Peer Community In
Evolutionary Biology

Unravelling the history of Neotropical plant diversification

Hervé Sauquet *based on peer reviews by* ***Thomas Couvreur*** *and* ***Hervé Sauquet***

Michael D. Pirie, Paul J. M. Maas, Rutger A. Wilschut, Heleen Melchers-Sharrott & Lars W. Chatrou (2017) Parallel diversifications of Cremastosperma and Mosannona (Annonaceae), tropical rainforest trees tracking Neogene upheaval of the South American continent. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Evolutionary Biology. 10.1101/141127

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South American rainforests, particularly the Tropical Andes, have been recognized as the hottest spot of plant biodiversity on Earth, while facing unprecedented threats from human impact [1,2]. Considerable research efforts have recently focused on unravelling the complex geological, bioclimatic, and biogeographic history of the region [3,4]. While many studies have addressed the question of Neotropical plant diversification using parametric methods to reconstruct ancestral areas and patterns of dispersal, Pirie *et al.* [5] take a distinct, complementary approach. Based on a new, near-complete molecular phylogeny of two Neotropical genera of the flowering plant family Annonaceae, the authors modelled the ecological niche of each species and reconstructed the history of niche differentiation across the region. The main conclusion is that, despite similar current distributions and close phylogenetic distance, the two genera experienced rather distinct processes of diversification, responding differently to the major geological events marking the history of the region in the last 20 million years (Andean uplift, drainage of Lake Pebas, and closure of the Panama Isthmus). As a researcher who has not personally worked on Neotropical biogeography, I found this paper captivating and especially enjoyed very much reading the Introduction, which sets out the questions very clearly. The strength of this paper is the near-complete diversity of species the authors were able to sample in each clade and the high-quality data compiled for the niche models. I would recommend this paper as a nice example of a phylogenetic study aimed at unravelling the detailed history of Neotropical plant diversification. While large, synthetic meta-analyses of many clades should continue to seek general patterns [4,6], careful studies restricted on smaller, but well controlled and sampled datasets such as this one are essential to really understand tropical plant diversification in all its complexity.

References:

[1] Antonelli A, and Sanmartín I. 2011. Why are there so many plant species in the Neotropics? Taxon 60, 403–414.

[2] Mittermeier RA, Robles-Gil P, Hoffmann M, Pilgrim JD, Brooks TB, Mittermeier CG, Lamoreux JL and Fonseca GAB. 2004. Hotspots revisited: Earths biologically richest and most endangered ecoregions. CEMEX, Mexico City, Mexico 390pp

[3] Antonelli A, Nylander JAA, Persson C and Sanmartín I. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. Proceedings of the National Academy of Science of the USA 106, 9749–9754. doi: [10.1073/pnas.0811421106](https://doi.org/10.1073/pnas.0811421106)

[4] Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson CL, Figueiredo JP, Jaramillo C, Riff D, Negri FR, Hooghiemstra H, Lundberg J, Stadler T, Särkinen T and Antonelli A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, 927–931. doi: [10.1126/science.1194585](https://doi.org/10.1126/science.1194585)

[5] Pirie MD, Maas PJM, Wilschut R, Melchers-Sharrott H and Chatrou L. 2017. Parallel diversifications of Cremastosperma and Mosannona (Annonaceae), tropical rainforest trees tracking Neogene upheaval of the South American continent. bioRxiv, 141127, ver. 3 of 28th Sept 2017. doi: [10.1101/141127](https://doi.org/10.1101/141127)

[6] Bacon CD, Silvestro D, Jaramillo C, Tilston Smith B, Chakrabartye P and Antonelli A. 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proceedings of the National Academy of Science of the USA 112, 6110–6115. doi: [10.1073/pnas.1423853112](https://doi.org/10.1073/pnas.1423853112)

Reviews

Evaluation round #2

Reviewed by **Thomas Couvreur**, 12 September 2017

Dear authors, I am pleased with the revised version of this article. The authors have attended all my concerns, which makes for a much more coherent article with very nice results. I don't have any firther comments to add. Thomas Couvreur, Montpellier 12/09/2017

Reviewed by **Hervé Sauquet**, 28 September 2017

I have checked in detail the revised manuscript and the authors' response to our comments from the first round. I am satisfied with this new version and appreciate the effort of the authors in following our suggestions. In particular, thank you for clarifying some issues with the fossil calibrations and doing the experiement of re-running the dating analyses with uniform priors for the secondary calibrations.

Evaluation round #1

DOI or URL of the preprint: **10.1101/141127**
Version of the preprint: 1

Authors’ reply, 28 August 2017

Download author’s reply

Decision by **Hervé Sauquet**, posted 07 July 2017

Revise

Dear authors,

Your preprint has now been reviewed by Thomas Couvreur and myself. You will find our comments attached. Although I was less critical than Thomas, who has more expertise in this field, I agree with most of his comments and believe that addressing them would make a stronger manuscript. Upon second thought, I also realize that this study did not use any of the recent parametric methods to reconstruct ancestral areas and biogeographic scenarios (such as Lagrange and BioGeoBears), yet most of the paper focuses on the biogeographic history of these two clades. It would be worthwhile explaining why in your text as some readers might also wonder about this.

I hope you will find these comments useful and would be very happy to recommend your preprint if you could address them. Although PCI Evol Biol is not a formal publication yet and we are all learning and testing the system here, I would suggest to treat this invitation to revise as you would for a traditional publication: please provide a point-by-point response to our comments and highlight your modifications in the revised manuscript.

I look forward to receiving your revised preprint.

Kind regards,

Hervé

Reviewed by **Thomas Couvreur**, 06 July 2017

This article sets out to test the timing and ecological dimensions of speciation within two moderate sized non sister Neotropical genera from the Annonaceae family (Cremastosperma (31 sp.) and Mosannona (14 sp.)). Both genera belong however to the same tribe (Malmeea within the Malmeoideae sub family). First, they reconstruct the phylogenetic relationships separately of each of the two genera based on plastid and nuclear markers (6 plastid for both genera, and 2 additional nuclear markers for Mosannona). Then, using a combined plastid data matrix including both genera and several other Malmeea genera, they estimated the divergence times using two secondary fossil calibrations in BEAST. In addition, species distribution modeling was inferred for species in both genera and niche identity and similarity were tested. The authors show congruent biogeographic patterns with closely related species being close both in geography and ecology. The timing of diversification is inferred to be consistent with Andean vicariance and Central American dispersal. In general the methods are thorough and well applied.

General Comments: This is a good and solid new addition to studies around the origin and diversification of Neotropical biodiversity. This article provides further evidence of the importance of two major geological events in the diversification of Neotropical plant diversification. The uplift of the Andes and the drainage of Lake Pebas in northwestern lowland Amazon. The congruence in the results of two well sampled non sister and co distributed genera adds support to the conclusions of the paper. I have however several comments. Title: It is curious that the two first words of your title never (almost) appear in the manuscript itself. “Parallel radiations”. What are radiations (definition?) and what does it mean when they are parallel? Diversification instead of radiation? Moreover, the article addresses other points than just the Andean orogeny. Maybe the title needs a rethink given this. I feel the article could do with a more focused writing. The introduction is very broad dealing very briefly with many different aspects of Neotropical biogeography. Some statements lack references both in the intro and the discussion (e.g. paragraph 2 “However, both species diversity …). The 5th paragraph (“In this paper..”) appears too early, suggesting that it is the end of the intro, but then the authors add on an extra page and half, revisiting the major biogeographic hypotheses in the light of Annonaceae… making it confusing and hard to follow. It is a pity as this leads to a hard to read and follow intro, making the article confusing. The discussion does not to refer to several important papers recently published.

Spécific comments Intro: What is the point of the second paragraph page 4 about molecular dating? This seems out of place and more of a discussion point. In any case I think it could be shorter. Last paragraph of the intro: the term “lake Pebas” appears for the first time in the hypothesis, and is not directly introduced. Methods: EMNTools: There are two different tests one can do: niche identity test and the background similarity test. Which one did you use and why? (see manual, and Couvreur et al 2011 for details). Page 7: species distribution modeling. This part is well done and the methods are well applied. Please indicate how many species have less than 10 unique occurrence points. Also please cite the following article where we showed that using remote sensing data in the tropics significantly improves models versus using worldclim. Why didn’t the authors use that data? Deblauwe, V., Droissart, V., Bose, R., Sonké, B., Blach-Overgaard, A., Svenning, J.C., Wieringa, J.J., Ramesh, B.R., Stévart, T., & Couvreur, T.L.P. (2016) Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. Global Ecology and Biogeography, 25, 443–454. Also it would be good to cite the following article which indicates that modeling is dependent on prevalence of the species more than on the strict number of occurrence. Statement 2 top of page 8 is thus not strictly correct. If you have a widespread species, 4 points will ot be enough, but at least 13. In contrast a strict local endemic, 3 points could be ok. van Proosdij, A.S.J., Sosef, M.S.M., Wieringa, J.J., & Raes, N. (2016) Minimum required number of specimen records to develop accurate species distribution models. Ecography, 39, 542–552. How was independence between soil layers measured? Seems odd, but maybe I am missing something as I don’t know what that type of data is made of.

Page 11: 1st paragraph: I wouldn’t call your sampling “dense” or “densely”. No doubt it is very respectable, but it isn’t dense. In fact, that paragraph is a bit out of place and not very interesting. This again, leads to a confusing article. I would just directly go for the main result here.

3rd paragraph of discussion: It is said that Andean centered genera are the exception. Why not cite them here? If they are the exception then there aren’t many, and it would make the rest of the sentence more comprehensible (multiple times, how many times?).

Page 12 1st paragraph. Is “era” the correct term here? Seems too large and includes periods and ages. Check. Several references missing for some of the statements (e.g. ref for the age of the Andea uplift etc). A ref to figure 3 would be nice after sentence 1. So in this paragraph you talk about the influence of the Andes on the origin of the species, yet no references are made to other studies that observe this same pattern… About Andean uplifts, I would recommend citing this new relevant paper: Pérez-Escobar, O.A., Chomicki, G., Condamine, F.L., Karremans, A.P., Bogarín, D., Matzke, N.J., Silvestro, D., & Antonelli, A. (2017) Recent origin and rapid speciation of Neotropical orchids in the world’s richest plant biodiversity hotspot. New Phytologist, 215, 891–905. 3rd paragraph: Lake Pebas. Seems to me that most of this should be in the introduction. Here I would expect more to discuss your results to other findings (eg Roncal et al 2013).

2nd paragraph: The use of “older estimates” versus younger “estimates” is confusing, especially as no results are cited (a table or a figure)… please improve the clarity of such statements. “Similar signatures” this sentence is vague I feel. Are the dates recovered by the cited studies the same? Another nice case of east west vicariance is Barfod, A.S., Trénel, P., & Borchsenius, F. (2010) Drivers of diversification in the vegetable ivory palms (Arecaceae: Ceroxyloideae, Phytelepheae) – Vicariance or adaptive shifts in niche traits? Diversity, phylogeny and evolution of Monocotyledons (ed. by O. Seberg, A.T. Peterson, A. Barfod, and A.M. Davis), Aarhus University Press, 225-243.

3rd paragraph: drainage of lake pebas. Please cite Roncal et 2013 as another study that presented this evidence in palms.

Page 14: Closure of Isthmus. I would also add the article Cody, S., Richardson, J.E., Rull, V., Ellis, C., & Pennington, R.T. (2010) The Great American Biotic Interchange revisited. Ecography, 33, 326–332. I am not convinced that plants are a good model to test hypotheses about closure of this Isthmus being more prone to long distance dispersal. The last paragraph about Annonaceae phylogenetics seems misplaced and not very interesting given the general theme of this paper. However, the discussion of the non monophyletic species is quite important, and should maybe be addressed in a separate paragraph somewhere. If the authors want to add a part about NGS then they will have to expand and better discuss the different options... such as sequence capture of nuclear regions etc. Also add references to past studies that have used these data to improve resolution (using full plastomes or nuclear genes).

Thomas Couvreur, Montpellier, 6th July 2017

Reviewed by Hervé Sauquet, 06 July 2017

This manuscript contributes to the growing number of studies aimed at understanding the drivers of diversification and biogeographic patterns in the Neotropics, considered to be the most biodiverse region in the World. As someone who is not too familiar with the specifics of this vast and rich field of research, I enjoyed very much reading the Introduction, which I thought set out the questions very clearly.

The study system here consists in two relatively small, closely related genera of the flowering plant family Annonaceae, Cremastosperma and Mosannona. The authors argue that this pair represents a good example of parallel radiations with both similarities and differences that might help us better understand the biogeographic history of the region. I was not entirely convinced by this and somehow wished that they had included more Neotropical clades (of Annonaceae and/or other plant families) in this study and applied the same methods to produce a more convincing contribution based on a larger sample of "radiations". This being said, the strength of this paper is the near-complete sample of species they obtained in each clade and the high-quality data compiled for the niche models, and I certainly believe that careful, in-depth studies like this one are important to publish and equally useful to large meta-analyses.

The results are interesting and not too surprising. Different clades experienced different biogeographic histories, as might be expected, but the detailed Discussion of how this may have happened is interesting. However, before recommending this paper, I believe a few minor points (below) are worth addressing to further strengthen the study.

Minor comments

Molecular dating: I agree that secondary calibration is a risky business (see also what we wrote about it in Sauquet et al. 2012) and that, given the known problems with evolutionary rates in Annonaceae (here you certainly want to cite the new paper by Paul Hoekstra et al. 2017 in Mol Phyl Evol), your solution to focus on Malmeeae only is a good idea to minimize error. However, given the paucity of fossil calibrations in Annonaceae, I would argue that you are still likely to get the wrong age estimates here. First, I think it would be essential to clarify which analysis exactly you are relying on from Pirie & Doyle (2012) since that study involved various experiments with calibrations. Then, I would suggest to remind the reader here of which calibration(s) exactly were used in your reference analysis. I know that most of the Annonaceae community has more or less accepted the Futabanthus fossil, but this flower remains incomplete and I have reservations regarding its use as a calibration point until phylogenetic analyses of the fossil are actually conducted (this is why we excluded it from the review of magnoliid calibrations by Massoni et al. 2015). Last, I think that the normal prior used for the secondary calibration is not ideal. While it might attempt to convey the true shape of the uncertainty around the age estimate of the node in question (which in general looks more lognormal than normal), the reality of BEAST analyses is that such priors tend to be poorly informative and estimated node ages can shift largely from them, which would be problematic in the case of a node age assumed to be known (the secondary calibration). Therefore, I would recommend to either provide evidence that these normal priors were effective or to rerun the analyses with uniform priors bounded by the 95% HPD from the original analysis. In summary, I believe this part of the manuscript could be improved by further justification of the choices made and discussion of how these choices may affect the conclusions presented here that are based on a direct comparison of estimated absolute ages and independently dated geological events.

I don't understand why patristic distances were calculated from PAUP* by re-estimating molecular branch lengths when the authors have RAxML, MrBayes, and BEAST trees at hand (all with branch lengths). Can't this be done easily in R without having to re-estimate branch lengths?

Figures 1 and 2: What is this "Unknown genus 0750"? Is it really useful to include in your analyses if you do not discuss it? The same question would apply to the various new species included in the analyses. the focus of this paper is clearly not taxonomic so my suggestion would be to remove these taxa and sequences and keep them for a future paper. I personally do not like very much the attempt to show both branch lengths and nearly all support values: this might be too ambitious for a single figure and the curved lines might be confusing to some readers. I am not fond of the grey triangles either: would it be possible to denote areas with simple colored rectangles as you have done for Figure 3? Last, I am not sure the dual trees are so useful, since there does not seem to be so much incongruence when you include or exclude taxa for which ndhF was unavailable. I would suggest to show only the most complete trees (B) and move the other ones (A) to supplementary figures. Should you decide to keep both in the same figure, I would recommend to add a mini-caption (a text box) to quickly denote which is which, otherwise the reader might think that this is nuclear vs. plastid markers or some similar contrast.

In addition to these comments, I attach an annotated copy of the manuscript with a few additional minor suggestions.

Hervé Sauquet