

# Species sympatry shapes brain size evolution in

## Primates

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**Abstract** | The main hypotheses about the evolution of animal cognition emphasise the role of

**conspecifics**. Yet, space is often simultaneously occupied by multiple species from the same

ecological guild. These sympatric species can compete for food, which may thereby stimulate or

hamper cognition. Considering brain size as a proxy for cognition, we tested whether species

sympatry impacted the evolution of cognition in frugivorous primates. We first retraced the

evolutionary history of sympatry between frugivorous primate lineages. We then fitted

phylogenetic models of the evolution of the size of several brain areas in frugivorous primates,

considering or not species sympatry. We found that the whole brain or brain areas used in

immediate information processing were best fitted by models not considering sympatry. By

contrast, models considering species sympatry best predicted the evolution of brain areas related to

long-term memory of interactions with the social or ecological environment, with a decrease of their

23 size the higher the sympatry. We speculate that species sympatry, by generating intense food  
24 depletion, leads to an over-complexification of resource spatio-temporality that counteracts the  
25 benefits of high cognitive abilities and thereby induces lower brain area sizes. In addition, we  
26 reported that species in sympatry diversify more slowly. This comparative study suggests that  
27 species sympatry significantly contributes to shaping primate cognition and diversification.

28 **Short title:** Sympatry shapes primates' brain size

29 **Keywords:** Brain size - Cognition - Diversification - Frugivory - Primates - Sympatry

30

## 31 INTRODUCTION

32 Cognition evolution is shaped by the balance between socio-ecological drivers promoting cognitive  
33 abilities (González-Forero and Gardner 2018) and physiological and energetic constraints limiting  
34 them (Navarrete, Schaik, and Isler 2011). Primates are pivotal species for cognitive studies (Byrne  
35 2000) because their cognition is thought to be promoted by interactions of individuals with  
36 conspecifics within the social unit (Byrne 2018; Dunbar and Shultz 2017), among generations  
37 (Wilson 1991; Whiten and Schaik 2007; Reader and Laland 2002; Herrmann et al. 2007; Tomasello  
38 2019; Schaik and Burkart 2011), between social units (Ashton, Kennedy, and Radford 2020), or with  
39 the rest of their environment (Clutton-Brock and Harvey 1980; Milton 1981; Rosati 2017).  
40 However, space is often occupied by many primate species sharing the same diet. Because of  
41 competition for food between these species, both direct and indirect interactions between  
42 **heterospecifics in sympatry are also likely to shape the evolution of their cognition.**

43 Retracing the evolutionary history of cognitive abilities proves to be challenging because there is  
44 still no consensual measurement for cognition applicable across all species. Up to now, a raw  
45 approximation consists in considering the (relative) brain size as a proxy for cognitive abilities, with  
46 larger sizes considered equivalent to more advanced cognitive abilities (Benson-Amram et al. 2016).  
47 Although the relevance of this assumption is heavily limited within species, in part because of  
48 plasticity (Gonda, Herczeg, and Merilä 2013), this holds true when comparing different species (e.g.,  
49 in primates, Reader and Laland 2002). Instead of considering the brain as a whole, the multifaceted  
50 aspect of animal cognition is then more precisely depicted by appreciating the mosaic nature of the  
51 brain (Barton and Harvey 2000). For instance, variations in the size of some specific brain areas  
52 have been robustly associated with variations in cognition related to the function of these areas  
53 (Healy and Rowe 2007). The brain is therefore a patchwork of areas cognitively specialised that  
54 may follow different evolutionary trajectories.

55 Because species sympatry might play on different aspects of the socio-ecological environment, the  
56 **brain areas might be differently affected by species sympatry**. First, sympatric species from the  
57 same dietary guild may show some dietary overlap. Thus, sympatry often leads to an increase in  
58 food depletion of the shared resource compared with an environment with only one foraging  
59 species (Minot 1981). As an indirect effect of depletion, sympatric species competing for the same  
60 food resource may therefore complexify the pattern of resource distribution and availability in  
61 space and time. This complexification may in turn affect the selective pressures upon brain areas  
62 involved in the storing of spatio-temporal information, such as the **Hippocampus** (Burgess, Maguire,  
63 and O'Keefe 2002, Hypothesis 1: memory is affected by sympatry). Second, all sympatric species  
64 may enrich the landscape of visual, olfactory or acoustic cues usable to locate available food (e.g.,  
65 Avarguès-Weber, Dawson, and Chittka 2013; Kashetsky, Avgar, and Dukas 2021). Consequently, it  
66 may impact the selective pressures upon brain areas involved in processing more immediate  
67 sensory information, such as the Main Olfactory Bulb (MOB), the Cerebellum (Koziol et al. 2014;  
68 Sokolov, Miall, and Ivry 2017), and the Neocortex (Wiltgen et al. 2004) (Hypothesis 2: cue  
69 processing is affected by sympatry). Besides indirect interaction(s) through foraging, cognition can  
70 also be triggered by direct “social” interactions with other individuals (Byrne 2018; Dunbar and  
71 Shultz 2017). **The Striatum, a brain area stimulated during social interactions (Báez-Mendoza and**  
72 **Schultz 2013), may therefore be affected by the increase of direct social interactions between**  
73 **heterospecifics** (Hypothesis 3: sociality is affected by sympatry).

74 Under these (non-exclusive) hypotheses, sympatry could stimulate or hamper cognition evolution.  
75 Memory stands as a valuable tool to infer food availability and location when food is rare and  
76 ephemeral but predictable (Milton 1981; Rosati 2017). Thus, having a better memory should be  
77 advantageous under reasonable food depletion. In addition, competition for the shared resource  
78 between species should promote anticipatory behaviour, hence high cognition, as expected for  
79 within-species competition (Ashton, Kennedy, and Radford 2020). In this case, the size of the

80 Hippocampus (reflecting long-term memory abilities) should be larger the higher the sympatry  
81 intensity (**Prediction 1.1**). On the other hand, intense depletion also increases environmental  
82 unpredictability. In the case of a frugivore searching for fruit, for instance, the perceived synchrony  
83 in fruit production between trees of the same or different species, used to infer food availability  
84 (Janmaat et al. 2012), can be lowered by depletion, eventually limiting the benefits of memory  
85 (Robira et al. 2021). Thus, with such a scenario and due to the energy constraints of maintaining a  
86 large brain, the Hippocampus size could be smaller in highly sympatric species (Prediction 1.2).  
87 Meanwhile, cues left out by heterospecifics and usable to locate available food might also add to  
88 environmental ones already available. Hence, sympatry could be associated with larger sizes of the  
89 MOB, the Cerebellum, or the Neocortex (Prediction 2). Finally, an increase in direct interactions  
90 between species, such as with the formation of mixed-group species (Goodale et al. 2010), should  
91 imply an upsurge of social stimuli leading to a larger size of the Striatum in sympatry (Prediction 3).

92 Here, we investigated whether species sympatry affected the evolution of cognition using  
93 frugivorous primates as a study example. Frugivorous primates are an interesting group for such a  
94 question because fruit is the archetype of a hard-to-find resource yet predictable (Janmaat et al.  
95 2016), for which cognition considerably shapes the foraging strategy (Trapanese et al. 2019). To  
96 infer the effect of species sympatry on cognition in frugivorous primates, we evaluated the support  
97 for models of brain size evolution accounting or not for species sympatry, and investigated the  
98 directionality of the selection induced by sympatry on brain size evolution. Finally, we tested for  
99 correlative patterns between brain size or current sympatry and the species diversification in all  
100 primates, to better understand the impact of cognition and interactions between primates on their  
101 evolutionary success.

## 102 **METHODS**

103 Data processing, analyses, and plots were computed with R software (v.4.1.2, R Core Team 2020).

## 104 **Data Collection**

### 105 **Phylogeny**

106 We used a block of chronogram trees of the primate taxon of the 10kTrees project (downloaded on  
107 May 2021, version 3), as well as a consensus tree of 1000 trees for the subsequent phylogenetic  
108 analyses. The trees contain 301 primate species (Figure 2). Note that in all these analyses, we  
109 discarded *Homo sapiens* and *Macaca sylvanus*. The latter was discarded because of its complete  
110 geographic isolation and repeated intervention of **human people** in population maintenance  
111 (Modolo, Salzburger, and Martin 2005). A summary of available data per species is presented in  
112 Supplementary Material Figure S3.

### 113 **Trait data**

114 Data were pooled from previous literature surveys (see Supplementary Material “Data availability”).  
115 Brain data were obtained from DeCasien and Higham (2019) for the whole brain and all mentioned  
116 other areas (Cerebellum, Hippocampus, Main Olfactory Bulb (MOB), Neocortex, Striatum), Powell,  
117 Isler, and Barton (2017) and Powell, Barton, and Street (2019) for the whole brain, Cerebellum and  
118 Neocortex size, Todorov et al. (2019) for Hippocampus and Neocortex size, Grueter (2015) for the  
119 whole brain size and Navarrete et al. (2018) for the whole brain, Cerebellum, Hippocampus and  
120 Striatum size. They were freely-available in the main manuscript or supplementary materials. For  
121 each primate species, the percentage of frugivory and/or folivory was obtained based on a freely  
122 available dataset from DeCasien, Williams, and Higham (2017), Powell, Isler, and Barton (2017), and  
123 Willems, Hellriegel, and Schaik (2013). The availability of trait and distribution range for the 301  
124 primate species represented in the primate phylogeny of the 10kTrees project is depicted in  
125 Supplementary Material Figure S3. From the **global endocranial brain volume, we obtained the**  
126 **Encephalization Quotient** (EQ,  $N_{EQ,max} = 182$ ) as follows (DeCasien, Williams, and Higham 2017)

$$EQ = 1.036 \times \text{Brain volume} / (0.085 \times \text{Body mass}^{0.775})$$

127 with the brain volume in  $\text{cm}^3$ ,  $1.036 \text{ g/cm}^3$  being the assumed homogeneous brain density, and the  
128 body mass in g. EQ indicates whether the brain size ranges above ( $> 1$ ) or below ( $< 1$ ) expected  
129 given the body mass. Body mass was obtained from DeCasien, Williams, and Higham (2017), Powell,  
130 Isler, and Barton (2017), Grueter (2015), Pearce et al. (2013). The sub-parts of the brain were  
131 chosen because they were involved in immediate sensory information processing (MOB,  $N_{MOB,max} =$   
132 39), in movement and/or general information processing and retention (Neocortex,  $N_{Neocortex,max}$   
133 = 69, Wiltgen et al. 2004; Cerebellum,  $N_{Cerebellum,max} = 70$ , Koziol et al. 2014; Sokolov, Miall, and  
134 Ivry 2017), short-term working memory and long-term spatio-temporal memory (Hippocampus,  
135  $N_{Hippocampus,max} = 63$ , Burgess, Maguire, and O'Keefe 2002). The Striatum ( $N_{Striatum,max} = 63$ )  
136 supports information processing during social interaction, reward assessment, planning or goal-  
137 oriented behaviours (Báez-Mendoza and Schultz 2013; Johnson, Meer, and Redish 2007). To  
138 investigate their evolutionary history, we used the ratio between their volume and body mass, so as  
139 to maximize comparability. As such, the use of specific area sizes relative to the body mass and not  
140 raw sizes depicts the evolution of cognitive abilities in terms of allocation rather than abilities per se  
141 (but see discussion in Deaner, Nunn, and Schaik 2000).

## 142 Ranging Data

143 The current biogeographic range of each primate species was assessed using ranging maps  
144 provided by the IUCN red list (IUCN 2021). Ranging data were available for 249 species among the  
145 301 represented in the 10kTrees primate phylogeny.

## 146 Retracing past sympatry between primate species

147 Based on the biogeographic distribution of each extant primate species, we first reconstructed the  
148 history of past sympatry between primate lineages. To do so, we followed Drury et al. (2018) and

149 first reconstructed the biogeographic history of each primate lineage to then retraced which pairs of  
150 primate lineages were likely to be simultaneously present at the same place. Leaning on Kamilar  
151 (2009), we considered that the biogeography of primates can be described by 12 discrete  
152 biogeographic areas with highly similar community structures shaped by both the environment  
153 geography and climatic correlates. These geographic areas, mapped using Google earth professional  
154 (v7.3.3), are represented in Figure 1. One to multiple biogeographic areas were assigned to each  
155 species as soon as 10 of their current distribution range overlapped on the surface with a given  
156 biogeographic area. We also replicated these biogeographic assignments by using instead a larger  
157 threshold of 30%. This upper threshold was chosen because a species could occupy as far as three  
158 areas, Figure 1). Overlap of primate current range with biogeographic areas was calculated with the  
159 “gIntersection” function from the *rgeos* package (Bivand and Rundel 2021) applied to Mercator-  
160 projected data to get the overlapping contour, and the “area” function from the *geosphere* package  
161 (Hijmans 2021), applied directly on unprojected longitudinal-latitude data for area size  
162 calculation.

163 Given these 12 biogeographic areas, we retraced the biogeographic history of primates with the  
164 *BioGeoBEARS* package (Matzke 2013), using the biogeographic stochastic mapping algorithm  
165 (Matzke 2016). We fitted non-time-stratified dispersal-extinction-cladogenesis (DEC) models  
166 specifically suiting analyses of range data since it accounts for spatially explicit processes of  
167 cladogenetic and anagenetic events (see Matzke (2013) for further details on these events). We  
168 fixed to three biogeographic areas the maximum number of areas that a lineage can simultaneously  
169 occupy since it offers the possibility to occupy a complete mainland continent while keeping  
170 computational time reasonable. DEC models were independently fitted when considering either a  
171 10% or a 30% threshold of range overlaps. Finally, to account for the uncertainty in biogeographic  
172 reconstructions, we sampled 10 histories of primate biogeographic ranges. We assumed that



173 primate lineages were in sympatry at a given time whenever the species occupied the same  
174 biogeographic area.

## 175 **Inferring past diets of primate lineages**

176 Next, we retraced the evolutionary history of frugivorous lineages in primates. We first classified  
177 extant species as either “frugivorous” or “folivorous” based on the availability of frugivorous rate  
178 and folivorous rate, prioritizing frugivory over folivory. A species was classified as frugivorous if the  
179 frugivory rate was at least above 20%. If this was not the case, or if the frugivory rate was  
180 unavailable, a species could be classified as folivorous if the folivory rate was at least above 40%.  
181 Otherwise, DeCasien, Williams, and Higham (2017) gave a binary classification of diet, species being  
182 categorised as frugivorous or folivorous, partly based on anatomical criteria. Whenever the rate was  
183 not available, we referred to this classification. In any other cases, the species was discarded. We  
184 also replicated these diet assignments by considering a threshold of 40% for frugivory and 60% for  
185 folivory.

186 Second, considering diet as a binary variable (frugivory versus folivory), we retraced the  
187 evolutionary history of such discrete traits based on a continuous Markovian process (extended Mk  
188 models) using a Bayesian inference (Bollback 2006), with the “simmap” function of the *phytools*  
189 package (Revell 2012) and internally setting up the prior probability of trait, but with no prior on  
190 the transition matrix. **Ancestral diet reconstructions** were performed using both combinations of  
191 dietary thresholds (20/40% and 40/60%). To account for the uncertainty in the reconstructions, we  
192 obtained 10 stochastic diet history timelines. The latter were used in combination with the history  
193 of primate ranges to assess whether a frugivorous species was in sympatry with another  
194 frugivorous species or not (i.e., we obtained reconstructions of the evolutionary history of sympatry  
195 between frugivorous primate lineages).

## 196 **Phylogenetic models**

197 We assessed the effect of sympatry on primate brain evolution using two approaches. First, we used  
198 phylogenetic models of trait evolution to assess the role of sympatry in the evolution of brain size.  
199 Second, we investigated how sympatry has influenced brain size evolution (i.e., selection towards  
200 smaller or larger brain sizes) by evaluating correlations between current levels of sympatry and  
201 brain sizes, using linear modelling. Besides, we also checked for correlative patterns between  
202 primate brain size and diversification rates to have insights into primate evolutionary success.

### 203 **Phylogenetic models of trait evolution: does species sympatry shape brain size evolution?**

#### 204 (a) Fitting models of trait evolution

205 We restricted the analyses to frugivorous species to test whether species sympatry has impacted  
206 the evolution of cognition, depicted either by the whole brain (using the **encephalic** quotient, EQ), or  
207 the size of the aforementioned specific brain areas relative to the whole-body mass (Figure 3). For  
208 such a task, we fitted phylogenetic models of the evolution of the size of the different brain areas  
209 independently (Drury et al. 2016). For models implying species sympatry, this was made possible  
210 by combining the historical timeline of diet and biogeography evolution, so that we could retrace  
211 the history of sympatry between frugivorous lineages. In practice, we obtained a series of  
212 interaction matrices (i.e., lines and columns correspond to frugivorous species, and each cell  
213 indicates whether a given species pair is in sympatry (value of 1) or not (value of 0)), along the  
214 phylogenetic tree (see Drury et al. 2016). This was used to fit models that considered species  
215 sympatry to model brain size evolution: the matching competition (MC) model (Nuismer and  
216 Harmon 2015) and density-dependent models ( $DD_{lin}$  and  $DD_{exp}$ , Drury et al. 2016). Specifically,  
217 these models expand classical models of stochastic evolution (Brownian Motion), by including an  
218 additional variable related to current brain size of sympatric species (MC), or by considering  
219 density-dependent evolutionary rate (DD models). Specifically, the matching competition model

220 (MC) considers the repulsion of traits of sympatric lineages from the same dietary guild due to  
221 competition (character displacement), that is  $z_i(t + dt) = z_i(t) + S(\mu(t) - z_i(t))dt + \sigma dB_i$  where  $z$   
222 is the brain size of a species  $i$  at time  $t$ ,  $\mu$  is the mean value of the trait of sympatric species,  $S$   
223 reflects the strength of the effect of species sympatry and  $\sigma dB_i$  is the drift with a constant  
224 evolutionary rate  $\sigma$  (Drury et al. 2016). Here,  $S$  is constrained to be negative, which means that  
225 sympatric species would tend to divergently evolve either lower, or higher, EQ or relative brain size.  
226 Linear ( $DD_{lin}$ ) or exponential ( $DD_{exp}$ ) density-dependence (Drury et al. 2016; Weir and Mursleen  
227 2013) means that the evolutionary rate,  $\sigma$ , of trait change, varies either positively or negatively as a  
228 function  $f$  of the number of frugivorous sympatric lineages, such as

$$\sigma_l = f_{lin}(l) = \sigma_0 + rl$$

$$\sigma_l = f_{exp}(l) = \sigma_0 \exp(rl)$$

229 where  $\sigma_0$  corresponds to the value of the initial ancestor,  $l$  indicates the number of lineages,  $r$  allows  
230 for modelling the speed and direction of the dependency to lineage number ( $r > 0$  leads to an  
231 increase of trait changes, while  $r < 0$  leads to a decline of the trait changes). We fitted models  
232 considering species sympatry using the “fit\_t\_comp” function from the *RPANDA* package (Morlon et  
233 al. 2016).

234 **Depending on the brain area and the frugivory threshold we considered, the models were fitted on**  
235 **different sample sizes: EQ: 148 to 182, Striatum: 56 to 63, MOB: 34 to 39, Neocortex: 61 to 69,**  
236 **Hippocampus: 56 to 63, Cerebellum: 62 to 70 frugivorous species. For a given set of models (i.e.,**  
237 **within a brain area), the sample was strictly identical, allowing within-set comparisons. Prior to**  
238 **fitting, trait parameters were log-transformed to reach more symmetrical distributions.**

239 We compared the support of models considering species sympatry to the support of simpler  
240 models assuming no effect of species sympatry on the evolution of brain sizes: the Brownian Motion

241 (BM), the Ornstein-Uhlenbeck process (OU, a model with an optimum value, see Blomberg,  
242 Rathnayake, and Moreau (2020) for a review), or the Early-Burst model (EB), for assessing a time-  
243 dependence of the evolutionary rate, irrespective of the intensity of species sympatry (Blomberg,  
244 Garland, and Ives 2003). These models without species sympatry were fitted using the  
245 “fitContinuous” function from the *geiger* package (Slater et al. 2012; Pennell et al. 2014). All these  
246 models were repeated 10 times, using 10 different combinations for the evolutionary history of  
247 primate biogeography and diet. They were then compared within an information-theoretic  
248 framework (Burnham and Anderson 2002), based on the weights of Akaike Information Criteria  
249 corrected for small samples (AICc) when considering all six models (MC,  $DD_{lin}$ ,  $DD_{exp}$ , BM, OU, EB).  
250 The model weight depicts how well the model fits the observed data compared with the other tested  
251 models.

#### 252 (b) Determining the effect of sympatry on brain sizes

253 If diversity-dependent models of traits evolution considering species sympatry can be used to  
254 assess whether or not species sympatry has impacted the evolution of the brain size by increasing  
255 or decreasing the tempo of trait evolution, they do not say anything about the directionality of the  
256 effect (i.e., are brain sizes in frugivorous sympatric primates increasing or decreasing?). To  
257 determine whether species sympatry positively or negatively affected the sizes of brain areas, we  
258 independently fitted Gaussian Pagel’s lambda phylogenetic regressions for each brain area of extant  
259 frugivorous species. This model is a derivative of the Brownian Motion model, where the  
260 phylogenetic variance-covariance matrix has all coefficients, but its diagonal ones, multiplied by  
261 lambda: it thus relaxes the hypothesis of Brownian Motion since we included brain areas for which  
262 the evolutionary history was best described by models considering sympatry (see [Results](#)). To fit  
263 these models, we used a frequentist-based approach with the “*phylolm*” function from the *phylolm*  
264 package (Ho and Ane 2014). We considered the least stringent frugivory assessment, with the

265 frugivory threshold fixed at 20% and the folivory threshold fixed at 40%. If due to data variability, a  
266 species did not robustly fit into the categorical classification “frugivorous versus folivorous” (i.e.,  
267 could be either of the two), it was considered as frugivorous nonetheless.

268 The response variable was the relative size of each brain area. Due to data variability, we took the  
269 mean of the possible values given the different datasets and assessed the sensitivity using non-  
270 averaged values (see Supplementary Material “Phylogenetic regressions: results, stability, and  
271 assumption”). In this model, we used as covariates (i.e., continuous predictors) two explicit  
272 measures of species sympatry intensity for each extant frugivorous species: (1) the number of  
273 frugivorous sympatric species (square-rooted to reach symmetrical distribution) and (2) the  
274 average percentage of overlapping current range (assessed based on IUCN data) with other  
275 sympatric frugivorous species. For a given species A, sympatry with another species B was  
276 considered when at least 10% of the range of species A overlaps with the range of species B. This  
277 was done to reduce the noise induced by coarse identification of species range.

278 Eventually, it means that the results for each model represent the average of 10 (uncertainty on  
279 diet/ranging evolution) x 10 (uncertainty in brain/diet rate data) x 2 (geographic overlap  
280 threshold) x 2 (frugivory threshold) x 2 (folivory threshold) = 800 sub-models. We stopped  
281 computations when the calculation of the likelihood was excessively long (> 1 week). The final  
282 sample size thus was 730 models. Wow!

283 To sum up, when assessing the interplay between sympatry and the evolution of frugivorous  
284 primates’ brain architecture, we considered sympatry under different forms. To assess whether it  
285 affected brain size evolution, sympatry was added to classical phylogenetic models of trait evolution  
286 as an additional variable depicting the mean trait value of sympatric species (MC models), or as a  
287 density-dependent term (i.e., the total number of sympatric lineages at a given time; in  $DD_{in}$  and  
288  $DD_{exp}$  models). Then, to assess the directionality of the effect of sympatry on brain sizes, sympatry

289 was used as a tested predictor in phylogenetic linear regressions, under two forms: the number of  
290 currently sympatric species, and the average range overlap with currently sympatric species.

## 291 Models of species diversification

292 Next, to investigate whether cognition and/or species sympatry have affected primate  
293 diversification, we inferred how primates diversified over time and across lineages. Lineage-specific  
294 net diversification rates (defined as speciation minus extinction rates) were estimated using an  
295 updated version of the *ClaDS* algorithm (Maliot, Hartig, and Morlon 2019) boosted for  
296 computational speed based on data augmentation techniques (Maliot and Morlon 2021).  
297 Particularly, we used *ClaDS2*, the model with constant turnover (i.e., constant ratio between  
298 extinction and speciation rates; see Supplementary Material “Primate diversification rate over time”  
299 for further explanations). We extracted the mean diversification rates through time and the lineage-  
300 specific diversification rate of each extant species.

301 We also fitted Gaussian Pagel’s lambda phylogenetic regressions of the different relative brain sizes  
302 against the net diversification rates, estimated for each extant species by the *ClaDS* algorithm.  
303 Because assumptions for a frequentist-based approach were unmet, we used a Bayesian-based  
304 approach. We used the “MCMCglmm” function of the *MCMCglmm* package (Hadfield 2010). Each  
305 chain was based on a burn-in period of 5000 iterations, among a total of 50 000 iterations, and was  
306 sampled every 50 iterations. We used the least informative priors. Fixed priors were let to default  
307 (Gaussian distribution of mean 0 and variance  $10^8$ ). Again, we took the mean of the brain trait  
308 values for the main model and assessed the sensitivity by re-running the model several times using  
309 non-averaged values.

310 To determine whether species sympatry was associated with lower or larger diversification rates,  
311 we fitted frequentist-based Gaussian Pagel’s lambda phylogenetic regressions with the lineage-  
312 specific diversification rate as the output variable, and used the two metrics for describing sympatry

313 (the number of frugivorous sympatric species and the average percentage of overlapping range with  
314 other sympatric frugivorous species) as the tested variables, as in (a).

315 Details on the implementation, stability, and uncertainty of phylogenetic regressions are provided in  
316 Supplementary Material (see “Phylogenetic regressions: results, stability, and assumption”).

## 317 **RESULTS**

318 The database we gathered contained between 34 to 182 frugivorous primate species (depending on  
319 the brain area considered). **After pondering by whole-body mass**, we observed ample variations in  
320 brain area relative sizes. For instance, the lemuriformes, which are known to prioritize smell  
321 compared with other primate species, have the largest relative MOB size (Lemuriformes: mean  $\pm$  SE  
322 =  $0.23 \pm 0.07$ , other:  $0.12 \pm 0.04$ , 3). Similarly, platyrrhini, and callitrichine primates in particular,  
323 are known to form poly-specific associations (Heymann and Buchanan-Smith 2000). The latter  
324 show the highest relative size of the Striatum (Platyrrhini: mean  $\pm$  SE =  $0.91 \pm 0.07$ , other:  $0.59 \pm$   
325  $0.07$ , 3). In terms of the measures of sympatry, we observed that on average ( $\pm$  SE), the considered  
326 primate species had 52% ( $\pm 2$ ) of their range overlapping with other species. That ranged from 0%  
327 of overlap (*Macaca nigra*), to 100% of overlap (*Cercopithecus pogonias*, *Alouatta pigra*, *Loris*  
328 *tardigradus*, *Hylobates moloch*, *Cercocebus galeritus*, *Presbytis melalophos*, *Semnopithecus entellus*).  
329 In terms of the distribution range, the considered primate species co-occurred on average with 6.38  
330 ( $\pm 0.39$ ) other primate species, ranging from 0 other species to 21.

331 To retrace the history of past species sympatry between frugivorous lineages, we first  
332 reconstructed primate biogeographic history when considering 12 biogeographic areas (Figure 1,  
333 Kamilar 2009) and their diet evolution. We then modelled the evolution of the size of the whole  
334 brain (EQ), or regionalised areas (Neocortex, Cerebellum, MOB, Hippocampus, and Striatum) when  
335 considering species sympatry or not. We found that models not considering species sympatry best

336 described the evolutionary history of the EQ, the Neocortex, and the Cerebellum (Figures 3 and 4),  
337 two areas specifically involved in immediate sensory information processing (Wiltgen et al. 2004;  
338 Koziol et al. 2014; Sokolov, Miall, and Ivry 2017), and also in memory consolidation for the  
339 Neocortex (Wiltgen et al. 2004). The fact that these biggest areas are best described by the Ornstein-  
340 Uhlenbeck process suggests a stabilization towards an optimal size, which may illustrate the trade-  
341 off between costs and benefits of brain development (Isler and Schaik 2009). By contrast, density-  
342 dependent models considering species sympatry ( $DD_{lin}$  and  $DD_{exp}$ ) were best supported in the  
343 foraging-related and social-related areas respectively: the Hippocampus, specialised in spatio-  
344 temporal memory (Burgess, Maguire, and O'Keefe 2002) and the Striatum, involved in social  
345 interactions (Báez-Mendoza and Schultz 2013). The fact that we inferred positive rates  $r$  of density-  
346 dependence (Figure 4) suggested an acceleration of the evolutionary tempo of trait evolution  
347 together with increased diversity of frugivorous sympatric lineages for the Hippocampus and the  
348 Striatum. The MOB, the area involved in sensory abilities, also tended to be best fitted by models  
349 considering sympatry as a whole. Yet, Brownian Motion (BM) was as likely as density-dependent or  
350 MC models, preventing firm conclusions on whether sympatry affected or not MOB size evolution  
351 (Figures 3 and 4), especially since this coincided with the most reduced sample size we had ( $N_{species}$   
352 = 34 to 39).

353 Next, we assessed whether species sympatry leads to “bigger” or “smaller” brain area sizes the  
354 more sympatric species. To do so, we fitted phylogenetic regressions in extant frugivorous species  
355 between the relative sizes of the different brain areas and two measures of sympatry (1) the  
356 average percentage of overlapping range with other frugivorous sympatric species, and (2) the  
357 number of such sympatric frugivorous species across their current entire distribution range. The  
358 number of sympatric species never significantly influenced the relative brain sizes (Table 1).  
359 Conversely, we found that the average percentage of overlapping range correlated with the relative  
360 size of brain areas that were better fit with models considering sympatry: the Hippocampus and the



361 Striatum (Hippocampus:  $t = -1.94$ ,  $p = 0.058$ ; Striatum:  $t = -2.26$ ,  $p = 0.028$ ). The correlations were  
362 all negative (Hippocampus: est. =  $-0.39$ , CI95% =  $[-0.76, -0.01]$ ; Striatum: est. =  $-0.4$ , CI95% =  $[-0.77, -$   
363  $0.04]$ ), which means that higher range overlap between sympatric species associates with lower  
364 relative size, insensitive to data and phylogenetic uncertainties (Appendix Table S1, Appendix  
365 Figure S8, Appendix Table S1). Given the acceleration of the evolutionary tempo with species  
366 sympatry ( $r > 0$  in the density-dependent models), it suggests that compared with isolated species,  
367 sympatric species are subject to a positive selection towards smaller brains, and not to a less intense  
368 selection for advanced cognitive abilities.

369 Finally, we investigated the evolutionary consequences of cognition and species sympatry by  
370 evaluating whether brain sizes and sympatry intensities correlated with the lineage-specific net  
371 diversification rates of primates (defined as speciation minus extinction rates). Overall, species  
372 diversification rates, estimated based on the primate molecular phylogeny, particularly boomed in  
373 the early and late Miocene, around 25 and 11 Myr ago (Appendix Figure S4). When accounting for  
374 phylogenetic dependence, no significant relationship between the net diversification rate and the  
375 relative size of brain areas was found (Table 2, Appendix Figure S8; see robustness in  
376 Supplementary Material Table S2). Although diversification was uncorrelated with brain size in  
377 frugivorous primates, it was influenced by the sympatry context. In particular, phylogenetic  
378 regressions highlighted a negative effect of the number of sympatric species on the diversification  
379 rate (est. =  $-5.04e-03$ , CI95% =  $[-0.01, 1.34e-04]$ ,  $t = 2.56e-03$ ,  $p < 0.001$ , Table 3, Appendix Figure S8,  
380 Appendix Table S3). In other words, the higher the number of sympatric species, the lower the  
381 diversification rate.

## 382 **DISCUSSION**

383 Bigger brains are not necessarily better, as the size of the brain is subject to a compromise between  
384 the energy it incurs, and the increase of fitness it allows. This is clearly emphasised by the fact that

385 the evolution of the biggest brain areas, the Cerebellum and the Neocortex, as well as the whole  
386 brain (EQ), were best fitted by the Ornstein-Uhlenbeck process. This suggests a stabilisation  
387 towards an optimal size resulting from an equilibrium between costs and benefits. Although  
388 allometric and developmental constraints, as well as spatial proximity in the brain, can induce  
389 correlation in the evolution of different brain areas (Gómez-Robles, Hopkins, and Sherwood 2014),  
390 brain areas underpin different cognitive functions and can thus be under different, independent,  
391 selective pressures (Barton and Harvey 2000). The functional regionalisation is for instance  
392 evidenced here by the differences in relative sizes across lineages in the MOB, with larger sizes in  
393 the lemuriformes that mostly rely on smell to forage. The differences in evolutionary trajectories are  
394 highlighted by the variations in the best fit models of size evolution for the different brain areas. We  
395 indeed show that sympatry is one factor that affects the selective regime under which only some  
396 brain area evolves: although the brain as a whole was insensitive to species sympatry, the latter  
397 nonetheless induced a change in the relative size of the Hippocampus and the Striatum. These areas  
398 are involved in individual-based and social-based information processing, pinpointing that the two  
399 components might be under strong selection in primates (DeCasien, Williams, and Higham 2017;  
400 Powell, Isler, and Barton 2017; González-Forero and Gardner 2018).

401 Overall, the fact that the Hippocampus, particularly relevant to process and memorise spatio-  
402 temporal information, is sensitive to sympatry, is consistent with the idea of an effect of sympatric  
403 species on resource spatio-temporality (Hypothesis 1). Competition is generally the first-thought  
404 mechanism to describe community structures (de Almeida Rocha et al. 2015) because it might affect  
405 the environment in which species evolve. We show that a higher intensity of sympatry is actually  
406 associated with smaller sizes of the Hippocampus (in accordance with Prediction 1.2). This suggests  
407 that indirect competition for food might contribute to convoluting the environment, and such an  
408 over-complexification of the resource spatio-temporality may render cognitive foraging not  
409 advantageous anymore. As a result, it might even generate a selection for smaller brains.

410 By contrast, potential indirect facilitation between species due to “social” cues (Hypothesis 2), is  
411 ruled out by the absence of an effect of sympatry on brain areas involved in immediate sensory  
412 information processing (e.g., Cerebellum or Neocortex). This absence of effect can stem from two  
413 possibilities. Either foragers do not exploit cues left out by sympatric heterospecifics. Otherwise, it  
414 has been shown that foragers tend to use social information over environmental (i.e., personal)  
415 information, in particular in non-perfectly predictable environments (Rafacz and Templeton 2003;  
416 Dunlap et al. 2016). Thus, if environmental complexity increases too much, “social” cues provided by  
417 heterospecifics might replace environmental ones. As such, stimulation intensity of the MOB, the  
418 Cerebellum, or the Neocortex would somehow remain equivalent when in sympatry or not. Further  
419 work should explicitly test for these possibilities.

420 As expected (Hypothesis 3), the Striatum size was relatively larger in callitrichines, particularly  
421 known to form mixed-species groups (Heymann and Hsia 2015). Yet, overall, the Striatum size was  
422 negatively affected by sympatry. This puzzle might take root in secondary, but key, functions  
423 supported by the Striatum, namely reward expectation, goal-directed behaviour, and planning  
424 abilities (Johnson, Meer, and Redish 2007). These three functions might as well be advantageous  
425 when foraging. As for the Hippocampus, then, the increase in environment unpredictability could  
426 diminish the benefits of these future-oriented skills.

427 Given the context-dependence of the direction of selection (towards bigger sizes when sympatry is  
428 low, smaller sizes otherwise), there is no surprise that we do not observe a correlation between the  
429 net diversification rate and the three brain areas affected by species sympatry. Surprisingly  
430 however, we found no positive association between the net diversification rate and the EQ, the  
431 Cerebellum or the Neocortex, which were insensitive to species sympatry. By contrast, a positive  
432 association between brain size and diversification was also found in birds (Sayol et al. 2019) given  
433 that bigger brains act as a buffer to environmental challenges (Sol et al. 2007). A visual inspection of  
434 the regressions clearly evidenced a positive trend if not considering phylogeny (EQ and Neocortex,

435 Figure S6). Sudden encephalisation in primates is clearly associated with a limited number of  
436 closely-related species (DeCasien, Williams, and Higham 2017; Melchionna et al. 2020). Thus, this  
437 clearly limits the statistical power of our phylogenetically-corrected analyses, as we cannot decipher  
438 whether larger brain size and faster species diversification result from a true biological link or  
439 appeared simultaneously but independently. This means that, despite what we found here, a  
440 positive association between brain size and species diversification remains a likely possibility (as  
441 previously suggested in primates, Melchionna et al. 2020). Species sympatry, however, induced a  
442 significant slowdown in primate diversification, a density-dependence trend frequently observed in  
443 many tetrapod clades (Condamine, Rolland, and Morlon 2019). This frames coherently with a  
444 competitive scenario, where the tempo of species diversification decreases when ecological niches  
445 are progressively filled up (Rabosky and Lovette 2008). Species competing for resources are  
446 thought to contribute to limiting competitors' range (Price and Kirkpatrick 2009), hence  
447 constraining population size and diversification rate (Pigot and Tobias 2013).

## 448 **CONCLUSION**

449 The use of brain size as a proxy for cognition is a central debate with no optimal solution (see  
450 grounded criticism from Deaner, Nunn, and Schaik 2000; Healy and Rowe 2007; Logan et al. 2018).  
451 The current flourishing of consortia, allowing for much more detailed and standardised  
452 anatomical measurements (e.g., in primates: Milham et al. 2018), or with standardised  
453 behaviourally explicit comparisons (e.g., on captive, Altschul et al. 2019; or wild primates, Janmaat  
454 et al. 2021), might alleviate biases stemming from brain size analysis, but this will take time to  
455 generate large-enough datasets. In the meanwhile, brain size is a proxy much appreciated in  
456 practice, because of its easy accessibility for a “large” number of species, while the multifaceted  
457 aspect of cognition can simply be taken into account by considering the brain as a mosaic of singular  
458 and independent regionalised areas that are cognitively specialised. Here, we showed that species

459 sympatry is an important factor shaping the evolutionary history of animals' brains, but the  
460 proximate mechanisms at play remain to be elucidated. Finally, it is very likely that any hypothesis  
461 on cognition evolution, generally discussed within species, could be broadened to a between-species  
462 context: foraging facilitation between species does exist (Olupot, Waser, and Chapman 1998;  
463 Havmøller et al. 2021), and so do polyspecific social associations (Porter 2001), as well as inter-  
464 species territory defence (Drury, Cowen, and Grether 2020; Losin et al. 2016) or imitation and  
465 copying (Persson, Sauciuc, and Madsen 2018; Pepperberg 2002). Similarly, prey-predator races  
466 could shape selection on cognitive abilities (Shultz and Dunbar 2006). As Alice said “It’s a great huge  
467 game of chess that’s being played—all over the world” (Carroll 1871, chap. II) and all individuals are  
468 just pieces to play with or against, no matter the species.

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479 (supplementary) material with their articles. Their indirect input is therefore tremendous. Both  
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481 **AUTHORS' CONTRIBUTION**

482 BR conceived the study, gathered, cleaned and analysed the data, drew the figures and wrote the  
483 first version of the manuscript and subsequently revised it. BP-L implemented the ClADS algorithm  
484 for our data, helped with running other analyses, and revised the manuscript multiple times. The  
485 authors declare having no conflict of interest. All authors gave final approval for publication and  
486 agree to be held accountable for the work performed therein.

487 **DATA ACCESSIBILITY**

488 The data and codes that support the findings of this study are openly available at  
489 [https://github.com/benjaminrobira/Meta\\_analysis\\_cognition\\_primates](https://github.com/benjaminrobira/Meta_analysis_cognition_primates).

490

491 **Table 1: Species sympatry correlates negatively with the size of some brain areas of extant frugivorous primate**  
 492 **species | Model estimates and significance of phylogenetic regressions to assess the relationship between relative**  
 493 **brain sizes and species sympatry. Est.=Estimate, CI2.5%=Lower border of the CI95%, CI97.5%=Upper border of**  
 494 **the CI95%, Sd=Standard deviation, t=Statistics t-value. The brain areas (as well as the associated sample sizes)**  
 495 **are indicated prior to each list of estimates. The transformations applied to variables are indicated between**  
 496 **parentheses (logarithm, log, or square-root, sqrt), as well as the ponderation by bodymass (/bodymass).**

	Est.	CI2.5%	CI97.5%	Sd	t	p-value
<b>EQ (log) (N=127)</b>						
Intercept	-0.17	-0.53	0.22	0.20	-	-
% of overlapped range	0.02	-0.08	0.13	0.05	0.41	0.68
Number of sympatric frugivores (sqrt)	0.02	-0.02	0.05	0.02	1.03	0.31
Lambda	0.98	0.94	1.00			
<b>Hippocampus (/bodymass, log) (N=50)</b>						
Intercept	-0.92	-1.95	0.05	0.53	-	-
% of overlapped range	-0.39	-0.76	-0.01	0.20	-1.94	0.06
Number of sympatric frugivores (sqrt)	0.08	-0.06	0.20	0.07	1.21	0.23
Lambda	0.99	0.92	1.00			
<b>Neocortex (/bodymass, log) (N=56)</b>						
Intercept	2.07	1.31	2.86	0.41	-	-

% of overlapped range	-0.23	-0.54	0.11	0.16	-1.46	0.15
Number of sympatric frugivores (sqrt)	0.02	-0.08	0.13	0.05	0.48	0.63
Lambda	0.99	0.91	1.00			
Cerebellum (/bodymass, log) (N=57)						
Intercept	0.60	-0.15	1.35	0.39	-	-
% of overlapped range	-0.08	-0.32	0.17	0.12	-0.7	0.49
Number of sympatric frugivores (sqrt)	-0.01	-0.1	0.07	0.04	-0.34	0.74
Lambda	1.00	0.96	1.00			
Striatum (/bodymass, log) (N=50)						
Intercept	-0.36	-1.18	0.44	0.44	-	-
% of overlapped range	<b>-0.40</b>	<b>-0.77</b>	<b>-0.04</b>	<b>0.18</b>	<b>-2.26</b>	<b>0.03</b>
Number of sympatric frugivores (sqrt)	0.03	-0.08	0.15	0.06	0.61	0.54
Lambda	0.98	0.85	1.00			
MOB (/bodymass, log) (N=31)						
Intercept	-2.76	-4.61	-0.93	1.00	-	-
% of overlapped range	-1.20	-2.65	0.35	0.80	-1.49	0.15
Number of sympatric frugivores (sqrt)	0.21	-0.18	0.56	0.19	1.12	0.27



Lambda

1.00 1e-07 1.00

497

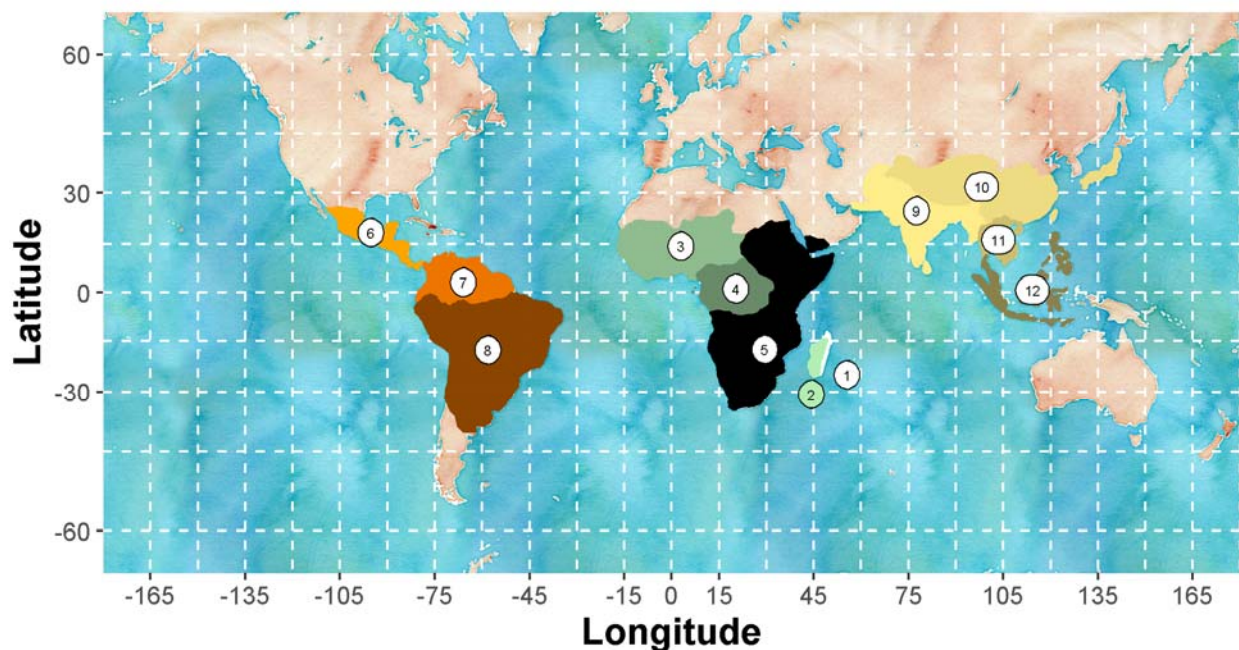
498 **Table 2: Relative brain sizes do not correlate with primate species diversification | Model estimates and**  
 499 **significance of Bayesian phylogenetic regressions to assess the correlation between the net diversification rates**  
 500 **and the relative brain sizes. Est.=Estimate, HDP2.5%=Lower border of the 95% Highest Posterior Density,**  
 501 **HDP97.5%=Upper border of the 95% Highest Posterior Density, Eff. samp.=Effective sample (adjusted for**  
 502 **autocorrelation). The brain areas (as well as the associated sample sizes) are indicated prior to each list of**  
 503 **estimates. The (log) indicates log-transformed variables, while the (/body mass) indicates variables pondered by**  
 504 **body mass.**

	<b>Est.</b>	<b>HDP2.5%</b>	<b>HDP97.5%</b>	<b>Eff. samp</b>	<b>pMCMC</b>
<b>Diversification EQ (N=148)</b>					
Intercept	0.12	0.08	0.16	900.00	-
EQ (log)	0.02	-7.91e-03	0.05	789.25	0.15
Lambda	0.83	0.76	0.9		
<b>Diversification Hippocampus (N=61)</b>					
Intercept	0.13	0.09	0.18	900.00	-
Hippocampus (/bodymass, log)	9.10e-03	-9.48e-03	0.03	900.00	0.34
Lambda	0.73	0.6	0.85		
<b>Diversification Neocortex (N=67)</b>					
Intercept	0.1	0.04	0.17	991.53	-

Neocortex (/bodymass, log)	7.26e-03	-0.02	0.03	900.00	0.56
Lambda	0.74	0.6	0.86		
Diversification Cerebellum (N=68)					
Intercept	0.12	0.07	0.16	900.00	-
Cerebellum (/bodymass, log)	3.94e-03	-0.02	0.03	989.21	0.76
Lambda	0.74	0.6	0.86		
Diversification Striatum (N=61)					
Intercept	0.12	0.08	0.17	900.00	-
Striatum (/bodymass, log)	9.11e-03	-0.01	0.03	900.00	0.44
Lambda	0.73	0.59	0.85		
Diversification MOB (N=37)					
Intercept	0.11	0.05	0.17	900.00	-
MOB (/bodymass, log)	-4.79e-03	-0.02	0.01	900.00	0.59
Lambda	0.65	0.46	0.83		

506 **Table 3: Species sympatry slowdowns primate diversification | Model estimates and significance of phylogenetic**  
 507 **regressions to assess the correlation between diversification rate and species sympatry. Est.=Estimate,**  
 508 **CI2.5%=Lower border of the CI95%, CI97.5%=Upper border of the CI95%, Sd= Standard deviation, t= Statistics t-**  
 509 **value. The brain areas (as well as the associated sample sizes) are indicated prior to each list of estimates. The**  
 510 **transformation (logarithm or square-root) is indicated in parentheses by the abbreviation (log or sqrt).**

	<b>Est.</b>	<b>CI2.5%</b>	<b>CI97.5%</b>	<b>Sd</b>	<b>t</b>	<b>p-value</b>
<b>Diversification (N=128)</b>						
Intercept	0.15	0.10	0.2	0.03	-	-
% of overlapped range	-5.40e-03	-0.02	9.35e-03	8.14e-03	-0.66	0.51
Number of sympatric frugivores (sqrt)	<b>-5.04e-03</b>	<b>-0.01</b>	<b>1.34e-04</b>	<b>2.56e-03</b>	<b>-1.97</b>	<b>0.05</b>
Lambda	0.96	0.89	0.99			



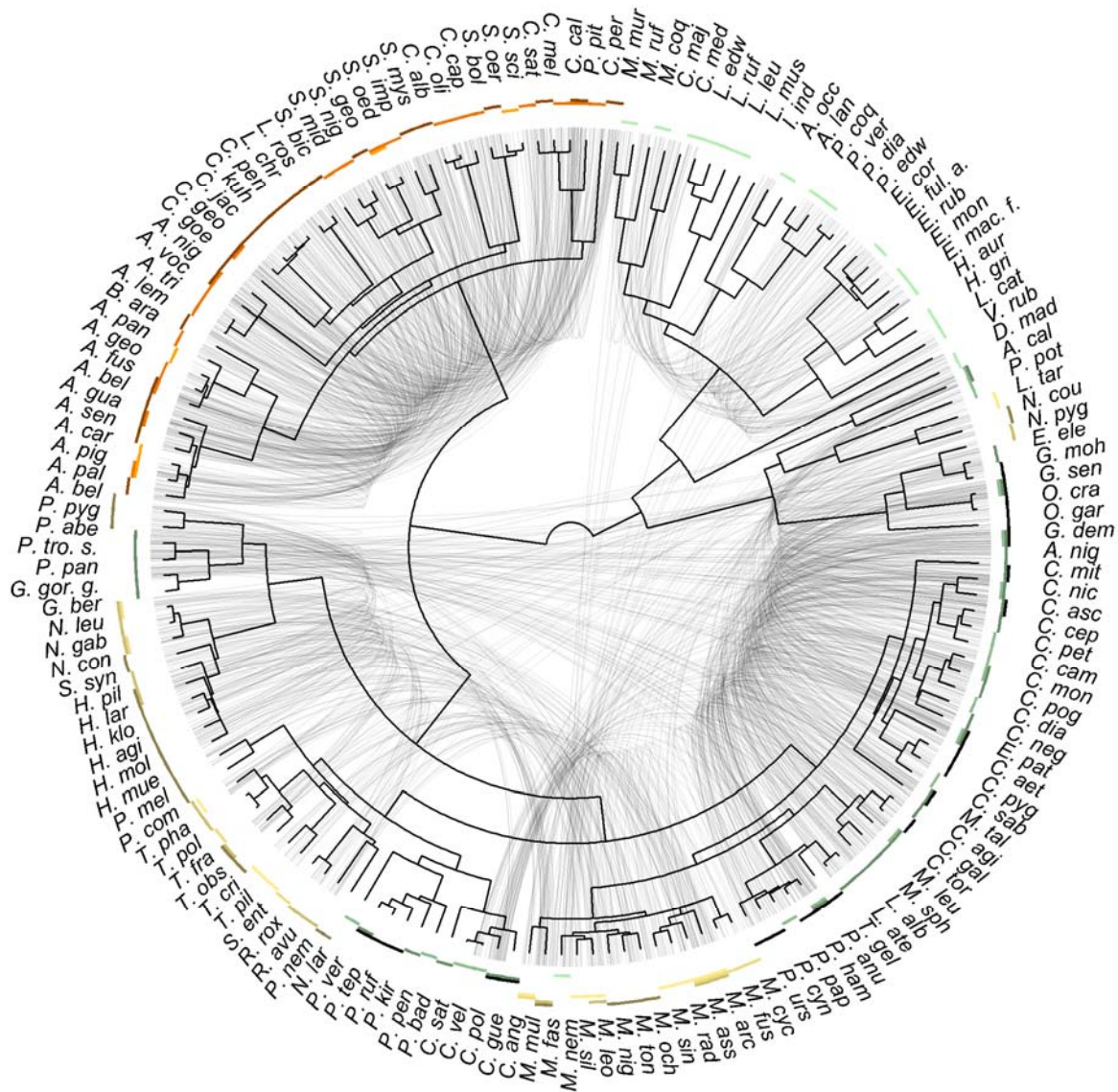
### Africa

### America

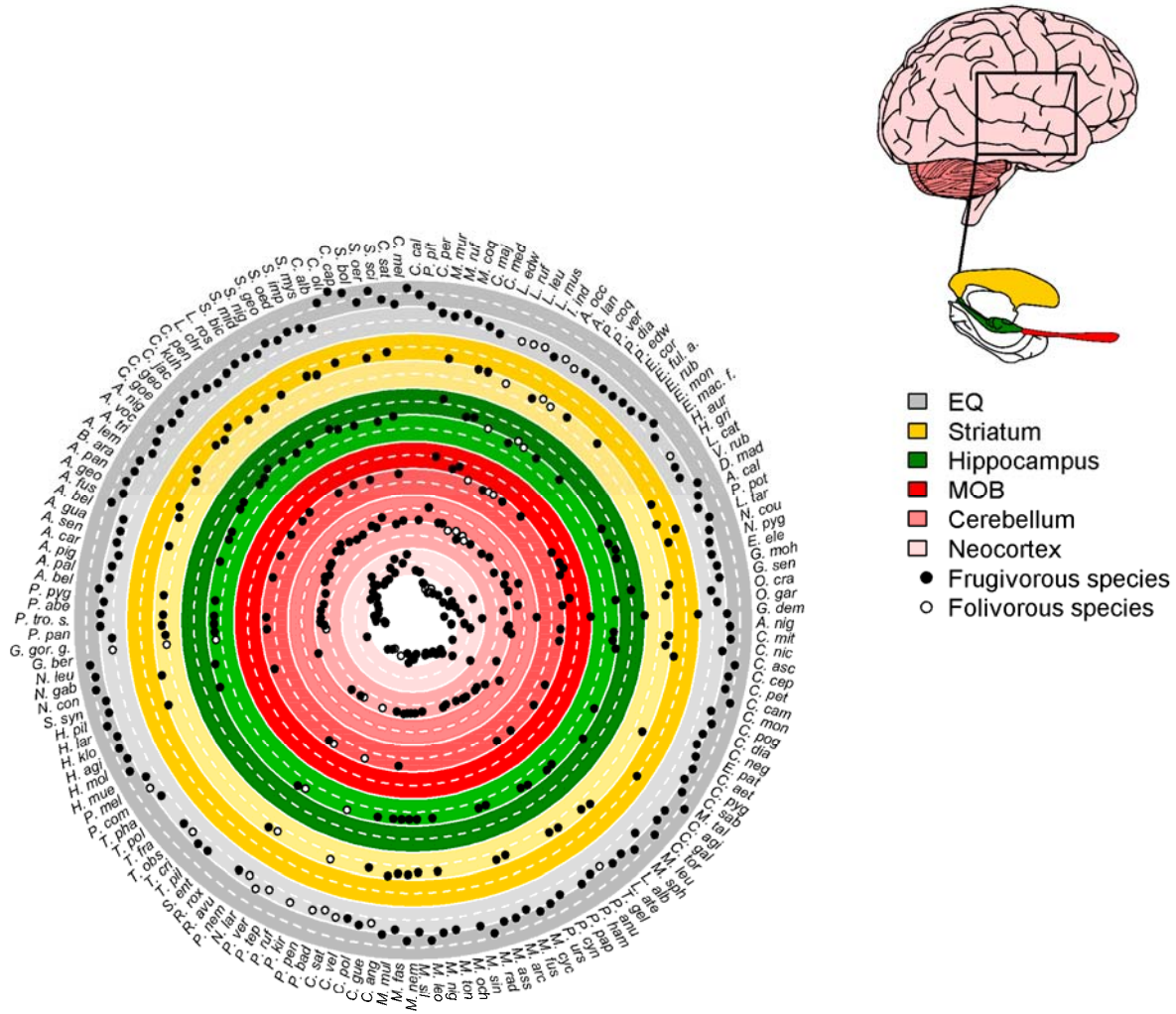
### Asia

- |                     |                          |                     |
|---------------------|--------------------------|---------------------|
| ○ East Madagascar   | ● Central America        | ● West Asia         |
| ● West Madagascar   | ● Northern South America | ● Central/East Asia |
| ● West Africa       | ● Southern South America | ● South Asia        |
| ● Central Africa    |                          | ● Asian islands     |
| ● East/South Africa |                          |                     |

511  
512 **Figure 1: Biogeographic areas used for reconstructing the history of sympatry in frugivorous primates**  
513 **represented on the Mercator projection of the world | Areas were defined as a combination of geographic and**  
514 **environmental criteria relative to the primate taxonomy following results from Kamilar (2009): (1) East**  
515 **Madagascar (2) West Madagascar (3) West Africa (4) Central Africa (5) East/South Africa (6) Central America (7)**  
516 **North South-America (8) South South-America (9) West Asia (10) Central/East Asia (11) South Asia (12) Asian**  
517 **peninsula and islands. Note that the north part of Africa and the south of Europe were discarded because *Macaca***  
518 ***sylvanus* was not considered.**



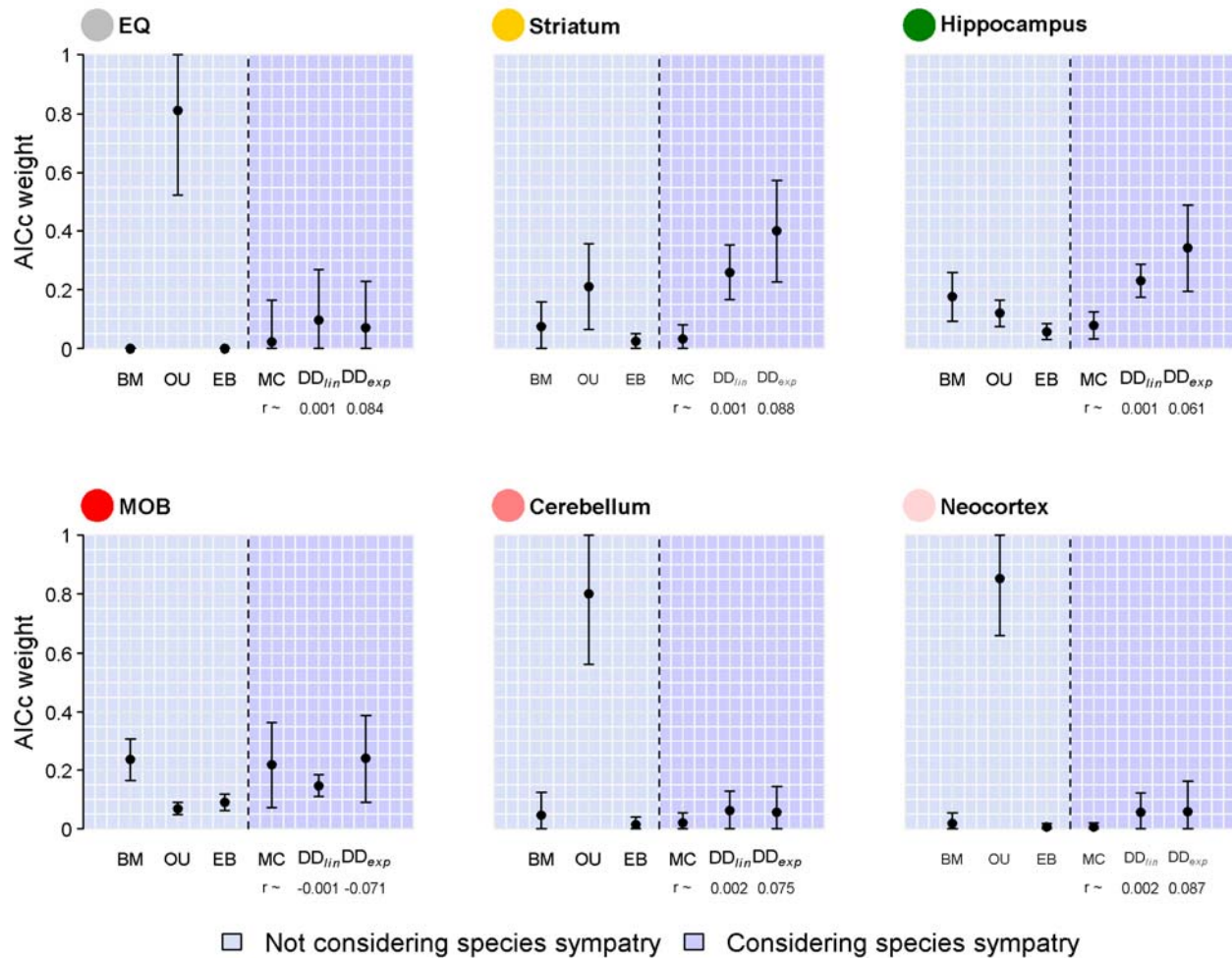
519  
520 **Figure 2: The intensity of species sympatry varies across the primate phylogeny | Primate phylogeny from the**  
521 **consensus tree of the 10kTrees project is depicted in the center, together with abbreviated species names. The**  
522 **corresponding non-abbreviated names can be found using Appendix Figure S3. Sympatric frugivorous (based on a**  
523 **frugivory threshold of 20% and folivory threshold of 40%) species are linked by light grey lines. The geographic**  
524 **areas occupied by a species are depicted by coloured rectangles. Presence was assessed given an overlap between**  
525 **the species range and the geographic area of 10%.**



526

527 **Figure 3: Variations in relative brain size areas among extant frugivorous primates | (Left) Circular plot of the**  
528 **relative sizes of the different brain areas. Colours indicate the rows for the different brain areas. The darker**  
529 **background emphasises when values are above average, while the lighter background emphasises when values**  
530 **are below average. The mean value (after scaling and based on one random sampling among possible values, but**  
531 **see Supplementary Material Figure S2 for visualization of measure variability) for the Encephalization Quotient**  
532 **(EQ) or relative size of brain areas, when available, is depicted by a plain circle for frugivorous species. The**  
533 **frugivorous threshold was fixed to 20% and the folivory threshold to 40%. (Right) The different studied brain**  
534 **areas (human brain as an illustration). In short, the MOB is involved in immediate olfactory information**

535 processing, the Neocortex and the Cerebellum support working memory and memory consolidation of immediate  
 536 sensory information processing (Wiltgen et al. 2004; Koziol et al. 2014; Sokolov, Miall, and Ivry 2017), and the  
 537 Hippocampus supports a working memory and a long-term spatio-temporal memory (Burgess, Maguire, and  
 538 O'Keefe 2002). The Striatum is involved in social information processing (Báez-Mendoza and Schultz 2013).



539  
 540 **Figure 4: The evolution of the Hippocampus and Striatum in frugivorous primates are best fitted by models of**  
 541 **trait evolution considering species sympatry | Plotted is the AICc weight, a measure of relative support for a given**  
 542 **model, for models not considering species sympatry (BM, OU, EB) or considering species sympatry (MC, DD<sub>lin</sub>,**  
 543 **DD<sub>exp</sub>). The points represent the average AICc weight obtained (when considering the six models from the same**  
 544 **run), while the vertical bars indicate the standard deviation given all tested conditions (see Phylogenetic models**  
 545 **of trait evolution: does species sympatry shape brain size evolution?).**



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