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1 **Unexpected higher convergence of human-great ape enteric viromes in central**  
2 **African forest than in a European zoo: A One Health analysis**

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28

29 **Abstract**

30 Human-animal pathogenic transmissions threaten both human and animal health, and the  
31 processes catalyzing zoonotic spillover and spillback are complex. Prior field studies offer  
32 partial insight into these processes but overlook animal ecologies and human perceptions and  
33 practices facilitating human-animal contact. Conducted in Cameroon and a European zoo, this  
34 holistic study elucidates these processes, integrating metagenomic, historical, anthropological  
35 and great ape ecological analyses, and real-time evaluation of human-great ape contact types  
36 and frequencies. Surprisingly, we find more enteric virome sharing between Cameroonian  
37 humans and great apes than in the zoo, a virome convergence between Cameroonian humans  
38 and gorillas, and adenovirus and enterovirus taxa as most frequently shared between  
39 Cameroonian humans and great apes. In addition to physical contact from hunting, meat  
40 handling and fecal exposure, overlapping human cultivation and gorilla pillaging in forest  
41 gardens explain these unexpected findings. Our multidisciplinary study identifies  
42 environmental co-use as a complementary mechanism for viral sharing.

43

44 **Key words:** anthroozoonosis, zooanthroponosis, great apes, virome, anthropology, Africa

45

## 46 Introduction

47 Pathogenic sharing between human and wild animal populations constitute major threats  
48 to human and animal health<sup>1,2</sup>. The virus SARS-CoV-2 illustrates the worst consequences of  
49 anthroozoonosis (zoonotic spillover) and the risks associated with zooanthroponosis  
50 (spillback): SARS-CoV-2 apparently emerged from bat populations and probably infected other  
51 intermediate animal hosts before moving into human populations, causing significant  
52 morbidity and mortality; zooanthroponosis may create animal reservoirs that can generate  
53 new SARS-CoV2 variants<sup>3-5</sup>. Pathogenic spillback from humans into wild animals, moreover,  
54 can hamper conservation of protected species. Such multispecies risks may catalyze new  
55 pandemics in the future<sup>6,7</sup>.

56 The processes leading to anthroozoonoses are complex, driven by genetic proximity  
57 between hosts, a pathogen's adaptative capacity, and human-animal contact, itself catalyzed  
58 by anthropogenic changes, including demographic expansion, land use that fragments  
59 habitats, economic changes, wild animal trade, hunting and butchering<sup>6,8,9</sup>. Modeling studies  
60 help to predict where, when, and who is at greatest risk for emerging anthroozoonoses<sup>10</sup>.  
61 Although less studied, zooanthroponoses appear to be facilitated by similar practices and  
62 processes<sup>2</sup>. Lacking, however, are fine-grained investigations of potential pathogen sharing  
63 between animals and people, and the ecologies, processes, and practices sustaining such  
64 sharing<sup>11</sup>.

65 Existing evidence and analyses only partially illuminate the dynamics of zoonotic spillovers  
66 and spillbacks. Identifying potential pathogens at risk of bidirectional sharing remains  
67 challenging and expensive<sup>12,13</sup>. Many analyses focus on single pathogens, genera or  
68 families<sup>14,15</sup> and overlook granular evidence of variable human-animal interactions facilitating  
69 or mediating against pathogen sharing. Certain human-animal contact investigations elucidate  
70 these cross-species interactions, but have been weakened by imprecise definitions of specific  
71 contact types and exclusive attention to blood-borne transmission through hunting and  
72 butchering, neglecting other transmission modes<sup>16,17</sup>. Finally, investigations integrating host  
73 animal ecologies are rare.

74 This article bridges viral, ecological, and anthropological investigation to produce holistic  
75 insight into potential pathogen sharing and the complex interactions facilitating it. It compares

76 the gut virome of humans, gorillas, and chimpanzees residing in two different sites (central  
77 African forest and European zoo), detailing their attendant socio-ecological systems<sup>18</sup> to  
78 explain how viral sharing may occur. We focus on human-great ape interactions because of  
79 the deep evolutionary relations between these primate species, long histories of shared  
80 pathogens (including those originating in different animal species<sup>19</sup>), and frequent interactions  
81 between humans and great apes in forest and zoo settings. We analyze the gastrointestinal  
82 virome for two reasons: biological collections were noninvasive for protected great ape  
83 species, and stools contain important quantities of environmentally-persistent viruses that  
84 can facilitate indirect transmission.

85 We hypothesize that host species and environment will influence the intestinal virome, as  
86 other intestinal bacteriome studies have shown<sup>20-24</sup>. We also predict that in both sites, the  
87 human virome would more closely resemble that of chimpanzees because of phylogenetic  
88 proximity, and because of close daily physical and environmental contact, viral sharing  
89 between humans and both great apes would be greater in the zoo than in the Cameroonian  
90 forest.

91 The first and principal site of investigation, located in the southeastern Cameroonian  
92 dense rainforest, is home to rural people who derive their livelihoods from farming, gathering,  
93 hunting and fishing and who live in close proximity to and share forest and farming spaces  
94 with sympatric species of lowland gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan*  
95 *troglodytes troglodytes*). The second site is a European zoo with sympatric chimpanzees (*P.t.*  
96 *verus*) and gorillas (*G.g. gorilla*) and their human zookeepers. This site served as a positive  
97 control for human-great ape contact. There, physical and environmental contact is high,  
98 continuous, and easily observed because of accessibility, offering conditions that facilitate  
99 viral sharing<sup>25</sup>.

100 The present study is a first comparing across two sites the shared gastrointestinal virome  
101 between humans and two nonhuman primate (NHP) species living in close proximity. Our  
102 metagenomic sequencing of human and great ape intestinal virome illuminates new, shared,  
103 potentially pathogenic viruses<sup>4</sup>. The human virome contains less-explored viral communities  
104 that are associated with disease conditions, trigger immune response, or may function as  
105 commensals,<sup>26,27</sup> and few published studies have explored great ape gastrointestinal virome,

106 pathogenic viruses and disease<sup>28-30</sup>. Crucially, our multidisciplinary analysis identifies gorilla  
107 and human co-use of small forest gardens as a complementary mechanism for viral sharing,  
108 in addition to physical contact through great ape hunting, meat handling and fecal exposure.

109 We begin with perspectives of people inhabiting the Cameroonian forest concerning their  
110 understandings of their history with great apes and socio-cultural perspectives that frame  
111 their current relations with gorillas and chimpanzees. We then quantify environmental and  
112 physical contacts between humans and great apes. These findings enable an interpretation of  
113 our intestinal virome results, in which we document the degree of intestinal virome-sharing  
114 between humans and great apes and chimpanzee-gorilla virome differences. Based on this  
115 One Health approach, we examine the relative influences of host phylogeny and proximity,  
116 ecology, and human perceptions and practices to identify mechanisms for cross-species viral  
117 sharing.

## 118 **Results**

### 119 ***Humans and great apes in Cameroon: a lengthy, shared history***

120 Our qualitative evidence on past and contemporary human-great ape relations reveals  
121 that Southeastern Cameroonians believed that they shared a lengthy history with great apes.  
122 Several mythical tales (*likano*), still recounted during evening festivities, portray a distant past  
123 in which people, chimpanzees, gorillas, and gods once lived together in settlements (Likano  
124 sessions, 12.07.2015, 08.07.2015). These tales indicate that cohabitation was ruptured when  
125 chimpanzees and gorillas committed social transgressions, resulting in their ejection from  
126 human society.

127 This deep history of cohabitation and interaction frames local assumptions that people  
128 and great apes share specific capacities. For our informants, great ape displays of certain  
129 emotions through their protection of other troupe members, mutual grooming, and sorrow  
130 reflected their commonalities with human capacities for love, emotional expression, and  
131 mutual protection. Great apes, however, displayed superior strength to humans, and  
132 interviews with local healers reveal that this strength rendered certain body parts (tibia or  
133 vertebrae of chimpanzees, bone marrow from gorillas) useful in remedies for human

134 weaknesses or ailments (Interviews 21.05.2016, 20.01.2016). The frequency of these uses is  
135 unknown.

136 These long-term histories framed current human-great ape interactions in other ways.  
137 Mythical tales recounting past human-great ape cohabitation, ruptured by great apes' exile,  
138 was a narrative structure mirrored in recent oral histories. Oral accounts underscored physical  
139 and emotional distancing between people and great apes that accelerated over the last 50  
140 years (Interviews 15.07.2015, 29.05.2017, 30.05.2017, 02.06.2017, 30.04.2016). As one aging  
141 hunter observed,

142 Before...gorillas slept next to the village. Now, they are there, but very rarely next to the  
143 village. They are afraid and very shrewd. Even the chimpanzees, there's a group between  
144 this and the next village...just a few meters from the road. But they don't cry out, they are  
145 prudent. It's rare to hear them, even though they are there (Interview 15.07.2015).

146 For some, this distancing resulted from intensified hunting since the 1970s with high-  
147 powered rifles (Interviews 13.05.2016, 14.05.2016, 02.06.2017). Perceptions of the changing  
148 sizes of gorilla and chimpanzee populations are mixed: some informants contend that great  
149 ape populations have remained stable, and others argue that they have declined (Interviews  
150 29.05.2017, 30.05.2017, 21.01.2016).

### 151 ***Differential human contacts with chimpanzees and gorillas in Cameroon***

152 Although Southern Cameroonians generally assumed that they shared a deep history with  
153 great apes, and over time were distanced from them, they did not recognize "great apes" as  
154 an NHP category. They distinguished chimpanzees (*waké*) from gorillas (*ko*), engaging with  
155 chimpanzees differently and less frequently than with gorillas.

156 Our data show that southeastern Cameroonians perceived chimpanzees as more  
157 intelligent than gorillas, capable of learning and displaying behaviors that approximate, but do  
158 not replicate, human behavior. Chimpanzees were more elusive than gorillas, living close to  
159 human settlements but remaining silent and invisible. Some specialist hunters also claimed  
160 that it was easier to kill a gorilla than a chimpanzee, contending that this relative ease partly  
161 resulted from gorillas' large size and practice of moving across the forest floor, rendering them  
162 more detectable than chimpanzees, who frequently traversed tree canopies (Interviews

163 31.05.2017, 18.01.2016). They also reported that emotionally, it was more difficult to kill a  
164 chimpanzee than a gorilla, because the former more closely resembled humans. As one  
165 former hunter confided, “You need a strong heart to kill a chimpanzee.”

166 Southeastern Cameroonians reported that gorillas were less discerning, clumsier, more  
167 destructive, more frequently encountered than chimpanzees, and more unpredictably  
168 aggressive (Interviews 18.01.2016, 19.01.2016, 20.01.2016, 21.01.2016). Reportedly unable  
169 to distinguish ripe from unripe foods, gorillas more often laid waste to forest gardens, whereas  
170 chimpanzees purportedly raided only ripe foods from these gardens. Among people  
171 responding to a questionnaire conducted in four villages, 94% (424/449) experienced crop  
172 raiding by all NHPs, including gorillas and chimpanzees. Gorillas were more involved in the last  
173 event of crop raiding (50%, 225/449), contrary to chimpanzees (2%, 7/449). Moreover, 82% of  
174 respondents (366/449) reported that gorillas more often damaged gardens, and just 2%  
175 (7/449) cited chimpanzees as more frequent pillagers.

176 Quantitative data on human physical and environmental contacts, collected in real time,  
177 also illuminates different human interactions with gorillas and chimpanzees. The mean  
178 frequency of human physical and environmental contact with gorillas was higher, but not  
179 significantly, than with chimpanzees; direct contact (seen alive, heard) did not differ between  
180 these great apes (Table 1). Based on questionnaires, physical contacts were more frequent  
181 (except for hunting) with gorillas than chimpanzees.

### 182 ***Human-great ape contact at the European zoo***

183 Zoo gorillas and chimpanzees lived separately but shared the same environment. Both  
184 species had an indoor enclosure with outdoor access on an island with similar vegetation.  
185 Islands were surrounded by channels through which water continually circulated. Our  
186 observations showed that zookeepers and great apes had notable daily environmental and  
187 physical contact. Although we did not quantify their contact frequency, we observed daily  
188 zookeepers in close proximity (<2m) to gorillas and chimpanzees, especially through the bars  
189 of cages. Zookeepers handled food during preparation to feed to chimpanzees and gorillas.  
190 Moreover, before the COVID-19 pandemic, they generally did not wear masks and gloves  
191 when entering the cages each day to remove straw bedding and feces, and when hosing cages  
192 with hot water every 3 to 5 days.



193 We observed occasional physical contact between zookeepers and chimpanzees (playing,  
 194 affectionate scratching, grooming), whereas no physical contact occurred between  
 195 zookeepers and gorillas. Additionally, zookeepers reported that chimpanzees fell ill more  
 196 often than gorillas, especially with respiratory infections during winter months.

197 **Table 1: Mean (%) contact frequencies (SD) according to great ape species and type of contact in Cameroon.**  
 198 Physical contact frequencies are from Narat et al. 2018. \*\*\* indicates a p-value <0.001 from the Mann-Whitney  
 199 statistical tests.

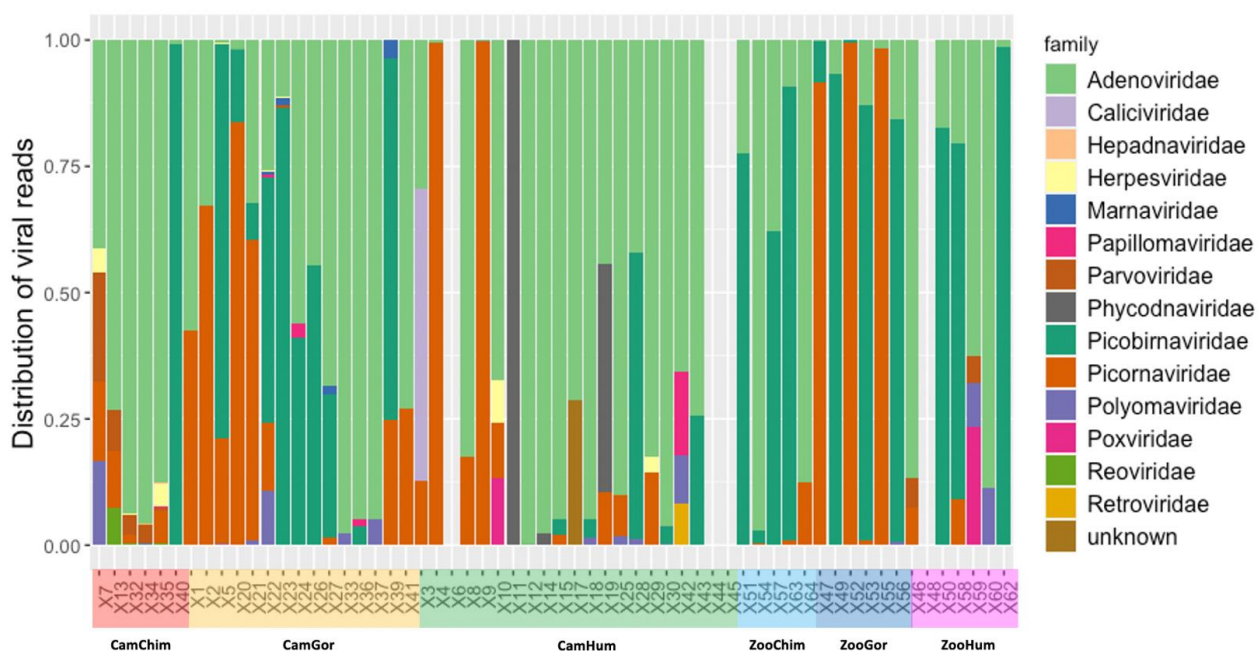
		Longitudinal survey N=18, data self-collected daily, 10 months		Questionnaire N=449	
Contact category	Type of contact	<i>Pan t. troglodytes</i>	<i>Gorilla g. gorilla</i>	<i>Pan t. troglodytes</i>	<i>Gorilla g. gorilla</i>
Environmental contact	Seen feces	2.3 (5.3)	3.5 (5.3)	Not addressed in questionnaires	
	Seen food remains	2.5 (5.3)	4.0 (5.6)		
	Seen nest	1.9 (3.5)	1.5 (2.3)		
	Seen footprints	2.2 (5.2)	3.8 (5.3)		
Direct contact	Seen alive	1.8 (5.1)	1.8 (4.1)	14.2 (31.4)	9.1 (22.3)
	Heard	3.2 (5.3)	2.6 (4.2)		
Physical contact	Hunt	0 (0, 0-0)	0 (0, 0-0)	0.08 (0.7)	0.07 (0.3)
	Butcher	0.1 (0.3)	0.2 (0.3)	0.7 (2.2)***	1.6 (7.3)***
	Cook	0.1 (0.4)	0.2 (0.6)	0.6 (2.1)***	1.0 (2.7)***
	Consume	0.2 (0.5)	1.1 (2.5)	0.7 (2.2)***	1.7 (7.3)***
	Buy/Sell	0.5 (1.2)	1.1 (2.6)	0.4 (1.6)***	1.3 (7.1)***

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202 **Fecal sample characterization and comparison**

203 We focused on vertebrate viruses because of their importance for viral transmission and  
 204 emergence. Among vertebrate viruses, 13 families, 26 genus and 61 species were identified.  
 205 The most frequent viral families observed in decreasing order were Adenoviridae (53  
 206 samples), Picobirnaviridae (30 samples) and Picornaviridae (29 samples). The distribution of  
 207 viral vertebrates reads per family for each sample tested is shown in Figure 1. The distribution  
 208 of viral reads across their natural host categories is depicted in Supplementary Figure 1.



209  
 210 **Figure 1: Distribution of viral vertebrate reads per viral family.** Each group is defined by its habitation site  
 211 (Cam=Cameroon, Zoo=European Zoo) and animal species (Chimp=Chimpanzee, Gor=Gorilla, Hum=Human)

212  
 213 The number of samples positive for each virus family among the ten most prevalent viral  
 214 families is detailed in Table 2. Adenoviridae, Picobirnaviridae and Picornaviridae were  
 215 identified in all human, gorilla and chimpanzee groups and Polymaviridae in all but zoo  
 216 chimpanzees. Herpesviridae, Papillomaviridae and Parvoviridae were identified only in stool  
 217 samples of apes and humans in Cameroon.

218 **Table 2: Number (%) of samples found positive for one of the 10 most prevalent vertebrate viral families by**  
 219 **group.** Each group is defined by its habitation site (Cam=Cameroon, Zoo=European Zoo) and animal species  
 220 (Chimp=Chimpanzee, Gor=Gorilla, Hum=Human).

	CamChimp n=6	CamGor n=15	CamHum n=23	ZooChimp n=5	ZooGor n=6	ZooHum n=7
<b>Adenoviridae</b>	6 (100%)	14 (93%)	17 (74%)	5 (100%)	5 (83%)	6 (86%)
<b>Caliciviridae</b>			1 (4%)			
<b>Hepadnaviridae</b>	1 (17%)					
<b>Herpesviridae</b>	4 (67%)	3 (20%)	2 (9%)			
<b>Papillomaviridae</b>	1 (17%)	2 (13%)	1 (4%)			
<b>Parvoviridae</b>	5 (20%)	1 (7%)	2 (9%)			
<b>Picobirnaviridae</b>	2 (33%)	10 (67%)	6 (26%)	4 (80%)	5 (83%)	3 (43%)
<b>Picornaviridae</b>	4 (67%)	9 (60%)	10 (43%)	2 (40%)	3 (50%)	1 (14%)
<b>Polyomaviridae</b>	2 (33%)	5 (33%)	5 (22%)		1 (17%)	2 (29%)
<b>Poxviridae</b>			1 (4%)			1 (14%)

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### ***Viral diversity and composition***

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Global virus richness was significantly higher in Cameroon chimpanzees than among Cameroonian humans or zookeepers (Observed and Chao index), although no difference between these same groups was observed with Shannon and Simpson indexes (Supplementary Figure 2a). When we focused only on vertebrate viruses, no significant difference was observed between the six different groups, despite a tendency for higher diversity in Cameroon chimpanzees (Supplementary Figure 2b).

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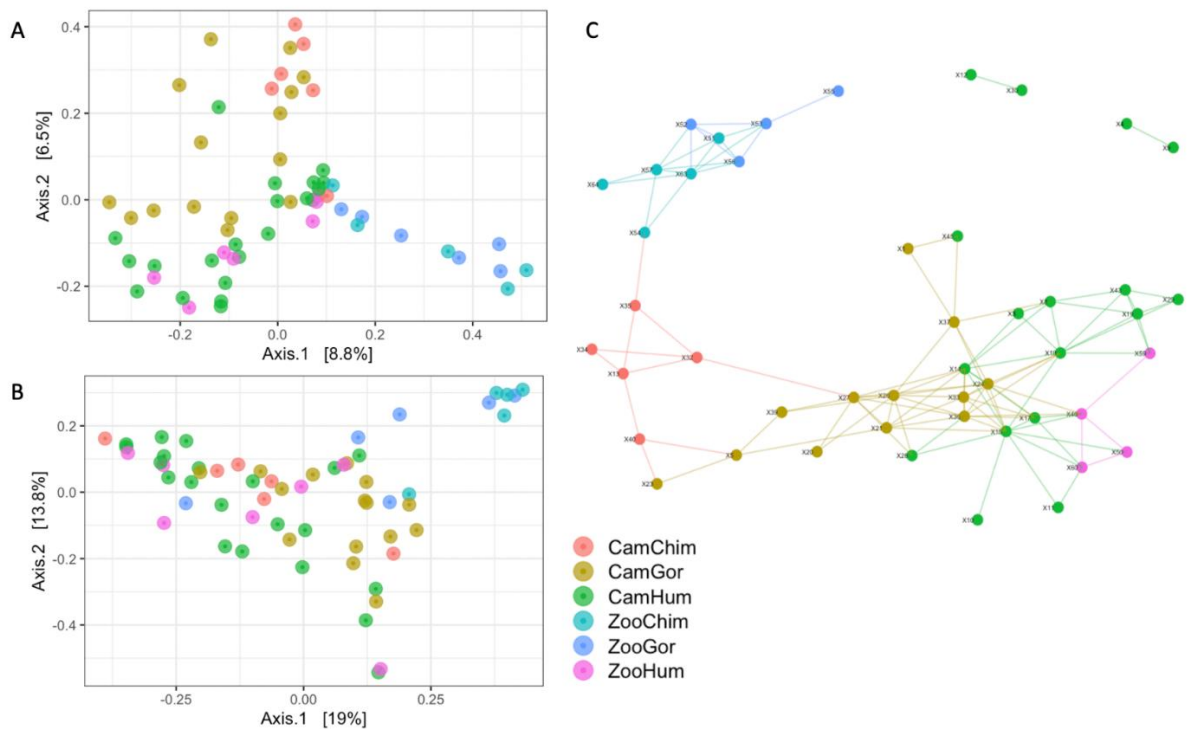
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The comparisons of virome composition using a PERMANOVA with Bray Curtis dissimilarity indices and weighted unifracs showed that the virome differed significantly across different groups ( $p$  values  $< 0.001$ ). An unsupervised analysis with a PCA among all samples showed that the global virome composition differed between host species, with a closer similarity between zoo chimpanzees and gorillas (Figure 2a and 2b). The network projection of virome similarity confirmed the proximity between viromes of zoo great apes. Viromes of zoo great apes resembled that of Cameroonian chimpanzees, which in turn was close to that of Cameroonian gorillas. Despite the distinct environments in which stools were collected, the Cameroonian and zoo human viromes closely resembled one another. Surprisingly, the network analyses revealed greater virome resemblance between Cameroonian humans and Cameroonian gorillas than between Cameroonian gorillas and other great apes in the Cameroon forest or the zoo (Figure 2c).



242

243 **Figure 2: PcoA analysis based on Bray-Curtis distances (A) and on weighted Unifrac distances (B). (C) Network**  
 244 **plot based on Bray-Curtis distances showing similarities among all sample virome profiles.** Only edges  
 245 connecting individuals (i.e., nodes) with > 90% similarity in their virome are shown. Each group is defined by its  
 246 habitation site (Cam=Cameroon, Zoo=European Zoo) and animal species (Chimp=Chimpanzee, Gor=Gorilla,  
 247 Hum=Human)

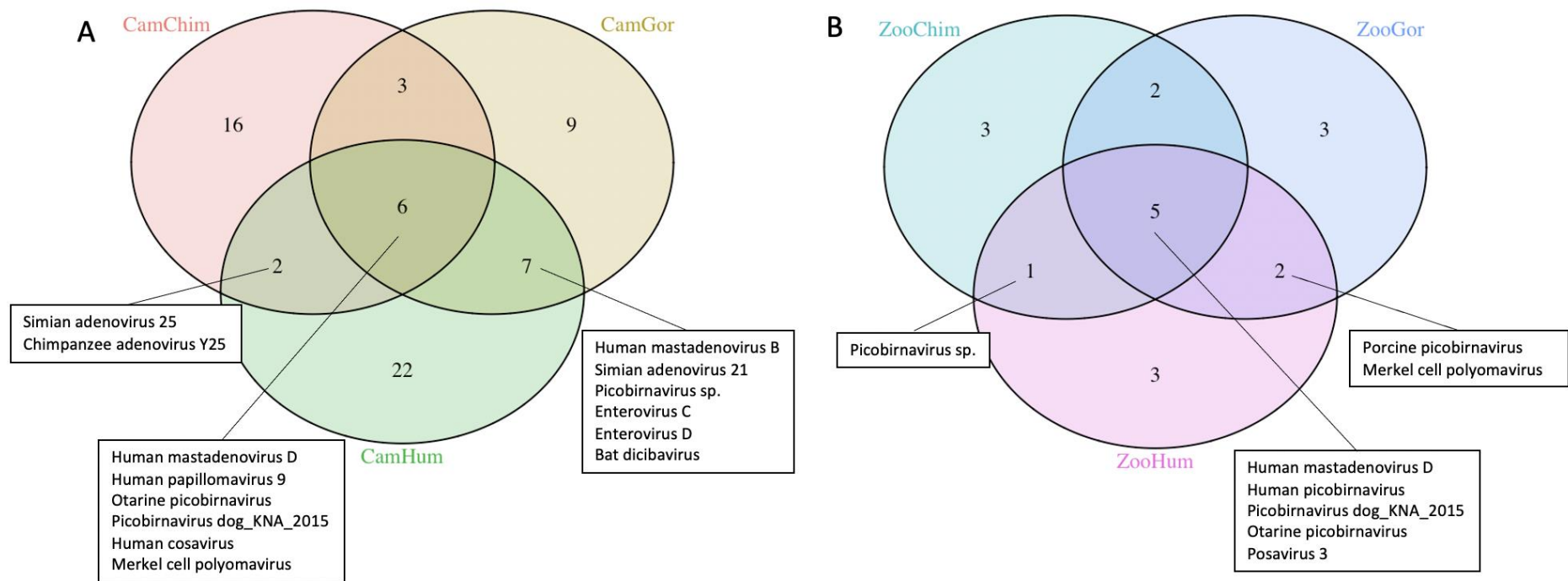
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## 249 ***Viral sharing***

250 We then investigated whether within a shared environment, great apes and humans  
 251 might harbor viruses with same lowest-common-ancestor (LCA) taxa identified. In Cameroon,  
 252 a total of 15 vertebrate viral LCA taxa identified in human stool samples were also found in  
 253 those of chimpanzees or gorillas: 13 viral LCA taxa in gorilla and human stools, 8 in chimpanzee  
 254 and human stools, and 5 shared by all 3 groups (Figure 3a). Among these vertebrate viral taxa,  
 255 the most represented genera were Mastadenovirus (n=5), Picobirnavirus (n=3), and Enterovirus  
 256 (n=3). In the European zoo, 8 viral LCA taxa were shared between humans and apes, with  
 257 a greater representation of the Picobirnavirus genus (n=5) (Figure 3b).

258 We analyzed the Mastadenovirus and Enterovirus genera, the vertebrate viruses that  
259 great apes and humans shared. Concerning the Mastadenovirus genus, we detected adenovi-  
260 rus species D among humans and great apes in Cameroon and in the European zoo. We found  
261 species E in Cameroonian humans, gorillas and chimpanzees, and species B in Cameroonian  
262 humans and gorillas. Although we detected Adenovirus species B and E in zoo great apes, we  
263 did not find them among zookeepers. Enterovirus C and D species were detected only in Cam-  
264 eroonian humans and gorillas.

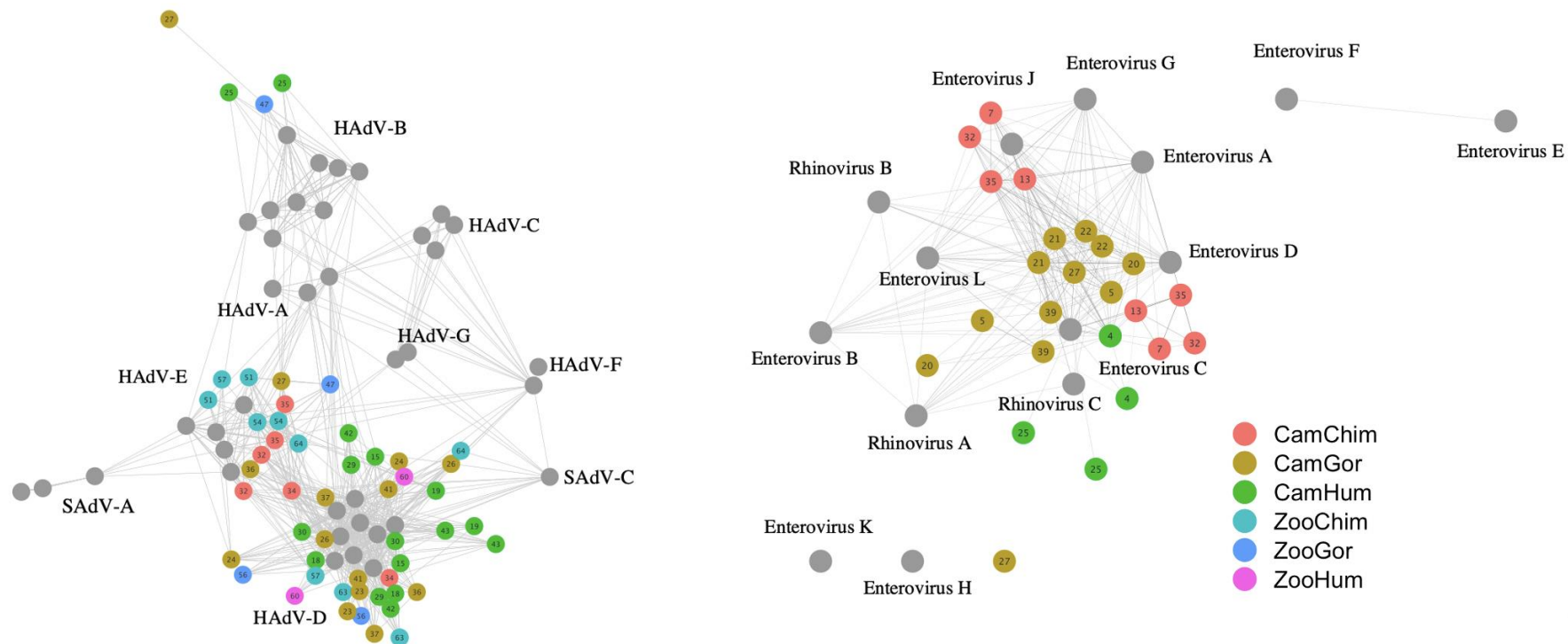
265 To evaluate the genetic proximity of the viral sequences, reads belonging to Mastade-  
266 novirus and Enterovirus genera were assembled to create contigs. Because the size of the  
267 contigs did not permit building of phylogenetic trees to compare different viruses, a network  
268 analysis on cytoscape was performed to assess genetic similarities between shared viruses.  
269 The sequence similarity network confirmed the detection of adenovirus species B, D and E  
270 (Figure 4a). The network showed close genetic distances between some adenovirus D col-  
271 lected among humans, chimpanzees and gorillas (Figure 4a), and between an enterovirus C  
272 species collected in one Cameroonian human and those collected from Cameroonian gorillas  
273 and chimpanzees (Figure 4b).



274

275 **Figure 3: Venn Diagrams of vertebrates viral lowest-common-ancestor (LCA) taxa identified in human and great ape stools in Cameroon (A) and European zoo (B).** Each  
 276 group is defined by its habitation site (Cam=Cameroon, Zoo=European Zoo) and animal species (Chimp=Chimpanzee, Gor=Gorilla, Hum=Human)

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278

279 **Figure 4: Sequence similarity network representation of Mastadenovirus (a) and Picornavirus (b) contigs.** Each node represents an individual contig or whole genome  
 280 reference sequences. Edges are defined based on the Blast Bit-score across individual samples. Each contigs is colored according to the group to which it belongs. Grey nodes  
 281 represent reference sequences. Each group is defined by its habitation site (Cam=Cameroon, Zoo=European Zoo) and animal species (Chimp=Chimpanzee, Gor=Gorilla,  
 282 Hum=Human)

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## 285 **DISCUSSION**

286 To shed light on shared human-great ape viromes and possible mechanisms of  
287 bidirectional viral sharing, this study brings together metagenomics analyses, oral histories,  
288 anthropological observation, great ape ecological analyses, and real-time evaluation of  
289 contact types and frequencies between people and great apes living in the African equatorial  
290 rain forest. It compares these results to a positive control in a European zoo, where we easily  
291 observed zookeeper-gorilla and zookeeper-chimpanzee interactions. We had two unexpected  
292 findings: the convergence of intestinal virome between Cameroonian humans and gorillas,  
293 and the higher proportion of human-great ape sharing in Cameroon. We expected that  
294 humans would share more of their intestinal virome with chimpanzees because of their  
295 phylogenetic proximity, and that viral sharing would be greater in the zoo, our positive control,  
296 because human zookeepers had closer, more frequent contact with zoo great apes.  
297 Additionally, certain adenovirus and enterovirus species were the most frequently shared  
298 viruses between Cameroonian great apes and humans. Our multidisciplinary analyses explain  
299 these biological findings in terms of southern Cameroonians' distinct perceptions and  
300 practices toward gorillas and chimpanzees, and gorilla and chimpanzee relative densities and  
301 behaviors.

302 The following explains each of our analyses around human-great ape interactions and  
303 risks associated with two viral genera, Mastadenovirus and Enterovirus, shared by  
304 Cameroonian humans and great apes. We then integrate these analyses to identify  
305 complementary mechanisms of human-great ape viral sharing in the central African forest:  
306 physical contact through hunting, meat handling, and fecal exposure; and environmental  
307 contact concentrated in small forest gardens, frequented by humans and great apes,  
308 especially gorillas.

### 309 **A historical framework for human-great ape interactions**

310 Although such evidence is not habitually integrated into metagenomics studies, our  
311 qualitative findings offer a historical framework that describes and still shapes human-great  
312 ape relations. Southeastern Cameroonians maintain that for millennia, they have interacted  
313 and shared forest spaces and foods with great apes; historical linguistic and archaeological  
314 investigations support this claim<sup>31,32</sup>. People now interact less with great apes than in previous



315 generations, but gorillas and chimpanzees still spark avid interest and ambivalence among  
316 southeastern Cameroonians. The compelling nature of great apes appears to result from their  
317 “charismatic” features; their behaviors lend themselves to human observation and elicit  
318 strong emotional responses among observers<sup>33</sup>.

319 Southeastern Cameroonian mythical tales and historical recollections make no  
320 reference to biological evolution. Consistent with historical, anthropological interpretations  
321 of mythical tales, southeastern Cameroonians appear to have distilled from their accumulated  
322 interactions with great apes their reflections about how humans, gorillas and chimpanzees  
323 resemble and differ from one another. These tales comment on an increasing emotional and  
324 physical distance between people and great apes, although there is little agreement on how  
325 it happened<sup>34–36</sup>. In the absence of long-term great ape population surveys, we cannot  
326 conclude that these NHP populations have been depleted. Certain people hunt great apes in  
327 this forest, whereas others do not<sup>37</sup>.

328 Our anthropological research shows that southeastern Cameroonians distinguish  
329 chimpanzees from gorillas, their perceptions shaping their practices around these great apes.  
330 Chimpanzee behavior, they concur, is closer than gorilla behavior to that of humans. Hence,  
331 southeastern Cameroonians avoid engaging with chimpanzees and are more reluctant to kill  
332 and butcher them, a tendency reinforced by chimpanzees’ avoidance of humans. Gorillas, by  
333 contrast, are reportedly more numerous. Their “less human” behavior apparently makes it  
334 easier for people to kill and butcher them. Human perceptions of differences between gorillas  
335 and chimpanzees seem to yield more frequent human physical and spatial contacts with  
336 gorillas than chimpanzees.

### 337 **More frequent human-gorilla contact than human-chimpanzee contact in Cameroon**

338 These qualitative findings align well with our quantitative analyses of human-great ape  
339 contact frequency. Our participatory longitudinal study found elevated, but not significant,  
340 human-gorilla spatial contact compared to that of humans and chimpanzees. Our  
341 questionnaire dataset, however, revealed significantly more frequent physical contact with  
342 gorillas. Most studies assessing human-great ape contact do not evaluate contact frequency<sup>38–</sup>  
343 <sup>40</sup>, an important but overlooked factor in understanding pathogenic transmission risks. Our  
344 previously published study evaluated quantitative and anthropological data concerning

345 human-great ape contact and different contact types with diverse NHP species<sup>41</sup>. Here,  
346 integrating quantitative contact analyses and qualitative evidence about such contacts  
347 permits insight into how southeastern Cameroonians may share specific viruses with great  
348 apes and closer virome resemblance to that of gorillas.

349 Our Cameroon investigation also describes the context and locations of these frequent  
350 human-great ape physical and environmental contacts. Our multi-village questionnaire  
351 showed that great apes were frequently involved in garden crop raiding, and gorillas more so  
352 than chimpanzees. Several primate ecological and behavioral factors may explain greater  
353 physical and environmental contact with gorillas. First, gorillas appear to be more abundant  
354 in the Cameroonian forest, leading to a higher probability of gorillas entering and raiding  
355 gardens may explain this phenomenon. Our previous work showed that signs of gorilla  
356 presence were 10 times higher than for chimpanzees in this forest<sup>41</sup>, in accordance with other  
357 studies finding that gorillas are more abundant or in similar densities to sympatric  
358 chimpanzees in the Republic of Congo, DR of Congo, Gabon, and Cameroon<sup>42-44</sup>.

359 In addition to different gorilla and chimpanzee relative densities, our southeastern  
360 Cameroonian informants also reported that gorillas crop raided more frequently and  
361 destructively. For many animals, including gorillas, these gardens were concentrated sites of  
362 food raiding and defecation. Gorillas and other nonhuman primates defecated freely in or  
363 around gardens. Gardens, frequently distant from villages where people constructed latrines,  
364 could also be sites of human defecation during their daily visits. In both cases, defecation could  
365 deposit environmentally persistent microbes.

366 Gorillas and chimpanzees may behave differently in forest gardens, leading gorillas to  
367 raid more often than chimpanzees. Most existing literature NHP crop raiding, however,  
368 focuses on chimpanzees in east and west Africa<sup>45-48</sup>. Just two studies address mountain gorilla  
369 (*Gorilla beringei*) crop raiding<sup>45,48</sup>. Gorilla and chimpanzee behavioral differences in socio-  
370 ecological systems require further investigation<sup>49</sup>. Nonetheless, small gardens may be focused  
371 “sharing platforms” for environmentally persistent microbes and their exchanges between  
372 humans and gorillas.

373 **Influence of host species and environment on intestinal virome**

374 Our results indicate that each species in its own environment harbored a specific  
375 virome composition, as expected. As with gut bacterial microbiota, phylogeny is a strong  
376 driver of species-specific enteric virome<sup>20,22,50</sup>. Our findings corroborate a previous  
377 investigation of the evolutionary and ecological origins of gut bacteriophage communities  
378 (phageome), demonstrating that the phageome structure and dynamics were influenced by  
379 superhost phylogeny and environment<sup>51</sup>.

380 Network and dissimilarity analyses revealed that human enteric viromes from  
381 Cameroon forest and the zoo were more similar despite habitation in different biotopes,  
382 whereas virome composition for great apes appeared to be shaped more significantly by  
383 ecology than by species. Additionally, the zoo environment seems to have exercised a greater  
384 influence on great ape virome than the forest did for Cameroon great apes. These results  
385 corroborate those reported by Moeller and colleagues<sup>52</sup>, in which gut microbiota of sympatric  
386 chimpanzees and gorillas bore greater resemblance to one another than gut microbiota of  
387 either allopatric bonobos and eastern lowland gorillas or allopatric chimpanzees from  
388 Tanzania and eastern lowland gorillas. Hence, our findings on human and great ape gut  
389 viromes reveal similar patterns to comparative gut microbiomes. Although phylogeny seems  
390 to exercise a greater impact on human gut virome and microbiome, environment apparently  
391 has a stronger influence on great ape viromes.

### 392 **Targeted assessment of bidirectional viral sharing risks**

393 Among vertebrate viruses known to cause disease in human beings, we identified  
394 Mastadenoviruses and Enteroviruses as the major viral genera that humans and great apes  
395 share in Cameroon. Both genera can be transmitted through physical contact and can remain  
396 infectious in the environment for several days.

397 Mastadenoviruses are associated with many diseases, including mild and severe  
398 respiratory infections, gastro-enteritis, encephalitis, cystitis, keratoconjunctivitis and  
399 hepatitis. Recently, severe hepatitis cases of unknown etiology among young children have  
400 been reported. Because an adenovirus has been detected frequently in these patients' feces  
401 or blood, investigators have hypothesized that the etiology of the severe hepatitis is an  
402 adenovirus, although investigations are ongoing<sup>53</sup>.

403 Adenovirus is a non-enveloped virus with a double-stranded DNA genome. Primate  
404 adenoviruses belong to the genus Mastadenovirus, which includes seven species (A to G) and  
405 more than 100 different types. Our analyses found adenovirus species D to be most frequently  
406 shared between humans and apes. Adenovirus species D displays frequent recombination  
407 events between different types. This tendency to recombine enables the emergence of new  
408 types that could escape from previously acquired anti-adenovirus host immunity and  
409 potentially trigger disease outbreaks in humans or great apes. Although adenoviruses are  
410 considered highly specific to hosts because of the genome's DNA structure, great ape-human  
411 transmission of adenovirus has been shown. A novel adenovirus (TMAdV, titi monkey  
412 adenovirus) discovered at the California National Primate Research Center caused a deadly  
413 outbreak in a closed colony of New World monkeys (titi monkeys; *Callicebus cupreus*) and  
414 infected humans in close contact<sup>54</sup>. Human-to-human transmission of TMAdV was also  
415 documented. Other studies have detected specific antibodies of baboon and chimpanzee  
416 adenoviruses among caregivers and zookeepers, confirming the capacity of NHP adenoviruses  
417 to infect humans<sup>55,56</sup>. Humans may also be capable of transmitting adenoviruses to great apes.  
418 Adenoviruses detected among NHPs elsewhere in Cameroon revealed sequences closely  
419 related to human adenoviruses<sup>57</sup>. Although no large adenovirus epidemics have been  
420 reported, these observations and our findings suggest an elevated risk of cross-species  
421 outbreaks.

422 Recently, machine learning analyzing viral genomes has been used to predict viral  
423 zoonotic risk. One study found significantly elevated predicted zoonotic risk in viruses from  
424 NHPs and identified adenoviruses among those viruses correlated with the probability of  
425 human infection, confirming prior investigations showing that NHP adenoviruses and  
426 retroviruses, bat rhabdoviruses, and rodent picornaviruses were more likely to be  
427 zoonotic<sup>58,59</sup>.

428 The second most frequent viral genus shared between humans and great apes was  
429 enterovirus, known to cause mild to severe disease in humans. Enteroviruses are positive-  
430 sense single-stranded RNA viruses with high mutation rates, frequent recombination events,  
431 and a potential for newly emerging types. Based on detection of specific antibodies or  
432 targeted PCR and specific viral protein sequencing, a few studies provide some evidence for  
433 anthroozoonosis and zooanthroponosis<sup>60</sup>. Although enterovirus origins are difficult to

434 ascertain because most have been described in humans, some studies have detected human  
435 enteroviruses in zoo-housed and free-ranging NHPs, with variable frequency depending on  
436 housing conditions or the degree of cohabitation in urban areas. In urban Bangladesh where  
437 NHPs and humans share the same environment, 100% of enteroviruses detected in NHPs were  
438 also known to circulate among the human population<sup>61</sup>. In contrast, in a Bangladesh zoo, most  
439 Picornaviruses detected in NHPs (53/64; 83%) were simian viruses, with only 8 (12.5%)  
440 detected in humans<sup>62</sup>. These results corroborate our findings, suggesting that environmental  
441 sharing without specific hygiene control measures enables cross-species transmission of  
442 enteroviruses. Another study investigating enterovirus genetic diversity in 615 stool samples  
443 collected between 2006 and 2008 from zoo and free-ranging NHPs in Cameroon, the rate of  
444 enterovirus detection was 20.2% among zoo NHPs and 3.5% in free-ranging NHPs. These  
445 viruses belong to virus types that circulate among humans in 94% of zoo NHP and 55% of free-  
446 ranging NHP positive samples<sup>25</sup>. The zoo NHP habitat (large enclosures), where frequent  
447 interactions between NHPs and employees and the public, was suspected as a key site  
448 facilitating viral transmission.

#### 449 **Humans, gorillas, intestinal virome, and targeted viruses: convergences in Cameroon**

450 Contrary to our prediction, viromes of Cameroon forest inhabitants and Cameroon  
451 gorillas more closely resembled one another than those of zookeepers and zoo gorillas and  
452 chimpanzees. The proportion of viral taxa shared between gorillas and humans was four times  
453 higher in Cameroon than in the European zoo, and among Cameroon humans and great apes,  
454 human-gorilla viral sharing was higher than for human-chimpanzee sharing.

455 Our historical-anthropological, ecological, and contact analyses suggest two  
456 complementary mechanisms to explain viral sharing: physical contact from hunting, meat  
457 handling and fecal exposure, and environmental contact through co-use of and fecal exposure  
458 in small forest gardens. Support for these mechanisms comes from multiple findings.  
459 Perceiving chimpanzees to resemble humans more closely than gorillas, Cameroonian  
460 participants avoided chimpanzees and had more frequent physical contact with gorillas  
461 through hunting and meat handling, although such activities were not highly frequent. Gorillas  
462 appeared more abundant and more active in crop-raiding than chimpanzees in gardens. Small  
463 forest gardens thus constituted focused sites of human-gorilla overlap and environmental

464 contact, where people and gorillas could leave behind environmentally persistent enteric  
465 viruses.

466 The positive control for human-great ape contact and viral sharing – the European zoo –  
467 generated unexpected results. Zookeepers and zoo great apes had daily contact and close  
468 spatial proximity in a relatively small site, but viral sharing was lower in the zoo than in  
469 Cameroon, possibly limited by zookeepers' occasional handwashing, but also by the above-  
470 mentioned mechanisms, and notably environmental contact in Cameroonian gardens.

471 Targeted viral discovery results are consistent with these two sharing mechanisms.  
472 Physical and environmental contact can facilitate sharing of Mastadenoviruses and  
473 Enteroviruses and could potentially lead to pathogenic spillover or spillback. An increased  
474 frequency of physical and environmental contacts between humans and great apes could  
475 facilitate the emergence of a novel viral disease in human or NHPs. Social sciences evaluation  
476 of human-NHP contact intensity and the introduction of viral surveillance programs where  
477 humans and NHPs are in close engagement would be essential for pandemic prevention.

478 Finally, our investigation reveals the explanatory richness of multidisciplinary  
479 investigations of cross-species pathogen sharing. Although limited to correlations, our  
480 anthropological-historical and ecological analyses and our granular study of contact type and  
481 frequency were essential for explaining the possible routes for viral sharing, illuminated by  
482 our metagenomics analyses and targeted viral discovery.

### 483 **Limitations of the study**

484 Our study has several limitations. First, we collected stool samples over one to two  
485 weeks, depending on the site and did not repeat collections. This collection strategy may have  
486 influenced our metagenomics analyses. We collected our Cameroon samples during the dry  
487 season. Seasonal availability of foods may influence virome composition, and in turn, the  
488 similarities and differences observed<sup>63</sup>.

489 Samples were limited in number, primarily because collecting great ape stools in forest  
490 settings is challenging. Our samples are, however, numerically sufficient to offer insight into  
491 shared gut viromes. We did not collect other NHP stool samples, notably among those with  
492 whom Cameroonian people have high-frequency physical or other contact; this investigation

493 focused on great apes because of their greater phylogenetic proximity with humans.  
494 Additional sampling would be important for understanding virome sharing between Old World  
495 monkeys and human beings in this forest.

496 Our study investigated the viromes from stool samples and cannot shed light on all  
497 potential human-great ape viral transmissions, notably blood-borne or respiratory viruses.  
498 Stool samples may, however, include viruses with a non-digestive tropism. Certain respiratory  
499 viruses can be detected in stool samples, such as naked viruses (picornavirus, adenovirus) or  
500 some enveloped viruses (such coronaviruses, influenza viruses) but usually with lower viral  
501 loads than in the respiratory tract<sup>64</sup>. We found no enveloped respiratory viruses in great apes  
502 or humans.

## 503 **CONCLUSION**

504 In recent decades, research into pathogenic anthroponosis and zoonosis  
505 has acquired crucial importance. The COVID-19 pandemic has heightened that importance,  
506 but also revealed the complex, potentially unexpected spillover and spillback pathways that a  
507 virus can take. The present study undertook a multidisciplinary One Health approach to  
508 examine shared virome and bidirectional viral sharing between humans and great apes and to  
509 illuminate associated processes, practices, and behaviors that may facilitate it. This  
510 multidisciplinary approach was essential in interpreting our unexpected biological results. More  
511 human-great ape sharing in Cameroon than in our control (the European zoo), a surprising  
512 convergence of human and gorilla virome in Cameroon, and apparent sharing of adenovirus  
513 and enterovirus taxa can only be understood by putting into dialogue metagenomics,  
514 historical, anthropological, and ecological analyses in southeastern Cameroon. These analyses  
515 point to lengthy human-great ape cohabitation and differential human perceptions of gorillas  
516 and chimpanzees, a greater willingness to hunt gorillas, gorillas' higher relative density and  
517 greater propensity to raid forest gardens. Interpreted together, our analyses in Cameroon  
518 point to two mechanisms facilitating such viral sharing: first, physical contact through great  
519 ape hunting, meat handling, and fecal contact, and second, environmental contact via focused  
520 co-use of small forest gardens by humans and gorillas.

521

## 522 MATERIAL AND METHODS

### 523 Study sites and study periods

524 We conducted research in several villages located between Yokadouma and Moloundou,  
525 Cameroon, and at the European zoo. Details of these two study sites are available elsewhere<sup>22</sup>.  
526 Team researchers (Victor Narat, Stephanie Rupp, Philippe Ambata, and Tamara Giles-Vernick)  
527 made a total of four field trips to Cameroon in 2015, 2016 and 2017 for six months total. We  
528 collected data and samples in the European zoo during a five-day research visit in November  
529 2017. To protect the anonymity of human populations and activities, we do not report the  
530 names of individual study sites.

### 531 Data collection

#### 532 *Qualitative data collection*

533 We collected qualitative data using anthropological participant-observation and semi-  
534 directed interviews (Supplementary method 1) with inhabitants of forest villages (Cameroon)  
535 and zookeepers (European zoo). In Southeastern Cameroon, we collected 93 in-depth  
536 individual and collective interviews with 83 men and 31 women, complemented by many  
537 informal discussions and 150 hours of participant-observation of forest activities and  
538 recitation of mythical tales.

539 Participant-observations enabled us to observe human interactions with and in  
540 proximity to chimpanzees and gorillas. Interviews permitted us to collect qualitative data  
541 concerning gorilla and chimpanzee behaviors, diet, habitats, and interspecies contacts, as well  
542 as human perceptions and practices with these animals. Participant-observation and semi-  
543 structured interviews were conducted in French or in the Bangando language; all interviews  
544 were recorded. We collected detailed notes for participant-observations.

545 In the zoo, Victor Narat and Tamara Giles-Vernick observed and documented  
546 zookeeper-great ape interactions and living conditions among the great apes sampled, includ-  
547 ing feeding regimens, living conditions, and cleaning practices of their habitats. We also ob-  
548 served and conducted semi-structured interviews with zookeepers to document great ape  
549 contacts with other animal species, including humans.



550

551 *Participatory longitudinal survey and transects in Cameroon*

552 We developed a longitudinal participatory survey for Cameroon volunteers and  
553 conducted this survey over 10 months. Eighteen volunteers (8 women and 10 men over 21  
554 years old) collected daily data on their contacts with gorillas and chimpanzees. Although a  
555 prior study addressed human-NHP physical contact<sup>41</sup>, the present article uses physical, direct  
556 and environmental contact data for gorillas and chimpanzees only (Table 1).

557 *Questionnaire*

558 Drawing from preliminary analyses of our qualitative data and participatory  
559 longitudinal survey, we developed and conducted a questionnaire (449 participants in four  
560 villages) to assess human contact frequency with gorillas and chimpanzees. Participants were  
561 asked if within the last day, week, month, year, or more than one year, they had had specific  
562 types of physical and direct (seen alive, heard) contacts with gorillas or chimpanzees. They  
563 also were asked to report on great ape involvement in crop raiding, namely the last great ape  
564 species raiding one of their fields, as well as the frequency of field raiding.

565 *Sample collection*

566 In Cameroon, after identifying great ape nesting sites, we collected fresh stool samples  
567 during the early morning, taking one stool per nest for a total of 15 gorilla samples and 6  
568 chimpanzee samples. At the zoo, we worked with zookeepers to collect stool samples  
569 immediately after feces emission, for a total of 6 samples for each species.

570 For human stool collection in Cameroon, we included adult participants over 21 years  
571 old with no current or chronic health problems. All participations received an information  
572 notice and informed consent form, explained orally in the Bangando language. Among  
573 potential participants, we conducted a questionnaire to determine whether they suffered  
574 from a recent or chronic illness or used medicines (including antibiotics), and what forest-  
575 based activities they pursued. All participants received a sampling tube which they used for  
576 individual stool collection. All stool samples were delivered within 12 hours of emission and  
577 were subsequently stored in RNAlater<sup>®</sup> tubes (Thermo Fisher)<sup>22</sup>. We successfully collected 24  
578 human samples.

579 For human stool collection at the European zoo, we invited zookeepers working full-  
580 or part-time with gorillas or chimpanzees to participate in this study. Stool collection followed  
581 the same procedure as in Cameroon, although zookeeper participants stored the sample  
582 directly in the RNAlater tube and sent immediately in a secured package the Microbiology  
583 Service, Saint Louis Hospital in Paris, France.

584 All stool samples were frozen at  $-80^{\circ}\text{C}$  within the 10 days of collection (for  
585 Cameroonian samples at Centre Pasteur, Yaoundé, and for zoo samples at Saint Louis Hospital,  
586 Paris). Further details of stool collection can be found in a previous publication<sup>22</sup>.

587 A total of 64 stools samples were analyzed, including 30 from humans (23 from  
588 Cameroon forest, 7 from European zoo), 21 from gorillas (15 from Cameroon forest, 6 from  
589 zoo), and 12 from chimpanzees (6 from Cameroon forest, 6 from zoo). Two samples, one from  
590 a Cameroon human (n°38) and another from a zoo chimpanzee (n°61), were removed from  
591 final analysis because the sequencing depth was too low (number of total reads < 5 million).  
592 We recovered a median of 40.6 million of reads per sample (range:  $4.11\text{E}+06 - 5.79\text{E}+07$ ) for  
593 DNA sequencing and of 40.7 million of reads per sample (range:  $1.58\text{E}+06 - 1.44\text{E}+08$ ) for RNA  
594 sequencing. Samples and sequencing information are shown in Supplementary Table 1. The  
595 median read per million (RPM) of viral reads per sample was 536 (range 38 – 97251, IQR: 137-  
596 2367) (Supplementary Table 2).

## 597 **Data analyses**

### 598 *Contact frequency with great apes in Cameroon*

599 We obtained daily contact data for 18 volunteers over 288 days on average (+/-  
600  $\text{SD}=21.4, 230-303$ ). We used presence/absence coding of data for one day, one volunteer, one  
601 type of contact and one great ape species. We then analyzed the frequency of contact (%) for  
602 each type of contacts, each species and each volunteer. We calculated the mean frequency  
603 for each type of contacts.

604 We calculated an estimated frequency of contact (%) using questionnaire data. We  
605 assigned a value that was the inverse of the number of days: 100 for daily contact, 14 for once  
606 weekly, 3 for once monthly, 0.3 for once yearly and 0.1 for more than once each year

607 (estimated here at once every three years for coding). Based on this scale, we calculated the  
608 mean frequency for each type of contact.

609 For our longitudinal survey and questionnaire datasets, we compared contact  
610 frequencies with the two great ape species using a Mann-Whitney statistical test.

611 To calculate crop raiding frequency, we analyzed the proportion of respondents who  
612 identified a chimpanzee or gorilla as the raiding species for last time their field or garden was  
613 pillaged. We also calculated the proportion of respondents citing chimpanzees or gorillas as  
614 the species more frequently responsible for crop raiding.

#### 615 *Qualitative data analyses in both sites*

616 Following transcription into French of all recorded interviews, we conducted manual  
617 coding of all qualitative data (transcriptions and notes), organizing data segments into  
618 categories pertaining to descriptions and perceptions of, discrete practices around, and  
619 interactions with great apes and other NHPs. From these codes, we used Thematic Analysis to  
620 identify broader, cross-cutting themes pertaining to human-great ape engagements.

#### 621 *DNA and RNA virome analysis with shotgun Next Generation Sequencing*

622 Fecal samples (solid phase) were re-suspended and diluted (50%) in phosphate  
623 buffered saline (PBS) and then centrifuged at 2500 g for 20 minutes. The supernatant was then  
624 filtered using an 0.45 $\mu$ M filter. To enrich for viral particles by reduction of host background,  
625 stool supernatant was filtered through a 0.45- $\mu$ m filter (Corning Costar Spin-X centrifuge tube  
626 filters), and an aliquot of 315  $\mu$ l of filtrate was pretreated before extraction by incubation with  
627 different nucleases: TURBO DNase (Invitrogen, Carlsbad, CA); Baseline-ZERO DNase (Ambion,  
628 Foster City, CA); Benzonase (NEB); RNase A (Promega) for 30 min, at 37 °C. Total nucleic acids  
629 were extracted using Nuclisens EAsymag (Biomerieux) according manufacturers protocol. For  
630 DNA libraries preparation, 25 $\mu$ L of extract was used. Depletion of methylated host DNA was  
631 performed using NEBNext<sup>®</sup> Microbiome DNA Enrichment Kit (NEB) according to the  
632 manufacturer instructions. DNA was then purified using zymo DNA Clean (Zymo) and eluted  
633 in 7.5 $\mu$ L of sterile water. DNA libraries were prepared using Nextera XT library preparation kit  
634 (Illumina). For RNA libraries preparation, Trio RNA Kit (Nugen) was used according to

635 manufacturer instructions. Libraries were sequenced on an Illumina HiSeq X using 150/150-  
636 bp paired-end sequencing.

### 637 *Bioinformatics analysis*

638 Raw reads were cleaned using TRIMMOMATIC<sup>65</sup>. Duplicated reads were removed using  
639 Dedupe<sup>66</sup>. Taxonomic assignment was carried out using Kraken2 with Viral, Bacterial and  
640 Human Refseq databases<sup>67</sup>. Kraken viral assigned reads were verified using Blastn on Refseq  
641 viral database. Reads with inconsistent assignment between Kraken and Blast methods were  
642 removed.

643 Alpha and Beta Diversity analysis were conducted using packages Phyloseq v1.22.3 and  
644 Vegan v2.5-4 in R v3.4.4<sup>68,69</sup>. For Alpha diversity, Simpson, Shannon, Chao1 and Richness index  
645 were calculated. For Beta diversity, Bray Curtis dissimilarity and Unifrac metrics were used.  
646 Principal coordinate analysis (PCoA) and network analysis was done with either Bray Curtis or  
647 weighted Unifrac distance. Permutational analysis of variance (PERMANOVA) was used to  
648 compare microbial communities between each group based on Bray Curtis dissimilarity  
649 indices, weighted and unweighted Unifrac distances using the adonis2 function with R package  
650 vegan.

651 Viral taxa shared between the human group and at least one great ape group  
652 (chimpanzee or gorilla) in Cameroon and in the zoo were identified.

653 As the genomic coverage of shared viruses between humans and apes did not allow  
654 the use of standard phylogeny methods, an alternative approach was used. Viral reads of  
655 interest were assembled into contigs with Spade<sup>70</sup>. Generated contigs and reference genomes  
656 (Supplementary Table 3) were compared using *All versus all BLAST*. Sequence similarity was  
657 assessed with the Bit-score and presented through sequence similarity networks with  
658 Cytoscape<sup>71</sup>.

### 659 **DATA AVAILABILITY**

660 RNA and DNA Metagenomic raw data are deposited on Sequence Read Archive (pending  
661 accession number). All other data are available upon reasonable request, except for  
662 qualitative data which cannot be shared because of ethical restrictions.

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822 VN contributed to study design, data collection, data encoding, data analyses and  
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824 MS contributed to study design, virome analyses and manuscript writing

825 MK and TH contributed to data encoding and analyses

826 SMD and NR contributed to virome analyses

827 SR contributed to study design, data collection and qualitative data analyses

828 PA contributed to data collection

829 RN contributed to study design and data collection

830 FS contributed to study design and virome analyses

831 JLG contributed to study design, virome analyses and manuscript writing

832 TGV contributed to study design, data collection, data analyses and manuscript writing and  
833 editing

834

## 835 **Competing interests**

836 The authors declare to have no competing interests.

837

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