

1 **Running title:** Primate fermented foods

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3 **Fermented food consumption in wild non-human primates and its ecological drivers**

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100 **ABSTRACT**

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102 **Objectives:** Although fermented food use is ubiquitous in humans, the ecological and
103 evolutionary factors contributing to its emergence are unclear. Here we investigated the
104 ecological contexts surrounding consumption of fruits in the late stages of fermentation by
105 wild primates to provide insight into its adaptive function. We hypothesized that climate,
106 socio-ecological traits, and habitat patch size would influence the occurrence of this
107 behavior due to effects on the environmental prevalence of late-stage fermented foods, the
108 ability of primates to detect them, and potential nutritional benefits.

109

110 **Materials and Methods:** We compiled data from field studies lasting at least nine months
111 to describe the contexts in which primates were observed consuming fruits in the late stages
112 of fermentation. Using generalized linear mixed-effects models, we assessed the effects of
113 18 predictor variables on the occurrence of fermented food use in primates.

114

115 **Results:** Late-stage fermented foods were consumed by a wide taxonomic breadth of
116 primates. However, they generally made up less than 3% of the annual diet and were
117 limited to a subset of fruit species, many of which are reported to have mechanical and
118 chemical defenses against herbivores when not fermented. Additionally, late-stage
119 fermented food consumption was best predicted by climate and habitat patch size. It was
120 more likely to occur in larger habitat patches with lower annual mean rainfall, higher
121 annual mean maximum temperatures, and lower annual mean minimum temperatures.

122

123 **Discussion:** We posit that primates capitalize on the natural fermentation of some fruits as
124 part of a nutritional strategy to maximize periods of fruit exploitation and/or access a wider
125 range of plant species. We speculate that these factors contributed to the evolutionary
126 emergence of the human propensity for fermented foods.

127

128 **Keywords:** fermentation, feeding ecology, climate, herbivore defense, human evolution

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130 **Research Highlights**

131

132 - Fruits in the late stages of fermentation are consumed by a wide range of primates but
133 only a subset of available fruit species is consumed in this form.

134

135 - Primate late-stage fermented fruit consumption is more common in large habitat patches
136 with lower annual mean rainfall and higher annual mean maximum temperatures.

137

138 - Consumption of late-stage fermented foods appears to be part of a primate nutritional
139 strategy to increase dietary breadth both qualitatively and temporally.

140 **1 INTRODUCTION**

141 Food fermentation – the anaerobic microbial degradation of carbon compounds into
142 ethanol and/or lactic acid – is a central part of human diet and culture (Tamang &
143 Kailasapathy, 2010). Humans from many cultures regularly incite or direct microbial
144 fermentation of a wide range of foods that include meat and dairy products, grains, fruits,
145 and vegetables (Battcock & Azam-Ali, 1998; Campbell-Platt, 1994; Deshpande, 2000;
146 Tamang, Holzapfel, Shin & Felis, 2017). Such foods make up 20 to 40% of the global food
147 supply (Campbell-Platt, 1994). Although not all fermented foods contain ethanol, the
148 majority of anthropological fermented food research to date targets ethanol as an indicator
149 of fermentation (e.g. Dominy, 2015; Dudley, 2002; Garnier & Valamoti, 2016; Hayden,
150 Canuel, & Shanse, 2013; Kuijt, 2009; Liu et al., 2018; Milton, 2004; Ross, Morgan, & Hill,
151 2002; Smalley et al., 2003).

152 Directed fermentation by humans has early origins. There is archaeological
153 evidence that humans have engaged in directed fermentation of fruits and grains and stored
154 the resulting ethanol in large quantities since ~4300 BC, although some suggest a date as
155 early as 12,500 cal BP (Garnier & Valamoti, 2016; Hayden et al., 2013). Evolutionary
156 changes in human genes for processing ethanol and for interacting with a major lineage of
157 fermenting bacteria (Lactobacillales) are compatible with an even earlier association with
158 fermented foods, dating back to the divergence of hominids from other primates at ~10
159 Mya (Carrigan et al., 2015; Janiak, Pinto, Duytschaever, Carrigan, & Melin, 2020; Peters et
160 al., 2019). Limited technology for processing and storing food at this time makes it likely
161 that our hominid ancestors relied more heavily on naturally occurring fermented foods.
162 However, some simple forms of directed fermentation, such as burying food items or
163 submerging them in water (Speth 2017), may have been possible.

164 Why humans have incorporated fermented products so prominently into their diet
165 across their evolutionary history is unclear. Fermentation is an effective food preservative
166 since it produces locally high concentrations of ethanol and lactic acid that ultimately
167 prevent microbial growth and associated food spoilage (Boulton, Singleton, Bisson, &
168 Kunkee, 1999; Pretorius, 2000; Skinner, Passmore, & Davenport, 1980; Thomson et al.,
169 2005). Additionally, the physiological effects of consuming ethanol (i.e. intoxication) are
170 believed to have facilitated social gatherings and rituals (Liu et al., 2018). Accordingly, the
171 modern and ancient contexts in which fermented food use has been documented often
172 suggest central roles of food preservation and socially motivated ethanol acquisition in
173 driving the ubiquity of human fermented food use (Dominy, 2015; Dudley, 2002; Kuijt,
174 2009; Liu et al., 2018; Milton, 2004; Ross, et al., 2002; Smalley et al., 2003). However,
175 given genetic evidence that human adaptations for fermented food consumption emerged
176 before the technology associated with its directed production and storage (Carrigan et al.,
177 2015; Janiak et al., 2020; Peters et al., 2019), fermented food consumption may have
178 provided another selective advantage earlier in our evolutionary history.

179 Given their high sugar content, fruits often ferment naturally (Dominy, 2004; Duar
180 et al., 2017; Dudley, 2002; Gorgus, Hittinger, & Schrenk, 2016; Martinson, Herre,
181 Machado, & Arnold, 2012; Nyanga et al., 2007; Ruiz Rodriguez et al., 2019; Weaver,
182 2016) making it likely that all frugivorous animals consume some minimum amount of
183 fermented foods. However, overripe fruits in late stages of fermentation commonly remain
184 in food patches after other fruits have been depleted. As described above, fermentation is
185 distinct from rot or decay in that it involves distinct microbes and precludes the production
186 of most toxic microbial byproducts (except ethanol). Therefore, it has been suggested that
187 fruits in the late stages of fermentation could have been a fallback food for increasingly

188 terrestrial hominids during periods of low food availability in patchy woodland
189 environments (Carrigan et al., 2015).

190 Foods in the late stages of fermentation could also convey nutritional benefits that
191 provide a selective advantage to consumers year-round. Compared to unfermented foods,
192 fermented foods have higher caloric, free amino acid, and vitamin content (NRC, 1998;
193 Gobbetti et al., 1994; LeBlanc et al., 2013; Mitchell & Herlong, 1986; Tamang, Shin, Jung
194 & Chae, 2016). In the wild, many fermented foods contain embedded insects, which
195 provide an additional protein source (Barnett et al., 2017; Barnett et al., in press; Braham,
196 2015; Hodge & Arthur, 1996; Xiaoming, Ying, Hong, & Zhiyong, 2010). Also,
197 fermentation improves digestibility of food by breaking down resistant starch, soluble fiber,
198 toxins, and secondary plant metabolites (Binita & Khetarpaul, 1997; Chaves-López et al.,
199 2014; Gupta, Gangoliya, & Singh, 2015; Rollan, Gerez & Leblanc, 2019). For example,
200 some toxic foods, such as blowfish and cassava, can only be consumed after fermentation
201 (Akinrele, 1964; Anraku et al., 2013). Together these properties not only directly affect
202 consumer nutrient intake and balance but may also result in a more favorable balance
203 among the nutrients of a food which in turn can play a critical role in food selection (Felton
204 et al., 2009). Therefore, foods in the late stages of fermentation could have represented a
205 critical nutritional resource to hominids, particularly as energetically expensive life history
206 traits such as long juvenile periods, short interbirth intervals, and large brains emerged
207 across evolutionary time (Aiello & Key, 2002; Antón, Potts, & Aiello, 2014; Leonard &
208 Robertson, 1992, 1997). The consumption of other high quality diet items such as meat and
209 cooked foods has also been hypothesized to have provided essential nutritional resources
210 for the development and maintenance of these traits in hominids (Aiello & Wells, 2002;

211 DeCasien, Williams, & Higham, 2017; Wrangham, 2009; Wrangham & Conklin-Brittain,
212 2003).

213 Fermented foods contain live microbes, substrates for microbial metabolism, and
214 microbial metabolites, which may affect consumer health and fitness either directly or
215 indirectly through impacts on the microbiome (Jacobsen et al., 1999; Kim et al., 2016;
216 Maldonado-Gómez et al., 2016; Marco et al., 2017). Given the broad effects of the
217 microbiome on host metabolism (Oliphant & Allen-Vercoe, 2019; Visconti et al., 2019),
218 immune function (Al Nabhani & Eberl, 2020), and neuroendocrine dynamics (Cryan et al.,
219 2019; Sylvia & Demas, 2018), fermented foods have the potential to affect consumer
220 physiology in many ways. Beyond intoxication caused by excessive consumption of
221 fermented foods with high ethanol content, none of these documented physiological effects
222 are negative. Therefore, fermented food consumption could have provided a selective
223 advantage to hominids in addition to the nutritional advantages discussed above. Indeed,
224 studies of human fermented food use consistently demonstrate a range of improved health
225 outcomes (e.g. Bourrie, Willing, & Cotter, 2016; Burton et al., 2017; Yartey, Nkrumah,
226 Hori, Harrison, & Armar, 1995). However, the wide variety of positive health effects that
227 fermented foods can produce via the microbiome make it difficult to predict specific
228 scenarios in which these properties would be most evolutionarily advantageous based on
229 current knowledge.

230 Even in the context of nutrition, modern human technology and cultural practices
231 complicate our ability to evaluate the potential fitness benefits of human fermented food
232 consumption. As a result, comparative data from non-human primates (hereafter primates)
233 are essential for exploring the adaptive function of this behavior. By determining how
234 pervasive consumption of late-stage fermented foods by wild primates is and the ecological

235 contexts in which it occurs, we can begin to more accurately assess the ecological and
236 evolutionary forces that drive it and contextualize it within human evolutionary history.
237 Nevertheless, few studies on this subject have incorporated primate data.

238 A handful of comparative genetic analyses of physiological adaptations for
239 fermented food consumption integrate data from multiple primate species (Carrigan et al.,
240 2015; Janiak et al., 2020; Peters et al., 2019). Additionally, some behavioral research has
241 investigated primate ethanol affinity in response to the Drunken Monkey Hypothesis
242 (Dudley, 2002, 2004). This hypothesis posits that humans direct the production of
243 fermented foods and consume them as a result of our affinity for ethanol, which stems from
244 our evolutionary past as frugivorous primates that used ethanol as an olfactory and/or
245 gustatory signal for energy-rich fruit (Dudley, 2002, 2004). Therefore, data from other
246 primates have been used to test the relationship between frugivory and ethanol affinity. The
247 results indicate that primates across the Order prefer solutions of 2-5% ethanol over water
248 (Dausch Ibañez, Hernandez Salazar, & Laska, 2019; Gochman, Brown, & Dominy, 2016;
249 Hockings et al., 2015; Kornet, Goosen, Ribbens, & Van Ree, 1990; Mandillo, Titchen, &
250 Miczek, 1998). However, data from spider monkeys (*Ateles geoffroyi*) indicate that sweet
251 solutions are preferred over ethanol regardless of calorie content (Dausch Ibañez et al.,
252 2019). Outside of this context, fermented food consumption is rarely mentioned in studies
253 of primate feeding ecology, despite the fact that not all fermented foods contain ethanol but
254 all of them likely confer a range of nutritional and health benefits to consumers.

255 As a first step to address this knowledge gap, we compiled qualitative data
256 describing overripe fruit consumption from primate field studies around the world to
257 estimate the minimum prevalence of late-stage fermented foods in wild primate diets,
258 regardless of ethanol content, and the ecological contexts in which the consumption of

259 these foods occurs. We hypothesized that local climate, primate socio-ecological traits, and
260 habitat patch size (Table S1) would predict the prevalence of primate consumption of late-
261 stage fermented foods. First, climate affects both the rate of fermentation and the rate of
262 ethanol evaporation (Isu & Njoku, 1998), thereby influencing the local prevalence of late-
263 stage fermented foods and the probability that primates will detect them via olfaction
264 (Dominy, 2004; Nevo & Valenta, 2018; Melin et al., 2019). Therefore, we predicted that
265 mean minimum annual temperature, mean maximum annual temperature, mean daily
266 temperature, mean annual rainfall, elevation, and latitude and longitude would be
267 associated with the occurrence of late-stage fermented food consumption in wild primates.
268 Given that fruit ferments easily in nature (Dominy, 2004; Duar et al., 2017; Dudley, 2002;
269 Gorgus, Hittinger, & Schrenk, 2016; Martinson, Herre, Machado, & Arnold, 2012; Nyanga
270 et al., 2007; Ruiz Rodriguez et al., 2019; Weaver, 2016), we predicted that primate species
271 and populations with high percentages of fruit in their diets and low percentages of leaves
272 and invertebrates would be more likely to encounter and consume late-stage fermented
273 food. Since home range, social group size, body size, and encephalization quotients are
274 often correlated with diet (Clutton-Brock & Harvey, 1980; Dunbar & Shultz, 2007, 2017;
275 Kudo & Dunbar, 2001), we also expected these variables to be associated with late-stage
276 fermented food consumption. Finally, due to the relationship between habitat patch size and
277 food availability more generally (Abbas et al., 2011; Fahrig, 2003; Laurance, Delamonica,
278 Laurance, Vasconcelos, & Lovejoy, 2000), we predicted that habitat patch size would
279 predict the prevalence of late-stage fermented foods and their consumption.

280

281 **2 | MATERIALS AND METHODS**

282 **2.1 | Behavioral data collection**

283 KRA, YZ, and TME identified a group of researchers who had completed a wild
284 primate field study of at least nine consecutive months using multiple approaches. We
285 searched two general online databases (<https://scholar.google.com>,
286 <http://xueshu.baidu.com>) using specific key words such as “primate” and “diet” combined
287 with primate family names one year at a time beginning with 2005. We also reviewed the
288 literature cited in multiple primate ecology books (Brady & Carville, 2012; Campbell,
289 Fuentes, MacKinnon, Bearder, & Stumpf, 2011; Davies & Oates, 1994; Dudley, 2014;
290 NRC, 2003; Rowe & Myers, 2016; Strier, 2016). Finally, we flagged abstracts from the
291 programs of primate conferences in 2018 and 2019, including the American Society of
292 Primatologists and the American Association of Physical Anthropologists.

293 KRA asked 151 researchers with relevant field studies and current email contact
294 information to report whether they had observed their study subjects consuming fermented
295 foods (i.e., plant foods clearly overripe or fermenting based on their color, physical traits,
296 smell, or other useful indicator traits). These food items could be found on the ground, but
297 this was not necessary for a food to be deemed 'fermented.' Most fruits consumed by
298 primates are likely to have undergone some degree of fermentation (Dominy, 2004), but
299 only late stages of fermentation with higher concentrations of ethanol and other microbial
300 products (Biale 1954) are likely to be identified using the sensorial cues we employed here.
301 Therefore, it is likely that we are excluding a substantial amount of fermented foods (e.g.
302 floral nectar and fruits with other levels of maturity (Aleksey Maro, personal
303 communication; Wiens et al., 2008; Weaver, 2016) from our analysis. However, without
304 systematic chemical and microbial analyses of primate food items, this conservative
305 approach represents the current best available option.

306 Additionally, foods, particularly fruits, in late stages of fermentation are more likely
307 to have physiological effects on consumers as a result of higher concentrations of microbes
308 and/or microbial by-products (Tamang et al., 2016). As a result, we may be strengthening
309 our statistical ability to detect ecological patterns by focusing on these late-stage fermented
310 foods. Given that the relative concentrations of ethanol and other microbial products--and
311 the likelihood of perception by human observers--are likely to vary by plant species,
312 quantitative data describing these variables for a range of food items are necessary to test
313 the extent to which primate ecology varies with food fermentation stage. However, that
314 analysis is beyond the scope of the current paper, and independent efforts to achieve this
315 goal are currently underway. We hope to address this question more effectively in the
316 future once additional data are available.

317 We collated data for 40 species of primates inhabiting 50 research sites (Table S1).
318 While these data encompass a small percentage of all extant primate species (7.9%, 40 out
319 of 504 recognized species; Estrada et al., 2017), 11 out of the 16 extant primate families
320 were represented across all continents inhabited by primates, and we included both tropical
321 and temperate environments. Therefore, we believe that our database fairly represents the
322 phylogenetic and geographic diversity of the order Primates. Study duration ranged from 9
323 to 312 months (median = 15 months), and we used data from multiple social groups or
324 communities of 18 species distributed across 13 sites.

325 We included data describing the location and length of their study, the elevation,
326 mean annual maximum and minimum temperatures, mean daily temperature, and mean
327 annual rainfall of the study site, the mean contribution of fruits, leaves, and invertebrates to
328 the diet of the study species, the frequency with which any fermented foods were consumed
329 relative to total observation time, and any other relevant details about the types of foods

330 consumed or associated behavior, such as seasonality or specific handling behaviors (Table
331 S1).

332

333 **2.2 | Physical and chemical traits of the late-stage fermented foods consumed**

334 For all late-stage fermented foods, we compiled data from each study site or the
335 literature describing presence/absence of a tough husk or skin, relative fiber content, and
336 presence/absence of secondary metabolites and their concentrations. We evaluated tough
337 husks qualitatively. A relative assessment of fiber content compared to other fruits at the
338 same site was possible for 35 fruits, and for 25 of these fruits the nutritional data were
339 available for that study site specifically. Secondary metabolite data were more difficult to
340 compile. Quantitative data were available for 11 fruit species at three sites. For the rest of
341 the fruits, we searched the literature using the fruit species name combined with terms such
342 as ‘toxin’ and ‘secondary metabolite.’ Because data describing secondary metabolite
343 content in fruits is sparse, in many cases we had to rely on literature describing medicinal
344 use that implied increased concentrations of identified or unidentified secondary
345 metabolites. Using this approach, we were able to find evidence of the occurrence of
346 secondary metabolites for 34 fruit species (Table 3).

347

348 **2.3 | Data analysis**

349

350 We assessed the influence of 18 predictor variables (Table 1) on the occurrence of late-
351 stage fermented food consumption via generalized linear mixed-effects models (GLMM;
352 Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with a binomial distribution and logit link
353 function using the function ‘lmer’ of the R package lme4 (Bates et al., 2015). We specified

354 the occurrence of late-stage fermented food consumption as a binary response variable, all
355 the predictor variables as fixed factors, and study site as a random factor to account for data
356 from repeated measures of the same species in different social groups at the same site. In
357 addition to socio-ecological, climate, and habitat patch size variables, we included study
358 length in all of our models to determine if shorter studies were biased against what we
359 assumed would be a relatively rare behavior (Souza-Alves et al., 2019). To avoid
360 overparameterization and problems of convergence with the global model, we did not
361 consider variable interactions (see Grueber, Nakagawa, Laws, & Jamieson, 2011). We also
362 did not include variables describing primate taxonomy because limited replication of
363 species reduced the power of the analysis to assess the impact of these variables.

364 Given differences in scale among the predictor variables, we standardized them
365 using the ‘standardize’ function of the package MuMIn (Barton, 2020) as recommended by
366 Grueber et al. (2011). We avoided multicollinearity problems by only including those
367 variables with Variance Inflation Factors (VIF) <3 into the models (Zuur et al., 2009) using
368 the ‘vifstep’ function of the package usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus,
369 2014). The seven variables with VIF >3 that we excluded from the global model were
370 female body mass, male body mass, male relative encephalization quotient, percentage of
371 leaves in the diet, percentage of invertebrates in the diet, mean daily temperature, and
372 elevation.

373 We selected models with an $\Delta AICc < 2$ as the most parsimonious (Grueber et al.,
374 2011). Given the occurrence of multiple equally parsimonious models, we also performed
375 full-model averaging on all models with an $\Delta AICc < 2$ to account for model uncertainty and
376 to identify the best predictors of patterns of late-stage fermented food consumption in our
377 data set (Grueber et al., 2011). We used the ‘model.avg’ function of the R package MuMIn

378 to identify the averaged model and the predictor weight ($\sum w_i$) of each variable. We
379 determined the coefficient of determination for each model with $\Delta AICc < 2$ using the
380 MuMIn ‘r.squaredGLMM’ function. We performed all statistical analyses in R 3.6.3 (R
381 CoreTeam, 2020).

382

383 **3 | RESULTS**

384 **3.1 | Occurrence of late-stage fermented food consumption in wild primates**

385

386 Out of 40 species of wild primates studied at 50 sites, 15 species (37.5%) were reported to
387 consume late-stage fermented foods at 23 sites in 12 countries across four continents.

388 Overall, late-stage fermented food consumption occurred infrequently (Table 2, S1). We
389 estimated that it constituted from 0.01% to 3% of the annual diet in most groups, although
390 there were seasonal differences. For example, we found that late-stage fermented fruits
391 could account for as much as 15% of the feeding records of *Cebus imitator* and *Alouatta*
392 *guariba clamitans* during some seasons. For some primates, such as *A. guariba clamitans*,
393 these seasons represented periods of low food availability (VBF personal observation),
394 whereas for many others, such as *C. imitator*, they did not (EKM personal observation).

395 While we recorded late-stage fermented food consumption in all our *Pan paniscus* and *C.*
396 *imitator* social groups (three and seven, respectively), not all populations or social groups
397 of the other species studied exhibited this behavior.

398

399 **3.2 | Main sources of fermented foods and behavioral strategies used**

400

401 Late-stage fermented food consumption was limited to fruits (Tables 2, 3, S1). The richness
402 of late-stage fermented fruits exploited ranged from one to nine fruit species for a given
403 primate species (Tables 2, 3, S1). *Pan paniscus* exhibited the highest richness of late-stage
404 fermented fruit species in the diet (N=9 fruit species), followed by *Ateles geoffroyi* (N=8),
405 *Alouatta guariba clamitans* (N=7), and *Cebus imitator* (N=5; Table 2). The remaining
406 primate species exploited between one and three fruit species (Table 2).

407 At least 31 of the 44 fruit species that were consumed in late stages of fermentation
408 have defenses in the form of difficult-to-break tough husks/skins (N=16) or secondary
409 metabolites, such as alkaloids, acetogens, saponins, and tannins (N=25; Table 3). Almost
410 all fruits (95%) were consumed both ripe/unfermented and overripe/fermented (Table 3). In
411 some cases, late-stage fermented fruits were only consumed when the patch was depleted of
412 ripe fruits (Table S1). We also reported cases in which very ripe or late-stage fermented
413 fruits appeared to be preferred over semi-ripe and unripe fruits. Specifically, *Cebus imitator*
414 at La Suerte, Costa Rica, was observed frequently knocking ripe *Dipteryx oleifera*
415 (Fabaceae) fruits to the ground and returning up to two weeks later to consume them (up to
416 15% of feeding time seasonally, EKM personal observation). These fruits were never
417 consumed unfermented by the capuchins. *Eulemur fulvus* at Ampijiroa, Madagascar (up to
418 5% of feeding time seasonally, PTR personal observation) and *Ateles geoffroyi* at Punta
419 Laguna, Mexico (up to 1% of feeding time seasonally, BPG personal observation) were
420 also reported to drop fruits to the ground and return to feed on them later. However, unlike
421 the capuchins, both lemurs and spider monkeys consumed the target fruits in different
422 stages of ripening, although the lemurs appeared to prefer fallen fruits over those on the
423 trees since they would consume fallen fruits first when both were available.

424

425 **3.3 | Main primate predictors of late-stage fermented fruit consumption**

426

427 Only climate and habitat patch size were significant factors predicting late-stage fermented
428 food consumption in wild primates. Other socio-ecological traits did not have a significant
429 effect in any of our top ranked models. We found six GLMMs equally parsimonious (ΔAIC
430 < 2) for explaining the observed patterns in late-stage fermented food consumption (Table
431 4). These models included mean maximum and minimum annual temperature, mean annual
432 rainfall, habitat patch size, mean minimum annual temperature, longitude, home range size,
433 and female relative encephalization quotient and explained approximately 99% of the
434 observed variance (Table 4). However, only mean annual maximum temperature, rainfall,
435 and habitat patch size were present in all six models. The model with the strongest
436 empirical support ($\Delta AICc = 0.00$) included these three variables and mean minimum annual
437 temperature (Table 4). The averaged model explained 99% of the observed variance, and
438 late-stage fermented food consumption was only significantly negatively influenced by
439 annual mean rainfall and mean annual minimum temperature, and positively influenced by
440 mean annual maximum temperature and habitat patch size (Table 4).

441

442 **4 | DISCUSSION**

443

444 We found that wild primates from all major evolutionary lineages consume foods in the
445 later stages of fermentation, although the behavior is relatively infrequent and limited to
446 only a few species of fruits at the sites where we recorded it. Additionally, climatic and
447 environmental variables generally predict the occurrence of late-stage fermented food
448 consumption better than socioecological variables. Specifically, late-stage fermented food

449 consumption is more common in hotter, drier environments and in larger, presumably less
450 fragmented, habitats. These findings provide an important foundation for understanding the
451 ecological and evolutionary forces that drive fermented food consumption in primates and
452 offer new insights into the emergence of this behavior in humans.

453

454 **4.1 | Occurrence of fermented food consumption in wild primates**

455

456 First, although reports of fermented food consumption are rare in most studies of wild
457 primate feeding ecology, this behavior is probably pervasive across the Order. We observed
458 late-stage fermented food consumption in more than one third of the primate species for
459 which we received data. However, given that our data were biased toward late-stage
460 fermentation and many fermented foods consumed by primates cannot be identified by
461 researchers without chemical analyses, it is likely that the prevalence of fermented food
462 consumption among wild primates is even higher. Fruits consumed by primates commonly
463 ferment naturally despite no clear signs to observers that fermentation has occurred
464 (Dominy, 2004; Dudley, 2002; Aleksey Maro, personal communication; Weaver, 2016).
465 Given that most primates, even those considered leaf-eaters, rely heavily on fruit during at
466 least part of the year (Campbell et al., 2011; Rowe, 2018; Sussman, 1991), it is likely that
467 most primates regularly consume fermented foods. This scenario becomes more probable
468 when we consider the fact that other foods such as nectar or gums may also often ferment
469 despite being difficult to observe (e.g. Wiens et al., 2008)

470 However, we do not expect that all primates consume fermented fruits. For instance,
471 primates of the subfamily Colobinae, which are physically unable to consume large
472 amounts of ripe fruits as a result of their sacculated foregut (Davies & Oates, 1994), as well

473 as immature fruit specialists, such as the Neotropical Pitheciinae, were not observed
474 consuming fermented fruit (at least not clearly overripe fruits) in any context in this study.
475 Additionally, the physical nature of some habitats can reduce access to fermented fruits.
476 For example, while not represented in our data set, swamps and riverbank forests reduce
477 opportunities for fruit fermentation on the ground, and fruits in these habitats are often
478 water-dispersed and rarely fleshy and easily fermentable (López, 2001).

479

480 **4.2 | Ecological contexts associated with late-stage fermented food consumption by** 481 **wild primates**

482

483 Despite how relatively common late-stage fermented fruit consumption appears to be
484 throughout the Order Primates, we found that it is selectively employed in specific
485 ecological contexts. Although most primates include many fruit species in their diets, in
486 most cases only one or two fruit species were consumed in the late stages of fermentation
487 by a given primate population or social group. In some cases, this pattern appeared to be a
488 result of primates extending the utility of a fruit patch. For example, in the rare instances
489 when *Pongo pygmaeus* was observed consuming late-stage fermented fruits, it was after the
490 patch had been depleted by other frugivores (ERV personal observation). Alternatively,
491 some primates, such as groups of *Alouatta guariba clamitans* in Santa Maria municipality,
492 Southern Brazil, appeared to rely on late-stage fermented fruits during periods of low or
493 altered food availability (VBF personal observation). Similarly, *Ateles geoffroyi* on Barro
494 Colorado Island, Panama utilized late-stage fermented *Quararibea asterolepis* during a
495 period of unusual fruiting patterns associated with the previous year's El Niño event, as did
496 other frugivorous mammals and birds (Campbell, 2000). These potential uses of late-stage

497 fermented foods as fallback foods are in line with previous hypotheses in other contexts
498 (Carrigan et al., 2015).

499 Other primates appeared to use fermentation to increase fruit edibility. Many fruits
500 contain secondary metabolites, and in some cases they may reach sufficient levels to have
501 meaningful physiological effects if consumed in large quantities (Cipollini & Levey, 1997;
502 Janzen, 1983). At least two-thirds of the fruit species consumed in the late stages of
503 fermentation by wild primates in this study had mechanical or chemical herbivore defenses
504 when unfermented. For seven of these species, primates were reported to reject fruits unless
505 they were very ripe or fermented. *Pan troglodytes* has been previously shown to
506 preferentially consume ripe fruits of plant species whose unripe fruits have high levels of
507 tannins since ripening reduces tannin content (Wrangham & Waterman, 1983). Therefore, it
508 is possible that fermentation was used by some of our study subjects in a similar way to
509 break down plant herbivore defenses. For example, *Dipteryx oleifera*, has a hard husk that
510 can only be breached by *Cebus imitator* when fermented (EKM personal observation).

511 Together, these patterns are compatible with the use of targeted consumption of
512 late-stage fermented fruits in multiple ways by primates as part of a broader nutritional
513 strategy to increase food availability and expand their dietary niches. We found preliminary
514 support for this interpretation. As predicted, our models indicated that late-stage fermented
515 food consumption was associated with climate and habitat patch size. In particular, late-
516 stage fermented food consumption was more common in drier environments with more
517 extreme mean annual maximum and minimum temperatures, as well as in larger habitat
518 patches. Habitats with higher mean annual maximum temperatures, lower mean annual
519 minimum temperatures, and lower annual rainfall are potentially more nutritionally
520 stressful for primates due to both chronic and seasonal reductions in food availability, as

521 well as distinct plant growth strategies that result in increased mechanical and/or chemical
522 defenses against herbivory (Coley & Barone, 1996; Onoda et al., 2011; Poorter & Kitajima,
523 2007; Zhao, Hartmann, Trumbore, Ziegler, & Zhang, 2013). In such environments, a
524 primate foraging strategy that relied more heavily on late-stage fermented foods could well
525 enhance survival during lean periods by both extending the utility of depleted food patches
526 and increasing digestibility of heavily defended plant foods. We do not have quantitative
527 data relating food availability or plant herbivore defenses to late-stage fermented food
528 consumption across sites, precluding our ability to rigorously test this hypothesis here.
529 However, future explorations of this relationship are warranted by our findings.

530 Our results also indicate other potentially important mechanisms driving patterns of
531 primate late-stage fermented food consumption. To some extent, it appears that late-stage
532 fermented food consumption occurs with more prevalence in habitats where primates are
533 more likely to come into contact with fruit in the late stages of fermentation. Higher mean
534 annual maximum temperatures are likely to result in more rapid rates of fermentation and
535 ethanol evaporation (Isu & Njoku, 1998), increasing the local prevalence of late-stage
536 fermented foods and the probability that primates will detect them via olfaction (Dominy,
537 2004; Nevo & Valenta, 2018; Melin et al., 2019). Furthermore, larger, potentially less
538 fragmented, habitats are often associated with an increased abundance and diversity of
539 fruiting trees (Abbas et al., 2011; Fahrig, 2003; Laurance, Delamonica, Laurance,
540 Vasconcelos, & Lovejoy, 2000). Therefore, there may be a higher probability that primates
541 in these habitats will encounter fermenting fruits. However, we found that late-stage
542 fermented food consumption was a function of both low mean annual minimum
543 temperatures and high annual maximum temperatures, and in our dataset, the effect of
544 habitat patch size appears to be driven by two particularly large sites, Goualougo and

545 Mandika in the Republic of Congo. As a result, it remains unclear whether factors
546 influencing the availability of late-stage fermented foods to primates truly shape patterns of
547 consumption more globally.

548

549 **4.3 | Potential evolutionary benefits of late-stage fermented food consumption**

550

551 The aforementioned relationships open up new perspectives on the emergence of food
552 fermentation as an important component of the human diet. If late-stage fermented food
553 consumption is part of an extant primate strategy for extending the time over which a
554 particular type of fruit can be fed on and/or increasing the nutritional accessibility of foods,
555 particularly in nutritionally harsh environments or environments with high levels of inter-
556 specific feeding competition, it may have served a similar role for our hominin ancestors.

557 As hominids diverged from other primates, they began to more consistently occupy a more
558 terrestrial niche (Sponheimer et al., 2013). It has been suggested that fermented fruits may
559 have emerged as a fallback food in this context (Carrigan et al., 2015), and the patterns we
560 observed in extant non-human primates provide some support for this hypothesis.

561 Additionally, hominins including *Paranthropus* and *Australopithecus* are believed to have
562 incorporated substantial amounts of hard and abrasive food items, as well as underground
563 plant storage organs, in their diets (Dominy, 2012; Kay, 1985; Plummer, 2004; Teaford &
564 Ungar, 2000). Underground plant storage organs are mechanically challenging, contain
565 more starch and fiber compared to most ripe fruits, and expose foragers to potentially high
566 amounts of diverse secondary plant metabolites that are toxic or can interfere with digestion
567 (Buonocore & Silano, 1986; Dominy, Vogel, Yeakel, Constantino, & Lucas, 2008; Stahl et
568 al., 1984; Waterman, 1984).

569 Fermentation could have reduced both the fiber and toxin levels in these food items.
570 In fact, fermentation is commonly used to process tubers in modern human contexts
571 (Akinrele, 1964; Ray & Sivakumar, 2009). While the transition to more settled, agrarian
572 communities is often associated with the advent of human fermented food production for
573 food preservation and ritual (Kuijt, 2009; Liu et al., 2018; Ross et al., 2002), the potential
574 nutritional benefits of fermentation should not be underestimated. We found evidence that
575 these benefits may be important drivers of late-stage fermented food consumption across
576 the Order Primates.

577 Other nutritional and non-nutritional factors that we could not quantify should also
578 be considered as proximate drivers of late-stage fermented food consumption in primates.
579 First, the nutritional benefits of late-stage fermented fruits could be further improved by the
580 presence of insects. Whilst generally composed of small individuals, insect assemblages in
581 fermenting fruit can be diverse and abundant (Braham, 2015; Feinsein, Mori, & Berkov,
582 2007; Hodge & Arthur, 1996). Insects can provide fat, protein, vitamins and amino acids
583 (Barnett et al., in press; Xiaoming et al., 2010), and fruit infested with them are known to
584 be selected by some primate species in other contexts (Barnett et al., 2017). Additionally,
585 fermentation is likely to alter food taste. Anecdotal researcher taste tests in our study
586 indicated positive changes in taste with fruit fermentation. Fermentation is generally
587 associated with sour or acid tastes, and humans tend to prefer sweet-sour tastes (Breslin,
588 2013; Katz, 2012). Little is known about sour taste receptors in primates and other
589 animals—or even sour taste preference (Montell, 2018; Roper, 2007). However, it is likely
590 that primates share an affinity for sour taste with humans. Taste has not been systematically
591 examined in wild primate foods, but it will likely provide additional insight into primate
592 food choices, both fermented and unfermented.

593 Finally, fermented foods are likely to provide health benefits to consumers as a
594 result of probiotic and prebiotic properties (Bourrie et al., 2016; Burton et al., 2017;
595 Löwenadler & Linberg, 1994; Marco et al., 2017; Summer et al., 2017; Tamang et al.,
596 2016; Veiga et al., 2014; Yartey et al., 1995). These properties are likely to be stronger in
597 late-stage fermented foods as a result of increased microbial activity, which may explain
598 why these foods are targeted by some primates. Currently, without chemical and microbial
599 data from primate foods as well as physiological and microbial data from primates, it is
600 impossible to assess these potential relationships. However, rapidly emerging evidence of
601 the importance of microbes for primate ecology and evolution (Amato, 2016; Amato,
602 Jeyakumar, Poinar, & Gros, 2019; Davenport et al., 2017; Dunn et al., 2020; Gaulke et al.,
603 2018) suggests that these interactions should not be overlooked.

604

605 **Conclusion**

606 We find that late-stage fermented fruits are consumed by a variety of non-human
607 primates globally. This behavior generally targets a specific subset of fruit species, some of
608 which contain herbivore defenses that are likely degraded by bacterial fermentation. It also
609 occurs more often in drier environments with more extreme mean annual temperatures, and
610 in larger habitat patches. As a result, we suggest that primate late-stage fermented food
611 consumption may be part of a nutritional strategy that increases food availability by
612 increasing the duration across which a particular fruit patch can be used, and expands
613 dietary niche space by degrading some toxins in ripe fruit and providing easily accessible
614 nutrients. It is possible that the human propensity for fermented food consumption is rooted
615 on this ancestral primate strategy, which was favored during the course of human evolution
616 by periods of nutritional stress caused by climate change events and migration to unknown

617 or unfavorable landscapes. Future studies should pair systematic assessments of spatial and
618 temporal patterns of wild primate fermented food consumption with nutritional and
619 microbial analyses of fermented and unfermented food items to further investigate these
620 relationships.

621

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633

634

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FIGURE LEGENDS

Figure 1. Wild primates consuming fermented fruits. (a) *Chlorocebus djadjamensis* consuming *L. abyssinica* at Kokosa, Ethiopia; credit Addisu Mekonnen (b) *Cebus capucinus imitator* consuming *D. oleifera* at La Suerte Biological Field Station, Costa Rica; credit: Liz Rasheed (c) *Pan paniscus* consuming *A. mannii* at LuiKatole, Democratic Republic of Congo; credit Gottfried Hohmann (d) *Ateles geoffroyi* consuming *M. zapota* at Punta Laguna, Mexico; credit Fabrizio Dell’Anna (e) *Alouatta guariba clamitans* consuming *P. guajava* at Parque São Paulo, Brazil; credit Claudio Godoy (f) *Macaca assamensis* consuming *N. cadamba* at Phu Khieo Wildlife Sanctuary, Thailand; credit Oliver Schülke (g) *Hapalemur meridionalis* consuming *Uapaca* sp. at Mandena, Madagascar; credit Tim Eppley (h) *Callithrix jacchus* consuming *P. pachycladus* at Baracuhy Biological Field Station, Brazil; credit: Filipa Abreu.

Figure 2. Fruits consumed fermented by wild primates. (a) *Lagenaria abyssinica*, credit: Addisu Mekonnen (b) *Stemmadenia obovata*, credit: Amanda Melin (c) *Vangueria madagascariensis*, credit: Tojotanjona Razanaparany (d) *Spondias mombin*, credit: Amanda Melin (e) *Landolphia myrtifolia*, credit Tojotanjona Razanaparany (f) *Diospyros kaki*, credit Bingua Sun.