

## Peer Review Information

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**Journal:** Nature Ecology & Evolution

**Manuscript Title:** Multiple paths to morphological diversification during the origin of amniotes

**Corresponding author name(s):** Neil Brocklehurst

### Editorial Notes:

### Reviewer Comments & Decisions:

<b>Decision Letter, initial version:</b>
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6th April 2021

\*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Brocklehurst,

Apologies again for the error that led to us failing to send a decision to you on your manuscript entitled "Multiple paths to morphological diversification during the origin of amniotes" within a timely manner. We're still trying to work out what happened and will pass the issue on to platform support to try to make sure it doesn't happen again. While the issue means we had only recruited two referees rather than the three we normally aim for, we've discussed the manuscript among the editorial team and we believe we have sufficient expertise with which to make a decision, and can now recommend a revision. The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file [OPTIONAL: in Microsoft Word format].

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

\* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

\* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to any guidelines provided in this letter.

\* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

**[REDACTED]**

**Note:** This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit [www.springernature.com/orcid](http://www.springernature.com/orcid).

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

**[REDACTED]**

Reviewer expertise:

Reviewer #1: tetrapod macroevolution

Reviewer #2: signed report

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

I have absolutely no qualms with this manuscript. It is executed according to high standards and will generate considerable interest among evolutionary palaeontologists. I recommend acceptance as is.

Reviewer #2 (Remarks to the Author):

Note that I am submitting my review both in the text box and also as a Word document; the latter contains a figure that cannot be included in the text box.

Brocklehurst & Benson examine both disparity and rates of change across phylogeny for early amniotes, documenting: 1) high rates of change accompanying near peak levels of disparity among the earliest (Late Mississippian – Early Pennsylvanian) amniotes; 2) slightly higher rates of change and levels of disparity among herbivorous amniotes relative to carnivorous (faunivorous) ones after herbivores appear in the Early Pennsylvanian, which continuous throughout most of the study interval; and, 3) a general increase in rates of change among herbivores through the Permian and into the Early Triassic (and for the Early through Middle Permian among carnivores) that has little effect on disparity, suggesting that amniotes character space already was saturated (exhausted) & that different lineages were adapting by recombining existing character states and/or evolving very similar states in parallel to each other. The authors do this using a large dataset of over 500 taxa and over 100 characters. (The number of states is not given, but probably should.) Moreover, they do this using very modern methods including tip-dating and birth-death-sampling priors derived from the Fossilized-Birth-Death method.

This paper probably could be published as is and get substantial attention. However, I think that there are some modifications that would increase the impact of this paper. I will outline these below. I would like to stress that, with one possible exception, I intend these to be constructive criticisms, not damning flaws of the paper.

My sole criticism that I think must be addressed concerns the theory discussed in the paper. Brocklehurst & Benson discuss early bursts solely in the context of ecological theory: on line 75, they attribute early bursts solely to the availability of niches. However, substantial work suggests that shifts in developmental regulation/restrictions plays a huge (and likely bigger) role than does ecology when we see "big bangs." Doug Erwin in particular (e.g., Erwin 2007 *Palaeont.* 50:57; 2012 *J. Exp. Zool. B: Mol. Dev. Evol.* 318:460; 2015 *Geobiology* 13:308) has propounded this idea, although past "giants" such as Valentine (1980 *Paleobiol.* 6:444) and Gould (1991 *Paleobiol.* 17:411) promoted the idea, too. (Erwin is hardly alone, too: the idea seems popular in the "EvoDevo" crowd.) These works were a key part of the "loose genes vs. empty ecospace" debate that inspired the precursors of "early burst" studies in the 1990's. The authors do not need to make a huge adjustment for this: simply modifying lines 74-75 defining early bursts for the readers to something like:

"...which then decelerate through time as niches become filled and/or new developmental/genetic constraints increase [REFS]"

would be adequate. This is small: but it will make a big difference in how a lot of paleobiologists and evolutionary-developmental biologists read the paper! Moreover, there are a couple of places where I think that the authors can contrast the expectations of the two models. For example, the general decline in rates that barely budges following the appearance of evolution of herbivores is consistent with increasing intrinsic constraints. Similarly, the fact that the character space gets saturated/exhausted suggests that there were limits on the numbers of easily distinguished states that could evolve.

My other suggestion is to discuss this study in the context of more inclusive and more exclusive studies, if there is room to do so. On one end, amniotes were part of a similar study of tetrapods by Ruta et al. (2006 Proc. R. Soc. B 273:2107); on the other end, there are multiple studies of amniote subclades (e.g., Sidor & Hopson 1998 Paleobiol. 24:254, Cisneros & Ruta 2010 J. Syst. Palaeo. 8:607, Ruta et al. 2013 Proc. R. Soc. B 280:20131071, Ruta et al. 2013 Proc. R. Soc. B 280:20131865). The results of this study fit in well with those of Ruta et al. (2006), which shows rates of change to decline through the Carboniferous for tetrapods as a whole. However, that study did not pick up an increase in rates in the later part of the Permian (perhaps due to the more limited sample size, but also perhaps because temnospondyls might have cancelled it out). Curiously, the Sidor & Hopson study did not suggest an early burst for basal synapsids; however, the cynodont study by Ruta et al. (2013) suggests both high early disparity for a synapsid subclade and high early rates of change; the anomodont study by Ruta et al. shows only high early disparity (no examination of rates was made). On the other side of the amniote tree, Cisneros & Ruta found that procolophonids show peak disparity early, too: but, again, they didn't examine rates. There are several other studies focusing on Mesozoic amniotes, but using younger taxa than examined here, so they do not represent subsets of these results. However, just this set of studies might be enough to discuss how the more specific studies fit in to the results from the more general ones and vice-versa.

Below are some more specific comments. Please note that I put these together before writing my general summary above, so there will be some repetition.

Lines 34-35 "Subsequent expansions of phenotypic diversity were not associated with increased evolutionary rates."

There are several sorts of "evolutionary rates": rates of anatomical change, rates of origination & extinction, rates of ecologic change, etc. Here and elsewhere, I think that the authors should state "rates of anatomical change." At the very least, they should state "rates of anatomical change (hereafter: 'evolutionary rates')." or something like that. I had to read through it a couple of times to make sure that they were not referring to diversification rates, which are expected to be high when rates of anatomical evolution are high under models Simpson's Adaptive Radiation Model, but not under others (see, e.g., Figure 4 in Erwin 1992 Hist. Biol. 6:25, attached in the Word document; Simpson's model is closest to the Adaptive Radiation I).

Lines 72 - 75 "This has been formalised by the "early burst" model, which attributes expansions of disparity primarily to a short-lived burst of high evolutionary rates occurring simultaneously in many lineages, which then decelerate through time as niches become filled [16-18]."

Although the term “early burst” was not formalized until the late aughts, the general concept (frequently but not exclusively called “big bangs” or just “high early disparity”) goes back Gould’s 1988 “Wonderful Life” and there are numerous studies on a variety of groups showing that rates of change across phylogenies are relatively high early in clade history (see summary in Erwin 2007 *Palaeont.* 50:57). A key point here is that increasing developmental regulation/constraint was emphasized just as much as the filling of ecosystems: this was the basis for the “loose genes vs. loose ecosystems” debate. In his 2007 paper and others (e.g., Erwin 2012 *J. Exp. Zool. B: Mol. Dev. Evol.* 318:460; 2015 *Geobiology* 13:308), Erwin argues that the developmental component is the more important one and probably responsible for more early bursts/big bangs/etc. than empty ecosystems. (This stated, ecology is not absent from Erwin’s model, as it clearly moderates/limits what is realized regardless of the potential.)

This is a long way of stating that this sentence really should read “... which decelerate through time as niches become filled and/or new intrinsic constraints evolve.” Moreover, I think that this is important because the pattern documented by the authors, in which the ecologic innovation of herbivory does not accompany accelerated rates of change whereas the elevated rates are concentrated in forms retaining the “primitive” carnivorous (faunivorous) life habits. This is what I would expect if a shakeup in intrinsic constraints rather than by exploiting new ecosystems. Given that we have well-documented arms-races between plants and insects, it seems very surprising that we didn’t see something similar between plants and amniotes: but if we did, then it was drowned out by the initial early burst among carnivorous amniotes.

Lines 138-141: “Evolutionary rates were more volatile in this early period of herbivore evolution, indicating greater between-branch variation in rates, but there is little indication of an overall rate increase in herbivores following the invasion of their new adaptive zone.”

It might be worth noting that phylogenetic context is really important when describing rates of change among herbivorous amniotes. If one looked at only herbivores, then one might describe elevated early rates, as they seem to decline by nearly 100% throughout the Pennsylvanian and into the Early Permian. However: this is just following the overall amniote pattern; so, it’s really “flotsam and jetsam” rather than anything to do with a new ecological role.

Line 184: “Character Saturation”

Although Foote (1994, cited in manuscript) used “saturation” to describe this pattern, molecular phylogeneticists already were using “character saturation” to describe what happens on long-branches: i.e., sufficient change that you expect many characters to change multiple times (see, e.g., Huelsenbeck & Crandall 1997 *Annu. Rev. Ecol. Evol.* 28:437; note that the term had been around for a while at that point and I’m not sure who first used it!). That’s why I used “character exhaustion” (Wagner 2000, cited in manuscript): when I initially used “character saturation,” people got a little confused because although the concepts are related, they are not identical. I am not sure how big of a difference this will make: but given that these analyses are being done in a phylogenetic context, and given that the methods used are very familiar to people from the molecular phylogenetics community, it might be safer to avoid possible confusion & use “exhaustion.”

Lines 195-196: “... inferred character state changes measured along the branches of the phylogeny (‘patristic distances’),”

Back in the day, the term “patristic dissimilarity” was used for this, whereas “patristic distance” was used to count the number of branches separating taxa. (The latter gets used a bit in conservation biology.) I think that the distinction is made in Sokal & Sneath (1973 Numerical taxonomy ). However, Figure 3 uses “Patristic Morphological Distance”, which works just as well. (However, the main text uses “morphological dissimilarity” and “pairwise character state dissimilarity” for morphological disparity, whereas Figure 3 uses “Morphological Distance” for simple pairwise dissimilarity: it probably would be best if the “dissimilarity” or “distance” was used for both simple pairwise and patristic contrasts.)

Lines 381-382: “Character saturation was tested by comparing the MORD morphological distance between pairs of taxa to the patristic morphological distance [82].”

As a side note, Bapst’ PaleoTree program (Bapst 2016 ) now does exhaustion/saturation. The output style also lets you examine relative frequencies of change among characters, which then can be used to test “sizes” of character spaces in the same way that ecologists will use abundance data to estimate total richness. (What the authors did for this study is completely fine, by the way.)

If the authors have any questions about my comments, then they are free to contact me at peterjwagner@unl.edu.

Peter Wagner  
University of Nebraska, Lincoln

References from Review not in Manuscript.

(NOTE: I am not recommending that all or even any be added to the manuscript; these are just to provide context for some of my statements.)

Bapst, D. W. 2016. paleotree. <https://github.com/dwbapst/paleotree>.

Cisneros, J. C. and M. Ruta. 2010. Morphological diversity and biogeography of procolophonids (Amniota: Parareptilia). *J. Syst. Palaeo.* 8:607 – 625. (10.1080/14772019.2010.491986)

Erwin, D. H. 1992. A preliminary classification of evolutionary radiations. *Hist. Biol.* 6:25 – 40. (10.1080/10292389209380423)

Erwin, D. H. 2007. Disparity: morphological pattern and developmental context. *Palaeont.* 50:57–73. (10.1111/j.1475-4983.2006.00614.x)

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Erwin, D. H. 2015. A public goods approach to major evolutionary innovations. *Geobiology* 13:308–315. (10.1111/gbi.12137)

Gould, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiol.* 17:411 – 423. (10.1017/S0094837300010745)

Huelsenbeck, J. P. and K. A. Crandall. 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. *Annu. Rev. Ecol. Evol.* 28:437 – 466. (10.1146/annurev.ecolsys.28.1.437)

Ruta, M., et al. 2013. Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anomodont therapsids. *Proc. R. Soc. B* 280:20131071. (10.1098/rspb.2013.1071)

Ruta, M., et al. 2013. The radiation of cynodonts and the ground plan of mammalian morphological diversity. *Proc. R. Soc. B* 280:20131865. (10.1098/rspb.2013.1865)

Ruta, M., et al. 2006. Evolutionary patterns in early tetrapods. I. Rapid initial diversification by

decrease in rates of character change. Proc. R. Soc. B 273:2107 – 2111. (10.1098/rspb.2006.3577)  
 Sidor, C. A. and J. A. Hopson. 1998. Ghost lineages and “mammalness”: assessing the temporal pattern of character acquisition in the Synapsida. Paleobiol. 24:254 – 273. (10.1666.0094-8373-24.2.254)  
 Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman.  
 Valentine, J. W. 1980. Determinants of diversity in higher taxonomic categories. Paleobiol. 6:444 – 450. (10.2307/2400542)

\*\*\*\*\*END\*\*\*\*\*

#### Author Rebuttal to Initial comments

#### Reviewer 2

**“My sole criticism that I think must be addressed concerns the theory discussed in the paper. Brocklehurst & Benson discuss early bursts solely in the context of ecological theory: on line 75, they attribute early bursts solely to the availability of niches. However, substantial work suggests that shifts in developmental regulation/restrictions plays a huge (and likely bigger) role than does ecology when we see “big bangs.” Doug Erwin in particular (e.g., Erwin 2007 Palaeont. 50:57; 2012 J. Exp. Zool. B: Mol. Dev. Evol. 318:460; 2015 Geobiology 13:308) has propounded this idea, although past “giants” such as Valentine (1980 Paleobiol. 6:444) and Gould (1991 Paleobiol. 17:411) promoted the idea, too. (Erwin is hardly alone, too: the idea seems popular in the “EvoDevo” crowd.) These works were a key part of the “loose genes vs. empty ecospace” debate that inspired the precursors of “early burst” studies in the 1990’s. The authors do not need to make a huge**

**adjustment for this: simply modifying lines 74-75 defining early bursts for the readers to something like:**

**“...which then decelerate through time as niches become filled and/or new developmental/genetic constraints increase [REFS]”**

**would be adequate. This is small: but it will make a big difference in how a lot of paleobiologists and evolutionary-developmental biologists read the paper!”**

- We have added discussion of the concepts highlighted by the reviewer. However we chose to add these to the following paragraph where we introduce the concept of constraint (lines 88-91). We describe there the distinction between intrinsic constraints (including developmental restrictions; “loose genes”) and extrinsic constraints (including competition and availability of new niches; “empty ecospace”).

- Note we did not intend to imply that early bursts should be attributed solely to the availability of niches, rather that the availability of niches has been suggested should lead to an early burst.

**“My other suggestion is to discuss this study in the context of more inclusive and more exclusive studies, if there is room to do so. On one end, amniotes were part of a similar study of tetrapods by Ruta et al. (2006 Proc. R. Soc. B 273:2107); on the other end, there are multiple studies of amniote subclades (e.g., Sidor & Hopson 1998 Paleobiol. 24:254, Cisneros & Ruta 2010 J. Syst. Palaeo. 8:607, Ruta et al. 2013 Proc. R. Soc. B 280:20131071, Ruta et al. 2013 Proc. R. Soc. B 280:20131865). The results of this study fit in well with those of Ruta et al. (2006), which shows rates of change to decline through the Carboniferous for tetrapods as a whole. However, that study did not pick up an increase in rates in the later part of the Permian (perhaps due to the more limited sample size, but also perhaps because temnospondyls might have cancelled it out). Curiously, the Sidor & Hopson study did not suggest an early burst for basal synapsids; however, the cynodont study by Ruta et al. (2013) suggests both high early disparity for a synapsid subclade and high early rates of change; the anomodont study by Ruta et al. shows only high early disparity (no examination of rates was made). On the other side of the amniote tree, Cisneros & Ruta found that procolophonids show peak disparity early, too: but, again, they didn’t examine rates. There are several other studies focusing on Mesozoic amniotes, but using younger taxa than examined here, so they do not represent subsets of these results. However, just this set of studies might be enough to discuss how the more specific studies fit in to the results from the more general ones and vice-versa.”**

- Discussion of how the results of our study compare to the broader study of Ruta et al. on all Paleozoic tetrapods, and of more restricted studies looking at individual clades, has been added (lines 167-168, 190-193)

**“Lines 34-35 “Subsequent expansions of phenotypic diversity were not associated with increased evolutionary rates.”**

**There are several sorts of “evolutionary rates”: rates of anatomical change, rates of origination & extinction, rates of ecologic change, etc. Here and elsewhere, I think that the authors should state “rates of anatomical change.” At the very least, they should state “rates of anatomical change (hereafter: ‘evolutionary rates’).” or something like that. I had to read through it a couple of times to make sure that they were not referring to diversification rates, which are expected to be high when rates of anatomical evolution are high under models Simpson’s Adaptive Radiation Model, but not under others (see, e.g., Figure 4 in Erwin 1992 Hist. Biol. 6:25, attached in the Word document; Simpson’s model is closest to the Adaptive Radiation I).”**



- We now specify on line 75 that when we say evolutionary rates we are referring to rates of anatomical change

**“Lines 138-141: “Evolutionary rates were more volatile in this early period of herbivore evolution, indicating greater between-branch variation in rates, but there is little indication of an overall rate increase in herbivores following the invasion of their new adaptive zone.”**

It might be worth noting that phylogenetic context is really important when describing rates of change among herbivorous amniotes. If one looked at only herbivores, then one might describe elevated early rates, as they seem to decline by nearly 100% throughout the Pennsylvanian and into the Early Permian. However: this is just following the overall amniote pattern; so, it’s really “flotsam and jetsam” rather than anything to do with a new ecological role.”

- This is now acknowledged (lines 140-143)

**“Line 184: “Character Saturation”**

Although Foote (1994, cited in manuscript) used “saturation” to describe this pattern, molecular phylogeneticists already were using “character saturation” to describe what happens on long-branches: i.e., sufficient change that you expect many characters to change multiple times (see, e.g., Huelsenbeck & Crandall 1997 *Annu. Rev. Ecol. Evol.* 28:437; note that the term had been around for a while at that point and I’m not sure who first used it!). That’s why I used “character exhaustion” (Wagner 2000, cited in manuscript): when I initially used “character saturation,” people got a little confused because although the concepts are related, they are not identical. I am not sure how big of a difference this will make: but given that these analyses are being done in a phylogenetic context, and given that the methods used are very familiar to people from the molecular phylogenetics community, it might be safer to avoid possible confusion & use “exhaustion.””

- We prefer to retain our use of “saturation”. The method employed to assess the phenomenon are now in press in a paper that uses the wording “character saturation,” and we feel it best to keep the wording consistent. To avoid the confusion the reviewer describes, we specify when we introduce the concept that it is character *state* saturation, and acknowledge that it is also referred to as exhaustion (line 202)

**“Lines 195-196: “... inferred character state changes measured along the branches of the phylogeny (‘patristic distances’),”**

Back in the day, the term “patristic dissimilarity” was used for this, whereas “patristic distance” was used to count the number of branches separating taxa. (The latter gets used a bit in conservation biology.) I think that the distinction is made in Sokal & Sneath (1973 Numerical taxonomy). However, Figure 3 uses “Patristic Morphological Distance”, which works just as well. (However, the main text uses “morphological dissimilarity” and “pairwise character state dissimilarity” for morphological disparity, whereas Figure 3 uses “Morphological Distance” for simple pairwise dissimilarity: it probably would be best if the “dissimilarity” or “distance” was used for both simple pairwise and patristic contrasts.)”

- We preferred to use “patristic distance” and “morphological dissimilarity” as being each more descriptive of what each measurement referred to: the patristic distance refers to the total evolutionary distance “travelled” by the two lineages since their common ancestor, while the “morphological dissimilarity” refers to the number of character state differences. Our use of “patristic distance” is consistent with the recent literature (e.g. it is the use employed by the R package used to measure it, cited in the text), and we do define each term in the text so we hope this will avoid confusion. We have standardised this usage with figure 3

**“Lines 381-382: “Character saturation was tested by comparing the MORD morphological distance between pairs of taxa to the patristic morphological distance [82].”**

**As a side note, Bapst’ PaleoTree program (Bapst 2016) now does exhaustion/saturation. The output style also lets you examine relative frequencies of change among characters, which then can be used to test “sizes” of character spaces in the same way that ecologists will use abundance data to estimate total richness. (What the authors did for this study is completely fine, by the way.)”**

- This is useful to know for future reference. However, as the method used in paleotree is slightly different to that employed here (using a parsimony-inferred evolutionary history of character state changes rather than patristic distances), we have not employed it here.

<b>Decision Letter, first revision:</b>
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21st May 2021

Dear Dr. Brocklehurst,

Thank you for submitting your revised manuscript "Multiple paths to morphological diversification during the origin of amniotes" (NATECOLEVOL-210112617A). It has now been seen again by the original reviewer 2 and their comments are below. The reviewer finds that the paper has improved in

revision, and therefore we'll be happy in principle to publish it in Nature Ecology & Evolution, pending minor revisions to satisfy the reviewers' final requests and to comply with our editorial and formatting guidelines.

If the current version of your manuscript is in a PDF format, please email us a copy of the file in an editable format (Microsoft Word or LaTeX)-- we can not proceed with PDFs at this stage.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution. Please do not hesitate to contact me if you have any questions.

**[REDACTED]**

Reviewer #2 (Remarks to the Author):

I've re-read the revised manuscript a couple of times, and I find that I have very little useful to offer in the way of constructive (or destructive!) criticisms. I think that the authors did a very good job of addressing my prior comments. In particular, I think that they address the relevant developmental theory appropriately; if nothing else, then nobody can criticize the paper for failing to consider the idea. I also think that the paper does a much better job of drawing this work into the larger body of works on both tetrapod evolution and general macroevolutionary theory: again, a lot of workers would have made the connection themselves, but now the readers don't have to forge those links. Regarding "saturation" vs. "exhaustion," I think that the present version is fine, and it does strike me that my concerns about how the two words were used 20 years ago might be about as relevant as Paleolithic tips for avoiding cave bears are to modern spelunkers.

The paper is pretty clearly written and I think that the methods are pretty easy to follow, too. In other words, the paper should be accessible to the biologists of all types, and not just paleobiologists.

I have a couple of fairly minor comments below.

Lines 247-249: "Indeed, evidence for early bursts of 248 morphological evolution, in which rates are high during the early history of a group, and then subsequently decrease are rare in comparative datasets of extant species [20,71,72]."

and

Lines 277-278: "The general scarcity of early-burst like patterns of rate variation in comparative studies (e.g. [17]) raises questions about their occurrence in early amniotes."

They are rare in analyses of extant taxa, but they are quite common in analyses of extinct taxa. Hughes et al. (2013 Proceedings of the National Academy of Sciences 110:13875–13879; see also Erwin 2007 Palaeontology 50:57–73) found that early bursts of disparity are commonplace. And (at the risk of blowing my own horn!), I found that inverse modeling indicated that these were commonly

associated with both high early rates of change and patterns consistent with shifting integration & modularity (Wagner 2018 Proceedings of the Royal Society B: Biological Sciences 285:20181604). There also are quite a few studies that use different types of "independent contrasts" methods to show that rates decline over time in trilobites, Ordovician gastropods, Ordovician crinoids, blastozoans, Ordovician bryozoans, Paleozoic coelocanth, Paleozoic lungfishes, etc.

So, I would stand the question on its head: why do fossil data show this but analyses of extant taxa fail to show it? It's possible that it's a methodological artifact of molecular trees allowing sufficiently deep divergences that "clock" models are OK. It's also possible that extinction winds up eliminating sufficient early disparity that it doesn't contribute to modern disparity. This study offers a possible example: at any one time, there are dozens of lineages contributing to amniote disparity at that time, but only about 4 of them (leading to: 1) mammals, 2) lizards+snakes+tuataras, 3) turtles, and 4) crocs+birds) go on to contribute to disparity that can be reconstructed in the late Paleozoic & early Mesozoic! It would be very difficult to reconstruct the range of anatomies documented in this study from extant tetrapods because of this.

However, that is pretty minor. This is a great analysis and I hope to see it published in NE&E soon.

Peter Wagner

Our ref: NATECOLEVOL-210112617A

25th May 2021

Dear Dr. Brocklehurst,

Thank you for your patience as we've prepared the guidelines for final submission of your Nature Ecology & Evolution manuscript, "Multiple paths to morphological diversification during the origin of amniotes" (NATECOLEVOL-210112617A). Please carefully follow the step-by-step instructions provided in the attached file, and add a response in each row of the table to indicate the changes that you have made. Please also check and comment on any additional marked-up edits we have proposed within the text. Ensuring that each point is addressed will help to ensure that your revised manuscript can be swiftly handed over to our production team.

**\*\*We would like to start working on your revised paper, with all of the requested files and forms, as soon as possible (preferably within two weeks). Please get in contact with us immediately if you anticipate it taking more than two weeks to submit these revised files.\*\***

When you upload your final materials, please include a point-by-point response to any remaining

reviewer comments.

If you have not done so already, please alert us to any related manuscripts from your group that are under consideration or in press at other journals, or are being written up for submission to other journals (see: <https://www.nature.com/nature-research/editorial-policies/plagiarism#policy-on-duplicate-publication> for details).

In recognition of the time and expertise our reviewers provide to Nature Ecology & Evolution's editorial process, we would like to formally acknowledge their contribution to the external peer review of your manuscript entitled "Multiple paths to morphological diversification during the origin of amniotes". For those reviewers who give their assent, we will be publishing their names alongside the published article.

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Reviewer #2:

Remarks to the Author:

I've re-read the revised manuscript a couple of times, and I find that I have very little useful to offer in the way of constructive (or destructive!) criticisms. I think that the authors did a very good job of addressing my prior comments. In particular, I think that they address the relevant developmental theory appropriately; if nothing else, then nobody can criticize the paper for failing to consider the idea. I also think that the paper does a much better job of drawing this work into the larger body of works on both tetrapod evolution and general macroevolutionary theory: again, a lot of workers would have made the connection themselves, but now the readers don't have to forge those links. Regarding "saturation" vs. "exhaustion," I think that the present version is fine, and it does strike me that my concerns about how the two words were used 20 years ago might be about as relevant as Paleolithic

tips for avoiding cave bears are to modern spelunkers.

The paper is pretty clearly written and I think that the methods are pretty easy to follow, too. In other words, the paper should be accessible to the biologists of all types, and not just paleobiologists.

I have a couple of fairly minor comments below.

Lines 247-249: "Indeed, evidence for early bursts of  
248 morphological evolution, in which rates are high during the early history of a group, and then  
subsequently decrease are rare in comparative datasets of extant species [20,71,72]."

and

Lines 277-278: "The general scarcity of early-burst like patterns of rate variation in comparative  
studies (e.g. [17]) raises questions about their occurrence in early amniotes."

They are rare in analyses of extant taxa, but they are quite common in analyses of extinct taxa.  
Hughes et al. (2013 Proceedings of the National Academy of Sciences 110:13875–13879; see also  
Erwin 2007 Palaeontology 50:57–73) found that early bursts of disparity are commonplace. And (at  
the risk of blowing my own horn!), I found that inverse modeling indicated that these were commonly  
associated with both high early rates of change and patterns consistent with shifting integration &  
modularity (Wagner 2018 Proceedings of the Royal Society B: Biological Sciences 285:20181604).  
There also are quite a few studies that use different types of "independent contrasts" methods to show  
that rates decline over time in trilobites, Ordovician gastropods, Ordovician crinoids, blastozoans,  
Ordovician bryozoans, Paleozoic coelocanth, Paleozoic lungfishes, etc.

So, I would stand the question on its head: why do fossil data show this but analyses of extant taxa  
fail to show it? It's possible that it's a methodological artifact of molecular trees allowing sufficiently  
deep divergences that "clock" models are OK. It's also possible that extinction winds up eliminating  
sufficient early disparity that it doesn't contribute to modern disparity. This study offers a possible  
example: at any one time, there are dozens of lineages contributing to amniote disparity at that time,  
but only about 4 of them (leading to: 1) mammals, 2) lizards+snakes+tuataras, 3) turtles, and 4)  
crocs+birds) go on to contribute to disparity that can be reconstructed in the late Paleozoic & early  
Mesozoic! It would be very difficult to reconstruct the range of anatomies documented in this study  
from extant tetrapods because of this.

However, that is pretty minor. This is a great analysis and I hope to see it published in NE&E soon.

Peter Wagner

**Author Rebuttal, first revision:**

**Reviewer 2**

**"Lines 247-249: "Indeed, evidence for early bursts of morphological evolution, in which rates are high  
during the early history of a group, and then subsequently decrease are rare in comparative datasets  
of extant species [20,71,72]."**

and

Lines 277-278: "The general scarcity of early-burst like patterns of rate variation in comparative studies (e.g. [17]) raises questions about their occurrence in early amniotes."

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So, I would stand the question on its head: why do fossil data show this but analyses of extant taxa fail to show it? It's possible that it's a methodological artifact of molecular trees allowing sufficiently deep divergences that "clock" models are OK. It's also possible that extinction wind up eliminating sufficient early disparity that it doesn't contribute to modern disparity. This study offers a possible example: at any one time, there are dozens of lineages contributing to amniote disparity at that time, but only about 4 of them (leading to: 1) mammals, 2) lizards+snakes+tuataras, 3) turtles, and 4) crocs+birds) go on to contribute to disparity that can be reconstructed in the late Paleozoic & early Mesozoic! It would be very difficult to reconstruct the range of anatomies documented in this study from extant tetrapods because of this."

- The fact that early bursts are apparently common in analyses of fossil data, while rare in analyses including only extant taxa, and the possible reasons for this, are now discussed (lines 287-301).
- We do however make a distinction between some of the apparent early bursts that the reviewer cites, where disparity is high early in a clade's history, and a true early burst where rates are high, as it is important to acknowledge that early increases in disparity may be a result of increased rates, relaxed constraints, or both. This distinction is made clear

<b>Final Decision Letter:</b>
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11th June 2021

Dear Neil,



We are pleased to inform you that your Article entitled "Multiple paths to morphological diversification during the origin of amniotes", has now been accepted for publication in Nature Ecology & Evolution.

Before your manuscript is typeset, we will edit the text to ensure it is intelligible to our wide readership and conforms to house style. We look particularly carefully at the titles of all papers to ensure that they are relatively brief and understandable.

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