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2 **Species sympatry shapes brain size evolution**  
3 **in Primates**

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**Abstract** | The main hypotheses related to animal intelligence evolution highlight the role of conspecifics. Yet, space is often simultaneously occupied by species sharing the same ecological guild. These sympatric heterospecifics can compete for food, thereby stimulating or hampering cognition. Considering brain size as a proxy for cognition, we used primates to test for the intertwining between species sympatry and cognition. We retraced the evolutionary history of several brain areas with evolutionary models considering or not sympatry. Sympatry-related models 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. By contrast, the whole brain or brain areas used in immediate information processing were best described by models not considering sympatry. Moreover, sympatry negatively affected primate diversification. Overall, this comparative study suggests that species sympatry contributes to shaping primate cognition and diversification. We speculate that this is due to an over-complexification of resource spatio-temporality.

☞ **Keywords:** Brain size - Cognition - Competition - Co-occurrence - Diversification

- Frugivory - Primates - Sympatry

➊ **Word Count:** 6106

## 18 Introduction

19 Cognition evolution is shaped by the balance between socio-ecological drivers pro-  
20 moting cognitive abilities<sup>1</sup> and physiological and energetic constraints limiting  
21 them<sup>2</sup>. Primates are pivotal species for cognitive studies<sup>3</sup> because their cognition is thought to  
22 be promoted by interactions of individuals with conspecifics within the social unit<sup>4,5</sup>, among  
23 generations<sup>6–11</sup>, between social units<sup>12</sup>, or with the rest of their environment<sup>13–15</sup>. However,  
24 space is often occupied by many species belonging to the same ecological guild. Because of  
25 competition for food, we can predict that indirect interactions with sympatric heterospecifics  
26 are also likely to strongly shape the evolution of cognition, because they either affect the  
27 resource landscape by depleting it (Hypothesis 1), or the landscape of usable “social” cues to  
28 locate available food (<sup>16</sup>; Hypothesis 2). In addition, direct interactions with heterospecifics,  
29 as much as with conspecifics<sup>5</sup>, might also affect cognition (Hypothesis 3).

30 Retracing the evolutionary history of cognitive abilities proves to be challenging because  
31 there is still no consensual measurement applicable across all species. Up to now, a raw  
32 approximation consists in considering brain size as a proxy for cognitive abilities, with  
33 larger size considered equivalent to more advanced cognitive abilities<sup>17</sup>. Yet, the brain is  
34 a mosaic of areas cognitively specialized<sup>18</sup>. These areas are likely to be under different  
35 selective pressures, and thus, to follow different evolutionary paths. In particular, they might  
36 be differently affected by species sympatry. First, brain areas involved in the storing of  
37 spatio-temporal information, such as the Hippocampus, home of an associative memory used  
38 for spatio-temporal navigation<sup>19</sup>, should in particular be affected if the resource landscape is  
39 complexified by sympatric species foraging on the same resource (Hypothesis 1: memory is  
40 affected). Second, brain areas involved in processing more immediate sensory information,  
41 such as the Main Olfactory Bulb (MOB), Cerebellum<sup>20,21</sup>, and the Neocortex<sup>22</sup> should  
42 be particularly affected if the landscape of cues varies with sympatry (Hypothesis 2: cue  
43 processing is affected). Besides individual foraging, cognition can also be triggered by direct

44 “social” interactions with other individuals<sup>4,5</sup>. The Striatum is a brain area stimulated during  
45 social interactions<sup>23</sup>, and should, therefore, be affected by direct social interactions with  
46 heterospecifics (Hypothesis 3).

47 Under these (non-exclusive) hypotheses, sympatry could stimulate or hamper cognition  
48 evolution. Reasonable food depletion should promote memory, which stands as a valuable tool  
49 to infer food availability and location when food is rare and ephemeral but predictable<sup>14,15</sup>. In  
50 this case, the size of the Hippocampus should be larger the higher the sympatry (Prediction  
51 1.1). On the other hand, maintaining a functional brain is energetically costly<sup>24</sup>, and if  
52 changes induced by sympatric species increase environmental unpredictability too much,  
53 which would make cognitive foraging not advantageous anymore<sup>25,26</sup>, the Hippocampus size  
54 should be smaller the higher the sympatry (Prediction 1.2). In the meanwhile, “social” cues  
55 left out by heterospecifics might also add to environmental ones. If species sympatry increases  
56 the load of usable cues to locate available food, we should then expect larger sizes of the  
57 MOB, the Cerebellum, or the Neocortex. Interactions between species can also occur directly,  
58 with the formation of mixed-group species<sup>27</sup>. This, in particular, should promote larger  
59 Striatum size in sympatry.

60 Here, we investigated the intertwining between species sympatry and cognition using  
61 frugivorous primates as a study example. Frugivorous primates are an interesting group for  
62 such a question because fruits are the archetype of a hard-to-find resource yet predictable<sup>28</sup>, for  
63 which cognition thus considerably shapes the foraging strategy<sup>29</sup>. To infer the effect of species  
64 sympatry on brain size evolution within frugivorous primates, we evaluated the support for  
65 evolutionary models accounting or not for sympatry, and investigated the directionality of  
66 the selection induced by sympatry history upon brain size evolution. Finally, we tested for  
67 correlative patterns between brain size or current sympatry and the evolutionary consequences  
68 (assumed to be reflected by species diversification) in all primates.

## 69 Results

70 We gathered a large database on the whole brain size, the size of the MOB, Cerebellum, and  
71 the Neocortex, involved in immediate sensory information processing, and the Striatum and  
72 the Hippocampus, related to either social and foraging-related memory, containing between 34  
73 to 182 frugivorous primate species (depending on the brain area considered). After pondering  
74 by whole-body mass, we observed ample variations in brain area relative sizes. For instance,  
75 the lemuriformes, that are known to prioritize smell compared to other primate species,  
76 have the largest relative MOB size (Lemuriformes: mean  $\pm$  SE = 0.23  $\pm$  0.07, other: 0.12  
77  $\pm$  0.04, 3). Similarly, platyrhini, and callitrichine primates in particular, are known to  
78 form poly-specific associations<sup>30</sup>. The latter show the highest relative size of the Striatum  
79 (Platyrhini: mean  $\pm$  SE = 0.91  $\pm$  0.07, other: 0.59  $\pm$  0.07, 3).

80 To get the evolutionary history of species sympatry between frugivorous lineages, we  
81 first reconstructed primate biogeography history ( $N_{species} = 214$ ;<sup>31,32</sup>) when considering 12  
82 biogeographic areas (Figure 1;<sup>33</sup>) and their diet evolution ( $N_{species} = 192$  to 269;<sup>34</sup>). We then  
83 calculated the likelihoods of models considering the role of species sympatry in the evolution  
84 of either the whole brain (using the encephalic quotient, EQ), or the size of the aforementioned  
85 specific brain areas relative to the whole-body mass (Figure. 3). We specifically considered  
86 the matching competition (MC) model<sup>35</sup> and density dependence models ( $DD_{lin}$  and  $DD_{exp}$ ),  
87 which assume a linear or exponential dependence of the brain sizes evolutionary rates on the  
88 number of sympatric lineages (<sup>36</sup> see [Models of trait evolution: does species sympatry shape](#)  
89 [brain size evolution?](#)). We compared the support of models considering species sympatry  
90 to the support of simpler models assuming no effect of species sympatry, like the Brownian  
91 Motion (BM), the Ornstein-Uhlenbeck process (OU) considering that traits are constrained  
92 around an optimal value (e.g. stabilizing selection; see<sup>37</sup> for a review), or the Early-Burst model  
93 (EB,<sup>38</sup>), the latter allowing to check for a time-dependence of the evolutionary rate, hence  
94 emphasizing that, if any, the density dependence is not an artefact due to time dependence.  
95 Support for each model was evaluated using an information-theoretic framework<sup>39</sup> based on

96 the weights of the Akaike Information Criteria corrected for small samples (AICc) when  
97 considering all six models (MC, DD<sub>lin</sub>, DD<sub>exp</sub>, BM, OU, EB, see [Models of trait evolution:](#)  
98 [does species sympatry shape brain size evolution?](#)).

99 We found that models not considering species sympatry were the most likely in describing  
100 the evolutionary history of the EQ, the Neocortex, and the Cerebellum (Figure 3 and 4),  
101 two areas specifically involved in immediate sensory information processing<sup>20–22</sup>, and also  
102 in memory consolidation for the Neocortex<sup>22</sup>. The fact that these biggest areas are best  
103 described by the Ornstein-Uhlenbeck process suggests a stabilization towards an optimal  
104 size, which may illustrate the trade-offs between costs and benefits of brain development<sup>40</sup>.  
105 By contrast, density-dependence models considering sympatry were best supported in the  
106 foraging-related and social-related areas respectively: the Hippocampus, specialised in spatio-  
107 temporal memory<sup>19</sup> and the Striatum, involved in social interactions<sup>23</sup>. The fact that we  
108 inferred positive rates  $r$  of density-dependence (Figure 4), suggested an acceleration of the  
109 evolutionary tempo of trait evolution together with increased diversity of sympatric lineages  
110 for the Hippocampus and the Striatum. The Main Olfactory Bulb (MOB), the area involved  
111 in sensory abilities, also tended to be best fitted by models considering sympatry as a whole:  
112 yet, Brownian-Motion was as likely as density-dependent or MC models, preventing firm  
113 conclusions on whether sympatry affected or not MOB size evolution (Figure 3 and 4).

114 Next, to understand the effect of sympatry on brain sizes (i.e. toward “bigger” or “smaller”  
115 brains the more sympatric species), we fitted phylogenetic regressions (see [Phylogenetic](#)  
116 [regressions a](#))). For these linear regressions, the predicted variable was the relative brain  
117 size values of the different areas. We considered as covariates the average percentage of  
118 overlapping range with other sympatric frugivorous species, as well as the number of such  
119 sympatric frugivorous species across their entire distribution range based on IUCN data<sup>41</sup>.  
120 On average ( $\pm$  SE), the considered primate species had 52% of their range overlapping with  
121 other species ( $\pm$  2). That ranged from 0% of overlap (*Macaca nigra*), to 100% of overlap  
122 (*Cercopithecus pogonias*, *Alouatta pigra*, *Loris tardigradus*, *Hylobates moloch*, *Cercopithecus*

<sup>123</sup> *galeritus*, *Presbytis melalophos*, *Semnopithecus entellus*). In terms of the distribution range,  
<sup>124</sup> the considered primate species co-occurred on average with 6.38 other primate species ( $\pm$   
<sup>125</sup> 0.39), ranging from 0 other species to 21. The number of sympatric species never influenced  
<sup>126</sup> significantly the relative size of the brain or other specific areas (Table 1). Conversely, we  
<sup>127</sup> found that the average percentage of overlapping range correlated with the relative size of areas  
<sup>128</sup> that were better fit with models considering sympatry: the Hippocampus and the Striatum  
<sup>129</sup> (Hippocampus:  $t = -1.94$ ,  $p = 0.058$ ; Striatum:  $t = -2.26$ ,  $p = 0.028$ ). The correlations  
<sup>130</sup> were all negative (Hippocampus: est. = -0.39, CI95% = [-0.76,-0.01]; Striatum: est. = -0.4,  
<sup>131</sup> CI95% = [-0.77,-0.04]), which means that higher range overlap between frugivorous species  
<sup>132</sup> associates with lower relative size, insensitive to data and phylogenetic uncertainty (Table S1,  
<sup>133</sup> Figure S8). Given the acceleration of the evolutionary tempo with species sympatry ( $r > 0$  in  
<sup>134</sup> the density-dependence models), it suggests that compared with isolated species, sympatric  
<sup>135</sup> species are subject to a positive selection towards smaller brains, and not to a less intense  
<sup>136</sup> selection for advanced cognitive abilities.

<sup>137</sup> Finally, we investigated the evolutionary consequences of brain evolution and sympatry by  
<sup>138</sup> evaluating whether brain sizes and sympatry level correlated with the net species diversification  
<sup>139</sup> rates (defined as speciation minus extinction rates). To do so, we used lineage-specific birth-  
<sup>140</sup> death models of species diversification<sup>42,43</sup>. Overall, species diversification rates, estimated  
<sup>141</sup> based on the primate molecular phylogeny, increased over time (Figure S4), particularly in  
<sup>142</sup> the early and late Miocene, around 25 and 11 Myr ago (Figure S4). When accounting for  
<sup>143</sup> phylogenetic dependence, no significant relationship between the net diversification rate and  
<sup>144</sup> the relative size of brain areas was found (Table 2, Figure S8; see robustness in Table S2).  
<sup>145</sup> Given the context-dependence of the direction of selection (towards bigger sizes when sympatry  
<sup>146</sup> is low, smaller sizes otherwise), there is no surprise that we do not observe a correlation  
<sup>147</sup> between the diversification rate and the three brain areas affected by species sympatry.  
<sup>148</sup> Surprisingly however, we found no positive association between the net diversification rate  
<sup>149</sup> and the EQ, nor with the relative sizes of the Cerebellum or the Neocortex, two areas

150 insensitive to species sympatry too. This is puzzling because this contradicts a recent study<sup>44</sup>.  
151 The visual inspection of the regressions however clearly evidenced a positive trend for the EQ  
152 and the Neocortex, if discarding phylogenetic non-independence (Figure S6). Indeed, sudden  
153 encephalisation in primates is clearly associated with a limited number of closely-related  
154 species<sup>44,45</sup>. This clearly limits the statistical power of our phylogenetically-corrected analyses,  
155 as we cannot decipher whether the connivance between brain size and species diversification  
156 results from a true biological link or appeared by chance. A positive association between  
157 brain size and diversification was also found in birds<sup>46</sup> given that bigger brains act as a buffer  
158 to environmental challenges<sup>47</sup>. This means that, despite what we found here, a positive  
159 association between brain size and species diversification evidenced in<sup>44</sup> remains a likely  
160 possibility. Finally, although diversification was uncorrelated with brain size in frugivorous  
161 primates, it was influenced by the sympatry context. In particular, phylogenetic regressions  
162 highlighted a negative effect of the number of sympatric species on the diversification rate  
163 (est. = -5.04e-03, CI95% = [-0.01,1.34e-04], t = 2.56e-03, p < 0.001, Table 3, Figure S8). In  
164 other words, the higher the number of sympatric species, the lower the diversification rate, a  
165 density-dependence trend that is frequently observed in many tetrapod clades<sup>48</sup>.

## 166 Discussion

167 Bigger brains are not necessarily better. The size of the brain is subject to a compromise  
168 between the energy it incurs, and the increase of fitness it allows. This is clearly emphasized by  
169 the fact that the biggest areas, the Cerebellum and the Neocortex, as well as the whole brain  
170 (EQ), were best described by the Ornstein-Uhlenbeck process. This evidence might suggest a  
171 stabilisation towards an optimal size resulting from an equilibrium between costs and benefits.  
172 As the brain is regionally specialised<sup>18</sup>, different brain areas could be under different selective  
173 pressures. This is evidenced, here, by the differences of relative sizes across lineages in the  
174 MOB or Striatum in particular. We further show that sympatry is one factor that affects

175 the selective regime under which some brain region evolves: although the brain as a whole  
176 was insensitive to species sympatry, the latter nonetheless induced a change in the relative  
177 size of the Hippocampus and the Striatum. These areas are involved in individual-based and  
178 social-based information processing, pinpointing that the two components might be under  
179 strong selection in primates<sup>1,45,49</sup>.

180 The negative influence of sympatry on the Striatum might be quite surprising. Direct  
181 interactions with heterospecifics should stimulate this area (Hypothesis 3). We observed that  
182 this area was relatively larger in callitrichines, particularly known to perform mixed-species  
183 groups<sup>50</sup>. When interacting with conspecifics, the Striatum underpins reward expectation,  
184 goal-directed behaviour, and planning abilities<sup>51</sup>. These skills are key within group, following  
185 a Machiavellian perspective<sup>4</sup>. Yet, these skills might also be relevant in a foraging context.  
186 It is thus possible that actions underpinned by the Striatum (e.g. planning/anticipating  
187 heterospecifics moves), might be key and up to now overlooked, when foraging in a multi-  
188 species context too.

189 Overall, the fact that only these two areas, particularly relevant to process and memorise  
190 spatio-temporal information, are sensitive to sympatry, is consistent with the idea of an  
191 effect of species affecting resource spatio-temporal patterns (Hypothesis 1). Competition is  
192 generally the first-thought mechanism to describe community structures<sup>52</sup> because it might  
193 affect the environment, and associate selective pressure, in which species evolve. We show  
194 that higher levels of sympatry is actually associated with smaller sizes of the Hippocampus  
195 or Striatum (in accordance with Prediction 1.2). This suggests that indirect competition  
196 for food might contribute to convoluting the environment which might generate a positive  
197 selection for smaller brains. Not only was brain evolution affected by sympatry, but sympatry  
198 induced a slowdown in diversification. Density-dependence within a clade is indeed generally  
199 associated with lower diversification rates<sup>53</sup>. In particular, species competing for resources  
200 are thought to contribute to limiting their ranges<sup>54</sup>, hence constraining population size and  
201 their subsequent diversification<sup>55</sup>. These observations thus strengthen the idea of scramble

202 competition between species that cascades both on species population dynamics and species  
203 cognition.

204 By contrast, potential indirect facilitation between species due to “social” cues (Hypothesis  
205 2), is ruled out by the absence of an effect of sympatry on brain areas involved in immediate  
206 sensory information processing (e.g. Cerebellum or Neocortex). This absence of effect can  
207 stem from two possibilities. Either sympatry, indeed, does not affect the landscape of cues  
208 for foragers. Otherwise, it has been shown that foragers tend to use social information  
209 over environmental (i.e. personal) information, in particular in non-perfectly predictable  
210 environments<sup>56,57</sup>. Thus, if environmental complexity increases too much, “social” cues  
211 provided by heterospecifics might replace environmental ones. From this point of view,  
212 the size of the MOB, the Cerebellum, or the Neocortex should, at the very least, remain  
213 unaffected by sympatry. This nonetheless deserves further attention.

214 To conclude, the use of brain size as a proxy for cognition is a central debate with no optimal  
215 solution (see grounded criticism from<sup>58–60</sup>). The current flourishing of consortia, allowing  
216 for much more detailed and standardized anatomical measurements (e.g. in primates<sup>61</sup>), or  
217 with standardized behaviourally explicit comparisons (e.g. on captive<sup>62</sup> or wild<sup>63</sup> primates),  
218 might alleviate biases stemming from brain size analysis, but this will take time to generate  
219 large-enough datasets. In the meanwhile, brain size is a proxy much appreciated in practice,  
220 because of its easy accessibility for a “large” number of species. Here, we showed that species  
221 sympatry is an important factor shaping the evolutionary history of animals’ brains, but the  
222 proximate mechanisms at play remain to be elucidated. Finally, it is very likely that any  
223 hypothesis on cognition evolution, generally discussed within species, could be broadened  
224 to a between-species context: foraging facilitation between species does exist<sup>64,65</sup>, and so do  
225 polyspecific social associations<sup>66</sup>, as well as inter-species territory defence<sup>67,68</sup> or imitation  
226 and copying<sup>69,70</sup>. Similarly, prey-predator races could shape selection on cognitive abilities<sup>71</sup>.  
227 As Alice said “It’s a great huge game of chess that’s being played—all over the world” (<sup>72</sup>,  
228 Chapter II) and all individuals are just pieces to play with or against, no matter the species.

229 **Methods**

230 Data processing, analyses, and plots were computed with R software (v.4.0.3, R Core Team  
231 [73]). Used codes and data are freely available at <https://github.com/benjaminrobira/Meta>  
232 analysis\_cognition\_primates. Note that in all these analyses, we discarded *Homo sapiens*  
233 and *Macaca sylvanus*. The latter was discarded in the analyses because of geographical  
234 complete isolation and repeated intervention of human people in population maintenance<sup>74</sup>.  
235 A summary of available data per species is presented in Appendix Figure 1.

236 **Data Collection**

237 **Phylogeny**

238 We used a block of chronogram trees of the primate taxon of the 10kTrees project (downloaded  
239 on May 2021, version 3), as well as a consensus tree of 1000 trees for the subsequent  
240 phylogenetic analyses. The trees contain 301 primate species.

241 **Trait data**

242 Brain data were obtained from<sup>75</sup> for the whole brain and all mentioned other regions (Cere-  
243 bellum, Hippocampus, Main Olfactory Bulb (MOB), Neocortex, Striatum),<sup>49</sup> and<sup>76</sup> for the  
244 whole brain, Cerebellum and Neocortex size,<sup>77</sup> for Hippocampus and Neocortex size,<sup>78</sup> for  
245 the whole brain size and<sup>79</sup> for the whole brain, Cerebellum, Hippocampus and Striatum size.  
246 They were freely available in the main manuscript or supplementary materials. When a  
247 species was represented multiple times within the dataset, we obtained a unique attribute by  
248 averaging it. From the global endocranial brain volume, we obtained the Encephalization  
249 Quotient (EQ,  $N_{EQ,max} = 182$ ) as follows<sup>45</sup>

250

251 
$$EQ = 1.036 \times \text{Brain volume} / (0.085 \times \text{Body mass}^{0.775})$$

252

253 with the brain volume in  $\text{cm}^3$ ,  $1.036 \text{ g/cm}^3$  being the assumed homogeneous brain density,  
254 and the body mass in g. EQ indicates whether the brain size ranges above ( $> 1$ ) or below  
255 ( $< 1$ ) expected given the body mass. Body mass was obtained from<sup>45,49,78,80</sup>. The sub-parts  
256 of the brain were chosen because they were involved in immediate sensory information  
257 processing (MOB,  $N_{MOB,max} = 39$ ), in movement and/or general information processing and  
258 retention (Neocortex,  $N_{Neocortex,max} = 69$ ,<sup>22</sup>; Cerebellum,  $N_{Cerebellum,max} = 70$ ,<sup>20,21</sup>), short-term  
259 working memory and long-term spatio-temporal memory (Hippocampus,  $N_{Hippocampus,max}$   
260 = 63,<sup>19</sup>). The Striatum ( $N_{Striatum,max} = 63$ ) supports information processing during social  
261 interaction, reward assessment, planning or goal-oriented behaviours<sup>23,51</sup>. To investigate  
262 their evolutionary history, we used the ratio between their volume and body mass, so as to  
263 maximize comparability. As such, the use of specific region sizes relative to the body mass  
264 and not raw sizes depicts the evolution of cognitive abilities in terms of allocation rather  
265 than abilities per se (but see discussion in<sup>58</sup>). Percentage of frugivory and/or folivory was  
266 obtained based on a freely available dataset from [DeCasien *et al.* [45]; Powell *et al.* [49];  
267 willems2013collective].

## 268 Ranging Data

269 Current geographic (maximal possible) range of each primate species was assessed using  
270 ranging maps provided by the IUCN red list<sup>41</sup>. Ranging data were available for 249 species  
271 among the 301 represented in the 10kTrees primate phylogeny.

## 272 Primate species sympatry

273 For primate biogeography, based on the structure (i.e. number of species and their phylogenetic  
274 relationships) of primate communities at different field sites, Kamilar *et al.*<sup>33</sup> determined  
275 clusters of sites with highly similar community structures that were shaped by both the  
276 environment geography and climatic correlates. We used this classification and manually  
277 mapped the geographic areas using Google earth professional (v7.3.3). These geographic

278 areas are represented in Figure 1 and correspond to Central America, the North and the  
279 South of South America respectively, West Africa, Central Africa, and East/South Africa,  
280 East and West of Madagascar respectively, West Asia, Central/East Asia, South Asia, and  
281 the Asian Islands. The chosen scale for the areas is large because (i) retracing the history  
282 of a large number of areas necessitates considerable computational means. In addition, this  
283 drastically increases the computational time for fitting the phylogenetic models of brain trait  
284 evolution too. Furthermore (ii), all species and particularly primate species suffer(ed) from  
285 recent extinction<sup>81</sup>, with a reduction of ranging areas at an unprecedented speed rate. Finer  
286 geographic characterization would therefore give too much weight to such anthropogenic  
287 effect that recently altered species distribution (e.g. evidenced on the North American fauna  
288 in<sup>82</sup>). One to multiple large-scale geographic areas were assigned to each species as soon  
289 as the species current distribution range overlapped in the surface at 10 (low threshold) or  
290 30% (high threshold; the maximum was chosen to 30% because on present data, a species  
291 could occupy as far as three areas, Figure 1). Overlap was calculated with the “gIntersection”  
292 function from the *rgeos* package<sup>83</sup> applied to Mercator-projected data to get the overlapping  
293 contour, and the “area” function from the *geosphere* package<sup>84</sup>, applied directly on unprojected  
294 longitudinal-latitude data for area size calculation.

295 We retraced the biogeographic history of the lineage ranges based on current observations of  
296 species range with the *BioGeoBEARS* package<sup>31</sup>, using the biogeographic stochastic mapping  
297 algorithm<sup>32</sup>. We fitted non-time-stratified dispersal-extinction-cladogenesis (DEC) models  
298 specifically suiting analyses of range data since it accounts for spatially explicit processes of  
299 cladogenetic and anagenetic events (see<sup>31</sup> for further details on these events). To reconstruct  
300 the evolution of species range, we fixed the maximum number of areas that could be occupied  
301 by a lineage at one time to three areas. A too high number of areas that can be occupied  
302 simultaneously drastically increases computational time. Here, we therefore chose that a  
303 species can at most occupy three areas since it offers the possibility to occupy a complete  
304 mainland continent. Finally, because these history reconstructions are likely to vary, for each

305 run of DEC models (considering both possible overlaps to consider species presence), we  
306 obtained 10 stochastic maps that were all used in subsequent phylogenetic model fits (see  
307 [Phylogenetic models](#)) to account for the uncertainty of these ancestral range estimations (see  
308 [Models of trait evolution: does species sympatry shape brain size evolution? \(b\)](#)).

309 **Dietary guilds**

310 We classified species as either “frugivorous” or “folivorous” based on the availability of  
311 frugivorous rate and folivorous rate , prioritizing frugivory over folivory. First, a species would  
312 be classified as frugivorous if the frugivory rate was at least above 20 (low threshold) or 40%  
313 (high threshold). If this was not the case, or frugivory rate was unavailable, a species could  
314 be classified as folivorous if the folivory rate was at least above 40 (low threshold) or 60%  
315 (high threshold). Otherwise,<sup>45</sup> gave a binary classification of diet, species being categorized  
316 as frugivorous or folivorous, partly based on anatomical criteria. Whenever the rate was not  
317 available, we referred to this classification. In any other cases, the species was discarded. To  
318 illustrate, if a species reached 30% of frugivory, and 65% of folivory (the rest being due, for  
319 instance, to insectivory), then, it would be categorized as, “frugivorous” if low thresholds  
320 are considered, or as “folivorous” in case high thresholds are considered. If we suppose now  
321 another species with 30% of frugivory and 50% of folivory, but considered by<sup>45</sup> as frugivorous,  
322 then, the species would be “frugivorous” for low threshold, and still “frugivorous” with high  
323 thresholds.

324 Frugivory was prioritized over folivory because we considered that since fruits are a highly  
325 palatable food source, it would be the key item that drives the foraging strategy (and associate  
326 consequence(s) on brain selection), even if less consumed. Additionally, to consider frugivory,  
327 we used a lower rate than for folivory for two reasons. First, such a static rate does not  
328 reflect potential seasonality in fruit-eating (e.g.<sup>85</sup>), which is generally shorter, hence a lower  
329 overall frugivory rate. Second, the frugivory rate is likely to be underestimated in part  
330 because primates generally spend more time feeding on leaves than fruits, while rates are

331 often based on relative feeding time, or observation frequency at the individual or group  
332 unit of feeding events. Finally, the methodology to obtain this rate could additionally vary  
333 (e.g. in addition to the two aforementioned estimations, one could also rely on the proportion  
334 of species targeted for their fruits/leaves). For all these reasons, we used two threshold levels  
335 (low, 20%, or high, 40%) to classify a species as frugivorous, as well as two threshold levels  
336 (low, 40%, or high, 60%) to classify a species as folivorous.

337 Considering diet as a binary variable (frugivory versus folivory), we retraced the evolutionary  
338 history of such discrete traits based on a continuous Markovian process (extended Mk models)  
339 and relying on a Bayesian approach<sup>34</sup>, using the “simmap” function of the *phytools* package<sup>86</sup>  
340 and internally estimating the prior probability of trait (i.e. at the root), but with no prior on the  
341 transition matrix. Again, the obtained character history is in no case certain. Therefore, for  
342 each run, we obtained 10 stochastic character maps that were used in subsequent phylogenetic  
343 model fits (see [Phylogenetic models](#)), to account for the uncertainty of these ancestral diet  
344 estimations (see [Models of trait evolution: does species sympatry shape brain size evolution?](#)  
345 (b)).

## 346 Phylogenetic models

### 347 Models of trait evolution: does species sympatry shape brain size evolution?

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

349

350 We focused only on frugivorous primates, because the sample size was otherwise insufficient,  
351 and fitted phylogenetic models of the evolution of the EQ or the relative size of a specific  
352 brain area considering or not species sympatry. Models were fitted on different sample  
353 sizes due to the non-availability of some data for some traits. Specifically, models using  
354 EQ included 148 to 182 frugivorous species. Other models included more reduced sample  
355 sizes (in species number): Striatum (56 to 63), MOB (34 to 39), Neocortex (61 to 69),  
356 Hippocampus (56 to 63), Cerebellum (62 to 70). Nonetheless, for a given set of models

357 (i.e. within brain area), the sample was strictly identical, allowing within-set comparisons.  
358 Prior to fitting, trait parameters were log-transformed to reach more symmetrical distributions.  
359 Models without species sympatry, Brownian Motion (BM), Ornstein-Uhlenbeck process (OU,  
360 model with stabilizing selection), or Early-Burst model (EB, for assessing a time-dependence  
361 of the evolutionary rate), were fitted using the “fitContinuous” function from the *geiger*  
362 package<sup>87,88</sup>. Using the evolutionary history of species distribution (see [Primate species](#)  
363 [sympatry](#)) and of diet (see [Dietary guilds](#)), we fitted models considering species sympatry  
364 using the “fit\_t\_comp” function from the *RPANDA* package<sup>89</sup>. These models notably  
365 account for interspecific interaction matrices that are built on the evolutionary history of  
366 species sympatry and diet. These interaction matrices retrace, along the phylogenetic tree,  
367 which frugivorous lineages were present within the same geographic areas (see<sup>36</sup>). We fitted  
368 three different models considering species sympatry. The matching competition model (MC)  
369 considers the repulsion of traits of sympatric lineages from the same dietary guild due to  
370 competition (character displacement)<sup>36</sup>. Here, that would mean that sympatric species would  
371 tend to divergently evolve either lower, or higher, EQ or relative brain size. Otherwise,  
372 we modelled trait evolution accounting for linear ( $DD_{lin}$ ) or exponential ( $DD_{exp}$ ) density-  
373 dependence<sup>36,90</sup>. Density-dependence means that the evolutionary rate,  $\lambda$ , of trait changes,  
374 varies either positively or negatively as a function  $f$  of the number of sympatric lineages  
375 sharing the same diet, such as

376

377 
$$f_{lin}(\lambda) = \lambda_0 + rl$$

378 
$$f_{exp}(\lambda) = \lambda_0 \exp(rl)$$

379

380 where  $\lambda_0$  corresponds to the value of the initial ancestor,  $l$  indicates the number of lineages,  $r$   
381 allows for modelling the speed and direction of the dependency to lineage number ( $r > 0$  leads  
382 to an increase of trait changes, while  $r < 0$  leads to a decline of the trait changes). All these  
383 models were repeated 10 times, using 10 different combinations of the evolutionary histories

384 of primate ranges and diets. They were then compared within an information-theoretic  
385 framework<sup>39</sup> based on the weights of Akaike Information Criteria corrected for small samples  
386 (AICc), when considering all six models (MC, DD<sub>lin</sub>, DD<sub>exp</sub>, BM, OU, EB). The model weight  
387 depicts how well the model fits the observed evolutionary pattern compared with the other  
388 tested models.

389

390 (b) Dealing with data uncertainty and parameterisation sensitivity

391

392 In this analysis, uncertainty can stem from two sources. First, the evolutionary history  
393 (phylogeny, diet, and ranging) was reconstructed based on Bayesian inference. They are  
394 susceptible to be uncertain at some points. Thus, we used a consensus phylogenetic tree  
395 from the 10kTrees project, which averages the phylogeny among 1000 possible estimated  
396 trees, given that running the models on several trees was too computationally demanding. In  
397 addition, we repeated diet and ranging history reconstructions 10 times.

398 Second, for each species, trait estimates could vary slightly among datasets (see Appendix  
399 Figure S2). Particularly, although correlations between measures from the different datasets  
400 seem good enough, it existed a variation in absolute measurements (Appendix Figure S2).

401 In addition, this study is based on several arbitrary thresholds, namely (i) to assess species  
402 sympatry (see Appendix Figure S1) and (ii) to assess the species dietary guild (see Appendix  
403 Figure S2) which can cause sensitivity of the results to the chosen parameters. To account for  
404 these three sources of variability, we refitted several times the six models of trait evolution  
405 (BM, OU, EB, MC, DD<sub>lin</sub> and DD<sub>exp</sub>) with (1) random samples of the dietary and brain  
406 traits in case of multiple values available (i.e. equal probability for each possible value to  
407 be selected), (2) used the low or high threshold for assessing frugivory, folivory, and species  
408 sympatry, and (3) various biogeography and dietary evolutionary history reconstructions.

409 Eventually, it means that the results for each model represent the average of 10 (uncertainty  
410 on diet/ranging evolutionary reconstructions) x 10 (uncertainty in brain/diet rate data) x

<sup>411</sup> 2 (geographic overlap threshold defining sympatry) x 2 (frugivory threshold) x 2 (folivory  
<sup>412</sup> threshold) = 800 sub-models. We stopped computations when the optimization of the  
<sup>413</sup> likelihood was excessively long (> 1 week). The final sample size thus was of 730 models  
<sup>414</sup> that covered all the ranges of tested parameters.

<sup>415</sup> **Models of species diversification**

<sup>416</sup> We investigated how primates diversified over time. Lineage-specific diversification rates were  
<sup>417</sup> estimated using an updated version of the *CladS* algorithm<sup>42</sup> boosted for computational  
<sup>418</sup> speed based on data augmentation techniques<sup>43</sup>. Particularly, we used *CladS2*, the model  
<sup>419</sup> with constant turnover (i.e. constant ratio between extinction and speciation rates). This  
<sup>420</sup> Bayesian approach considers speciation rate heterogeneity by modelling small shifts in the  
<sup>421</sup> rate at speciation events. In other words, the two new lineages are assumed to inherit new  
<sup>422</sup> speciation rates that are sampled from a log-normal distribution with an expected mean  
<sup>423</sup> value  $\log(\alpha\lambda)$  (where  $\lambda$  represents the initial speciation rate and  $\alpha$  is a trend parameter),  
<sup>424</sup> and a standard deviation  $\sigma$ . Three independent chains were run until their convergence  
<sup>425</sup> was validated by a Gelman-Rubin diagnostic criterion<sup>91</sup>. The analysis relied on the use of a  
<sup>426</sup> consensus tree of primate phylogeny from<sup>92</sup>. The latter provides a robust phylogenetic tree  
<sup>427</sup> for 367 primate species (while the 10kTrees primate phylogeny has only 301 species).

<sup>428</sup> Such analysis necessarily depends on a prior estimation of the sample representativeness,  
<sup>429</sup> that is, the fraction of sampled taxa (present in the phylogenetic tree) among all possible  
<sup>430</sup> existing ones. Estrada et al.<sup>93</sup> estimated that, given current knowledge, the primate clade  
<sup>431</sup> should be composed of 504 species. This means that the current sampling fraction is around  
<sup>432</sup> 73%. We thus parameterized the *CladS* algorithm with this value for the estimated sampling  
<sup>433</sup> fraction. Yet, given that the extant number of primate species is subject to controversy,  
<sup>434</sup> and because the estimated sampling fraction may affect diversification rate estimations, we  
<sup>435</sup> replicated our analyses with a range of sampling fractions from 95% down to 60%. At the  
<sup>436</sup> end of each run, we extracted the maximum of the *a posteriori* net diversification rate of each

437 extant primate species, as well as the mean diversification rate (given all lineages) through  
438 time.

439 **Phylogenetic regressions**

440 (a) Determining the effect of sympatry on brain sizes

441

442 To determine the nature of the relationship between species sympatry and relative sizes of  
443 brain regions, we fitted Gaussian Pagel's lambda phylogenetic regressions (i.e. a derivative of  
444 the Brownian Motion model, for which the phylogenetic variance-covariance matrix has all  
445 coefficients, but its diagonal ones, multiplied by lambda) for each brain region individually  
446 and for frugivorous species only. We used Pagel's lambda model so as to relax the hypothesis  
447 of Brownian Motion since we included brain areas for which the evolutionary history was  
448 best described by models considering sympatry. Here specifically, we considered the least  
449 stringent frugivory assessment, with the frugivory threshold fixed to 20% and the folivory  
450 threshold fixed to 40%. If, due to data variability, a species did not robustly fit into the  
451 categorical classification "frugivorous versus folivorous" (i.e. could be either of the two), it  
452 was considered as frugivorous nonetheless.

453 The response variable was the relative size of brain areas. Due to data variability, we took  
454 the mean of the possible values given the different datasets, and assessed the sensitivity using  
455 non-averaged values (see [Phylogenetic regressions: results, stability, and assumption](#)). In this  
456 model, the covariates (i.e. continuous predictors) were the average percentage of overlapping  
457 range with other sympatric frugivorous species, and the number of frugivorous sympatric  
458 species (the second was square-rooted, to reach symmetrical distribution). For a given species  
459 A, sympatry with another species B was considered when species B range overlapped on more  
460 than 10% of the range of species A. This was done to reduce the noise induced by coarse  
461 identification of species range.

462

463 (b) Diversification and brain size

464

465 In the same way as explained above, we fitted Gaussian Pagel's lambda phylogenetic regressions  
466 of the different relative brain sizes against the net diversification rates (i.e. the difference  
467 between speciation and extinction rates), estimated for each extant species by the *CladS*  
468 algorithm. Again, we took the mean of the brain trait values for the main model and assessed  
469 the sensitivity by re-running the model several times using non-averaged values.

470

471 (c) Diversification and species sympatry

472

473 To determine whether species sympatry was associated with specific diversification patterns  
474 (and thus if diversification rates were regionalized), we fitted Gaussian Pagel's lambda  
475 phylogenetic regressions with the diversification rate as output variable, and used the two  
476 metrics for describing sympatry (the average percentage of overlapping range with other  
477 sympatric frugivorous species, and the number of frugivorous sympatric species) as tested  
478 variables, as described in (a).

479

480 (d) Model implementation

481

482 (i) Effect of sympatry on brain sizes

483

484 Models were fitted using the "phylolm" function from the *phylolm* package<sup>94</sup>, with the  
485 lambda parameter (with  $\lambda$  indicating the strength of the phylogenetic signal, where  $\lambda=1$   
486 corresponds to Brownian Motion, i.e. the maximal influence of the phylogenetic history on  
487 the trait evolution) estimated by maximum-likelihood (argument "model" set to "lambda").  
488 Bootstrapping over 1000 independent replicates was done to obtain confidence intervals.  
489 Other function parameters were set to default. Prior to fitting, covariates were transformed

490 so as to reach more symmetrical distributions when adequate. Necessary assumptions on the  
491 normal distribution of residuals and homoscedasticity were visually assessed and pointed out  
492 no violation (see Appendix [Model assumptions](#)). We did not observe correlation issue among  
493 predictors neither ( $VIF_{max} < 2$ ,<sup>95</sup>).

494

495 (ii) Diversification and brain size

496

497 We could not compute phylogenetic regressions to link diversification and brain traits in  
498 frugivorous primates using a frequentist approach because it led to a violation of homoscedas-  
499 ticity. Instead, we fitted Bayesian phylogenetic regressions using the “MCMCglmm” function  
500 of the *MCMCglmm* package<sup>96</sup>. Each chain was based on a burnin period of 5000 iterations,  
501 among a total of  $5 \times 10^4$  iterations, and was sampled every 50 iterations. We used the least  
502 informative priors. Fixed priors were let to default (Gaussian distribution of mean 0 and  
503 variance  $10^8$ ). Priors on random effects and residuals were set to follow an inverse-Wishart  
504 distribution with a variance at a limit ( $V$ ) of 1, and a degree of belief ( $nu$ ) of 0.02. We  
505 checked model convergence by fitting three chains, and calculated the Gelman-Rubin criterion  
506 (max value  $< 1.0042$ ; Gelman & Rubin [91]), as well as checked autocorrelation (max absolute  
507 value  $< 0.07$ ) using the respective “gelman.diag” and “autocorr.diag” functions from the *coda*  
508 package<sup>97</sup>. In Appendix [Model assumptions](#), we present traces and distributions of posterior  
509 estimates. We further checked the quality of the posterior by visually assessing the Q-Q plot  
510 of the posterior with that of a Gaussian distribution of mean 0 and sd 1 (see Appendix [Model](#)  
511 [assumptions](#)). We present the estimate together with the 95% credibility interval centered on  
512 the mode (Highest Density Posterior, HDP), together with a MCMC p-value (pMCMC) that  
513 corresponds to the probability that the estimate ( $\beta$ ) is positive if the mean estimate ( $\hat{\beta}$ ) is  
514 negative (i.e.  $P(\beta > 0 | \hat{\beta} < 0)$ ), or if the mean estimate is positive, the probability that the  
515 estimate is negative (i.e.  $P(\beta < 0 | \hat{\beta} > 0)$ ).

516

517 (iii) Diversification and sympatry

518

519 We fitted phylogenetic regression as explained in (i). In particular, verification of model  
520 assumption and stability pointed out no source of worry (see [Phylogenetic regressions: results,](#)  
521 [stability, and assumption](#)).

522

523 (d) Model robustness

524

525 To assess frequentist model stability with regards to singular points, we computed the DfBetas  
526 (variation in estimates) by discarding one observation at a time of the “standard” dataset  
527 used to fit the main model, based on the consensus tree .

528 To assess the sensitivity to (i) the variability in data and (ii) phylogeny uncertainty, we  
529 refitted the models using 50 phylogenetic trees among the 10000 possible trees from the  
530 10kTrees project. For each of these trees, we fitted the model 50 times, allowing random  
531 sampling for data when we had multiple values (e.g. if body mass was provided by different  
532 datasets etc.). For the diversification analysis specifically, we also assessed the sensitivity to  
533 changes in primate sampling fraction by refitting the models for values ranging between 60  
534 to 95% (as specified before), using the “standard” dataset and the consensus tree.

535 The results of these assessments (min-max of estimates) are shown in Appendix [Model](#)  
536 [stability](#). It emphasizes the weak sensitivity of the results.

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## 551 **Authors' contribution**

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

Table 1: Species sympatry correlates negatively with the sizes of some brain areas : 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 size) are indicated prior to each list of estimates. The transformation applied to variables are indicated between brackets (logarithm, log, or square-root, sqrt), as well as the ponderation by bodymass (/bodymass).

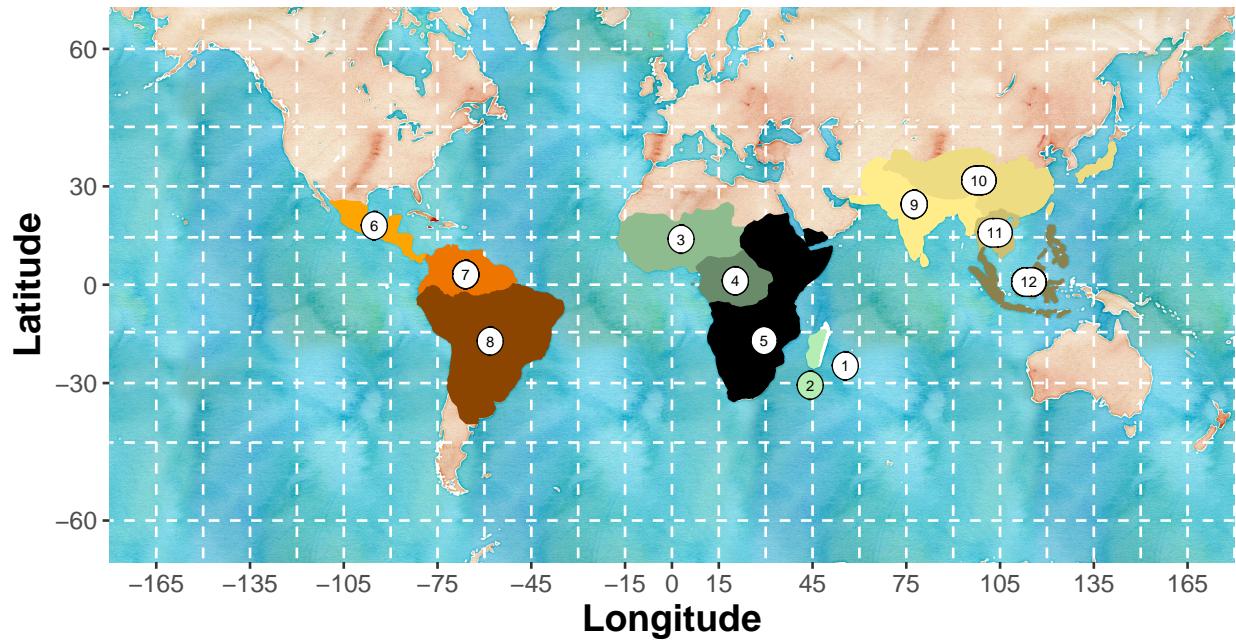
	Est.	CI2.5%	CI97.5%	Sd	t	p-value
EQ (log) (N=127)						
Intercept	-0.17	-0.53	0.22	0.20	-	-
% of overlapped range	0.02	-0.08	0.13	0.05	0.41	0.68
Number of sympatric frugivores (sqrt)	0.02	-0.02	0.05	0.02	1.03	0.31
Lambda	0.98	0.94	1.00			
Hippocampus (/bodymass, log) (N=50)						
Intercept	-0.92	-1.95	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	<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			

Table 2: The relative brain sizes did not impact 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 size) are indicated prior to each list of estimates. The logarithm transformation was applied to variable and is indicated between brackets (log), as well as the ponderation by bodymass (/bodymass).

	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		

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 size) 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)	<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 |                          |                     |

Figure 1: Geographic areas used for ancestral range reconstruction of 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<sup>33</sup>: (1) East Madagascar (2) West Madagascar (3) West Africa (4) Central Africa (5) East/South Africa (6) Central America (7) Northern South America (8) Southern 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.

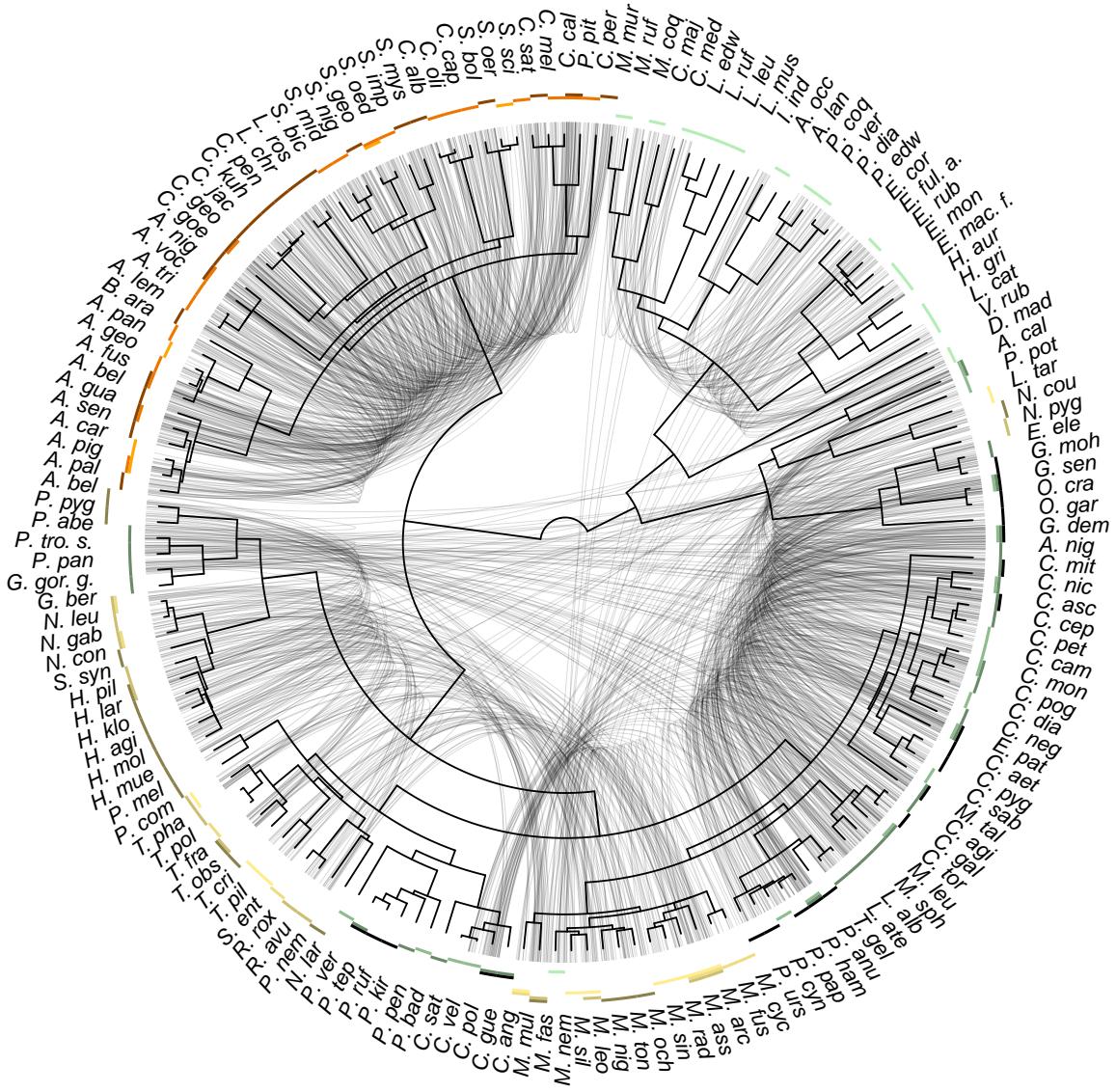


Figure 2: Levels of species sympatry vary across the primate phylogeny | Primate phylogeny from the consensus tree of the 10kTrees project is depicted in the center, together with abbreviated species names. The corresponding non-abbreviated names can be found using Appendix Figure S3. Sympatric frugivorous (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%.

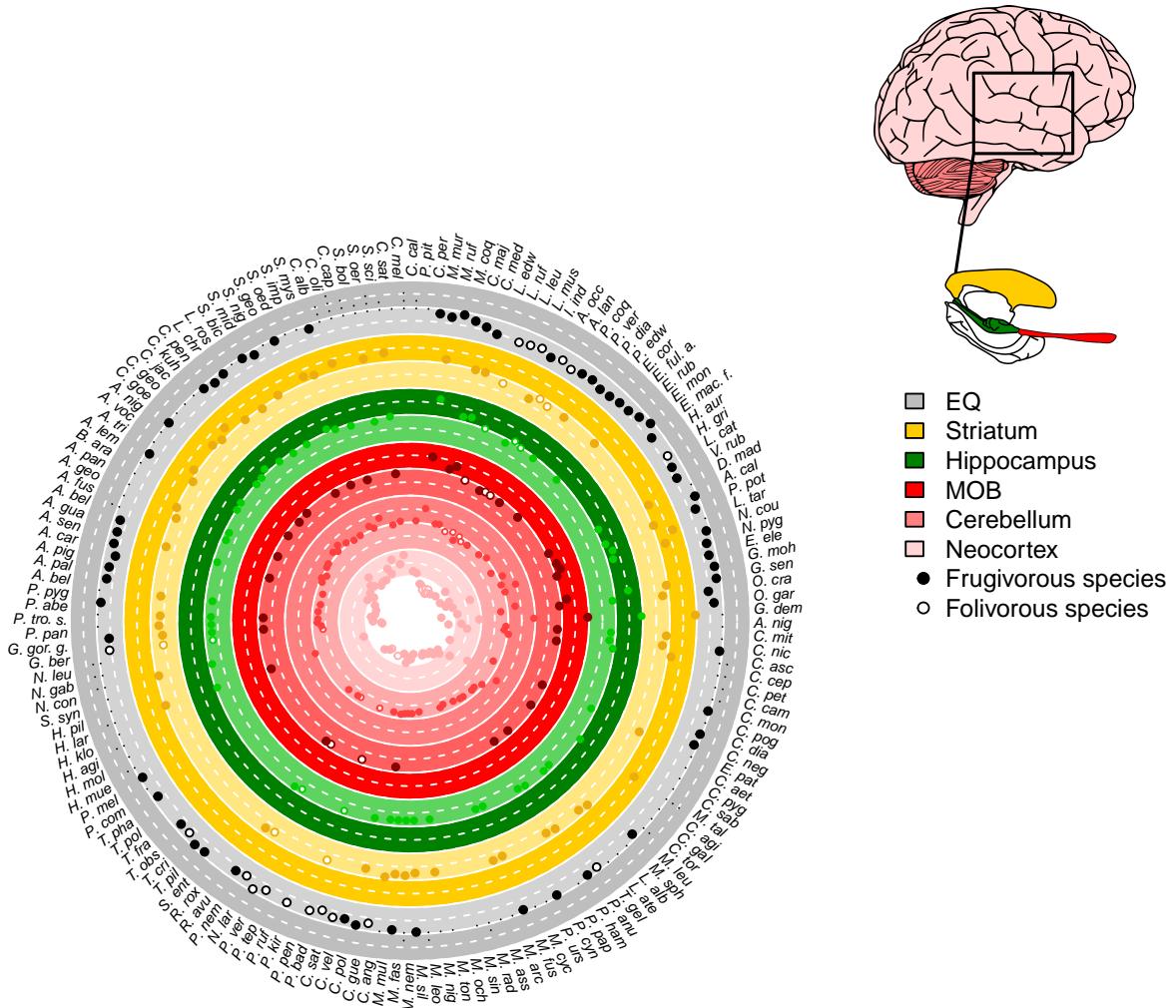


Figure 3: Variations in relative brain size areas among frugivorous primates | (Left) Circular plot of the relative sizes of the different brain areas. Colours indicates the rows for the different brain areas. The darker background emphasises when values are above average, while the lighter background emphasises when values are below average. The mean value (after scaling and based on one random sampling among possible values, but see S2 for visualization of measure variability) for the Encephalization Quotient (EQ) or relative size of brain regions, when available, is depicted by a plain circle for frugivorous species. The frugivorous threshold was fixed to 20% and the folivory threshold to 40%. (Right) The different studied brain areas (human brain as an illustration). In short, the MOB is involved in immediate olfactory information processing, the Neocortex and the Cerebellum support working memory and memory consolidation of immediate sensory information processing<sup>20–22</sup>, and the Hippocampus supports a working memory and a long-term spatio-temporal memory<sup>19</sup>. The Striatum is involved in social information processing<sup>23</sup>.

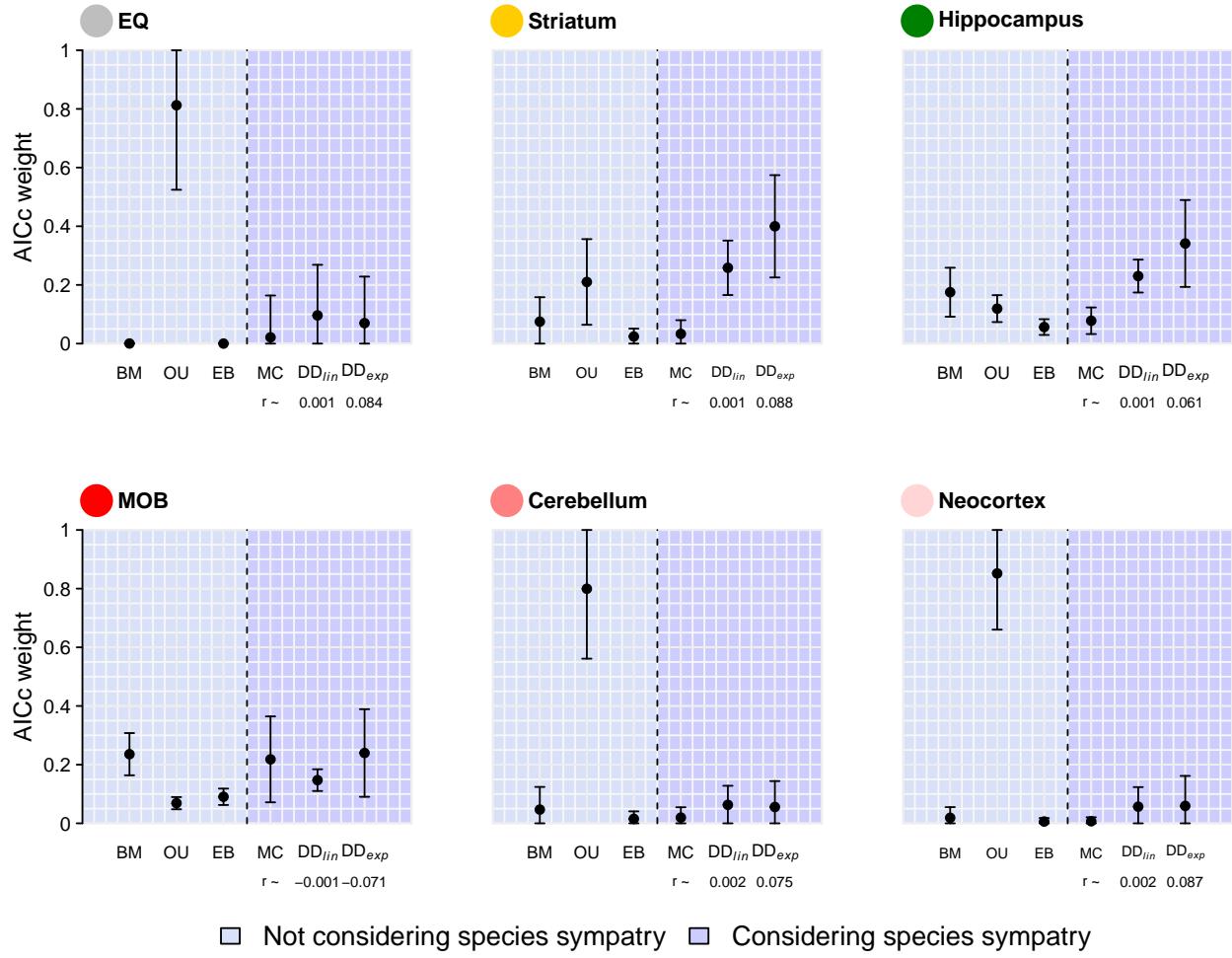


Figure 4: The evolution of the Hippocampus and Striatum in frugivorous primates are best fitted by models of trait evolution considering species sympathy | Plotted is the AICc weight, a measure of relative support for a given model, for models not considering species sympathy (BM, OU, EB) or considering species sympathy (MC,  $DD_{lin}$ ,  $DD_{exp}$ ). The points represent the average AICc weight obtained (when considering the six models from the same run), while the vertical bars indicate the standard deviation given all tested conditions (see [Models of trait evolution: does species sympathy shape brain size evolution?](#)).

557 **Appendix**

558 **Data availability**

559 Availability of trait and distribution range for the 301 primate species represented in the  
560 primate phylogeny of the 10kTrees project is depicted in Appendix Figure [S3](#).

561 **Data variability**

562 We present below the results of the assessments of data variability depending on the considered  
563 thresholds (for frugivory, folivory or overlap) and the data set that is used, specifically related  
564 to distribution ranges, or anatomical/behavioural traits.

565 **Sensitivity to variation in distribution range**

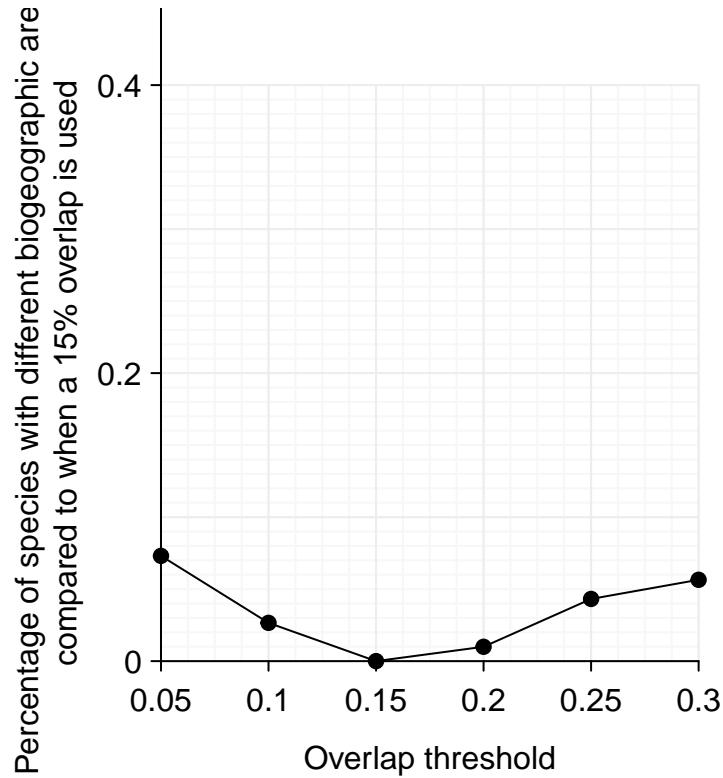


Figure S1: Percentage of species with differently identified biogeographic areas in function of the overlap threshold (reference is an overlap threshold of 15%) | For a given species, a biogeographic area difference means that at least one biogeographic area considers absence/presence of the species while this was not the case with the 15% threshold. 15% was chosen as the reference since halfway to the chosen maximum of 30%. 30% was chosen as the maximum because based on current observations, a species occupied at best three different biogeographic areas.

566 Sensitivity to variation in trait value

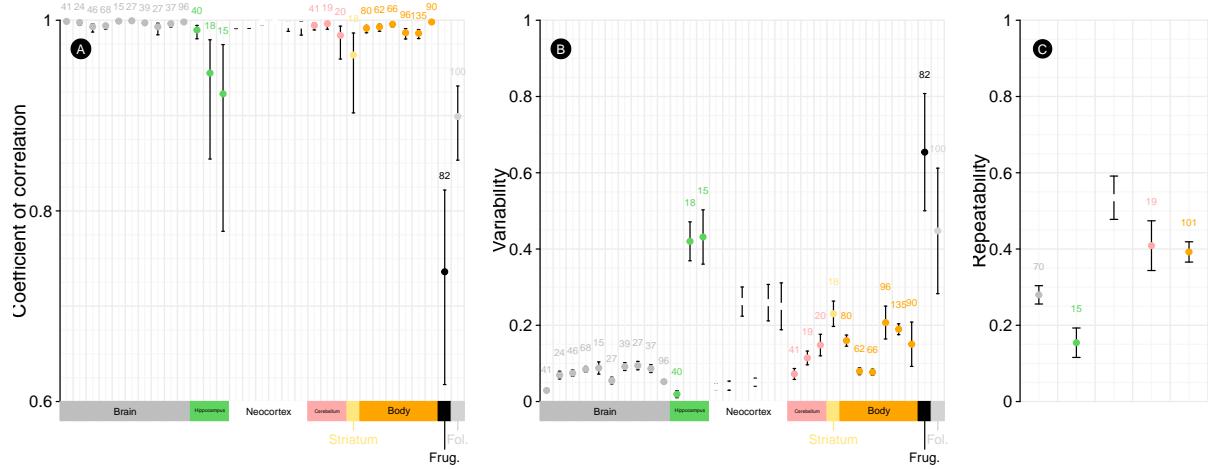


Figure S2: Variation in trait values among reference datasets | Colours are associated with a specific trait: Brain, Hippocampus, Neocortex, and Cerebellum refers to the volume of the area (in  $\text{mm}^3$ ), Body refers to the body mass (in g), Frug. indicates the frugivory rate and Fol. indicates the folivory rate. (A) Correlation: The points depict the coefficient of correlation while the bar depicts the 95% confidence interval (CI). (B) Variability: The points depict the average of the mean ratio  $m$  of the absolute of differences with paired values; If we reduce the equation, we have  $m = |(v_1^2 - v_2^2)|/(2v_1v_2)$ , where  $v_1$  and  $v_2$  are the two paired values from two different datasets and are different from 0. If  $v_1$  and  $v_2$  equal 0, then  $m = 0$ . If  $v_1$  or  $v_2$  equals 0 (case for the diet rates constrained between  $[0,1]$ ), then we fixed the null value to 0.01. The bar depicts the standard error. (C) Repeatability: Repeatability was assessed for traits that were included in at least three datasets. Before calculation, traits were pondered *within* species by the *within* species max value. The point represents the mean repeatability  $r$  calculated as  $\sigma_{\text{between}}^2/(\sigma_{\text{between}}^2 + \sigma_{\text{within}}^2)$ , with the  $\sigma_{\text{between}}^2$  and  $\sigma_{\text{within}}^2$  corresponding the variance *between* or *within* species. The bar depicts the standard error. For all graphics, sample sizes are indicated above the upper value of the CI/error interval.

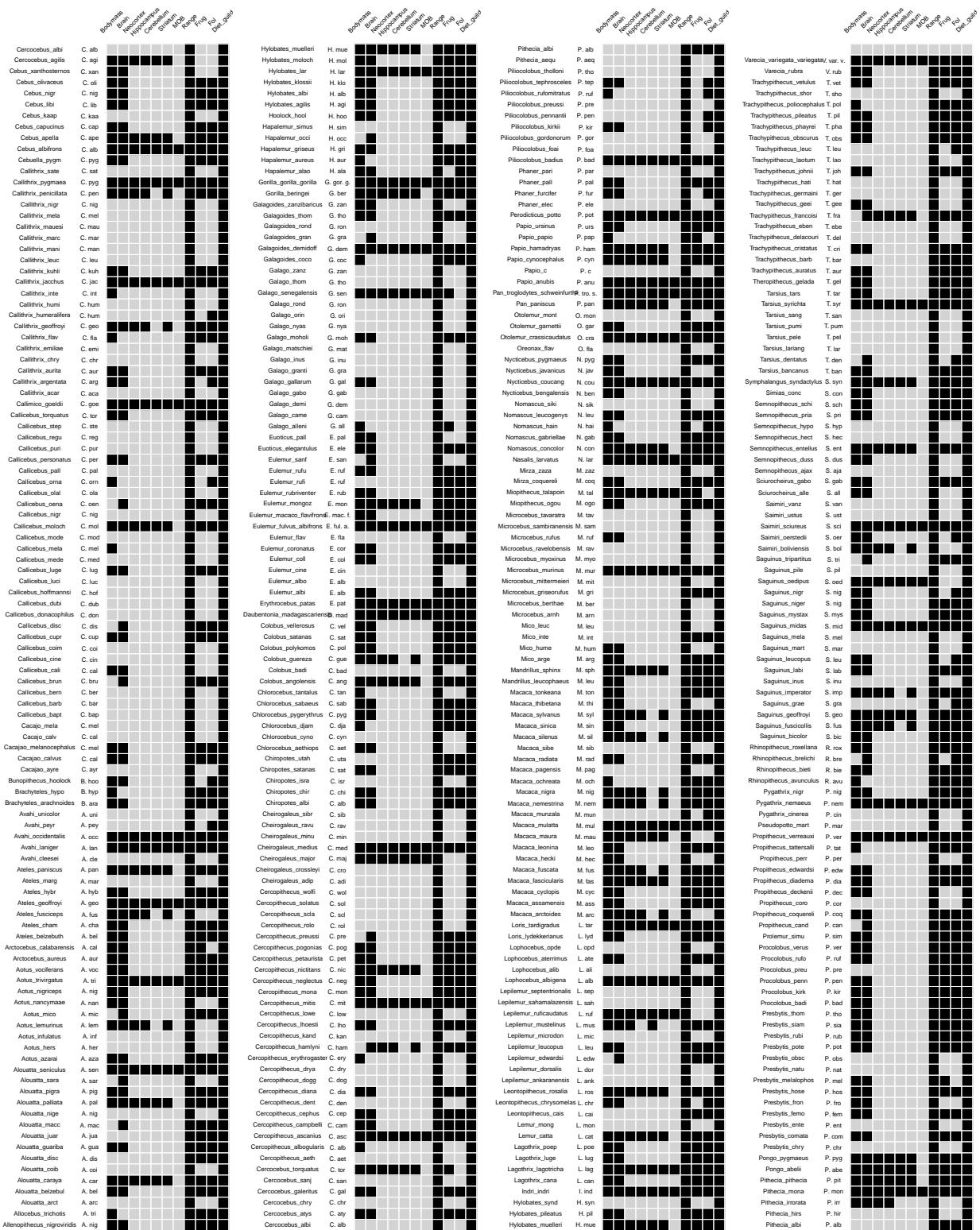


Figure S3: Data availability | Black boxes indicate data availability while grey boxes indicate absence of data.

567 **Primate diversification rate over time**

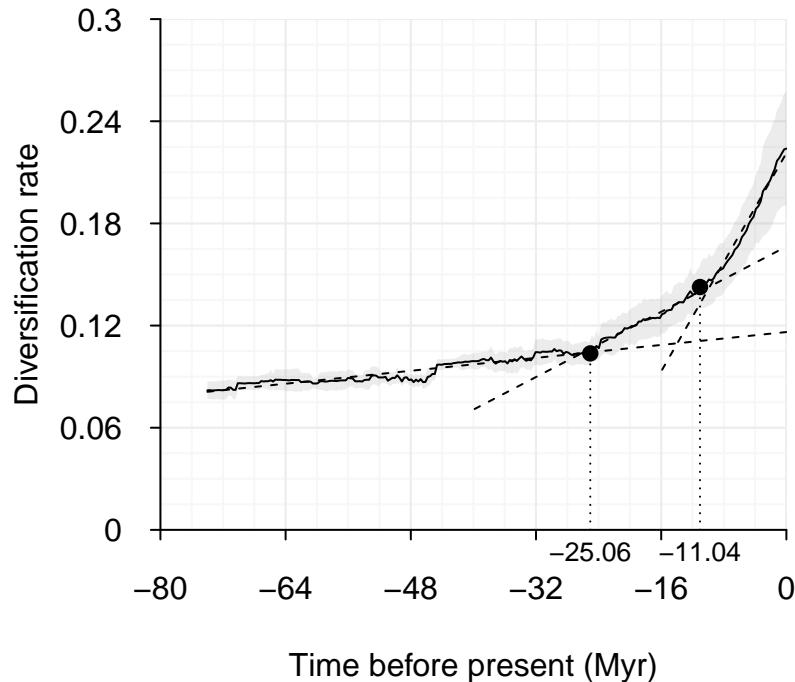
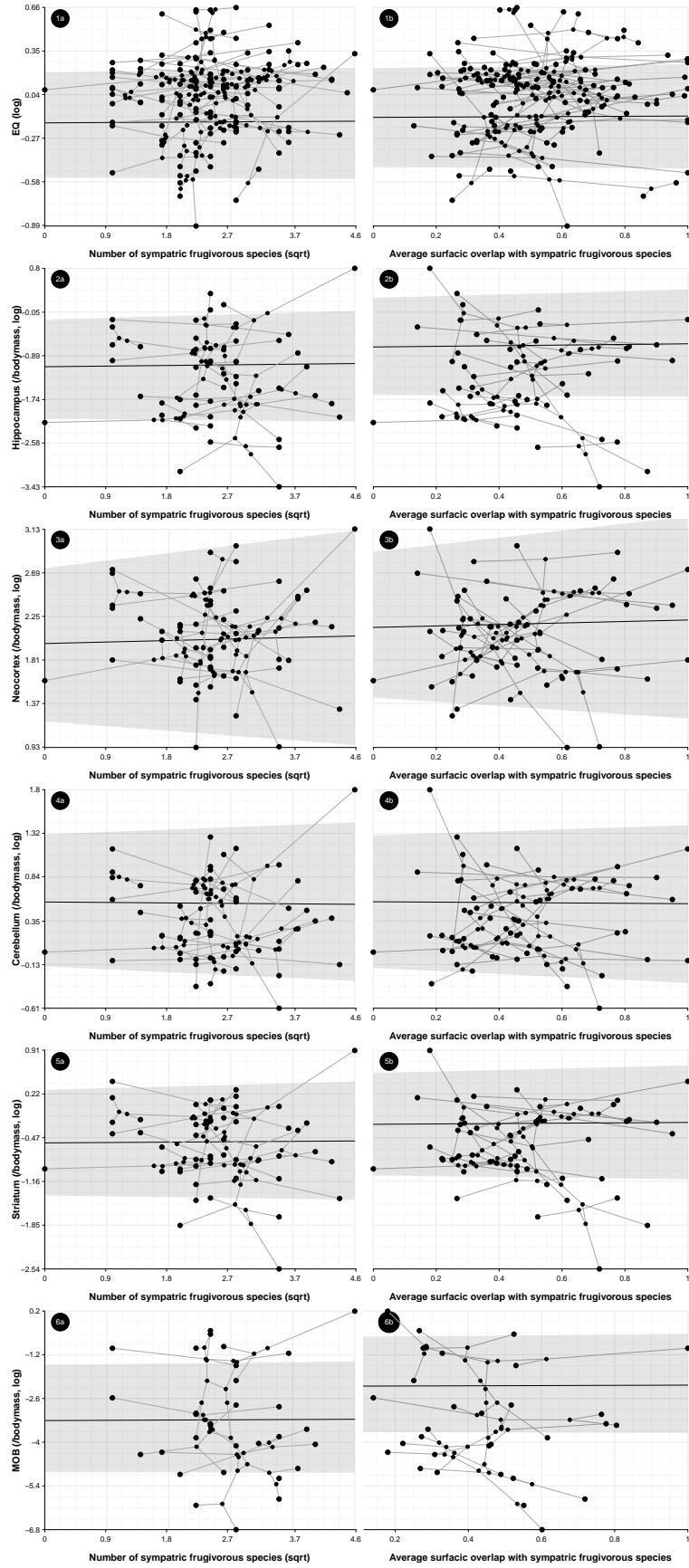


Figure S4: Net diversification rate over time in the Primate taxon | The average diversification rate estimated based on an assumed sampling fraction of primate species ranging from 60 to 95% (at a step of 10%; then 5% from 90%) is depicted by the plain line. The grey background depicts the standard deviation. The two breakpoints, depicted by the plain dots and the vertical dotted bars, were estimated based on a three-linear regression segmentation using the *strucchange* package [Zeileis *et al.* [98]; Zeileis *et al.* [99]; Zeileis [100]; see the vignette package for statistical details]. The three fitted regressions are displayed by the dashed lines. The choice of two breakpoints was first assessed by choosing the number of breakpoints minimizing the Bayesian Information Criterion. The identified breakpoints, coinciding with previous studies<sup>101,102</sup>, correspond to the emergence of more favourable environmental conditions stemming from a progressive warming after harsh temperature cooling that started earlier in the Oligocene until reaching a mid-Miocene Climatic Optimum<sup>103</sup>.

568 **Phylogenetic regressions: results, stability, and assumption**

569 **Model results**

570 (a) Phylogenetic regressions: effect of sympatry on brain sizes



**Figure S5:** Phylogenetic regressions of relative brain size as a function of sympatry level indices | Left graphics show the effect of the number of sympatric species on the brain size, when the effect of the average percentage of overlapping range with sympatric frugivorous species is averaged, while the right graphics do the opposite. Raw data are depicted with points, while the segments that link them correspond to the projected phylogenetic tree. The model fit is shown with the plain black line and the associated 95% confidence interval is depicted by the transparent grey background.

## (b) Phylogenetic regressions: diversification and brain size

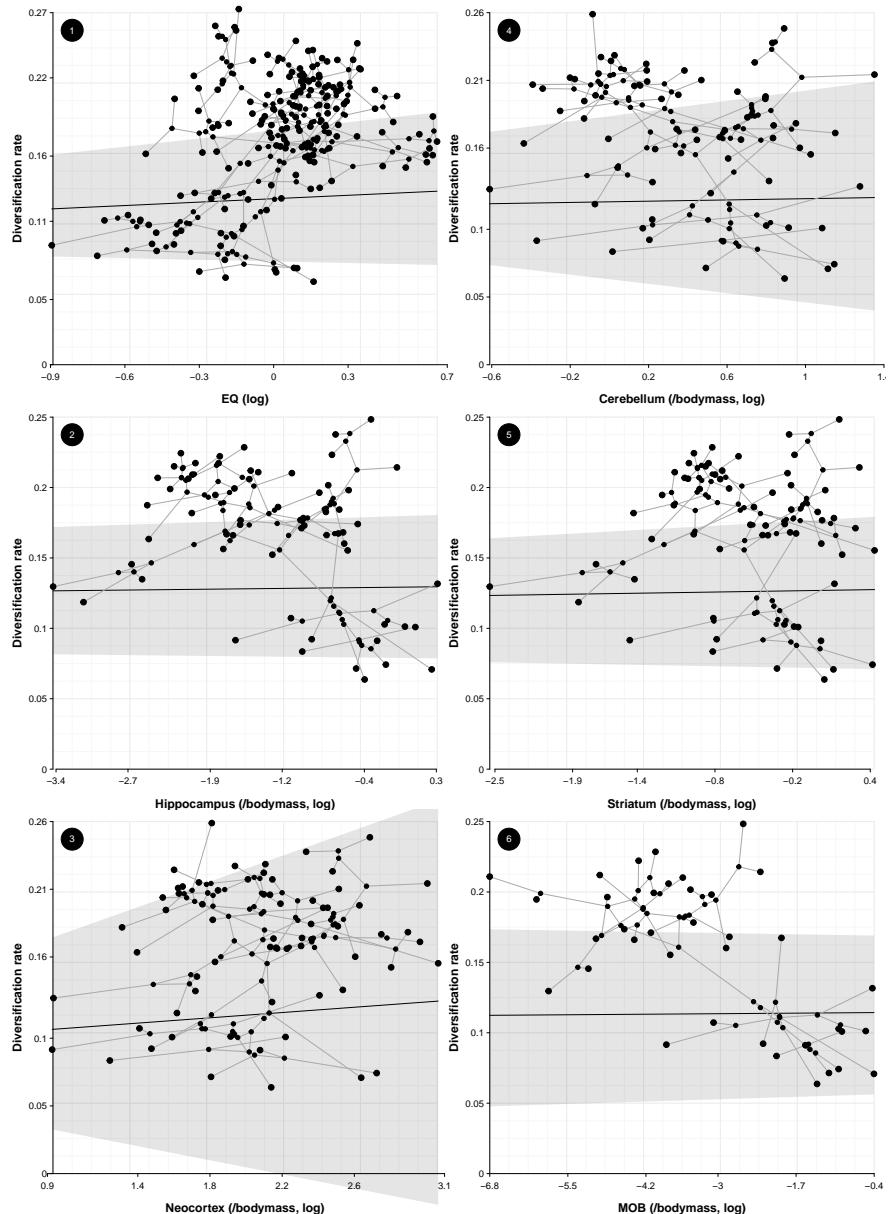


Figure S6: Phylogenetic regressions of the net diversification rate as a function of the size of the different brain areas | Raw data are depicted with points, while the segments that link them correspond to the projected phylogenetic tree. The model fit is shown with the plain black line and the associated 95% highest density posterior is depicted by the transparent grey background.

## (c) Phylogenetic regressions: diversification and sympathy

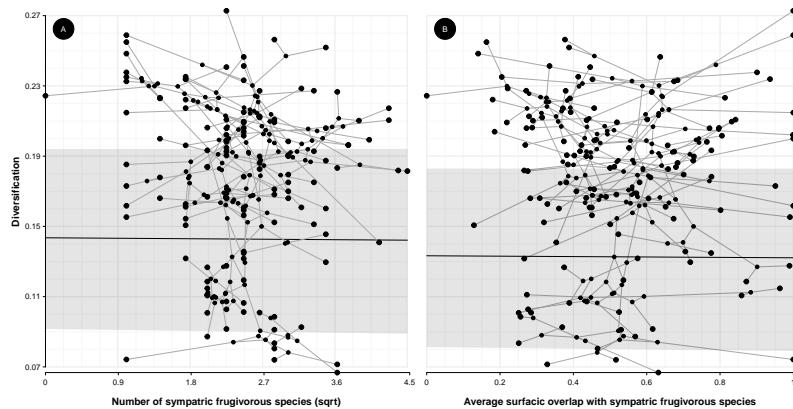


Figure S7: Phylogenetic regressions of the net diversification rate as a function of sympathy level indices | The left graphic depicts the effect of the number of sympatric species on the brain size, when the effect of the average percentage of overlapping range with sympatric frugivorous species is averaged, while the right graphic does the opposite. Raw data are depicted with points, while the segments that link them correspond to the projected phylogenetic tree. The model fit is shown with the plain black line and the associated 95% confidence interval is depicted by the transparent grey background.

## (d) Forest plot of estimates

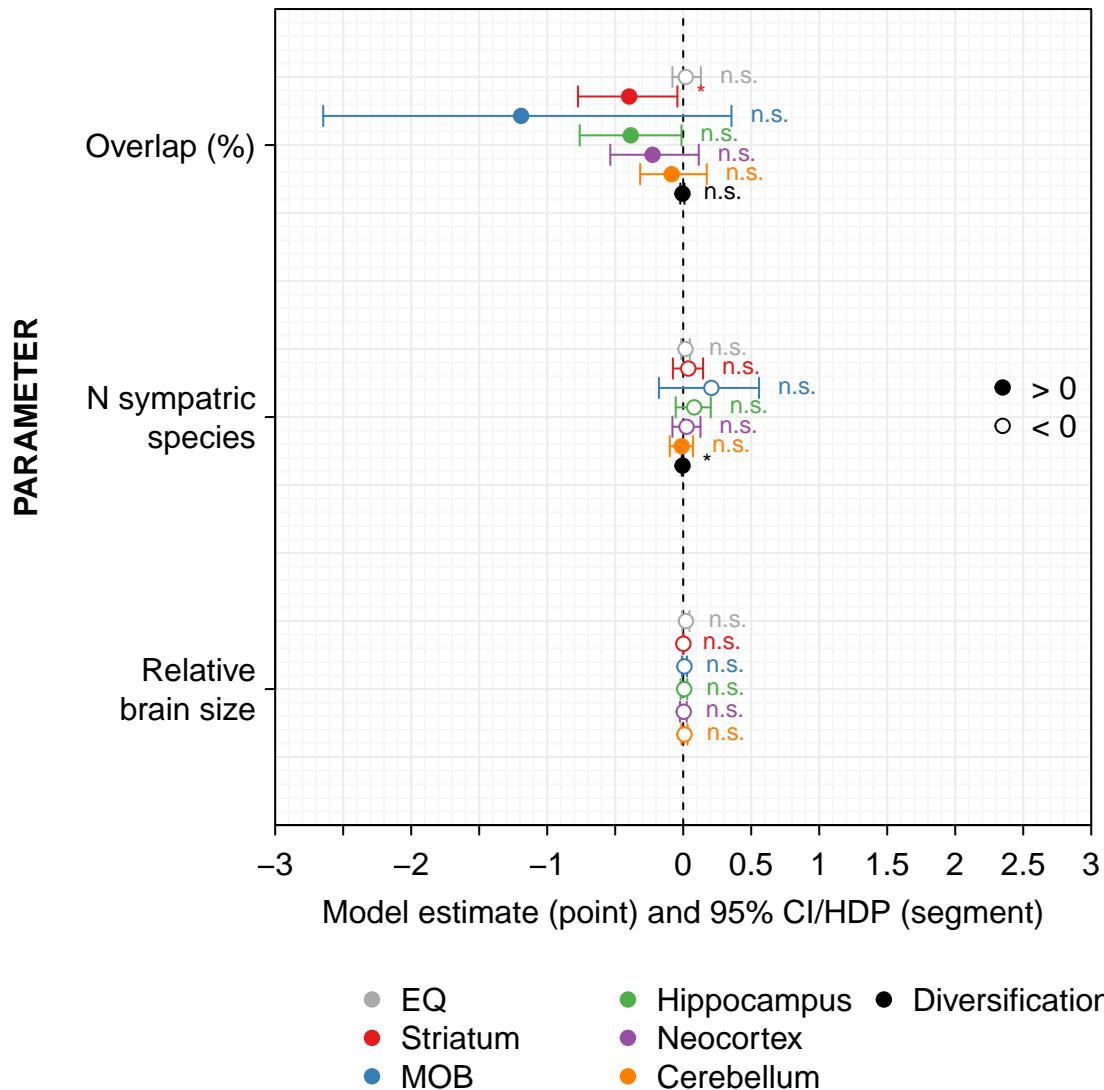


Figure S8: Forest plot of the phylogenetic regressions | CI: 95% Confidence Interval, HDP: Highest Posterior Density (when brain size is the predictor, they are barely visible because reduced). Plain dots depict negative effects, open dots depict positive effects.

574 **Model stability**

575 We present below statistical indicators related to changes in estimates when re-fitting the  
576 model considering sub-samples (i.e. DfBetas and Cook's distance), as well as when accounting  
577 for data variability (i.e. re-sampling among possible values given all datasets) or when  
578 using different parameterisation (i.e. "sampling fraction" of known species for diversification  
579 analyses).

580

581 (a) Phylogenetic regressions: effect of sympatry on brain sizes

Table S1: Sensitivity analysis of phylogenetic regressions to assess the relationship between relative brain sizes and species sympatry | Depicted is the minimum and maximum of estimates when one observation was removed at a time (DfBetas) or when varying the used phylogenetic tree and the data sampling (Phylogeny/Data).

Trait	Variable	Regression			DfBetas		Phylogeny/Data		
		Est. min.	Est.	Est. max.	Est. min.	Est.	Est. max.		
Cerebellum (/bodymass, log)	Intercept	0.55	0.6	0.67	0.22	0.6	0.7		
	% of overlapping range	-0.16	-0.08	-0.03	-0.49	-0.08	-4.84e-03		
	Number of sympatric frugivores	-0.04	-0.01	5.27e-03	-0.01	-0.01	0.17		
	Lambda	1	1	1	0.3	1	1		
EQ (log)	Intercept	-0.19	-0.17	-0.13	-0.41	-0.17	-0.05		
	% of overlapping range	7.14e-04	0.02	0.06	-0.38	0.02	0.09		
	Number of sympatric frugivores	5.37e-03	0.02	0.02	2.70e-03	0.02	0.1		
	Lambda	0.98	0.98	0.99	0.35	0.98	1		
Hippocampus (/bodymass, log)	Intercept	-1.03	-0.92	-0.82	-1.16	-0.92	-0.41		
	% of overlapping range	-0.5	-0.39	-0.2	-1.37	-0.39	-0.28		
	Number of sympatric frugivores	0.04	0.08	0.1	0.03	0.08	0.21		
	Lambda	0.99	0.99	1	0.79	0.99	1		
MOB (/bodymass, log)	Intercept	-3.23	-2.76	-2.62	-2.99	-2.76	-2.55		
	% of overlapping range	-1.83	-1.2	-0.8	-1.5	-1.2	-0.87		
	Number of sympatric frugivores	0.11	0.21	0.33	0.13	0.21	0.26		
	Lambda	1	1	1	1	1	1		
Neocortex (/bodymass, log)	Intercept	1.95	2.07	2.23	1.73	2.07	2.32		
	% of overlapping range	-0.31	-0.23	-0.03	-0.55	-0.23	-0.02		
	Number of sympatric frugivores	-0.02	0.02	0.06	-0.04	0.02	0.15		
	Lambda	0.98	0.99	1	0.23	0.99	1		
Striatum (/bodymass, log)	Intercept	-0.45	-0.36	-0.26	-0.76	-0.36	-0.07		
	% of overlapping range	-0.46	-0.4	-0.28	-0.92	-0.4	-0.22		
	Number of sympatric frugivores	4.03e-03	0.03	0.06	0.01	0.03	0.18		
	Lambda	0.98	0.98	1	0.79	0.98	1		

582 (b) Phylogenetic regressions: diversification and brain size

Table S2: Sensitivity analysis of phylogenetic regressions to assess the relationship between species diversification and relative brain sizes | Depicted is the minimum and maximum of estimates when varying the used phylogenetic tree and the data sampling (Phylogeny/Data), or when the sampling fraction varied (Sampling fraction).

Regression		Phylogeny/Data			Sampling fraction		
Model	Variable	Est. min.	Est.	Est. max.	Est. min..1	Est..1	Est. max..1
Cerebellum (/bodymass, log)	Intercept	0.12	0.12	0.12	0.11	0.12	0.13
	Trait	7.60e-04	3.94e-03	4.17e-03	1.91e-04	3.94e-03	6.13e-03
	Lambda	0.69	0.74	0.74	0.72	0.74	0.75
EQ (log)	Intercept	0.12	0.12	0.12	0.11	0.12	0.13
	Trait	7.51e-03	0.02	0.02	6.04e-03	0.02	0.02
	Lambda	0.77	0.83	0.83	0.8	0.83	0.85
Hippocampus (/bodymass, log)	Intercept	0.13	0.13	0.13	0.12	0.13	0.14
	Trait	3.73e-03	9.10e-03	9.10e-03	4.07e-03	9.10e-03	9.10e-03
	Lambda	0.69	0.73	0.73	0.72	0.73	0.75
MOB (/bodymass, log)	Intercept	0.1	0.11	0.11	0.1	0.11	0.12
	Trait	-9.89e-03	-4.79e-03	-4.76e-03	-7.64e-03	-4.79e-03	-4.10e-03
	Lambda	0.6	0.65	0.65	0.64	0.65	0.65
Neocortex (/bodymass, log)	Intercept	0.1	0.1	0.11	0.1	0.1	0.12
	Trait	4.69e-03	7.26e-03	7.26e-03	1.60e-03	7.26e-03	7.26e-03
	Lambda	0.69	0.74	0.74	0.72	0.74	0.75
Striatum (/bodymass, log)	Intercept	0.12	0.12	0.13	0.12	0.12	0.14
	Trait	5.89e-03	9.11e-03	9.41e-03	6.27e-03	9.11e-03	9.13e-03
	Lambda	0.69	0.73	0.73	0.72	0.73	0.75

Table S3: Sensitivity analysis of phylogenetic regressions to assess the relationship between species diversification and sympatry | Depicted is the minimum and maximum of estimates when one observation was removed at a time (DfBetas) or when varying the used phylogenetic tree and the data sampling (Phylogeny/Data)

Model:	DfBetas				Phylogeny/Data			Sampling fraction	
	Variable	Est. min.	Est.	Est. max.	Est. min.	Est.	Est. max.	Est. min.	Est.
Intercept		0.14	0.15	0.15	0.15	0.15	0.15	0.14	0.15
% of overlapping range		-8.58e-03	-5.40e-03	5.85e-05	-5.73e-03	-5.40e-03	-5.73e-03	-8.6e-03	-5.40e-03
Number of sympatric frugivores		-6.03e-03	-5.04e-03	-4.24e-03	-5.2e-03	-5.04e-03	-5.2e-03	-9.06e-03	-5.04e-03
Lambda		0.96	0.96	0.97	0.96	0.96	0.96	0.94	0.96
									0.99

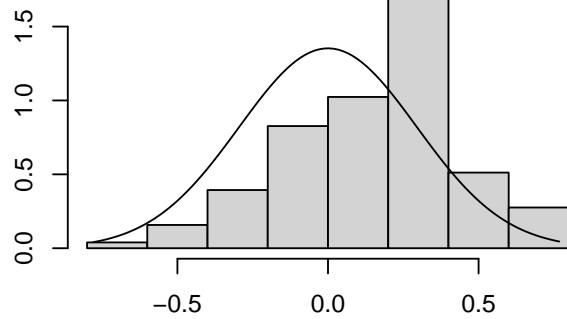
583 (b) Phylogenetic regressions: diversification and sympathy

584 **Model assumptions**

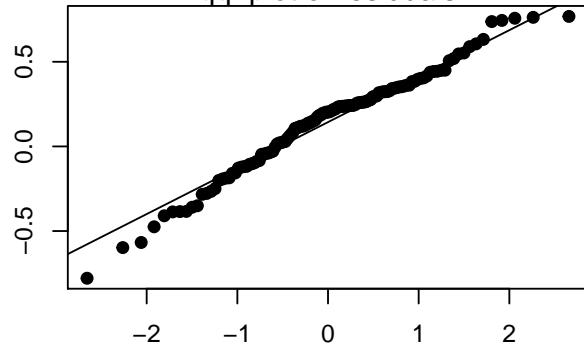
585 We present below the visual assessment of linear modelling assumptions (histogram of  
586 residuals, Q-Q plot, and scatterplot of fitted values vs residuals).

587 (a) Phylogenetic regressions: effect of sympatry on brain sizes

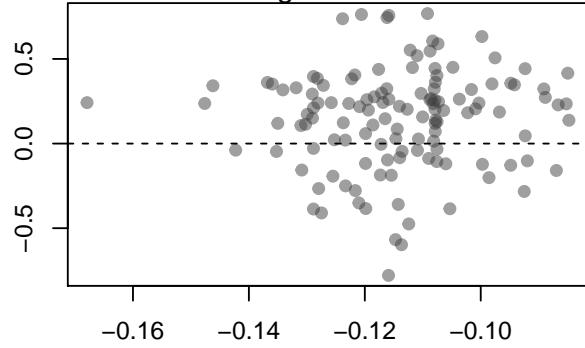
histogram of residuals



qq-plot of residuals

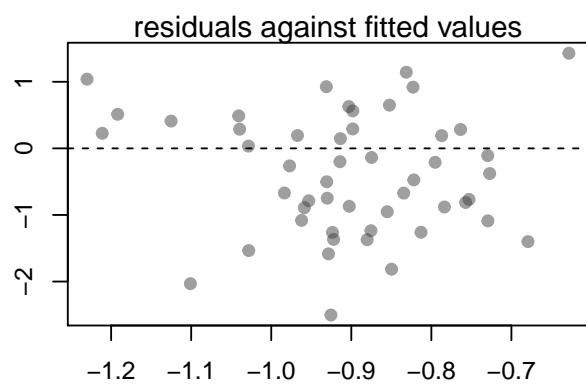
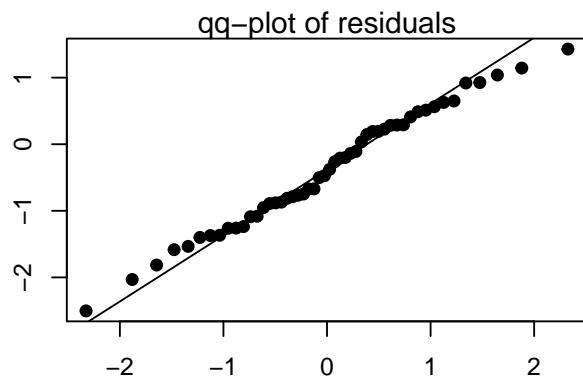
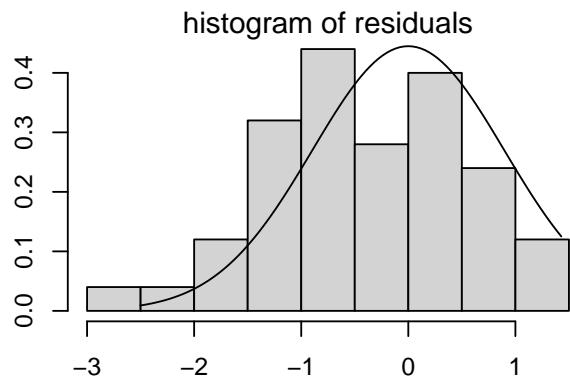


residuals against fitted values

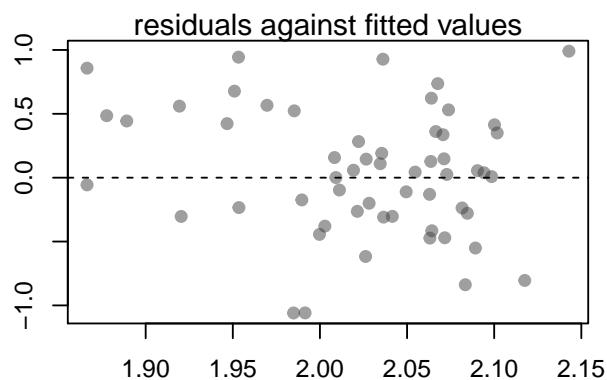
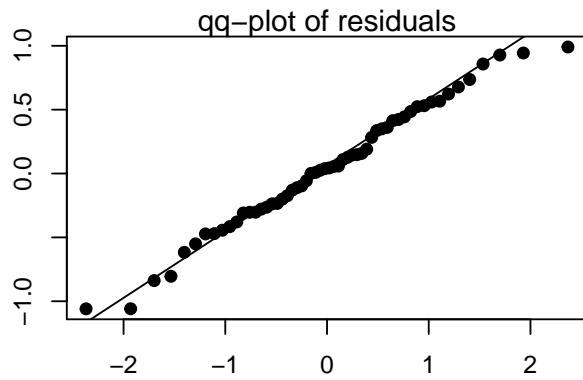
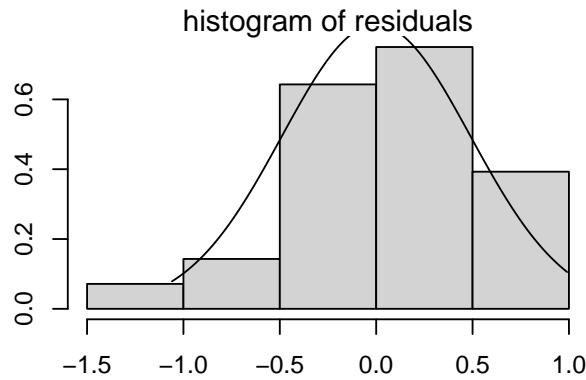


Model:  
EQ (log)

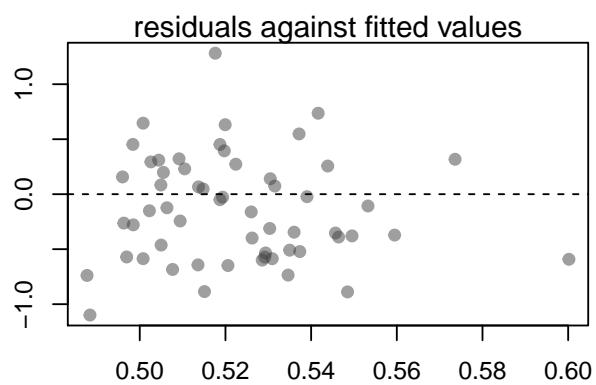
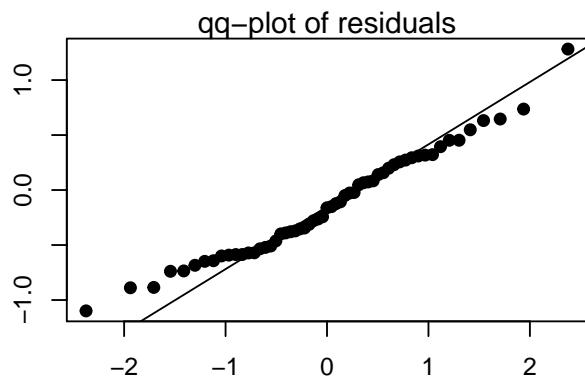
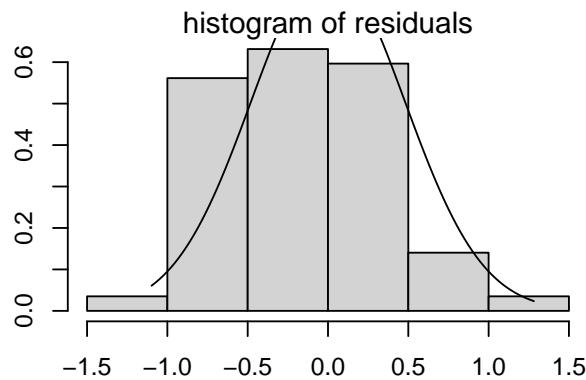
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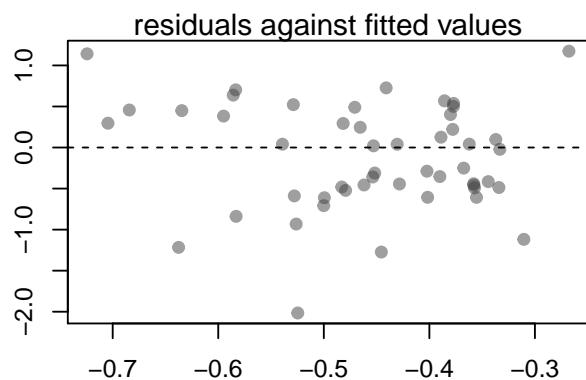
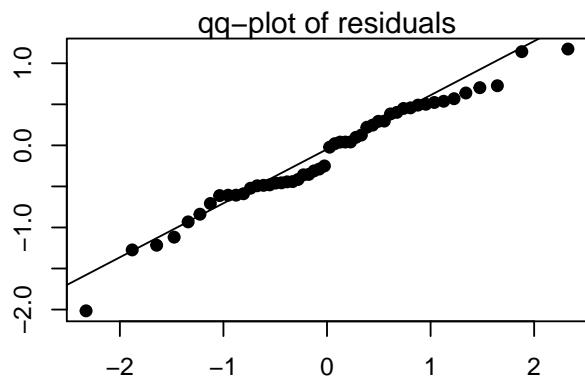
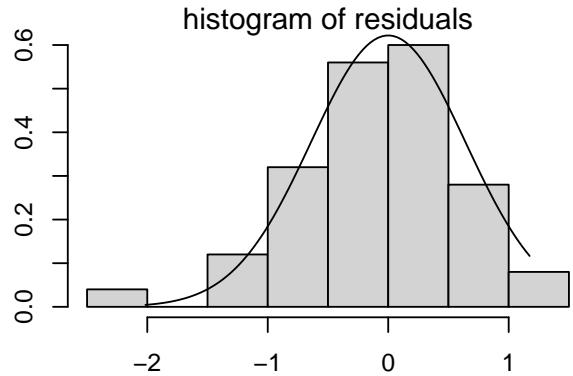
Model:  
Hippocampus (/bodymass, log)



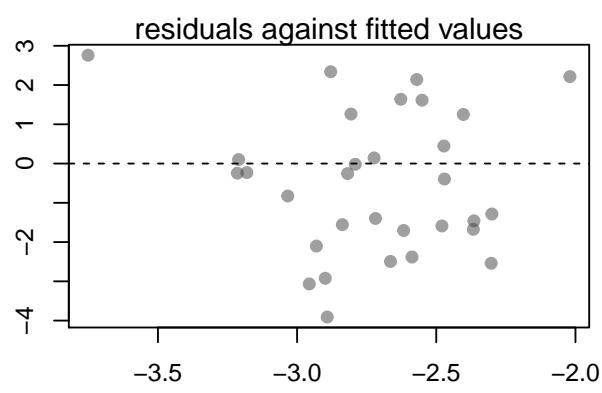
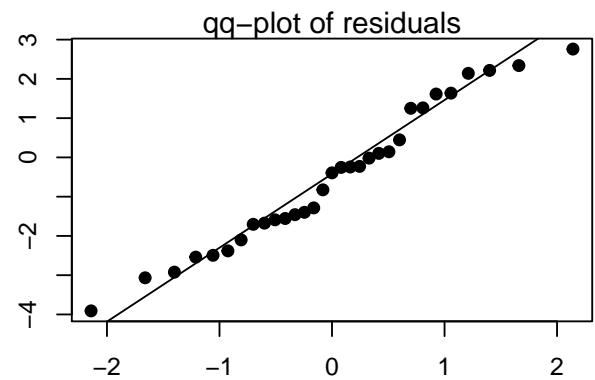
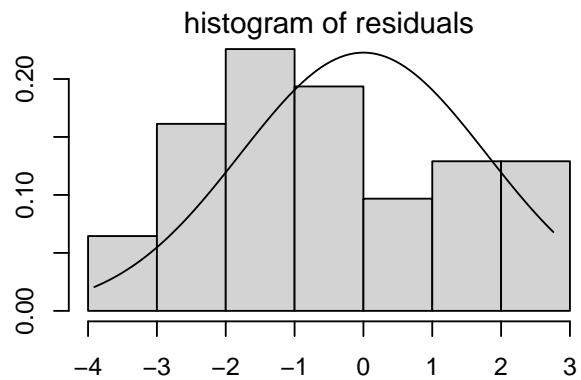
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Neocortex (/bodymass, log)



Model:  
Cerebellum (/bodymass, log)

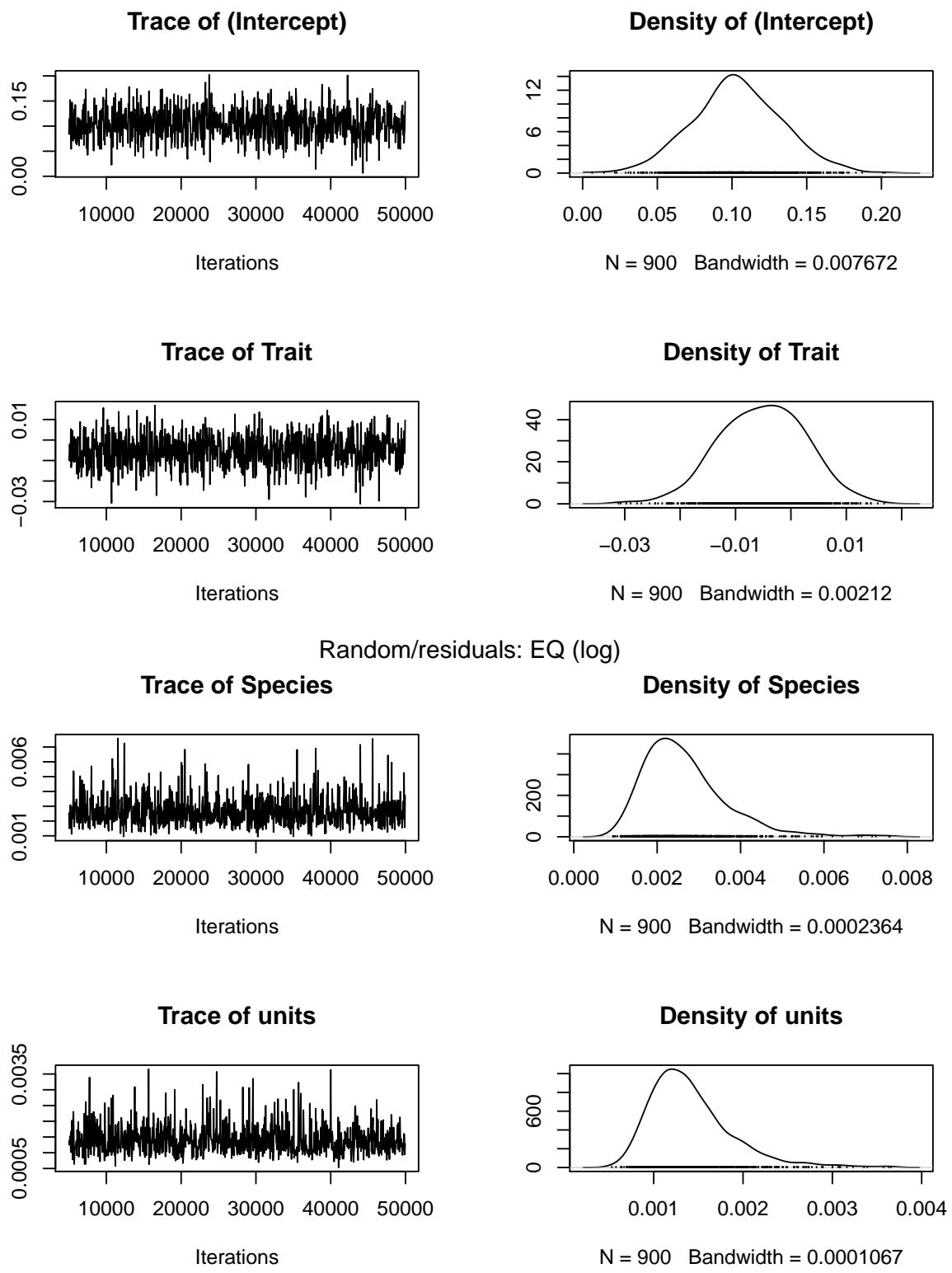


Model:  
Striatum (/bodymass, log)



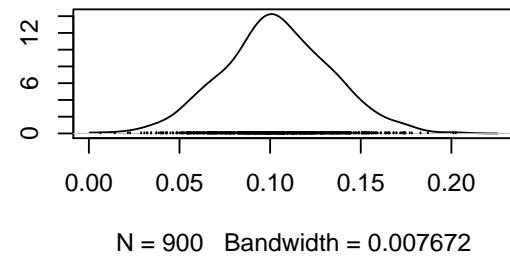
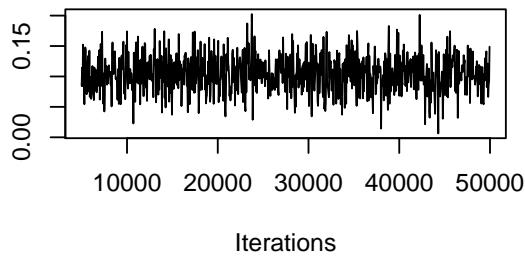
Model:  
MOB (/bodymass, log)

594 (b) Phylogenetic regressions: diversification and brain size  
Fixed effects: EQ (log)

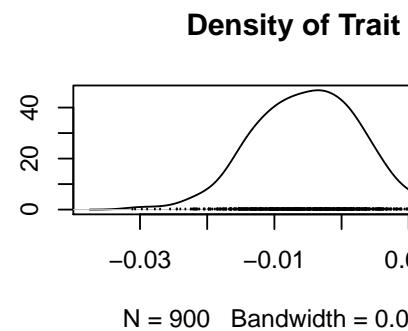
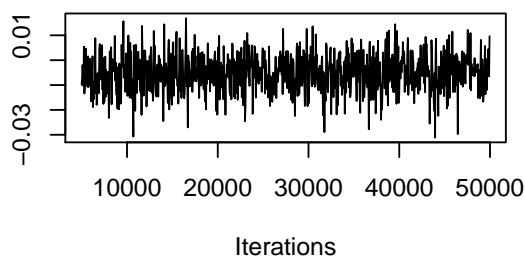


Fixed effects: Hippocampus (/bodymass, log)

**Trace of (Intercept)**

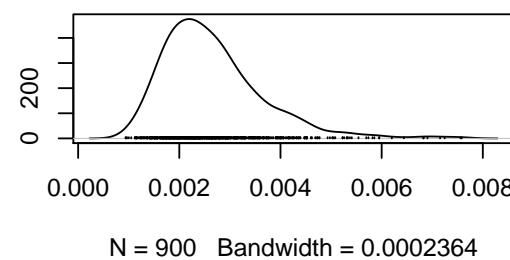
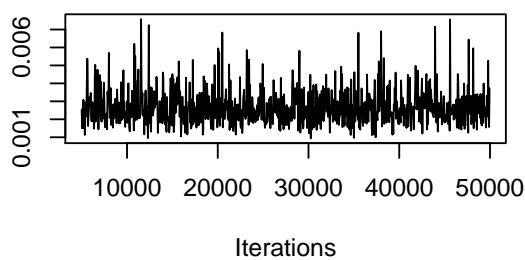


**Trace of Trait**

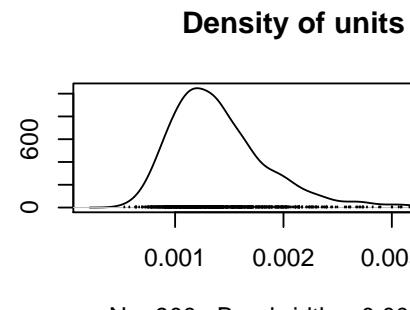
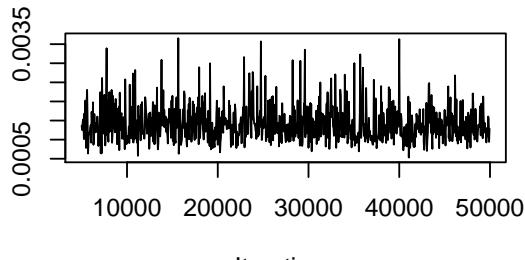


Random/residuals: Hippocampus (/bodymass, log)

**Trace of Species**

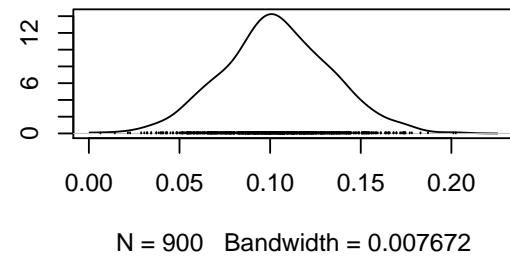
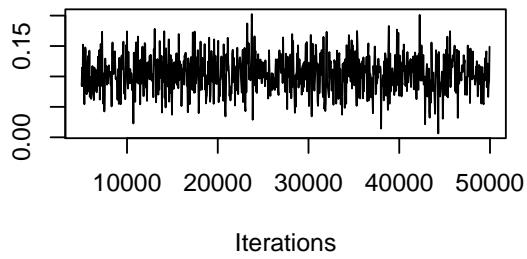


**Trace of units**

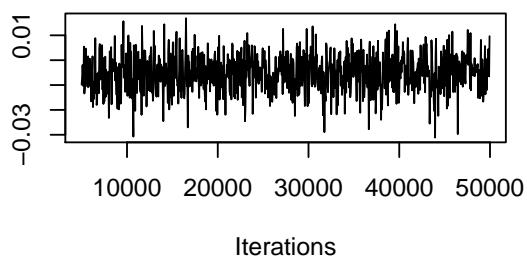


Fixed effects: Neocortex (/bodymass, log)

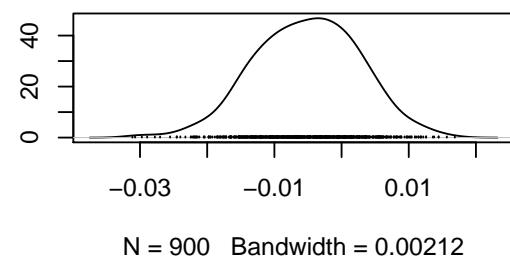
**Trace of (Intercept)**



**Trace of Trait**



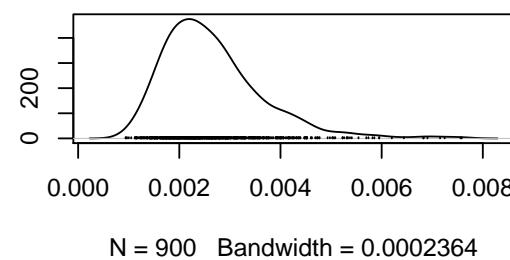
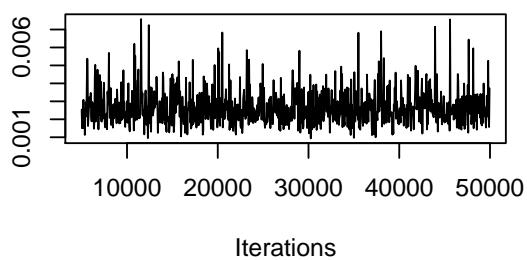
**Density of Trait**



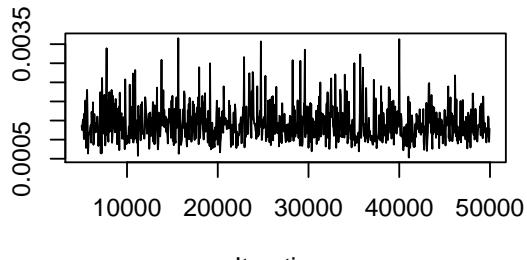
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Random/residuals: Neocortex (/bodymass, log)

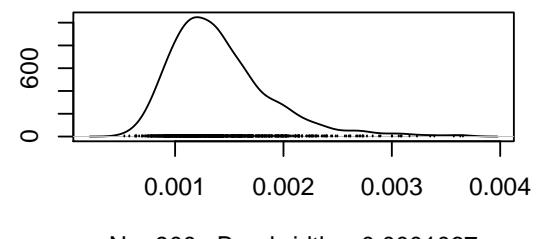
**Trace of Species**



**Trace of units**



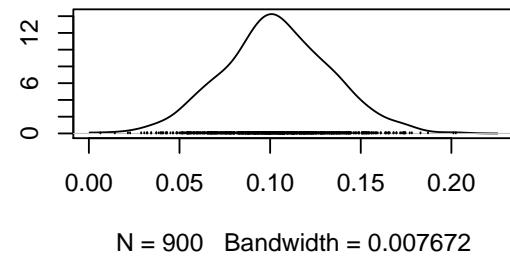
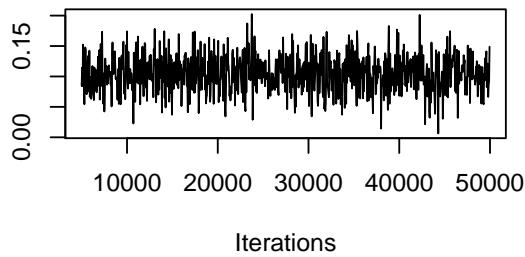
**Density of units**



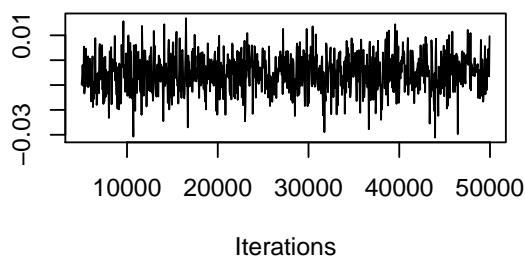
Fixed effects: Cerebellum (/bodymass, log)

**Trace of (Intercept)**

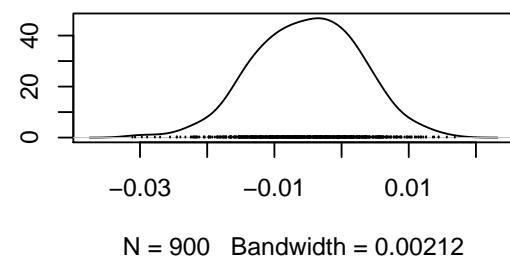
**Density of (Intercept)**



**Trace of Trait**



**Density of Trait**

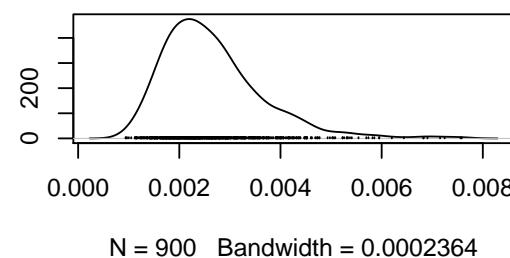
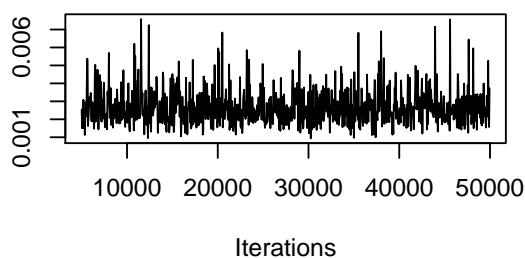


601

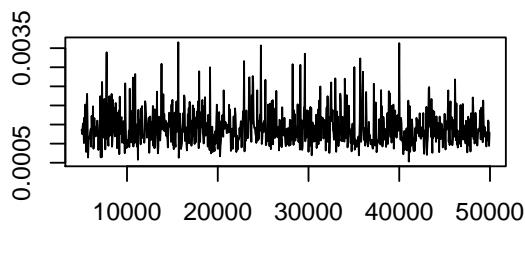
Random/residuals: Cerebellum (/bodymass, log)

**Trace of Species**

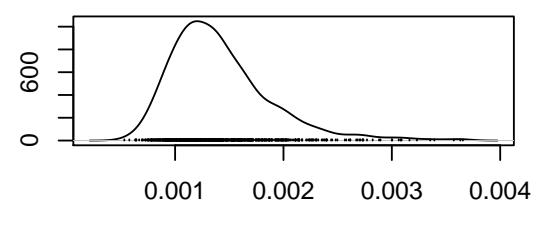
**Density of Species**

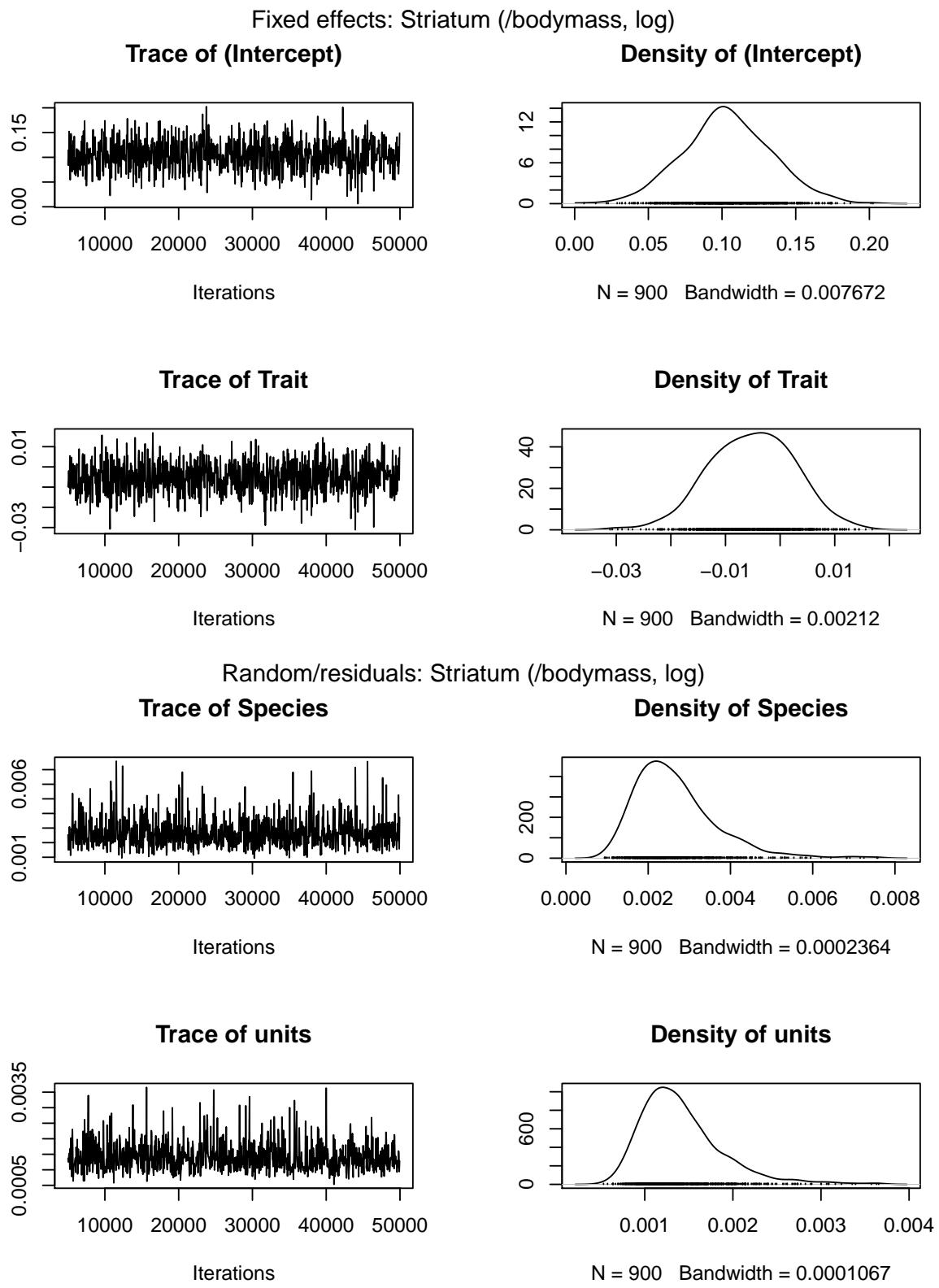


**Trace of units**



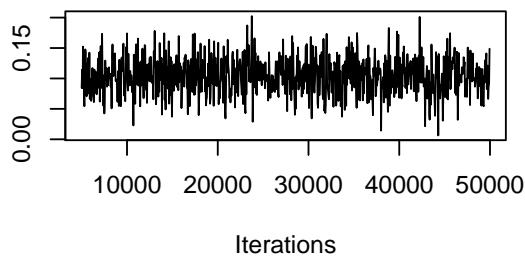
**Density of units**



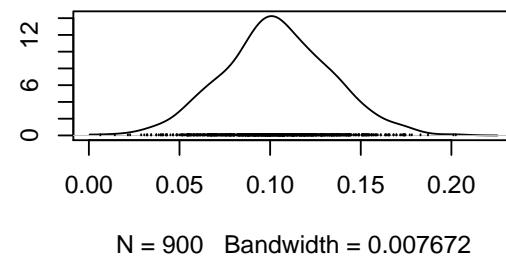


Fixed effects: MOB (/bodymass, log)

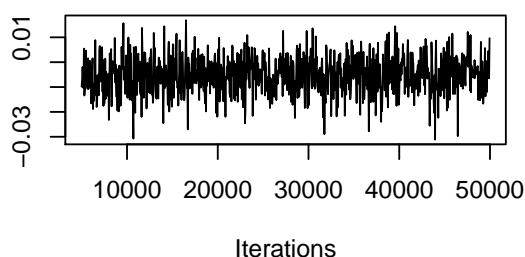
**Trace of (Intercept)**



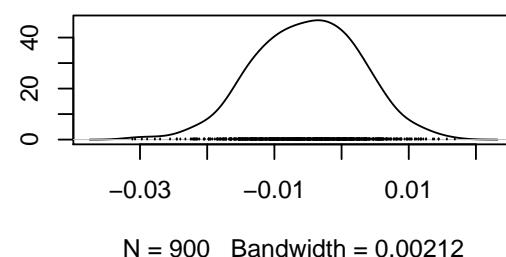
**Density of (Intercept)**



**Trace of Trait**



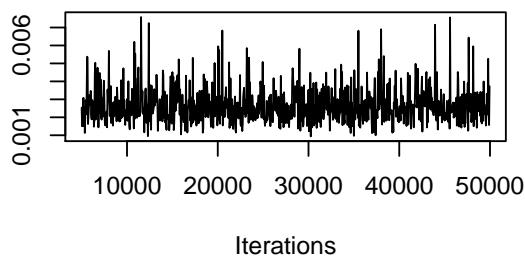
**Density of Trait**



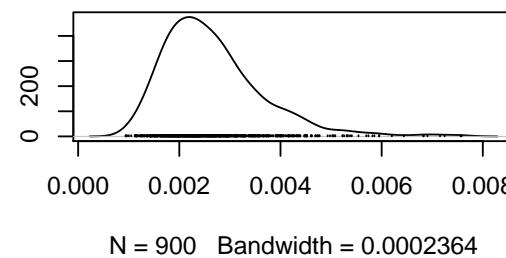
605

Random/residuals: MOB (/bodymass, log)

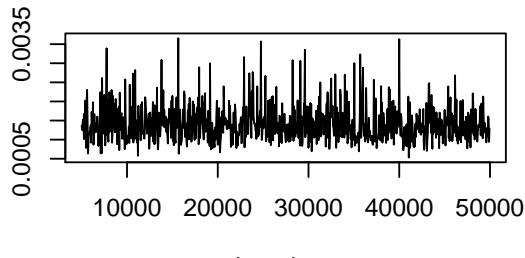
**Trace of Species**



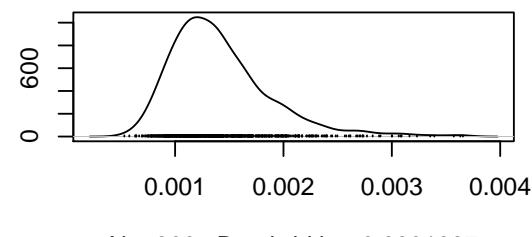
**Density of Species**



**Trace of units**



**Density of units**



606

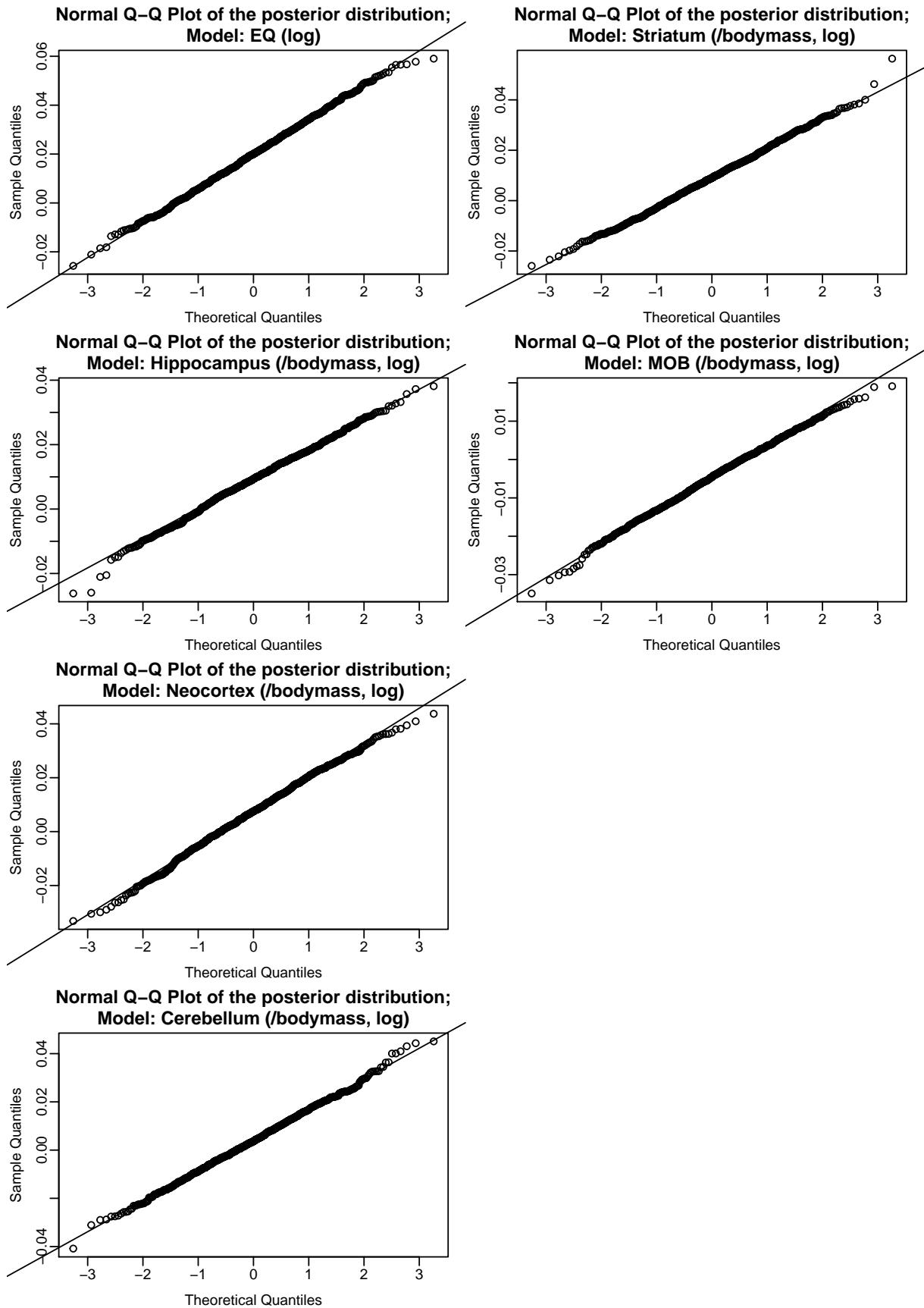


Figure S9: Model assumption check ‘Diversity and brain size’ | Q-Q plot of the posterior distribution and the expected Gaussian distribution

607 (b) Phylogenetic regressions: diversification and sympatry

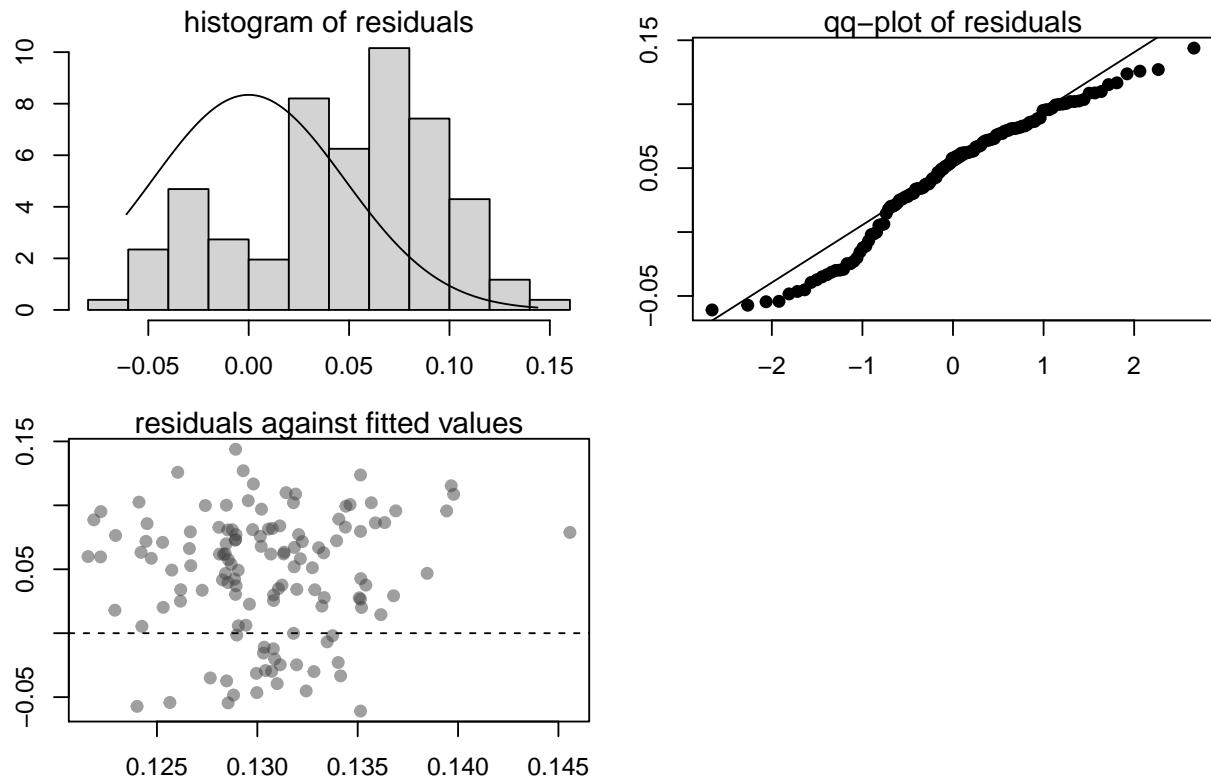


Figure S10: Model assumption check ‘Diversity and sympatry’| Depicted are the histogram of residuals, the Q-Q plot, and the scatter plot of the fitted values *vs* the residuals.

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