Dear Dr. Condamine,

We appreciated that you considered our manuscript with such careful attention and thank you for your time. We also greatly valued the benevolence of the reviewers while making constructive criticisms. We have done our best to address most of their criticisms. In particular, we checked the quality of the data set, as concerns were raised about the validity of the data used, and we repeated the analysis by weighting each brain area by the size of the whole brain (instead of the whole body mass), as this was suggested by several reviewers. We argue that weighting by body mass or whole brain nevertheless refers to different biological situations and therefore propose these two options conservatively. Finally, we now discuss the limitations of our work, especially in terms of data availability, measures of sympatry, and model assumptions.

We now provide a point-by-point response to each of the reviewers' comments. Our responses are in blue, and are preceded by the reviewer's point. We have quoted our changes in between quotation marks and highlighted them in the main text with a red font.

With our very best regards,

Benjamin Robira and Benoit Perez-Lamarque.

Dear authors,

Thank you for submitting your work (manuscript #548) to PCi Evol. Biol., which is much appreciated.

We have now received the comments from 5 expert reviewers (Dr. Orlin Todorov and four anonymous reviewers), which you will find associated to this decision. All five reviewers expressed positive comments about the manuscript, on which I agree.

However, I also agree with the comments raised during this round of review, and I would like to see a revised version of the manuscript. I think it's important to have clear definition of sympatry/co-existence to make predictions clearer. The definition of diet (frugivory) can be important to clarify too, especially to make improvements comapred to previous studies. In addition, there is apparently some issues with data combination, and a few issues with the analyses of the data. I do think these comments are crucial to take into account. The recent primate tree of Wisniewski et al. (2022 - PRSB) has been proposed, but I have important reservations about this tree. I reviewed this paper and many problems remains in the tree. Also their biogeographic analyses are poor, but I agree that this should be discussed in light of your inferences. I also think a revised title would better reflect the results.

Overall, I am opitmistic that such a revision process can lead to a recommendation but the study first needs improvements to attain this point. I hope these reviews will help you to improve your study.

On a personal opinion, I really enjoy the study and I concur with the general opinion that the manuscript addresses a passionating question, is already good and of high quality. I am impressed to see the amount and quality of data put together to address the question. As a macroevolutionary biologist, I remain a bit disappointed with the lack of figure showing the diversification rates over time. I see you have one in the Supplementary Material, what about using this to draft a figure for the main text? I know you have tables reporting the results for the diversification rates. I would also recommend the authors to put the ClaDS tree in the Supplementary Material, or along the figure with rates through time in a min-text figure. A last point that would be worth looking at is the fossil record

of primates. I leave this opportunity open to the authors but in macroevolution, fossils provide direct evidence for presence and species' traits.

I look forward to see a revised version of your manuscript. If you have any questions, please do not hesitate to reach me.

All the best,

Fabien Condamine, for PCi Evol. Biol.

We thank you for this feedback. Among the suggestions, we have addressed the following points:

- we provide in introduction a very basic definition of sympatry (now L58-59 "...the coexistence of primate species in the same biogeographic area (henceforth referred to as sympatry)..."), as this was also raised by a reviewer. We would like to highlight that we also refer to a more practical and quantitative definition of sympatry that we used (in methods: L328-336 "…when assessing the interplay between species sympatry and the evolution of frugivorous primates' brain architecture, we considered sympatry under different forms. To assess whether it affected brain size evolution, sympatry was added to classical phylogenetic models of trait evolution as an additional variable depicting the mean trait value of sympatric species (MC models), or as a density-dependent term (i.e. the total number of sympatric lineages at a given time; in DD_lin and DD_exp models). Then, to assess the directionality of the effect of sympatry on brain sizes, sympatry was used as a tested predictor in phylogenetic linear regressions, under two forms: the number of currently sympatric species, and the average range overlap with currently sympatric species"). We finally discuss the implications and limitations of this definition of sympatry in lines the "Limits" section (precisely in the paragraph L578-600).

- we now introduced the dietary guilds classification (L64-65).

- we changed the title to "Primate sympatry shapes the evolution of their brain architecture"

- we have now added two figures: one depicting the diversification rate over time and its relationship with sympatry (now Figure 5), and another one on the ancestral reconstruction of primate diet with comparison to fossil evidence (now Supplementary Figure S1). The latter figure indicates that our ancestral reconstruction of primate diet are consistent with fossil dental evidences used to inferred past diets (from Merceron et al., 2009 and Ramdarshan et al., 2012). We present this on lines 390 and 568-569. In addition, we have compared the results of our diversification analyses obtained with ClaDS2 with estimates of fossil diversity of primates through time (computed in Springer et al., 2012). We now indicate in the manuscript that we are estimates of diversification rates seems consistent with fossil data (lines 569-571). Straightforwardly, any further comparison to brain fossils could not be made, as such fossils give no information on the brain architecture in terms of size of the different brain areas, which leave no imprints on external fossilized skulls.

- we also worked on the layout of the figures (e.g. Figure 2 depicting biogeographic areas)

- we finally added a whole paragraph on the limits of our study (L545-600), to discuss many of the fair points raised by reviewers about the dataset, the methodology used, as well as definition (on diet, sympatry etc.).

Reviews

Reviewed by anonymous reviewer, 23 Jun 2022 19:33

Comments to the Author

Review of "Species sympatry shapes brain size evolution in Primates" (PCIEvolBiol #548)

This is an interesting manuscript that explores an important and controversial topic in evolutionary neurobiology – the selective forces shaping brain size and structure variation in nonhuman primates. The goal of this manuscript is to test whether sympatry predicts species differences in brain size or the size of certain brain regions (in frugivorous primates specifically). To accomplish this, they assemble new neuroanatomical data and apply phylogenetic comparative methods. They conclude that sympatry leads to a reduction in the size of the hippocampus and striatum, and that species in sympatry diversified more slowly.

This manuscript is very well written, and the analyses are thoughtfully executed. However, there some issues with the methods used (e.g., use EQ as a dependent variable, pooling of data from methodologically distinct resources, choice of brain regions to analyze). Accordingly, I suggest major revisions to this manuscript – my feedback it organized by section below.

Title

- I believe the title should more accurately reflect the results. In particular, the results suggest sympatry may affect the relative size of specific brain regions, not overall brain size, so a title of "Species sympatry shapes brain structure evolution in Primates" (or something similar) would be more appropriate.

We have changed the title as following "Primate sympatry shapes the evolution of their brain architecture".

Introduction

- The authors provide extremely clear and well-structured hypotheses and predictions. This is pretty rare in comparative work and is very much appreciated by this Reviewer.

We thank the reviewer for noticing it and making such a positive note.

- Prediction 2: Given that this prediction is centered on sensory information processing, why not examine V1 and AOB (instead of the whole neocortex)? Data is available for these areas.

In fact, the models require a lot of computational effort. We were limited by this, so we carefully inspected which brain areas most closely matched our reasoning, and for which the sample size was sufficient. If we are not mistaken, in the collated datasets, AOB was only available from the data collected by Decasien et al. (2017), where MOB data were also provided. Considering only the availability of measurements, 43 species were available for MOB measurements, but only 30 for AOB measurements. As they have similar functions, we therefore preferred the MOB. Similarly, the V1 region was only available for 70 species, compared to 98 for the whole neocortex. We therefore favoured the latter. We have added this explanation in supplementary material.

- Prediction 3: What about the role of the AOB in social contexts?

For the reason mentioned above, the AOB was therefore not considered. The AOB could indeed be important for the social context, for example for the olfactory recognition of the major histo-

incompatibility complex which may be important in sexual selection in primates. We do not deny that the sense of smell is indeed used for other purposes, outside the context of foraging. However, we believe that its role is more prominent in foraging (although most primates favour vision), and less so in social interaction. Thus, to keep it simple and understandable, we have chosen to mention the MOB only for the processing of environmental information cues during foraging.

Methods

- The methods are clearly explained.

Thank you for this positive note.

- The Navarette data should only be combined with other datasets for the neocortex and cerebellum, but not for the hippocampus or striatum (see their Erratum: https://doi.org/10.1159/000496658).

We had checked this erratum which dates from January 2019, so before this study was carried out. In the latter, they state that they have corrected the online supplementary materials, which we used.

If the author of the erratum further refers to the systematically lower values of hippocampal and striatum sizes in this dataset, it is not clear what the source of these discrepancies is, which are highlighted, moreover, on the basis of very small sample sizes (N < 10). One possibility is a less accurate measurement here, but as the authors point out, this could be due to within-species variability, previous inaccurate measurement, etc. We therefore cautiously took this variability into account by running the models on different random samplings across all datasets, which did not reveal any major differences between the different runs. In fact, we believe that the intra-species variation is smaller than the inter-species variation (a condition for the brain size measure to be a good indicator of cognition), and therefore this intra-species variability should be of minor importance. We now discuss it clearly in the "Limits" section, after the discussion (L545-600).

- Do % of overlapped range and # of sympatric species covary? It would be informative to see the results with these predictors modelled separately.

We thank the reviewer for this comment, as we noticed that this information was in the supplementary material but never mentioned in the main text. We have checked that the two variables do not covary to a large extent, which is a precondition for fitting the linear models, with the variance inflation factor (known by its acronym VIF). Therefore, we see no point in modelling them separately. We have now indicated this in the main text lines 366-371 (and removed it from supplementary) "Prior to fitting, covariates were transformed so as to reach more symmetrical distributions when adequate. Necessary assumptions on the normal distribution of residuals and homoscedasticity were visually assessed and pointed out no violation (see Supplementary Material, Model assumptions). In addition, we did not observe correlation issues among predictors (Variance Inflation Factor, $VIF_{max} < 2$, Mundry 2014)."

- PGLS models:

- EQ should not be used as a dependent variable to model relative brain size. Rather, body size should be included as a covariate and brain size as a dependent variable.

To address this point in more detail, we refer the reviewer to the Supplementary Material (Section "Accounting for allometry in models of brain size evolution"), in which we now address this question. We demonstrate why taking body size as a covariate does not appear to be a reasonable approach. In particular, we point out that it has (1) little biological relevance given both variables face similar constraints, (2) probably causes statistical problems of correlations between predictors, (3) may hamper the effects of other covariates. Instead we now carry two types of analyses: we measured the sizes of the different brains areas (i) relatively to the whole body mass or (ii) relatively to the whole brain size. This therefore measures different types of energetic allocations, with or without being directly impacted by the absolute body size (see below).

- It may be more appropriate to model region size relative to rest of brain size (rather than body size), since if sympatry drives selection on body size, this could confound results.

We agree that modelling the relationship between brain area size and whole-body size, or whole-brain size, does not point to the same biological scenario. Pondering by body size reflects a change in overall energy allocation, whereas reflection by brain size reflects a change in brain architecture. Since the latter is also interesting, and still relevant to the hypotheses we mentioned, we have also run it now. We added a sentence to mention it in the method section "Second, we also the analyses considering the ratio between the brain area volume and the whole brain volume, as this might reflect within brain energy reallocation (i.e., mosaic evolution of the brain). This yielded similar results (see Supplementary Material, Weighting the size of brain areas by whole brain size), thus we mainly focus on results considering the ratio with body mass. " and in the results "We also conducted the analyses considering weighting by whole brain size, which more likely reflects the mosaic evolution of the brain. Both approaches yielded similar results (see Supplementary Material, Weighting the size of brain areas by whole brain size), therefore we only present the case when weighting by body mass.

In addition, we also checked whether body mass was affected by sympatry. We observed that the best supported model was the matching-competition (MC) model. In other words, sympatric species tend to diverge in their body mass by being either large or small (i.e. character displacement). Thus, it explains why no overall trend was identified using PGLS (i.e. testing for a linear relationship between sizes and sympatry). We underline this in the results with the sentence L432-437: "Furthermore, we also investigated the influence of sympatry on body mass, which could be a confounding explanation for the observed patterns (Smaers et al. 2021). We found that the evolutionary history of body mass is best explained by MC models (Supplementary Figure S6). In other words, species in sympatry tend to diverge towards being large or small. There is thus no overall linear relationship of the whole body mass with sympatry, explaining why we found no effect of sympatry variables on body mass in PGLS; see Supplementary Table S2).". MC models are in nature very different from DD models, which were the best supported one for some brain areas. Thus, the sympatry effect on body mass should be unrelated to the one observed on brain size.

Results

- The results are clear and well-written.

- It is not accurate to report significant results for the hippocampus when p = 0.058 (>0.05), unless the authors are using a different significance cutoff.

We now consider a strict binary cutoff at 0.05. We have therefore changed the wording to "Conversely, we found that the average percentage of overlapping range **significantly** correlated, **or tended to correlate,** with the relative size of brain areas that were better fitted with models considering sympatry...".

Discussion

- Line 383: "Bigger brains are not necessarily better" – when comparing brains across species, we also need to consider species differences in brain composition

This is true, and indeed the whole point of this paper (although it is certainly not the first time, nor the last, this has been put forward). As this part of the sentence seems to be misleading, we have deleted it.

- Line 409: "As a result, it might even generate a selection for smaller brains." – There is no evidence for this.

We agree with the reviewer that the current evidence is not for the whole brain, but only for certain areas. We have therefore reworded the sentence as follows (L493-494): "As a result, it might even generate a selection for smaller brain areas involved in foraging".

- How do the reported results for the hippocampus relate to previous work on the socioecological correlates of this region (Todorov et al. 2019; DeCasien et al. 2019; Schilder et al. 2019)?

It is difficult for us to draw parallels with the cited studies, as they deal with the influence of within-species socio-ecological approximation on cognition (e.g. food preference, group size, etc.), whereas the present study aims to determine how possible cross-species interactions are related to cognition. To refer readers to these key findings nonetheless, we now highlight that (L480-484): "The hippocampus in particular, may have played a considerable role in the evolution of primate-like behaviours (Schilder, Petry, and Hof 2020), driven by the changes that primates faced in their ecological environment (e.g. the spatio-temporal distribution of the food, DeCasien and Higham 2019), or by the social environment that they faced (e.g. the number of conspecifics to interact with, Todorov et al. 2019; DeCasien and Higham 2019).

I hope the authors find these comments helpful in revising their manuscript.

We did indeed find these comments very helpful, and we kindly appreciated the time the reviewer took to make them. We hope that our responses meet their expectations.S

Reviewed by anonymous reviewer, 13 Jun 2022 14:05

This a very interesting manuscript where the authors test the hypothesis that species competition for resources in Primates differentially impacts the evolutionary trajectories of the (relative) sizes of several brain regions. To do this they compile a comparative dataset of trait (brain regions' sizes), distribution, and phylogenetic data, and implement a battery of phylogenetic comparative methods mostly based on evolutionary modelling. The paper is carefully and well written, it is

methodologically very sound and it is a fantastic example of a well conducted study based on a phylogenetic comparative method approach. I highlight the careful consideration the authors had for dealing with uncertainty both in the data as in the analytical pipeline, which is rare to see in the field.

Thank you for these positive comments.

Nonetheless, I have a main concern regarding the author's approach. While I admit that the hypothesis is very intriguing, I suspect that there could be a significant conflation of sympatry with competition. First of all, because current sympatry might reflect coexistence, not competition.

We agree that sympatry is not synonymous with competition and we hope that this is not the message we have conveyed. In fact, we suggest that competition is certainly the explanatory mechanism (here specifically indirect competition), but we have mentioned hypotheses where there might be some kind of (indirect) mutualism/facilitation (i.e. Hypothesis 3). We deliberately use the term sympatry and not competition. To be clearer, we now state in the introduction (L58-62): " Because the coexistence of primate species in the same biogeographic area (henceforth referred to as sympatry) can affect multiple aspects of their social-ecological environment, brain areas may be affected differently by sympatry. Considering a simplistic functional picture of the primate brain, one can hypothesise how sympatry might, through direct or indirect competition or cooperation, influence the relative benefits of cognition (i.e. the balance between its benefits and its costs).". We also removed the mention of competition for food to replace it with the idea of interaction around food. Thus, we now state (L42-44) "Because of direct and indirect interactions linked to resource availability, the presence of heterospecifics..." instead of "Because of competition for food between these species, both direct and indirect interactions between heterospecifics…".

Second, and specially in Primates, under the label of "frugivory" there is a plethora of different dietary strategies, as basically all Primates could be considered frugivorous animals. Although this is a problem that many other papers also have, here it could be potentially more problematic as what the authors are trying to model explictly are the effects of competition on cognition. But if there's no or little resource compsumption overlap, it could be argued that there would be hardly any competition despite sympatry.

Competition, through depletion, could be particularly influential on the memorisation of spatio-temporal patterns of food species included in the diet of primate species. However, it is important to note that associative reasoning, which might be essential in the evolution of cognition (Lind, 2018; Lind and Vinken, 2021) and might support foraging, is not necessarily and solely based on contingency between plant species in an animal species' diet (see Robira et al., 2021). For example, a species could use the phenological cross-correlation between two species (e.g. A and B), while targeting only one of the two species (e.g. B, and A is only used to infer the phenological status of B). If another animal species exploits the other species (i.e. A), then this weakens the phenological relationship between A and B, making it more difficult to infer the status of B. Thus, it is possible that the behaviour of any frugivore species, even with poor dietary overlap, might influence the environment perceived, and processed, by another forager. This is what we argue when we discuss the idea of increase in noise overall. We now added it more clearly in the introduction L72-77.

In fact, it is known that currently sympatric primates tend to partition niche space quite considerably. By looking at the data it is not completely clear for me which species were finally considered as frugivorous, but for example, all or most platyrrhine primates seem to be above the 20% threshold for being considered frugivorous.

However, this hides the fact that some species specialize in eating insects and tree exudates (Callithricins), others are seed predators (Pithecids, they forage for hard fruits impossible to eat for other species to get to the seeds through morphological adaptations) and others (Alouatta) rely heavily and seasonally on leaves without being as "folivorous" as colobines.

The reviewer is correct, but it is important to note that in the case where insect feeding, or tree exudates, is most important, the species would have been discarded. Indeed, folivory and frugivory rates were not necessarily equal to one. This approach therefore alleviates some of the conflicting situations raised here by the reviewer. We have now clarified this in lines 216-219 and 316-317.

 Moreover, they segregate vertically in the three-dimensional canopy. This is not to say that there's no competition or that there wasn't in the past, and while I don't have a clear solution to this problem (and I aknowledge that the author's used two different thresholds for assignign categories), I would like to see a more nuanced discussion and interpretation of results regarding this possibility. Big dietary categories are useful for macroecological studies as they allow to incorporate a lot of data, but the lack of detail perhaps is at some point harmful. I would like to see the authors thoughts on this reflected in the paper. Nonetheless, that the niche partitioning in primates could have also a "cognitive dimension" is a possibility that has been rised previously in other primate brain studies too (see for example Aristide et al 2016 PNAS for brain evolution in platyrrhine primates).

We believe that the point raised by the reviewer is not incompatible with the consideration of large feeding guilds, such as "frugivores", even though the actual feeding overlap within the guild may be small. Indeed, as dietary specialisation might rhyme with cognitive specialisation, it is possible that the "number of sympatric species" actually reflects the "level of niche partitioning" that is at play, and thus the level of "cognitive specialisation" that is observed. Although some species may specialise in hard-to-reach food, thus requiring high cognition, specialisation is generally associated with reduced flexibility, and thus cognitive abilities. We have now added it to the introduction as follows (L102-111): "Furthermore, the competition between sympatric species from a given dietary guild may be lowered by specialising in different food resources, i.e. niche partitioning. While a species might specialise in food that is difficult to access and requires high cognition (e.g. through the use of tools), specialisation is generally associated with reduced flexibility and thus lower cognitive abilities (Henke-von der Malsburg, Kappeler, and Fichtel 2020). A strong association between niche partitioning and cognitive specialisation has been previously raised in primates (Aristide et al. 2016). From this perspective, a high level of sympatry could be enabled by high cognitive specialisation toward specific food types, requiring less long-term memory abilities, and could also result in smaller hippocampus sizes in highly (specialised) sympatric species.".

Additionally, and although I think the authors did their best to tackle uncertainty regarding biogeographic reconstructions, explictly akwnoledging the limits of extant-only/neontological approaches would be recommended. For example, the authors would not want to miss the recent paper by Wiesniecki et al (2022) PROC. B: https://royalsocietypublishing.org/doi/full/10.1098/rspb.2021.2535

We agree with the reviewer's view. Biogeographic reconstructions are still in their infancy, despite their recent growth and considerable improvements. In particular, the size of biogeographic zones, although ecologically and phylogenetically relevant (as shown by the work of Kamilar cited), is a crude approximation. Furthermore, biogeographic history should not only take into account species movements, but also tectonic history and other such topographic/historical events that might act as barriers to movement. The models we used do not do this. In addition, we do not include fossil data in our biogeographic reconstructions, which provide quantitatively limited improvement (see Wiesniecki article and associated reviews), and can suffer from other sources of biases (e.g. rarity of fossils with heterogeneous distribution). We acknowledge these limitations in a dedicated paragraph about the limitations of the study (L562-577).

Reviewed by anonymous reviewer, 13 Jun 2022 18:59

I have read with interest the preprint "Species sympatry shapes brain size evolution in Primates". I have several comments and suggestions which I hope the authors will find useful to improve their work.

We thank the reviewer considerably for such a detailed review and sympathy despite many disagreements. We have done our best to answer the doubts and questions that have been raised.

Major comments:

My first concern regards the hypothesis, as it is unclear why sympatry is expected to influence brain evolution. As noted by the authors, the social brain hypothesis has been porposed as a general explanation for brain evolution. I note that although the hypothesis was initially developped with primates in mind, it has been extended to other vertebrates (see e.g. Dunbar and Shultz 2007), although support for it beyond primates is mixed. The social brain hypothesis suggests that more complex interactions among members of a given species will lead to selection for greater cognitive abilities. The emphasis of the social brain hypothesis, as I understand it at least, is on the interactions among members of a given group. In fact, part of the reason of the mixed support in non-primate vertebrates is the fact that group size per se is actually a rather bad proxy for social complexity, and we lack the detailed observations of social interactions among group members that exist for primates in other species. The social brain hypothesis might well not apply to non-primates, but some of the tests likely do not capture its essence, that it that complex social interactions favor larger brain size. In fact, in their review Dunbar and Shultz (2007) propose different proxies for social complexity for non-primates (see e.g. Fig 3). Thus, following from this argumentation, sympatry is just as likely a bad proxy for interspecific interactions between sympatric species, as some sympatric species are unlikely to interact much while others might do so much more. This is one of the reasons why I find the argumentation presented in the manuscript unconvincing.

As it is commonly stated that "all models are wrong, but some are more useful than others", we would argue that "all proxies are wrong, but some are more useful than others". We used a very large definition of sympatry as "being in the same area at the same time", This is advantageous as it includes a very broad set of possibilities on what would be the proximate meaning of sympatry (e.g. direct or indirect mutualism to competition), it relaxes initial constraints when modelling past history (otherwise, the current picture of sympatry would be such narrow that the inference of past history would be too biased), and it even can remove biases due to recent changes (e.g. important effect of human activity on primate population and distribution). However, we do agree that this can have

considerable impact on our conclusions, as illustrated with the case of group size for social cognition. Thus, we now clearly specify that our proxy may have consequences in our analyses in the discussion, in the "Limits" section (L578-600).

Secondly, and related to the point above, the authors propose that sympatry could both lead to increased or decreased sizes of brain structures, which makes me wonder how they expect to actually reject their hypothesis, if any relationship between sympatry and brain structure size would support it. The argument in favour of decreased brain size is actually rather weak, as they suggest high competition would lead to reduced resource availability and thus less investment into brain size. This seems somewhat far-fetched, as studies have proposed a diversity of means by which individuals may mitigate the negative effects of interspecific competition for resources, through behavioural changes, or changes in which resources are exploited or prefered.

We are surprised that the argument of reduced food availability (and increased noise in the inference of availability, which is also central to our reasoning) is considered weak, as it is the mainstay of theories on the evolution of foraging cognition (see Rosati, 2017 for example). We have reinforced our argumentation in the introduction (see L63-77).

However, the reviewer is right that species may also develop different behavioural strategies in relation to changes in food availability patterns. On this aspect, we would nevertheless like to point out that this is not inconsistent with what we argue in this article. First, species may rely on food species as environmental cues (e.g. through cross-correlation of phenology to infer temporal availability, Robira et al., 2021) that are not part of their diet. Depletion (and thus increased variability) imposed by other animal species could therefore still play on the performance of a given level of cognition in the environment. We now added it in the introduction L72-77: "This complexification may also occur when the dietary overlap is inexistent, as foragers may rely on phenological cross-correlations between plant species (e.g. if plant species A produces fruits earlier in the season than plant species B, thus the availability of B fruits can be predicted based on the availability of A fruits, even though A is not consumed by the forager, Robira et al. 2021). Food depletion may thus weaken these cross-correlations and make food availability predictions less reliable."

Second, diet is generally associated with cognitive abilities (e.g. Decasien et al., 2017). Thus, dietary specialisation could also be related to variation in cognitive abilities. In particular, although on rare occasions dietary specialisation may lead to higher cognitive abilities (e.g. if the specialisation is on a food that involves the use of a tool), specialisation is generally associated with a lower amount of information to process (in terms of quantity and diversity), and should therefore also imply lower cognition. This is therefore also not inconsistent with what we have observed. Given the comment of reviewer 2, we now introduce it L102-111 "Furthermore, the competition between sympatric species from a given dietary guild may be lowered by specialising in different food resources, i.e. niche partitioning. While a species might specialise in food that is difficult to access and requires high cognition (e.g. through the use of tools), specialisation is generally associated with reduced flexibility and thus lower cognitive abilities (Henke-von der Malsburg, Kappeler, and Fichtel 2020). A strong association between niche partitioning and cognitive specialisation has been previously raised in primates (Aristide et al. 2016). From this perspective, a high level of sympatry could be enabled by high cognitive specialisation toward specific food types, requiring less long-term memory abilities, and could also result in smaller hippocampus sizes in highly (specialised) sympatric species.".

A reduction in brain size seems like quite a high price to pay, especially given the rather well documented benefits of enlarged brain size (see e.g. Benson-Amram et al. 206, Sol et al. 2005, Sol et al. 2008, Jimenez-Ortega et al. 2020, to name a few).

As noted in the article, brain size is the result of drivers and constraints, and thus a balance between benefits and costs. Indeed, cognition is not without costs: the most direct are energetic costs, but there are also developmental costs, interference (see Fagan et al., 2013 for a discussion of spatial memory, for example), etc. It has thus been clearly demonstrated that species experiencing seasonality (i.e. the opposition between an energy-rich and an energy-poor period) have a smaller relative brain size than others (the costly brain hypothesis, illustrated in van Woerden et al., 2010: 2014), although the brain size nevertheless allows them to buffer the challenge of this seasonal pattern (the buffer hypothesis, illustrated in van Woerden et al., 2012). Thus, one should not confuse absolute benefits, which as the reviewer notes, are always large, with relative benefits, which can vary considerably. It is the latter that we are concerned with here. To reinforce this point, we have added (bold) to the initial sentence L89-90: "Under these (non-exclusive) hypotheses, sympatry could stimulate or hinder the evolution of cognition by affecting the **relative** benefits that cognition provides".

In addition, and perhaps more importantly, it is unclear why sympatry would lead to changes in brain size at the species-level, rather than increased variance among populations, based on the degree of / number of sympatric species. What I mean is that if sympatry causes competition, it would be only the populations that compete with other species for food which would be under the selection pressure to modify brain size / brain structure size, it is unclear why populations not under said selection pressure would change at all. For example, populations of two sympatric species show greater pre-cigotic isolation than allopatric populations of the same species.

We are not sure we understand the reviewer's point of view, but it might arise from the difference of time scales (between macroevolution and microevolution). Here, we look for (and find) macroevolutionary imprints of sympatry on brain size evolution: species that tend to leave in sympatry with other primates are more affected than species that don't. We can expect also to see differences between populations (on shorter time scales) but it will require (i) that brain size evolution is fast enough to be different between recently isolated populations and (ii) to have enough samples per population to compare populations in sympatry versus in non-sympatry. Making such micro-evolutionary analyses between populations are out of the scope of our study, but it will be an interesting follow-up analyses of our study.

In addition, body size is not taken into account in the hypothesis, but I would imagine that larger species are likely to be much less affected by sympatry than smaller ones, as the larger species will be much more efficient at defending a limited resource against heterospecific competitors than smaller species, hence the effect of sympatry might not be equal across all species.

Again, we reinforce the fact that the assumptions are not just about competition. Secondly, according to this reasoning, there would therefore be a positive advantage to have larger body size in sympatry. As an additional analysis, we therefore investigated whether sympatry influenced body mass, both by using models of trait evolution including sympatry, or by running the PGLS with body mass as an output variable, in a manner analogous to models run on brain size. We found that body mass was best predicted by MC models, coherently with the idea that species tend to evolve divergent body masses (i.e. character displacement). The supported models about the effect of sympatry on brain size (DD models) thus highlight a very different dynamics, which renders unlikely a confounding effect of body mass (see results L432-437).

I also have important concerns regarding the data and methods used to test the hypothesis.

Firstly, brain size, and more importantly brain structure sizes, were collated from different sources. How did you ensure that the data were comparable? Methods, sample sizes, etc likely differed across studies. How did you deal with sexual size dimorphism? Were data collated for both males and females? I imagine all were adult specimens?

It is well known that data from different datasets can vary (see reviewer 1's point about the Navarette dataset, for example). Much of the data collected on brain size is opportunistic and has been scattered over time, inducing a change in methodology. Yet, we believe that it remains a valuable source for analysis. Therefore, to account for this variability, we deliberately ran the models several times by randomly sampling a value from the possible data sets. This revealed an insignificant variation in the results, which we believe is sufficient to highlight the robustness to possible measurement differences. This is now discussed in a dedicated section entitled "Limits" (L546-561).

For brain size the authors estimate encephalization quotients, but use of an ANCOVA approach would be much more appropriate from a statistical point of view (see e.g. Freckleton 2002, García-Berthou 2001, Nakagawa et al. 2017).

ANCOVAs are used when a predictor is categorical. In our phylogenetic regressions, to which we assume the reviewer is referring, we used only continuous predictors. Nonetheless, the reviewer remark might generally have been about the use of relative brain size as variable of interest, as it is suggested the weight as a predictor variable, following the cited work. We have investigated this possibility with simulations (see Supplementary Material), and show that considering body mass (or brain size) as a predictor, and not a weight, should not yield to different results and might even be more biased. Thus, we did not follow this advice.

For brain structure sizes the authors use a ratio between brain volume and body mass, which is much more worrying given that relative brain size is assumed to vary among species, as they calculate EQ. If relative brain size is assumed to vary among species, and the authors assume that there is at least some degree of mosaic evolution of brain structures, whole brain size would be the appropriate means to adjust structure sizes based on allometry, i.e. the expectation is that the structure size will respond to changes in brain size or at least will change in size relative to the whole brain. Again, as mentioned above, analyses should be done including brain size as a co-variate in all analyses.

We would like to point out that EQ is only one variable tested here, and that it was insensitive to sympatry. We also present a new analysis that highlights how body mass is sensitive to sympatry history. However, other reviewers have raised the point that it would make more sense to weight the different brain areas by whole brain size. We therefore also provide results when whole brain size is used as weight instead of body mass. Results were unchanged. We now present these two types analyses (by weighting by the body mass or by weighting by the whole brain size) as these two analyses have different interpretations.

Regarding the addition of body size as a covariate and the non-use of relative brain size as an output variable, we refer to our response to the other reviewers, where we show, based on simulations, that this is a biased approach in our case.

To estimate sympatry the authors used distribution maps from the IUCN red list. However, the maps are estimates of species distributions, but not always specifically based on actual observations of species. How did the authors verify that said maps coincided with actual registered sightings of the species, especially given these were used to estimate sympatry.

The reviewer is right. The IUCN maps are not necessarily based on actual observations. They are also adjusted according to expert opinion, specifically for each species. We humbly admit that we are far less qualified than these experts to comment on these distributions for each species. We therefore regret that it is not possible for us to test the validity of these maps more rigorously. We now discuss this limitation of our work, including those linked to IUCN maps, lines 578-600. However, we must emphasise that the IUCN maps are used repeatedly in macro-ecological studies, as there is no other such comprehensive source of species range.

I also worry about the use of biogeographic analyses to estimate 'history of sympatry' along the primate phylogeny. Such reconstructions of ancestral distributions make the assumption that the factors that determine a species' distribution range have remained stable from present to the past, which seems unlikely.

As we understand it, the reviewer is addressing the point here that the biogeographic reconstruction model does not take into account the evolution of habitat suitability, which is true. However, it is likely that the current habitat preferences of extant species do not match those of the species' ancestor. It seems reasonable to assume that the habitat preferences of species have evolved in parallel with changes in habitat conditions. Therefore, the extent estimate should remain insensitive to current criticisms. It is true, however, that the quality of these reconstructions depends on a large number of factors that are oversimplified in the scenarios currently considered (see our response to reviewer 2), as well as on the size of the biogeographic areas we have considered. To consider this uncertainty in the biogeographic reconstructions, we re-run the analyses 10 times with different biogeographic reconstructions (see lines 298-301). We now discuss the limits of biogeographic reconstruction lines 578-600.

In the Methods section the authors surprise readers by anouncing that they also checked for correlative patterns between primate brain size an ddiversification rates, however this does not relate to their original hypotheses, or it is unclear how it relates to them. I would suggest that either they include this question in the Introduction or just leave it out, as it seems rather tangential to the hypothesis being tested.

We think this is important because diversification is a marker that can help determine the importance of certain traits: for instance, a positive correlation between a given trait and diversification can be a sign of evolutionary success. We now better introduced these ideas at the end of the introduction (see L118-122 and 129-132).

In line 208-209 the authors state that they "fitted phylogenetic models the evolution of the size of different brain areas independently". However, this assumes completely moisaic evolution of brain structure sizes, which is not the case for primates (see e.g. Barton and Harvey 2000, Finlay and Darlington 1995).

The reviewer is right. We are aware of this point, and it could be resolved by a structural equation modelling approach, in which the different brain sizes are predictors of each other. However, we were confronted with the large inhomogeneity of the sampling of the different brain sizes: the number of species with all the different brain areas measured is considerably too small to perform structural equation modelling. As we were not aware of any other methods to account for the residual dependence between the sizes of the different areas, we therefore considered independent models. To acknowledge this choice, we now state (the bold part is the change) L236-238 "using linear models **independently for each brain area. Although it does not explicitly consider the potential**

independence between brain areas, we modelled independently each brain area to preserve the maximum power (i.e. the largest sample size) in each analysis"

Furthermore, some of the models of trait evolution are specifically designed to test whether inter-specific competition could influence phenotypic evolution, however as I argue above, I would expect changes in particular functional traits linked to resource acquisition, it is unclear why brain size, or brain structures, would respond directly to competition. The DD models assume rates of phenotypic evolution are influenced by species richness (see Morlon et al 2016), but these are based on theory on adaptive radiations, where available niches become filled as the radiation progresses (and lineage diversity increases) and thus niche partition becomes increasingly finer, all of which is expected to influence the rate of phenotypic evolution. It is not clear how these models relate to the hypothesis being tested here.

The DD model (described in Drury et al., 2016) assumes that the rates of trait evolution are (positively or negatively) affected by the number of lineages. Adaptive radiation can indeed be modelled using the DD model (then, we expect a negative relationship between trait evolution and time of lineages). Here, we find a positive relationship, meaning that the tempo of brain size evolution increases with the number of sympatric lineages. In other words, the DD model can be applied to a broader context of density-dependences and not only adaptive radiations. We have clarified this in our methods section (lines L276-279).

Finally, in the Results the authors first find that models that do not include sympatry best explained the evolutionary history of EQ, neocortex and cerebellum. They apparently also fitted OU models to explain trait evolution, however it is unclear why they expected an OU model (especially with a single optimum value) to explain evolution of brain and brain structure sizes. In addition interpretation and fit of such simple OU models has been questioned (see Cooper et al. 2015).

OU models are among the "null" models that do not take sympatry into account in our analyses. Since brain size is strongly limited by energy intake, one would indeed expect brain size to evolve around an optimal value, as modelled by OU models. Interpreting the good fit of OU model as a sign of stabilizing selection has indeed been questioned. Yet, in our discussions, we do not interpret the OU explaining the evolutionary history of EQ, neocortex and cerebellum as a support of a simple stabilizing selection *per se*, we only interpret it as a likely sign that the evolution of these brain areas is induced by multiple constraints (see L401-402 and 453-457).

Reviewed by anonymous reviewer, 19 Jun 2022 00:04

The paper aims at evaluating the effect of sympatry on the evolution of brain size in Primates species. The main assumption of the study is that cognitive abilities are associated with the number of species sharing the same environment due to competition for food between species and direct and indirect interactions between heterospecifics. The topic of brain evolution in Primates has been extensively studied, and the role of ecological and social factors has been tested with variable results according to the sampling design. In this context, the topic of this study is important because it provides a new perspective focusing on the interaction among primate species. However, I found that some ideas and criteria used to define the variables under study should be better explained (see comments below).

In the Introduction, the authors should clearly explain the definition of sympatry used throughout the study. According to the methods used, it seems sympatry is defined as species sharing the same biogeographic area. Given the wide geographic extension of the areas analyzed, the inclusion of two

species as sympatric not necessarily implies a direct interaction between them (e.g., Ayres and Clutton-Brock, 1992). Consequently, the hypotheses proposed, which assume a competition for food and direct and indirect interactions between heterospecific sympatric species, are hard to test based solely on such biogeographic areas. At least, the caveats of this approach need to be discussed.

We now define sympatry in the introduction L58-59 as "the coexistence of species in the same area (henceforth referred to sympatry)". In addition, we agree with the caveat highlighted by the reviewer, which in fact echoes the comment of reviewers 2 and 3. As we have said, these biogeographic zones have ecological and phylogenetic relevance, but they are still large indeed. It is important to bear in mind, however, that the current assessment of sympatry at a fine scale, or the current pattern of interactions between species, does not necessarily reflect what was happening in the past, and even in the recent past, given the unprecedented rapid changes that the Earth has undergone, not least due to human activity. We now discuss these limitations in the "Limits" section (L562-577).

The hypotheses tested assume a direct association of each brain area with only one function, which is problematic because some brain areas include several regions with different functions. For example, hypothesis #2 assumes that the neocortex is associated with processing immediate sensory information (such as the primary motor and visual cortex) even though it also comprises multimodal areas. Similarly, the hippocampus is not only related to spatial navigation and memory but is organized into regions with different functional specializations (see Todorov et al., 2019).

The multifunctional role of the hippocampus was also highlighted by reviewer 5, and the hippocampus is now added to hypothesis 3. Yet, it is important to note that the area largely influenced for other purposes (e.g., sociality, like CA2) are occupying a much lower volume than areas devoted to spatial navigation and memory. Furthermore, the cognitive specialisation of the brain is like a Russian doll: it may be infinite because the brain is a very complex organ. In our view, this simplification, with a hierarchy of function for each area, is a necessary step in conducting such analyses, and that is why we have done it. However, we agree that this is only a pale copy of reality and therefore acknowledge that our approach is simplified (i.e. almost "one area, one function") now at the beginning of the article (L60-62 "Considering a simplistic functional picture of the primate brain, one can hypothesise how sympatry might, through direct or indirect competition or cooperation, influence the relative benefits of cognition (i.e. the balance between its benefits and its costs).").

Regarding the material and methods, the study relies on publicly available data on brain size and body mass to estimate the EQ and the relative size of five brain regions. The authors estimated the relative size of the different brain areas relative to body size instead of brain size. There are different approaches to estimating relative brain size and there are no a priori criteria to prefer one instead of the other but depends on the aim of the study. In this sense, brain size relative to body mass is usually used to discuss the resource allocation between tissues while the second approach is used in the framework of mosaic brain evolution. Given the hypotheses tested, the latter method seems to be more informative, although the authors might have good reasons to prefer the other method, which needs to be better explained.

We agree with the reviewer's comment as this is how we see it too, particularly with regard to the biological interpretation of body or brain size weightings. We considered that weighting by body mass was the most relevant approach to highlighting energy reallocation. However, as this point was also raised by other reviewers, and as we see the relevance of both biological facets (i.e. energy reallocation and the effect of brain architecture) and their compatibility with the hypothetical

evolutionary scenarios, we now provide the analysis weighting both body mass and brain size (added in the supplementary material for the latter). This shows no difference in our findings. We have indicated this in the Methods, Results and Discussion section (L392-396, 430-431, and 464-474).

Moreover, brain size relative to body mass can vary due to changes in body size (Smaers et al., 2021), although the latter variable was not included in the models. Particularly in platyrrhines, previous studies show that the evolution in body size was the main factor responsible for changes in phenotypic traits, including the skull, a structure closely related to the brain (Marroig and Cheverud, 2001). The allometric effect of body size should be taken into account along with other variables such as group size, which has also been related to brain evolution in primates (Dunbar, 1998; among others).

Variation in relative brain size as a consequence of variation in body mass is also, in our view, the reason we focused on relative brain size defined as the ratio of brain size to whole body mass. Maintaining a large brain despite selection for smaller body size could be considered a sign of positive selection for cognition. Thus, we accounted for the allometric effect, specifically by using brain size versus body size. Because the idea of a confounding effect of sympatry on body mass and brain size has been raised by other reviewers nonetheless, we repeated the analysis with body mass as the output variable. We refer to the response to reviewer 1 for more details.

Regarding the potential effect of other variables, we do not deny this, but we see very little direct relationship with sympatry. Thus, we do not deny that these variables, such as group size, must have an influence on brain size, but their effect would not be confounded by the one we highlight. Nevertheless, to draw the reader's attention to these other effects, we now state in the conclusion "Overall, it seems crucial to scrutinise more carefully how sympatry fits with other socio-ecological variables that have been shown to influence brain size evolution (e.g. diet, group size, home range etc.; see e.g. Decasien et al., 2017; 2019; Powell et al., 2017)...".

The probable confounding factor of group size for testing Hypothesis #3 should be at least discussed.

We agree that some of the observed variations can be explained by group size, as variations in group size have been repeatedly shown to be associated with variations in brain size, although there is considerable debate about the quality of group size as a good indicator of social complexity (Dunbar and Schultz, 2007). However, we do not see how this is a 'confounding variable', as there is no other a priori reason to believe that group size is associated with sympatry. However, a possibility remains that sympatry effect is overshadowed by group size (and actually, many other factors that have been shown to influence sympatry). Hence, we now refer to the effect of group size and other variables as mentioned in our answer to the previous comment. We have clarified this on lines 578-581 and in the conclusion.

Minor comments. Figure 3 is difficult to read, and the relative brain size among species is hard to compare.

We cannot disagree fully with the reviewer but we found no better solution than a circular plot given the important number of specie. We tried to improve the relative comparison by plotting the data on the external layers of the circle, instead of going up to its center, and changed colors. We hope this sufficiently improves clarity for rough comparisons.

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Reviewed by Orlin Todorov, 07 Jun 2022 01:50

Thanks for inviting me to review the manuscript entitled "Species sympatry shapes brain size evolution in Primates". The paper is well written, the problem is tackled appropriately through the application of state-of-the-art phylogenetic comparative methods and the sample collated from the literature is comprehensive. The chosen approach, namely to look into brain partitions besides whole (relative) brain size is commendable. I am providing line-to-line comments here and the lines referred to have been highlighted in the pdf file I am attaching.

I consider the paper to be worthy of publication in a high-ranking journal, but there are a few problems that need to be addressed. Some of the reasoning in the introduction might need to be addressed (i.e. sympatry or congener sympatry?), some models might need to be reanalysed (see my comments regarding normalisation and derivation of EQ) and there might be methodological solution already available that directly address the problem with sample size (as the authors sacrifice the majority of their sample size in most of their analyses). I also have reservations regarding the use of ancestral state estimation without calibrating with data from the fossil record (in this case 'diet').

We sincerely thank the reviewer for looking at our work critically, while always remaining courteous. As each of these concerns is commented on point by point, we respond to them below.

Comments:

Title: Primates does not need capitalisation. We have modified it accordingly.

Ln12 – For an opening statement, this is not necessarily true. Some of 'the main hypotheses' emphasize the role of the environment.

We acknowledge that our wording was confusing and led to such a misunderstanding. We did not mean that none of the hypotheses took the environment into account, but rather that the consideration of 'other individuals' in these theories was equivalent to the consideration of 'other conspecifics'. We therefore rephrased as follows (L13-14): "The main hypotheses on the evolution of animal cognition emphasise the role of conspecifics on their socio-ecological environment".

Ln42 – This seems to be as valid not only for other primate species, but for many other animals, i.e. birds, other mammals etc that will also compete with primates for similar food sources. How can/would one account for that? If the problem is phrased as 'sympatry' then most definitely competition between primates and other frugivorous species must be taken into account? Maybe rephrase the whole issue as 'congeners sympatry' also in the title?

Yes, indeed, interactions arising from sympatry can be between individuals belonging to a relatively close phylogenetic clade but also to a distant phylogenetic clade. What is important is the overlap of the ecological niche achieved. An extension of this work would therefore take this into account. However, it seems reasonable to assume that, within broadly defined food guilds (see reviewer 2's comment as a critique on this aspect), the realised niches of closely related species might actually overlap more, compared to what happens if we consider species in the same food guild that have nevertheless diverged significantly. To take the possibility mentioned by the reviewer into account, however, one would have to consider not only primates but all frugivores here. With the material at our disposal, this is not computationally feasible. Therefore, we have changed the term "Species sympatry" in the title to "Primate sympatry" to reflect more accurately what was the work done here.

Ln56 – This is a really good point! I like the idea of looking into different brain partitions instead of whole brain / relative brain size.

Ln62 - I don't think you need to capitalize brain partitions.

Thank you for pointing this out, we have removed all capital letters for the brain areas in the text (main and supplementary).

Ln71 – But also the hippocampus? It has been shown that hippocampal volume is related to sociality in primates (Todorov, 2019 – it is in the citation list of the manuscript).

Indeed, we have now added the hippocampus to hypothesis 3. However, we would like to emphasize, as illustrated in Figure 1 of the reviewer's article (Todorov et al., 2019), that areas associated to sociality are of much lower size than areas associated to foraging. This is why we believe that effects of foraging should dominate.

Ln81 – In terms of memory and primates, using a proxy (as hippocampus) might be ok (can you refer to a paper in the manuscript showing that there is a correlation between memory performance and hippocmpal size in primates?), but we do have direct measures of memory for many primates – MacLean, 2014 (MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., ... & Zhao, Y. (2014). The evolution of self-control. Proceedings of the National Academy of Sciences, 111(20), E2140-E2148.)

We had indeed highlighted that direct measures of cognition existed and were correlated with brain size, holding the work of Benson-Amram et al. (2016) on mammalian carnivores. We have now added reference to MacLean et al. (2014) as well.

Ln100 – Just humans should be OK instead of human people?

Yes, we have modified accordingly.

Ln125 – Looking at your code, there seems to be a concerning misunderstanding here.

summaryData$EQ   <-   summaryData$Brain*1.036*(10**-3)/(0.085*summaryData$Bodymass**0.775) #Following decasien, according to #Jerison, H. J. Evolution of the Brain and Intelligence (Academic, 1973).

What you are doing here is you are multiplying the brain volume as per Jerrison's formula, but then you multiply by 10^3 – this is not needed, as the derived value is already a conversion from gr to mm3 (the 1.036 being the conversaion factor)

This multiplication is done to get the correct unit, as brain size is expressed in cm^3 in our data set. However, even if it had been an unintentional error, it would not have had any consequence, as it is the output variable, and a constant multiplicative term. Thus, it would not have affected the significance of the tests, but only the value of the estimates, which are of little interest here. No action thus taken here.

Ln 138 - Additionally, when obtaining 'relative brain partition size' the partition size is being divided by bodymass:

summaryData$ratioNeocortex <- summaryData$Neocortex/summaryData$Bodymass

This is also inappropriate, as in order to control for the allometry it is better normalized by the whole brain size. I.e. brain partitions scale allometrically to whole brain size, not body size (they scale to body size too, but as a consequence of scaling to brain size).

See for example Triki, Z., Granell-Ruiz, M., Fong, S., Amcoff, M., & Kolm, N. (2022, May 2). Brain morphology correlates of learning and cognitive flexibility in a fish species (Poecilia reticulata).

Another approach is to scale it to another (more conserved) brain area as in Vanier, D. R., Sherwood, C. C., & Smaers, J. B. (2019). Distinct Patterns of Hippocampal and Neocortical Evolution in Primates. Brain, behavior and evolution, 93(4), 171–181. https://doi.org/10.1159/000500625

We thank the reviewer for pointing this out, they are not the only one and other reviewers have also suggested this. For the discussion on the choice between body mass and brain size, we refer to our response to reviewer 1 and the Supplementary Material to which we added a paragraph to discuss this point. We have clarified this L247-251 "Models of trait evolution testing the effect of species sympatry on one brain area relative to the whole body mass (models (i)) test whether the total allocation towards specific brain area is affected by species sympatry. In contrast, models of trait evolution testing the effect of species sympatry on one brain area relative to the whole brain size (models (ii)) test whether the within-brain energy reallocation (i.e. mosaic evolution) is affected by sympatry."

       The choice of another area, on the contrary, seems to us to be inappropriate from an evolutionary point of view. The mosaic structure of the brain does not mean that the brain areas are completely independent of each other, nor does it mean that the (residual) dependence between the brain areas is equal between any pair of brain regions. It may therefore be a dangerous choice, as we may be relying on a brain area that is evolving at the same time as the one we are interested in. We are therefore reluctant to identify this 'conserved' brain area, and given the limited dataset (and therefore the brain areas available that were not of interest to us but relatively large to use as weights), we did not venture to do so.

Additional methods comment – Seeing that you are sacrificing huge portion of your sample size (301) in the model fitting (N=70, 69, 39), have you considered using multiple imputation technique to deal with missing values? See Todorov, 2021; Nakagawa, 2011

Todorov, O. S., Blomberg, S. P., Goswami, A., Sears, K., Drhlík, P., Peters, J., & Weisbecker, V. (2021). Testing hypotheses of marsupial brain size variation using phylogenetic multiple imputations and a Bayesian comparative framework. Proceedings of the Royal Society B, 288(1947), 20210394.

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We are aware of these techniques, unfortunately, most of the missing data concern the output variable (brain size), thus using such methods won't be applicable in this context.

Ln190 – Re Ancestral diet reconstruction this method has been shown to be very unreliable when there is absence of fossil data to 'correct' for estimations on the ancestral nodes. If you cannot obtain data on extinct primate's diet (at least a few and I am sure there can be found in the literature) I would advise against the use of ancestral state reconstruction.

We are aware of these criticisms and understand the reluctance of the reviewer. However, this approach is necessary for the evolutionary models we compute and has been applied repeatedly (e.g. in the work of Jonathan Drury, who developed the algorithm we used).

To allay some of these concerns, we now present the evolutionary map of the diet that we have reconstructed in Supplementary Figure S1. We have confronted this map with the fossil evidence, to show that the inferred dietary history is, for the time being, consistent with current fossil-based knowledge of diet evolution in primates (estimated from dental microwear textures; Ramdarshan, Merceron, and Marivaux 2012; Merceron et al. 2009). We have now discussed this point L566-569. "Dental microwear textures in tooth fossils can indeed be used to reconstruct past diet and we found that our estimates of ancestral primate diets were consistent with available fossil evidence (Ramdarshan, Merceron, and Marivaux 2012; Merceron et al. 2009, see Supplementary Figure S1). "

Ln206 – encephalization, not encephalic. Also re the use of EQ, you might want to check van Schaik, 2021, where they advise using caution when using EQ.

van Schaik C, P, Triki Z, Bshary R, Heldstab S, A: A Farewell to the Encephalization Quotient: A New Brain Size Measure for Comparative Primate Cognition. Brain Behav Evol 2021;96:1-12. doi: 10.1159/000517013

Thank you for correcting this (rather fundamental) term, and we sincerely apologise for this error.

We had also read the publication of van Schaik et al. (2021), but this happened after we submitted this work. In addition, EQ was mainly done as for a control purpose. We have even worked on raw brain data (not shown) which gave similar results. Therefore, we do not believe it is necessary to elaborate further on van Schaik (2021)'s recent suggestion, as our results are very robust to any proxy of cognition used. However, we have added it to the list of citations discussing the use of brain size (and its derivatives) for the study of cognition at the beginning of our conclusion.

Ln234 – Multiple imputation can solve a lot of problems here

As we have already answered, we do not think that data imputation is a solution for the missing data here, as missing data are mostly on the output variable.

Ln319 – This can be rephrased.

We have rephrased as follows L374-375: "When pondering by whole body mass, we observed ample variations in the relative size of the studied brain areas".

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