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

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

Short title: Sympatry shapes primates' brain size

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INTRODUCTION

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

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

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

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

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

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

METHODS

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

Data Collection

Phylogeny

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

Trait data

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

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

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

Ranging Data

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

Retracing past sympatry between primate species

Based on the biogeographic distribution of each extant primate species, we first reconstructed the 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 assignations 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-latitudinal 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).

Phylogenetic models

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

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

(a) Fitting models of trait evolution

We restricted the analyses to frugivorous species to test whether species sympatry has impacted the evolution of cognition, depicted either by the whole brain (using the encephalic quotient, EQ), or the size of the aforementioned specific brain areas relative to the whole-body mass (Figure 3). For such a task, we fitted phylogenetic models of the evolution of the size of the different brain areas independently (Drury et al. 2016). For models implying species sympatry, this was made possible by combining the historical timeline of diet and biogeography evolution, so that we could retrace the history of sympatry between frugivorous lineages. In practice, we obtained a series of interaction matrices (i.e., lines and columns correspond to frugivorous species, and each cell indicates whether a given species pair is in sympatry (value of 1) or not (value of 0)), along the phylogenetic tree (see Drury et al. 2016). This was used to fit models that considered species sympatry to model brain size evolution: the matching competition (MC) model (Nuismer and Harmon 2015) and density-dependent models (DD_{lin} and DD_{exp}, Drury et al. 2016). Specifically, these models expand classical models of stochastic evolution (Brownian Motion), by including an additional variable related to current brain size of sympatric species (MC), or by considering 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 $z_i(t+dt) = z_i(t) + S\big(\mu(t) - z_i(t)\big)dt + \sigma dB_i$ where z
222 is the brain size of a species i at time t, μ is the mean value of the trait of sympatric species, S
223 reflects the strength of the effect of species sympatry and σdB_i is the drift with a constant
224 evolutionary rate σ (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, σ, 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 σ_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.

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_{lin} 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 (Maliet, Hartig, and Morlon 2019) boosted for
296 computational speed based on data augmentation techniques (Maliet 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,

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

CONCLUSION

The use of brain size as a proxy for cognition is a central debate with no optimal solution (see grounded criticism from Deaner, Nunn, and Schaik 2000; Healy and Rowe 2007; Logan et al. 2018). The current flourishment of consortia, allowing for much more detailed and standardised anatomical measurements (e.g., in primates: Milham et al. 2018), or with standardised behaviourally explicit comparisons (e.g., on captive, Altschul et al. 2019; or wild primates, Janmaat et al. 2021), might alleviate biases stemming from brain size analysis, but this will take time to generate large-enough datasets. In the meanwhile, brain size is a proxy much appreciated in practice, because of its easy accessibility for a "large" number of species, while the multifaceted aspect of cognition can simply be taken into account by considering the brain as a mosaic of singular 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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AUTHORS' CONTRIBUTION

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

DATA ACCESSIBILITY

The data and codes that support the findings of this study are openly available at **https://github.com/benjaminrobira/Meta_analysis_cognition_primates**.

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

	Est.	CI2.5%	CI97.5%	Sd	t	p-value
EQ (log) (N=127)						
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			
Hippocampus (/bodymass, log) (N=50)						
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			
Neocortex (/bodymass, log) (N=56)						
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	**-0.40**	**-0.77**	**-0.04**	**0.18**	**-2.26**	**0.03**
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

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

	Est.	HDP2.5%	HDP97.5%	Eff. samp	pMCMC
Diversification EQ (N=148)					
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		
Diversification Hippocampus (N=61)					
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		
Diversification Neocortex (N=67)					
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		

505

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

	Est.	**CI2.5%**	**CI97.5%**	**Sd**	**t**	**p-value**
Diversification (N=128)						
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)	**-5.04e-03**	**-0.01**	**1.34e-04**	**2.56e-03**	**-1.97**	**0.05**
Lambda	0.96	0.89	0.99			

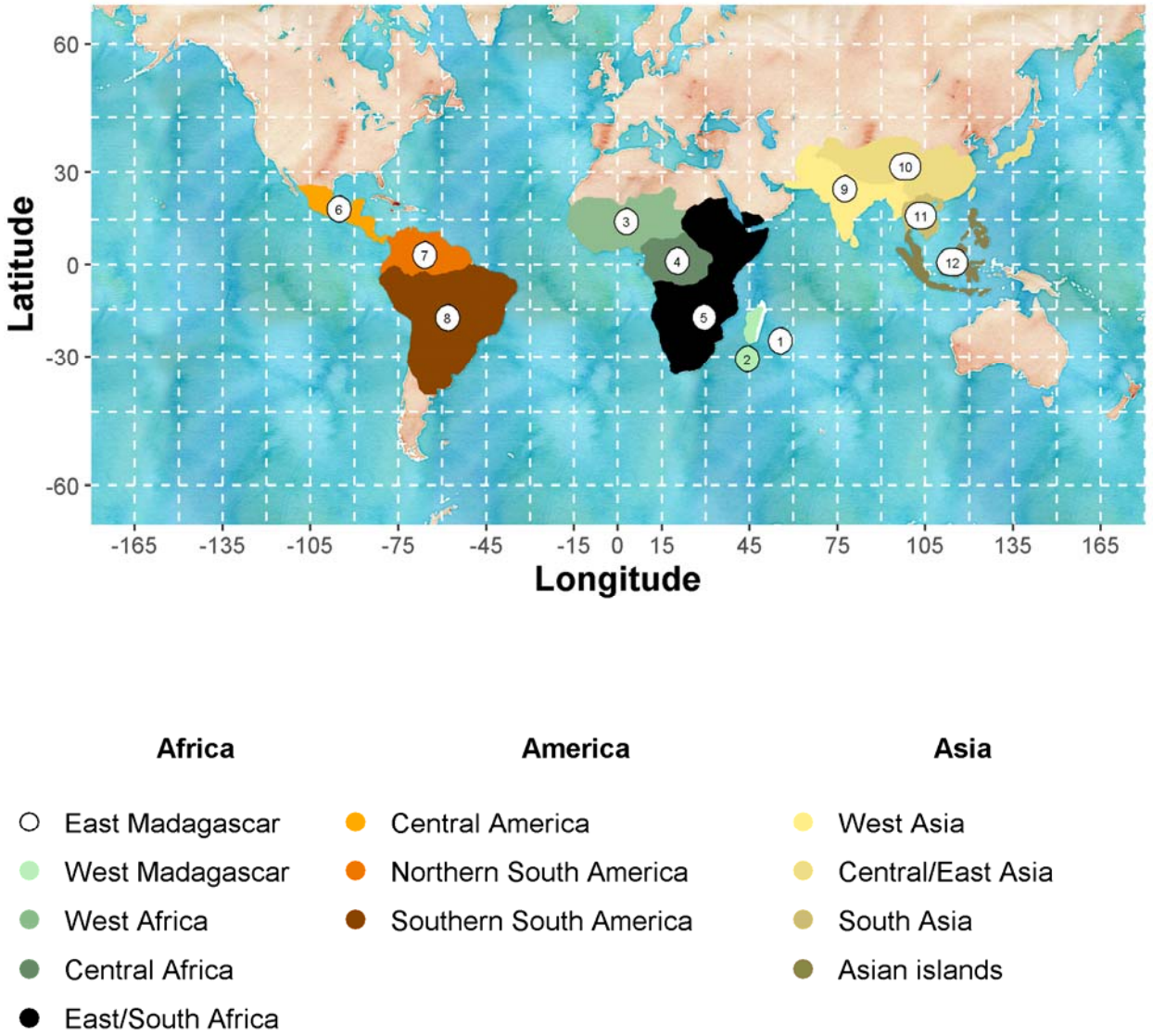
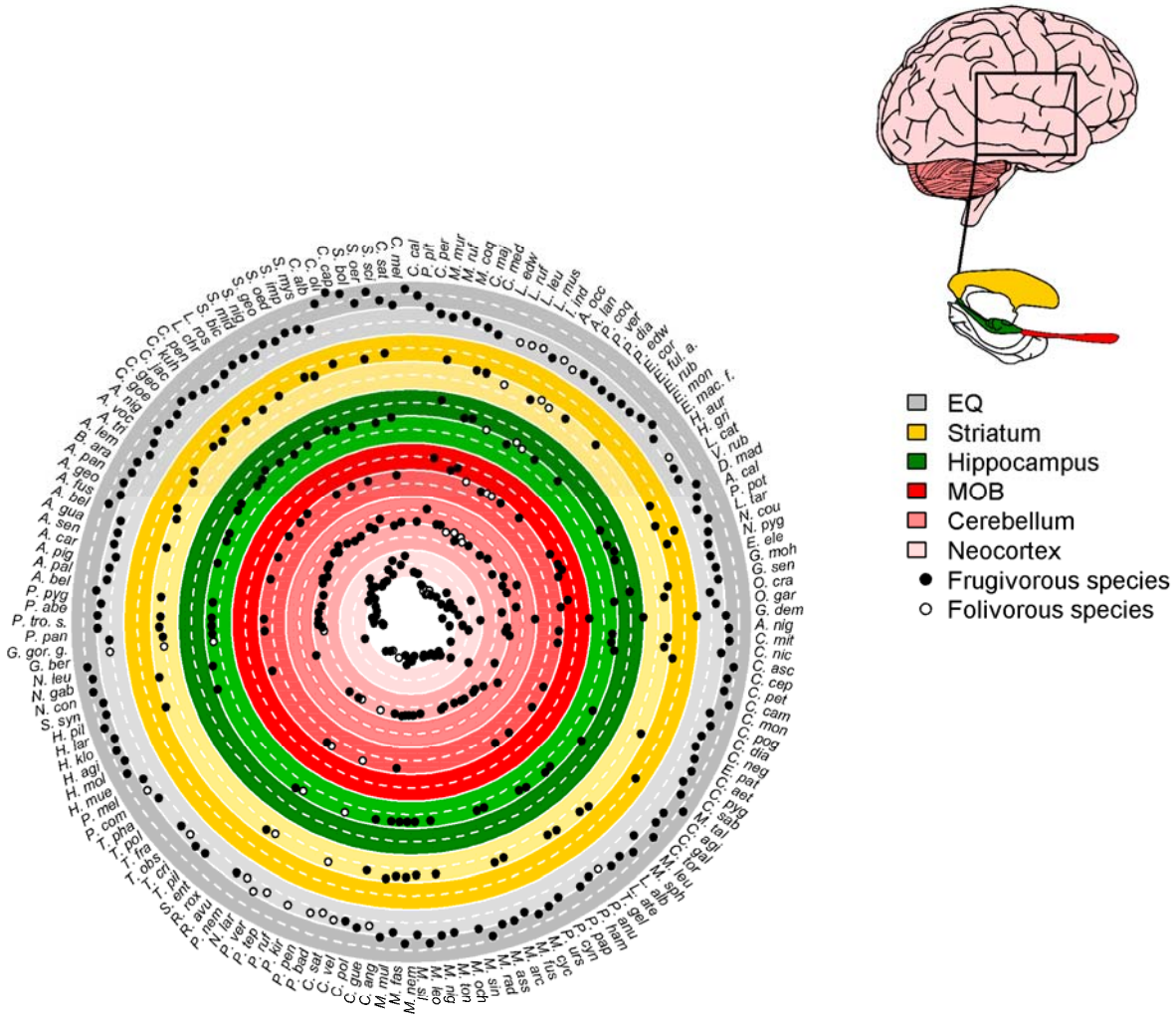


Figure 1: Biogeographic areas used for reconstructing the history of sympatry in frugivorous primates represented on the Mercator projection of the world | Areas were defined as a combination of geographic and environmental criteria relative to the primate taxonomy following results from Kamilar (2009):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

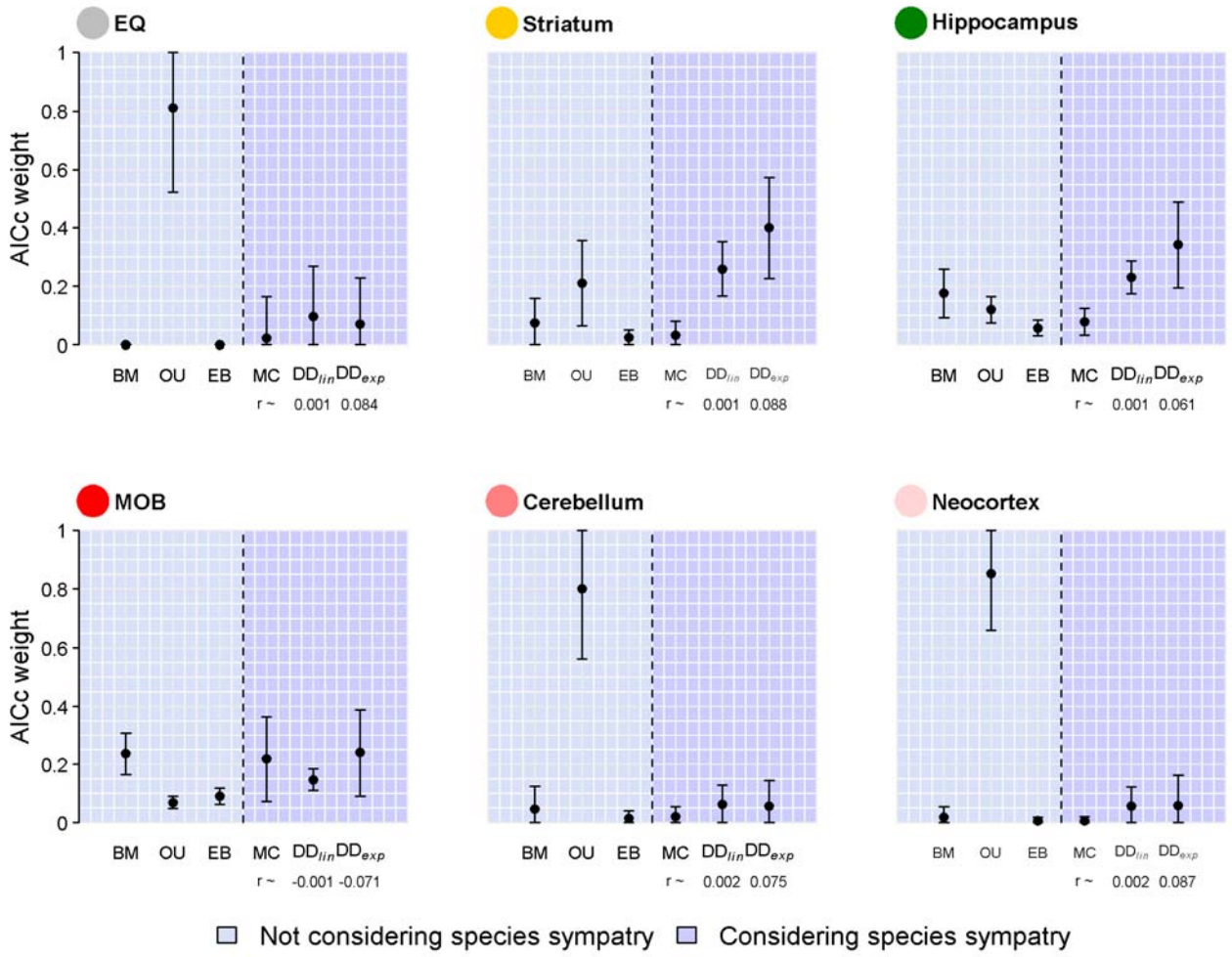
Figure 2: The intensity of species sympatry varies across the primate phylogeny | Primate phylogeny from the consensus tree of the 10kTrees project is depicted in the center, together with abbreviated species names. The corresponding non-abbreviated names can be found using Appendix Figure S3. Sympatric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

REFERENCES

Altschul, Drew M., Michael J. Beran, Manuel Bohn, Josep Call, Sarah DeTroy, Shona J. Duguid, Crystal L. Egelkamp, et al. 2019. "Establishing an infrastructure for collaboration in primate cognition research." *PLoS ONE* 14 (10): e0223675. https://doi.org/10.1371/journal.pone.0223675.

Ashton, Benjamin J., Patrick Kennedy, and Andrew N. Radford. 2020. "Interactions with conspecific outsiders as drivers of cognitive evolution." *Nature Communications* 11 (1): 1–9. https://doi.org/10.1038/s41467-020-18780-3.

Avarguès-Weber, A., E. H. Dawson, and L. Chittka. 2013. "Mechanisms of social learning across species boundaries" 290 (1): 1–11. https://doi.org/10.1111/jzo.12015.

Báez-Mendoza, Raymundo, and Wolfram Schultz. 2013. "The role of the striatum in social behavior." *Frontiers in Neuroscience* 7 (7 DEC): 233. https://doi.org/10.3389/fnins.2013.00233.

Barton, Robert A., and Paul H. Harvey. 2000. "Mosaic evolution of brain structure in mammals." *Nature* 405 (6790): 1055–58. https://doi.org/https://doi.org/10.1038/35016580.

Benson-Amram, Sarah, Ben Dantzer, Gregory Stricker, Eli M. Swanson, and Kay E. Holekamp. 2016. "Brain size predicts problem-solving ability in mammalian carnivores." *Proceedings of the National Academy of Sciences of the United States of America* 113 (9): 2532–37. https://doi.org/10.1073/pnas.1505913113.

Bivand, Roger, and Colin Rundel. 2021. *Rgeos: Interface to Geometry Engine - Open Source ('GEOS')*. https://CRAN.R-project.org/package=rgeos.

Blomberg, Simone P., Theodore Garland, and Anthony R. Ives. 2003. "Testing for phylogenetic signal in comparative data: Behavioral traits are more labile." *Evolution* 57 (4): 717–45. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x.

568 Blomberg, Simone P., Suren I. Rathnayake, and Cheyenne M. Moreau. 2020. "Beyond brownian
569 motion and the ornstein-uhlenbeck process: Stochastic diffusion models for the evolution of
570 quantitative characters." *American Naturalist* 195 (2): 145–65. https://doi.org/10.1086/706339.

571 Bollback, Jonathan P. 2006. "SIMMAP: Stochastic character mapping of discrete traits on
572 phylogenies." *BMC Bioinformatics* 7 (1): 1–7. https://doi.org/10.1186/1471-2105-7-88.

573 Burgess, Neil, Eleanor A. Maguire, and John O'Keefe. 2002. "The human hippocampus and spatial
574 and episodic memory." *Neuron* 35 (4): 625–41. https://doi.org/10.1016/S0896-6273(02)00830-9.

575 Burnham, Kenneth P., and David R. Anderson. 2002. *Model selection and multimodel inference: A*
576 *practical Information-theoretic approach*. Second. New York: Springer.

577 Byrne, Richard W. 2000. "Evolution of primate cognition." *Cognitive Science* 24 (3): 543–70.
578 https://doi.org/10.1207/s15516709cog2403_8.

579 ———. 2018. *Machiavellian intelligence retrospective*. Vol. 132. 4. Oxford University Press Oxford.
580 https://doi.org/10.1037/com0000139.

581 Carroll, Lewis. 1871. *Through the looking glass*. Macmillan London U.K.

582 Clutton-Brock, T. H., and Paul H. Harvey. 1980. "Primates, brains and ecology." *Journal of Zoology*
583 190 (3): 309–23. https://doi.org/10.1111/j.1469-7998.1980.tb01430.x.

584 Condamine, Fabien L., Jonathan Rolland, and Hélène Morlon. 2019. "Assessing the causes of
585 diversification slowdowns: temperature-dependent and diversity-dependent models receive
586 equivalent support." *Ecology Letters* 22 (11): 1900–1912. https://doi.org/10.1111/ele.13382.

587 de Almeida Rocha, Juliana Monteiro, Míriam Plaza Pinto, Jean Philippe Boubli, and Carlos Eduardo
588 Viveiros Grelle. 2015. "The role of competition in structuring primate communities under different

productivity regimes in the amazon." *PLoS ONE* 10 (12): e0145699. https://doi.org/10.1371/journal.pone.0145699.

Deaner, Robert O., Charles L. Nunn, and Carel P. van Schaik. 2000. "Comparative tests of primate cognition: Different scaling methods produce different results." *Brain, Behavior and Evolution* 55 (1): 44–52. https://doi.org/10.1159/000006641.

DeCasien, Alex R., and James P. Higham. 2019. "Primate mosaic brain evolution reflects selection on sensory and cognitive specialization." *Nature Ecology and Evolution* 3 (10): 1483–93. https://doi.org/10.1038/s41559-019-0969-0.

DeCasien, Alex R., Scott A. Williams, and James P. Higham. 2017. "Primate brain size is predicted by diet but not sociality." *Nature Ecology and Evolution* 1 (5): 1–7. https://doi.org/10.1038/s41559-017-0112.

Drury, Jonathan P., Julien Clavel, Marc Manceau, and Hélène Morlon. 2016. "Estimating the effect of competition on trait evolution using maximum likelihood inference." *Systematic Biology* 65 (4): 700–710. https://doi.org/10.1093/sysbio/syw020.

Drury, Jonathan P., Madeline C. Cowen, and Gregory F. Grether. 2020. "Competition and hybridization drive interspecific territoriality in birds." *Proceedings of the National Academy of Sciences of the United States of America* 117 (23): 12923–30. https://doi.org/10.1073/pnas.1921380117.

Drury, Jonathan P., Joseph A. Tobias, Kevin J. Burns, Nicholas A. Mason, Allison J. Shultz, and Hélène Morlon. 2018. "Contrasting impacts of competition on ecological and social trait evolution in songbirds." *PLoS Biology* 16 (1): e2003563. https://doi.org/10.1371/journal.pbio.2003563.

Dunbar, Robin I. M., and Susanne Shultz. 2017. "Why are there so many explanations for primate brain evolution?" *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1727): 20160244. https://doi.org/10.1098/rstb.2016.0244.

612 Dunlap, Aimee S., Matthew E. Nielsen, Anna Dornhaus, and Daniel R. Papaj. 2016. "Foraging bumble
613 bees weigh the reliability of personal and social information." *Current Biology* 26 (9): 1195–99.
614 https://doi.org/10.1016/j.cub.2016.03.009.

615 Gómez-Robles, Aida, William D. Hopkins, and Chet C. Sherwood. 2014. "Modular structure facilitates
616 mosaic evolution of the brain in chimpanzees and humans." *Nature Communications* 5 (1): 1–9.
617 https://doi.org/10.1038/ncomms5469.

618 Gonda, Abigé, Gábor Herczeg, and Juha Merilä. 2013. "Evolutionary ecology of intraspecific brain
619 size variation: A review." *Ecology and Evolution* 3 (8): 2751–64. https://doi.org/10.1002/ece3.627.

620 González-Forero, Mauricio, and Andy Gardner. 2018. "Inference of ecological and social drivers of
621 human brain-size evolution." *Nature* 557 (7706): 554–57. https://doi.org/10.1038/s41586-018-0127-x.

622 Goodale, Eben, Guy Beauchamp, Robert D. Magrath, James C. Nieh, and Graeme D. Ruxton. 2010.
623 "Interspecific information transfer influences animal community structure." *Trends in Ecology and*
624 *Evolution* 25 (6): 354–61. https://doi.org/10.1016/j.tree.2010.01.002.

625 Grueter, Cyril C. 2015. "Home range overlap as a driver of intelligence in primates." *American*
626 *Journal of Primatology* 77 (4): 418–24. https://doi.org/10.1002/ajp.22357.

627 Hadfield, Jarrod D. 2010. "MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
628 MCMCglmm R Package." *Journal of Statistical Software* 33 (2): 1–22. https://www.jstatsoft.org/v33/i02/.

629 Havmøller, Linnea W., J. Carter Loftus, Rasmus W. Havmøller, Shauhin E. Alavi, Damien Caillaud,
630 Mark N. Grote, Ben T. Hirsch, Lucia L. Tórrez-Herrera, Roland Kays, and Margaret C. Crofoot. 2021.
631 "Arboreal monkeys facilitate foraging of terrestrial frugivores." *Biotropica* 53 (6): 1685–97.
632 https://doi.org/10.1111/btp.13017.

633 Healy, Susan D., and Candy Rowe. 2007. "A critique of comparative studies of brain size."
634 *Proceedings of the Royal Society B: Biological Sciences* 274 (1609): 453–64.
635 https://doi.org/10.1098/rspb.2006.3748.

636 Herrmann, Esther, Josep Call, María Victoria Hernández-Lloreda, Brian Hare, and Michael
637 Tomasello. 2007. "Humans have evolved specialized skills of social cognition: The cultural
638 intelligence hypothesis." *Science* 317 (5843): 1360–66. https://doi.org/10.1126/science.1146282.

639 Heymann, Eckhard W, and Hannah M. Buchanan-Smith. 2000. "The behavioural ecology of mixed-
640 species troops of callitrichine primates." *Biological Reviews* 75 (2): 169–90.
641 https://doi.org/10.1111/j.1469-185X.1999.tb00044.x.

642 Heymann, Eckhard W, and Shin S Hsia. 2015. "Unlike fellows–a review of primate–non-primate
643 associations." *Biological Reviews* 90 (1): 142–56.

644 Hijmans, Robert J. 2021. *Geosphere: Spherical Trigonometry*. https://CRAN.R-
645 project.org/package=geosphere.

646 Ho, Lam Si Tung, and Cecile Ane. 2014. "A Linear-Time Algorithm for Gaussian and Non-Gaussian
647 Trait Evolution Models." *Systematic Biology* 63: 397–408.

648 Isler, Karin, and Carel P. van Schaik. 2009. "The Expensive Brain: A framework for explaining
649 evolutionary changes in brain size." *Journal of Human Evolution* 57 (4): 392–400.
650 https://doi.org/10.1016/j.jhevol.2009.04.009.

651 IUCN. 2021. *The IUCN Red List of Threatened Species*. Downloaded on the 19/01/2021.
652 https://www.iucnredlist.org.

653 Janmaat, Karline R. L., Christophe Boesch, Richard Byrne, Colin A. Chapman, Zoro B. Goné Bi,
654 Josephine S. Head, Martha M. Robbins, Richard W. Wrangham, and Leo Polansky. 2016. "Spatio-
655 temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral

656 nature of ripe fruit." *American Journal of Primatology* 78 (6): 626–45.
657 https://doi.org/10.1002/ajp.22527.

658 Janmaat, Karline R. L., Colin A. Chapman, R. Meijer, and Klaus Zuberbühler. 2012. "The use of fruiting
659 synchrony by foraging mangabey monkeys: A 'simple tool' to find fruit." *Animal Cognition* 15 (1):
660 83–96. https://doi.org/10.1007/s10071-011-0435-0.

661 Janmaat, Karline R. L., Miguel de Guinea, Julien Collet, Richard W. Byrne, Benjamin Robira, Emiel van
662 Loon, Haneul Jang, et al. 2021. "Using natural travel paths to infer and compare primate cognition in
663 the wild." *iScience* 24 (4): 102343. https://doi.org/10.1016/j.isci.2021.102343.

664 Johnson, Adam, Matthijs AA van der Meer, and A. David Redish. 2007. "Integrating hippocampus and
665 striatum in decision-making." *Current Opinion in Neurobiology* 17 (6): 692–97.
666 https://doi.org/10.1016/j.conb.2008.01.003.

667 Kamilar, Jason M. 2009. "Environmental and geographic correlates of the taxonomic structure of
668 primate communities." *American Journal of Physical Anthropology* 139 (3): 382–93.
669 https://doi.org/10.1002/ajpa.20993.

670 Kashetsky, Tovah, Tal Avgar, and Reuven Dukas. 2021. "The cognitive ecology of animal movement:
671 Evidence from birds and mammals." *Frontiers in Ecology and Evolution* 0 (September): 633.
672 https://doi.org/10.3389/FEVO.2021.724887.

673 Koziol, Leonard F., Deborah Budding, Nancy Andreasen, Stefano D'Arrigo, Sara Bulgheroni, Hiroshi
674 Imamizu, Masao Ito, et al. 2014. "Consensus paper: The cerebellum's role in movement and
675 cognition." *Cerebellum* 13 (1): 151–77. https://doi.org/10.1007/s12311-013-0511-x.

676 Logan, Corina J., Shahar Avin, Neeltje Boogert, Andrew Buskell, Fiona R. Cross, Adrian Currie, Sarah
677 Jelbert, et al. 2018. "Beyond brain size: Uncovering the neural correlates of behavioral and cognitive

specialization." *Comparative Cognition and Behavior Reviews* 13 (na): 55–90. https://doi.org/10.3819/CCBR.2018.130008.

Losin, Neil, Jonathan P. Drury, Kathryn S. Peiman, Chaya Storch, and Gregory F. Grether. 2016. "The ecological and evolutionary stability of interspecific territoriality." *Ecology Letters* 19 (3): 260–67. https://doi.org/10.1111/ele.12561.

Maliet, Odile, Florian Hartig, and Hélène Morlon. 2019. "A model with many small shifts for estimating species-specific diversification rates." *Nature Ecology and Evolution* 3 (7): 1086–92. https://doi.org/10.1038/s41559-019-0908-0.

Maliet, Odile, and Hélène Morlon. 2021. "Fast and accurate estimation of species-specific diversification rates using data augmentation." *Systematic Biology*. https://doi.org/10.1093/sysbio/syab055.

Matzke, Nicholas J. 2013. "Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing." *Frontiers of Biogeography* 5 (4): na. https://doi.org/10.21425/f5fbg19694.

———. 2016. "Stochastic mapping under biogeographical models." *PhyloWiki BioGeoBEARS* na (na): na.

Melchionna, M., A. Mondanaro, C. Serio, S. Castiglione, M. Di Febbraro, L. Rook, J. A. F. Diniz-Filho, et al. 2020. "Macroevolutionary trends of brain mass in Primates." *Biological Journal of the Linnean Society* 129 (1): 14–25. https://doi.org/10.1093/biolinnean/blz161.

Milham, Michael P, Lei Ai, Bonhwang Koo, Ting Xu, Céline Amiez, Fabien Balezeau, Mark G Baxter, et al. 2018. "An open resource for non-human primate imaging." *Neuron* 100 (1): 61–74.

Milton, Katharine. 1981. "Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development." *American Anthropologist* 83 (3): 534–48. https://doi.org/10.1525/aa.1981.83.3.02a00020.

Minot, Edward O. 1981. "Effects of interspecific competition for food in breeding blue and great tits." *The Journal of Animal Ecology* 50 (2): 375. https://doi.org/10.2307/4061.

Modolo, Lara, Walter Salzburger, and Robert D. Martin. 2005. "Phylogeography of Barbary macaques (*Macaca sylvanus*) and the origin of the Gibraltar colony." *Proceedings of the National Academy of Sciences of the United States of America* 102 (20): 7392–97. https://doi.org/10.1073/pnas.0502186102.

Morlon, H, E Lewitus, FL Condamine, M Manceau, J Clavel, and J Drury. 2016. "RPANDA: An r Package for Macroevolutionary Analyses on Phylogenetic Trees." *Methods in Ecology and Evolution* 7: 589–97. https://CRAN.R-project.org/package=RPANDA.

Navarrete, Ana F., Erwin L. A. Blezer, Murillo Pagnotta, Elizabeth S. M. De Viet, Orlin S. Todorov, Patrik Lindenfors, Kevin N. Laland, and Simon M. Reader. 2018. "Primate Brain Anatomy: New Volumetric MRI Measurements for Neuroanatomical Studies." *Brain, Behavior and Evolution* 91 (2): 109–17. https://doi.org/10.1159/000488136.

Navarrete, Ana F., Carel P. van Schaik, and Karin Isler. 2011. "Energetics and the evolution of human brain size." *Nature* 480 (7375): 91–93. https://doi.org/10.1038/nature10629.

Nuismer, Scott L., and Luke J. Harmon. 2015. "Predicting rates of interspecific interaction from phylogenetic trees." *Ecology Letters* 18 (1): 17–27. https://doi.org/10.1111/ele.12384.

Olupot, William, Peter M. Waser, and Colin A. Chapman. 1998. "Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible

721 strategies?" *International Journal of Primatology* 19 (2): 339–53.
722 https://doi.org/10.1023/A:1020391901832.

723 Pearce, Fiona, Chris Carbone, Guy Cowlishaw, and Nick J. B. Isaac. 2013. "Space-use scaling and
724 home range overlap in primates." *Proceedings of the Royal Society B: Biological Sciences* 280 (1751):
725 20122122. https://doi.org/10.1098/rspb.2012.2122.

726 Pennell, MW, JM Eastman, GJ Slater, JW Brown, JC Uyeda, RG Fitzjohn, ME Alfaro, and LJ Harmon.
727 2014. "Geiger V2.0: An Expanded Suite of Methods for Fitting Macroevolutionary Models to
728 Phylogenetic Trees." *Bioinformatics* 30: 2216–18.

729 Pepperberg, Irene M. 2002. "Allospecific referential speech acquisition in grey parrots (*Psittacus*
730 *erithacus*): Evidence for multiple levels of avian vocal imitation." *Imitation in Animals and Artifacts*,
731 109–31.

732 Persson, Tomas, Gabriela Alina Sauciuc, and Elainie Alenkær Madsen. 2018. "Spontaneous cross-
733 species imitation in interactions between chimpanzees and zoo visitors." *Primates* 59 (1): 19–29.
734 https://doi.org/10.1007/s10329-017-0624-9.

735 Pigot, Alex L., and Joseph A. Tobias. 2013. "Species interactions constrain geographic range
736 expansion over evolutionary time." *Ecology Letters* 16 (3): 330–38. https://doi.org/10.1111/ele.12043.

737 Porter, Leila M. 2001. "Benefits of polyspecific associations for the Goeldi's monkey (*Callimico*
738 *goeldii*)." *American Journal of Primatology* 54 (3): 143–58. https://doi.org/10.1002/ajp.1019.

739 Powell, Lauren E., Robert A. Barton, and Sally E. Street. 2019. "Maternal investment, life histories
740 and the evolution of brain structure in primates." *Proceedings of the Royal Society B: Biological*
741 *Sciences* 286 (1911): 20191608. https://doi.org/10.1098/rspb.2019.1608.

Powell, Lauren E., Karin Isler, and Robert A. Barton. 2017. "Re-evaluating the link between brain size and behavioural ecology in primates." *Proceedings of the Royal Society B: Biological Sciences* 284 (1865): 20171765. https://doi.org/10.1098/rspb.2017.1765.

Price, Trevor D., and Mark Kirkpatrick. 2009. "Evolutionarily stable range limits set by interspecific competition." *Proceedings of the Royal Society B: Biological Sciences* 276 (1661): 1429–34. https://doi.org/10.1098/rspb.2008.1199.

R Core Team. 2020. "R: A language and environment for statistical computing." Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org https://www.r-project.org/.

Rabosky, Daniel L., and Irby J. Lovette. 2008. "Density-dependent diversification in North American wood warblers." *Proceedings of the Royal Society B: Biological Sciences* 275 (1649): 2363–71. https://doi.org/10.1098/rspb.2008.0630.

Rafacz, Michelle, and Jennifer J. Templeton. 2003. "Environmental unpredictability and the value of social information for foraging starlings." *Ethology* 109 (12): 951–60. https://doi.org/10.1046/j.0179-1613.2003.00935.x.

Reader, Simon M., and Kevin N. Laland. 2002. "Social intelligence, innovation, and enhanced brain size in primates." *Proceedings of the National Academy of Sciences of the United States of America* 99 (7): 4436–41. https://doi.org/10.1073/pnas.062041299.

Revell, Liam J. 2012. "Phytools: An r Package for Phylogenetic Comparative Biology (*and Other Things*)." *Methods in Ecology and Evolution* 3: 217–23.

Robira, Benjamin, Simon Benhamou, Shelly Masi, Violaine Llaurens, and Louise Riotte-Lambert. 2021. "Foraging efficiency in temporally predictable environments: Is a long-term temporal memory really advantageous?" *Royal Society Open Science*.

Rosati, Alexandra G. 2017. "Foraging cognition: Reviving the Ecological Intelligence Hypothesis." *Trends in Cognitive Sciences* 21 (9): 691–702. https://doi.org/10.1016/j.tics.2017.05.011.

Sayol, Ferran, Oriol Lapiedra, Simon Ducatez, and Daniel Sol. 2019. "Larger brains spur species diversification in birds." *Evolution* 73 (10): 2085–93. https://doi.org/10.1111/evo.13811.

Schaik, Carel P. van, and Judith M. Burkart. 2011. "Social learning and evolution: The cultural intelligence hypothesis." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1567): 1008–16. https://doi.org/10.1098/rstb.2010.0304.

Shultz, Susanne, and Robin I. M. Dunbar. 2006. "Chimpanzee and felid diet composition is influenced by prey brain size." *Biology Letters* 2 (4): 505–8. https://doi.org/10.1098/rsbl.2006.0519.

Slater, GJ, LJ Harmon, D Wegmann, P Joyce, LJ Revell, and ME Alfaro. 2012. "Fitting Models of Continuous Trait Evolution to Incompletely Sampled Comparative Data Using Approximate Bayesian Computation." *Evolution* 66: 752–62.

Sokolov, Arseny A., R. Chris Miall, and Richard B. Ivry. 2017. "The cerebellum: Adaptive prediction for movement and cognition." *Trends in Cognitive Sciences* 21 (5): 313–32. https://doi.org/10.1016/j.tics.2017.02.005.

Sol, Daniel, Tamás Székely, András Liker, and Louis Lefebvre. 2007. "Big-brained birds survive better in nature." *Proceedings of the Royal Society B: Biological Sciences* 274 (1611): 763–69. https://doi.org/10.1098/rspb.2006.3765.

Todorov, Orlin S., Vera Weisbecker, Emmanuel Gilissen, Karl Zilles, and Alexandra A. De Sousa. 2019. "Primate hippocampus size and organization are predicted by sociality but not diet." *Proceedings of the Royal Society B: Biological Sciences* 286 (1914): 20191712. https://doi.org/10.1098/rspb.2019.1712.

Tomasello, Michael. 2019. *The cultural origins of human cognition*. Harvard university press. https://doi.org/10.2307/j.ctvjsf4jc.

Trapanese, Cinzia, Benjamin Robira, Giordana Tonachella, Silvia Di Gristina, Hélène Meunier, and Shelly Masi. 2019. "Where and what? Frugivory is associated with more efficient foraging in three semi-free ranging primate species." *Royal Society Open Science* 6 (5): 181722. https://doi.org/10.1098/rsos.181722.

Weir, Jason T., and Sara Mursleen. 2013. "Diversity-dependent cladogenesis and trait evolution in the adaptive radiation of the auks (*Aves: Alcidae*)." *Evolution* 67 (2): 403–16. https://doi.org/10.1111/j.1558-5646.2012.01786.x.

Whiten, Andrew, and Carel P. van Schaik. 2007. "The evolution of animal 'cultures' and social intelligence." *Philosophical Transactions of the Royal Society B: Biological Sciences* 362 (1480): 603–20. https://doi.org/10.1098/rstb.2006.1998.

Willems, Erik P., Barbara Hellriegel, and Carel P. van Schaik. 2013. "The collective action problem in primate territory economics." *Proceedings of the Royal Society B: Biological Sciences* 280 (1759): 20130081. https://doi.org/10.1098/rspb.2013.0081.

Wilson, AC. 1991. "From molecular evolution to body and brain evolution." In *Perspectives on Cellular Regulation: From Bacteria to Cancer*, 331–40. J. Wiley & Sons.

Wiltgen, Brian J., Robert A. M. Brown, Lynn E. Talton, and Alcino J. Silva. 2004. "New circuits for old memories: The role of the neocortex in consolidation." *Neuron* 44 (1): 101–8. https://doi.org/10.1016/j.neuron.2004.09.015.