – review and editing (equal).

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Ethics Statement

We carried out all methods in accordance with relevant guidelines and regulations and they are reported in accordance with ARRIVE guidelines. All howler monkey fieldwork followed the joint International Primatological Society and American Society Primatologists Code of Best Practices for Field Primatology (http://www.asp.org/resources/docs/Code%20of_Best_Practices%20Oct%202014.pdf) and the research protocol was approved by the Scientific Committee of the School of Health and Life Sciences of the Pontifical Catholic University of Rio Grande do Sul (project no. 9701/2020 SIPESQ). The Normative Instruction #3 of September 1, 2014 of the Chico Mendes Institute of Biodiversity Conservation (ICMBio) states that no authorization is required for the collection of fecal samples from wild free-ranging animals outside of nature reserves and natural underground cavities. We registered all six sample shipments in the National System for the Management of Genetic Heritage and Associated Traditional Knowledge (SisGen) under the access codes AD4AD5E, RC70BF3, R8C122D, R765DEB, R92604A and RF9EE59 to comply with the Brazilian Law no. 13,123/2015. The import of the samples by KRA was authorized by the Center for Disease Control and Prevention (CDC) PHS permit no. 20220802-2766 A.

Data Availability Statement

Raw DNA sequences are available from the authors upon request. Feature tables and metadata are included in the supplemental material. Analysis code is available on GitHub (https://github.com/Kramato-lab/guariba_food_supplementation).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.