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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^{1,2}. 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 variants³⁻⁵. 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^{6,7}.

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^{6,8,9}. Modeling studies
60 help to predict where, when, and who is at greatest risk for emerging anthroozoonoses¹⁰.
61 Although less studied, zooanthroponoses appear to be facilitated by similar practices and
62 processes². Lacking, however, are fine-grained investigations of potential pathogen sharing
63 between animals and people, and the ecologies, processes, and practices sustaining such
64 sharing¹¹.

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^{12,13}. Many analyses focus on single pathogens, genera or
68 families^{14,15} 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^{16,17}. 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 systems¹⁸ 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 species¹⁹), 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 shown²⁰⁻²⁴. 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 *troglydytes troglydytes*). 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 sharing²⁵.

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 viruses⁴. The human virome contains less-explored viral communities
104 that are associated with disease conditions, trigger immune response, or may function as
105 commensals,^{26,27} and few published studies have explored great ape gastrointestinal virome,

106 pathogenic viruses and disease²⁸⁻³⁰. 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.

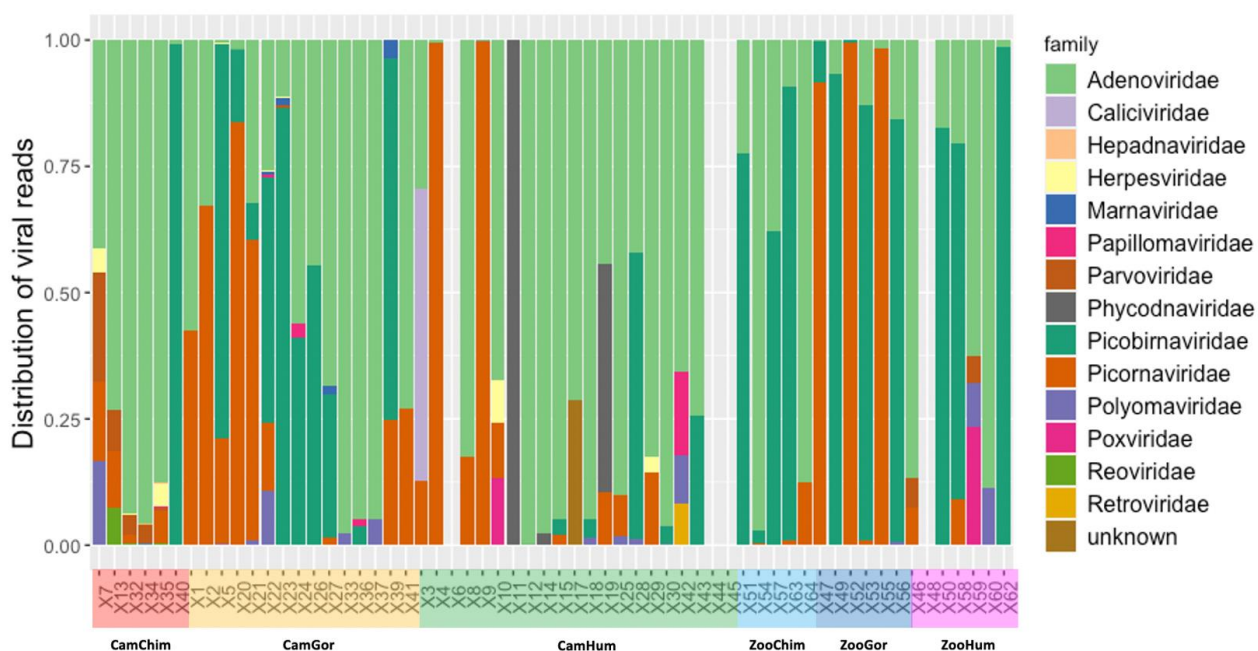
		Longitudinal survey N=18, data self-collected daily, 10 months		Questionnaire N=449	
Contact category	Type of contact	<i>Pan t. troglodytes</i>	<i>Gorilla g. gorilla</i>	<i>Pan t. troglodytes</i>	<i>Gorilla g. gorilla</i>
Environmental contact	Seen feces	2.3 (5.3)	3.5 (5.3)	Not addressed in questionnaires	
	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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201

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
Adenoviridae	6 (100%)	14 (93%)	17 (74%)	5 (100%)	5 (83%)	6 (86%)
Caliciviridae			1 (4%)			
Hepadnaviridae	1 (17%)					
Herpesviridae	4 (67%)	3 (20%)	2 (9%)			
Papillomaviridae	1 (17%)	2 (13%)	1 (4%)			
Parvoviridae	5 (20%)	1 (7%)	2 (9%)			
Picobirnaviridae	2 (33%)	10 (67%)	6 (26%)	4 (80%)	5 (83%)	3 (43%)
Picornaviridae	4 (67%)	9 (60%)	10 (43%)	2 (40%)	3 (50%)	1 (14%)
Polyomaviridae	2 (33%)	5 (33%)	5 (22%)		1 (17%)	2 (29%)
Poxviridae			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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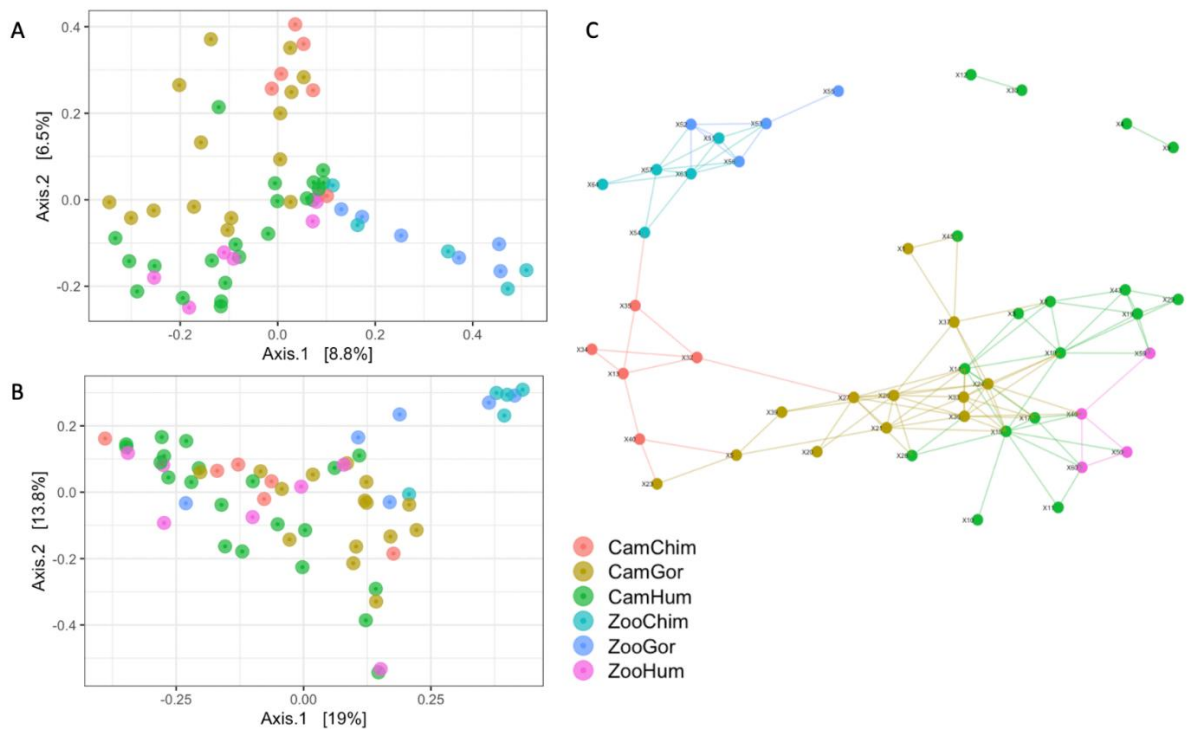
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The comparisons of virome composition using a PERMANOVA with Bray Curtis dissimilarity indices and weighted unifracs showed that the virome differed significantly across different groups (p values < 0.001). An unsupervised analysis with a PCA among 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)

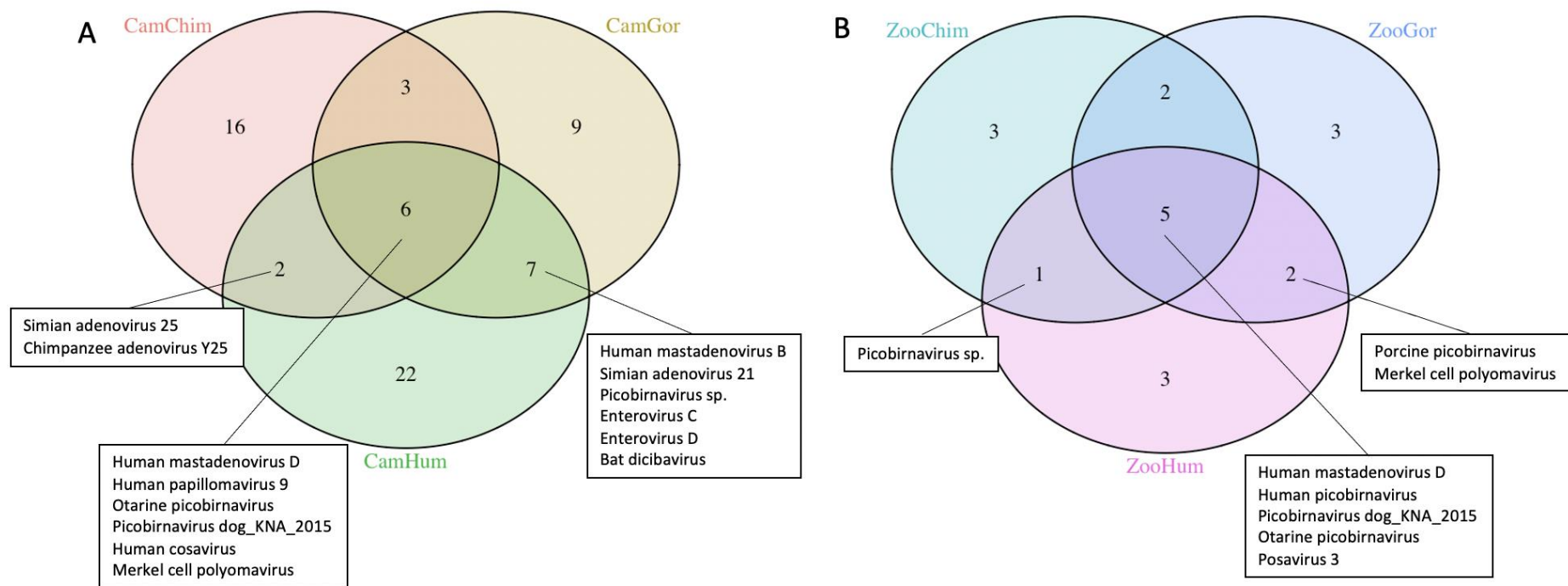
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249 ***Viral sharing***

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 Enterovi-
 256 rus (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.

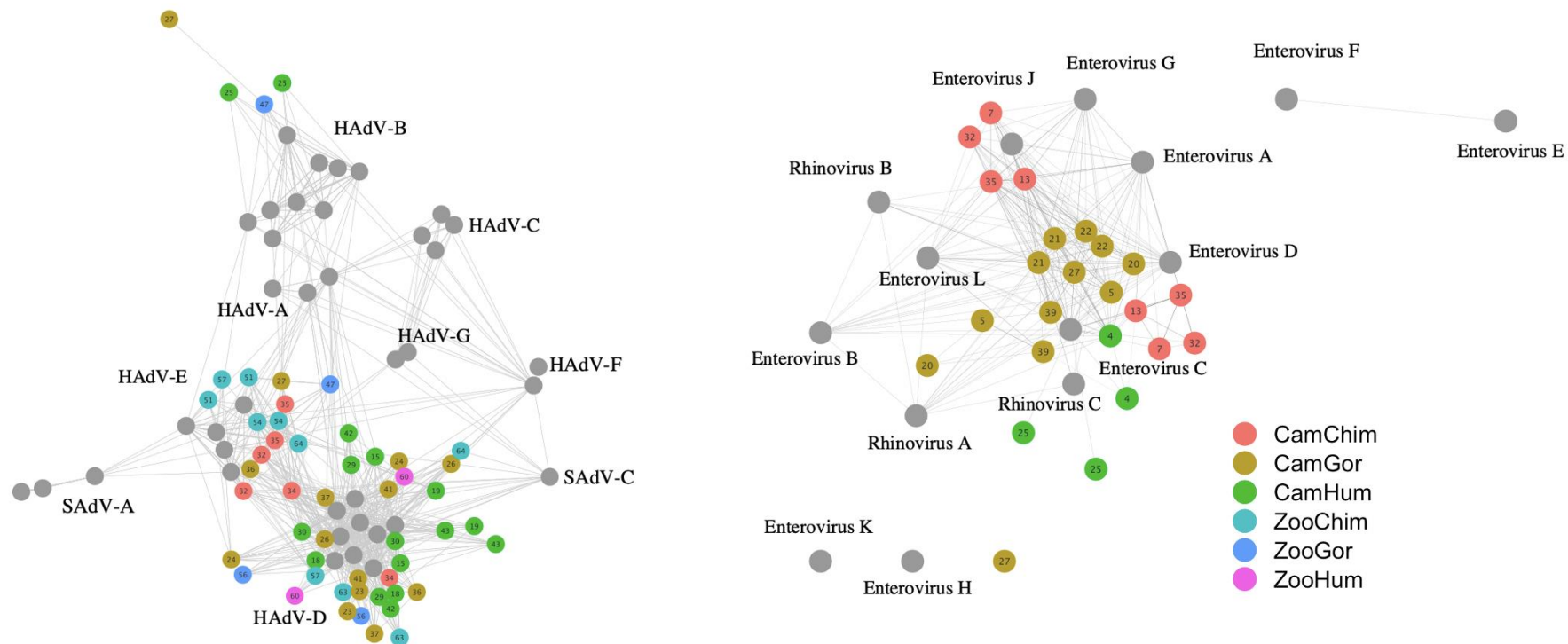
265 To evaluate the genetic proximity of the viral sequences, reads belonging to Mastade-
266 novirus and Enterovirus genera were assembled to create contigs. Because the size of the
267 contigs did not permit building of phylogenetic trees to compare different viruses, a network
268 analysis on cytoscape 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)

283

284

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^{31,32}. 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 observers³³.

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^{34–36}. 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 not³⁷.

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^{38–}
343 ⁴⁰, 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 species⁴¹. 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 forest⁴¹, 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 Cameroon⁴²⁻⁴⁴.

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 Africa⁴⁵⁻⁴⁸. Just two studies address mountain gorilla
369 (*Gorilla beringei*) crop raiding^{45,48}. Gorilla and chimpanzee behavioral differences in socio-
370 ecological systems require further investigation⁴⁹. 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^{20,22,50}. 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 environment⁵¹.

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 colleagues⁵², 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 ongoing⁵³.

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 contact⁵⁴. 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^{55,56}. 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 adenoviruses⁵⁷. 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^{58,59}.

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 zooanthroponosis⁶⁰. 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 population⁶¹. 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 humans⁶². 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 samples²⁵. 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 observed⁶³.

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 tract⁶⁴. 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 elsewhere²².
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 contact⁴¹, 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[®] tubes (Thermo Fisher)²². 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°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 publication²².

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 μ M filter. To enrich for viral particles by reduction of host background,
625 stool supernatant was filtered through a 0.45- μ m filter (Corning Costar Spin-X centrifuge tube
626 filters), and an aliquot of 315 μ 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 μ L of extract was used. Depletion of methylated host DNA was
631 performed using NEBNext[®] 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 μ 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 TRIMMOMATIC⁶⁵. Duplicated reads were removed using
639 Dedupe⁶⁶. Taxonomic assignment was carried out using Kraken2 with Viral, Bacterial and
640 Human Refseq databases⁶⁷. 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^{68,69}. 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 Spade⁷⁰. 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 Cytoscape⁷¹.

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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811

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821 **Author contributions**

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
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834

835 **Competing interests**

836 The authors declare to have no competing interests.

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