One (more) step towards a dynamic view of the Latitudinal Diversity Gradient

Joaquín Hortal and *Juan Arroyo* (ID) *based on peer reviews by Juan Arroyo* (ID)*,*
Joaquin Calatayud, *Joaquín Hortal*, *Arne Mooers* and 2 anonymous reviewers

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The Latitudinal Diversity Gradient (LDG) has fascinated natural historians, ecologists and evolutionary biologists ever since [1] described it about 200 years ago [2]. Despite such interest, agreement on the origin and nature of this gradient has been elusive. Several tens of hypotheses and models have been put forward as explanations for the LDG [2-3], that can be grouped in ecological, evolutionary and historical explanations [4] (see also [5]). These explanations can be reduced to no less than 26 hypotheses, which account for variations in ecological limits for the establishment of progressively larger assemblages, diversification rates, and time for species accumulation [5]. Besides that, although in general the tropics hold more species, different taxa show different shapes and rates of spatial variation [6], and a considerable number of groups show reverse patterns, with richer assemblages in cold temperate regions (see e.g. [7-9]). Understanding such complexity needs integrating ecological and evolutionary research into the wide temporal and spatial perspectives provided by the burgeoning field of biogeography. This integrative discipline ¬–that traces back to Humboldt himself (e.g. [10])– seeks to put together historical and functional explanations to explain the complex dynamics of Earth's biodiversity. Different to quantum physicists, biogeographers cannot pursue the ultimate principle behind the patterns we observe in nature due to the interplay of causes and effects, which in fact tell us that there is not such a single principle. Rather, they need to identify an array of basic principles coming from different perspectives, to then integrate them into models that provide realistic –but never simple– explanations to biodiversity gradients such as LDG (see, e.g., [5; 11]). That is, rather than searching for a sole explanation, research on the LDG must aim to identify as many signals hidden in the pattern as possible, and provide hypotheses or models that account for these signals. To later integrate them and, whenever possible, to validate them with empirical data on the organisms' distribution, ecology and traits, phylogenies,

fossils, etc. Within this context, Meseguer & Condamine [12] provide a novel perspective to LDG research using phylogenetic and fossil evidence on the origin and extinction of taxa within the turtle, crocodile and lizard (i.e. squamate) lineages. By digging into deep time down to the Triassic (about 250 Myr ago) they are able to identify several episodes of flattening and steepening of the LDG for these three clades. Strikingly, their results show similar diversification rates in the northern hemisphere and in the equator during the over 100 Myr long global greenhouse period that extends from the late Jurassic to the Cretaceous and early Neogene. During this period, the LDG for these three groups would have appeared quite even across a mainly tropical Globe, although the equatorial regions were apparently much more evolutionarily dynamic. The equator shows much higher rates of origination and extinction of branches throughout the Cretaceous, but they counteract each other so net diversification is similar to that of the northern hemisphere in all three groups. The transition to a progressively colder Earth in the Paleogene (starting around 50 Myr ago) provokes a mass extinction in the three clades, which is compensated in the equator by the dispersal of many taxa from the areas that currently pertain to the Holarctic biogeographical realm. Finally, during the coldhouse Earth's climatic conditions of the Neogene only squamates show significant positive diversification rates in extratropical areas, while the diversity of testudines remains, and crocodiles continue declining progressively towards oblivion in the whole world. Meseguer & Condamine [12] attribute these temporal patterns to the so-called asymmetric gradient of extinction and dispersal (AGED) framework. Here, the dynamics of extinction-at and dispersal-from high latitudes during colder periods increase the steepness of the LDG. Whereas the gradient flattens when Earth warms up as a result of dispersal from the equator followed by increased diversification in extratropical regions. This idea in itself is not new, for the influence of climatic oscillations on diversification rates is well known, at least for the Pleistocene Ice Ages [13], as is the effect of niche conservatism on the LDG [14]. Nevertheless, Meseguer & Condamine's AGED provides a synthetic verbal model that could allow integrating the three main types of processes behind the LDG into a single framework. To do this it would be necessary to combine AGED's cycles of dispersal and diversification with realistic models of: (1) the ecological limits to host rich assemblages in the colder and less productive temperate climatic domains; (2) the variations in diversification rates with shifts in temperature and/or energy regimes; and (3) the geographical patterns of climatic oscillation through time that determine the time for species accumulation in each region. Integrating these models may allow transposing Meseguer & Condamine's [12] framework into the more mechanistic macroecological models advocated by Pontarp et al. [5]. This type of mechanistic models has been already used to understand the development of biodiversity gradients through the climatic oscillations of the Pleistocene and the Quaternary (e.g. [11]). So the challenge in this case would be to generate a realistic scenario of geographical dynamics that accounts for plate tectonics and long-term climatic oscillations. This is still a major gap and we would benefit from the integrated work by historical geologists and climatologists here. For instance, there is little doubt about the progressive cooling through the Cenozoic based in isotope recording in sea floor sediments [15]. Meseguer & Condamine [12] use this evidence for separating greenhouse, transition and coldhouse world scenarios, which should not be a problem for these rough classes. However, a detailed study of the evolutionary correlation of true climate variables across the tree of life is still pending, as temperature is inferred only for sea water in an ice-free ocean, say earlier half of the Cenozoic [15]. Precipitation regime is even less known. Such scenario would provide a scaffold upon which the temporal dynamics of several aspects of the generation and loss of biodiversity can be modelled. Additionally, one of the great advantages of selecting key clades to study the LDG would be to determine the functional basis of diversification. There are species traits that are well known to affect speciation and extinction probabilities, such as reproductive strategies or life histories (e.g. [16]). Whereas these traits might also be a somewhat redundant effect of climatic causes, they might foster (i.e. "extended reinforcement", [17]) or slow diversification. Even so, it is unlikely that such a model would account for all the latitudinal variation in species richness. But it will at least provide a baseline for the main latitudinal variations in the diversity of the regional communities (*sensu* [18]) worldwide. Within this context the effects of recent ecological, evolutionary and historical processes, such as environmental heterogeneity, current diversification rates or glacial cycles, will only modify the general LDG pattern resulting from the main processes contained in

Meseguer & Condamine's AGED, thereby providing a more comprehensive understanding of the geographical gradients of diversity.

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Reviews

Evaluation round #3

DOI or URL of the preprint: https://doi.org/10.1101/236646
Version of the preprint: 3

Authors' reply, 21 February 2019

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Decision by Joaquín Hortal and Juan Arroyo, posted 06 February 2019

Needs a revision; see AE report

First of all, please accept our apologies for the delay with this review. You present a novel and very bold hypothesis about (one of) the causes of latitudinal diversity gradients, and you do so in a quite complete and thorough way. So analysing all aspects of it has required some time, which together with the change of recommender and one of the busiest periods of the last years has done the rest. We are very sorry for that.

Briefly, the current version of your study is in great shape, but needs some final tweaking. Besides our own reading, two additional reviewers made an in-depth review of it, and they identify some key points that merit some revisions. Most of these revisions are of relatively minor importance, as they are directed to improve the clarity of the manuscript and, importantly, the presentation of your results and analyses. As stated above, you tackle a novel issue and you do it thoroughly, so it is not surprising that some bits remain obscure even though the main lines of your work are quite convincing (but see my cautionary note below). So please follow the advice made by the reviewers, and try to clarify and/or discuss the points they make in a way that (a) the

reasons behind your methodological choices are clear for the readers; and (b) the uncertainty associated to your results and their and implications are communicated better.

With regard to (a) both reviewers provide some clues about where the text needs improvement and some clarifications. Perhaps the most significant of them is Joaquín Calatayud's concern #2. This may be solved by reporting the state node probabilities as supplementary material, and making a brief statement that, given their distribution, the uncertainty associated to their estimations does not affect the overall estimation of the number of times each type of dispersal event (i.e. equatorward/poleward) happened. However, if the actual results do not provide solid evidence when uncertainty in state node estimations is displayed (i.e. if it not self-evident that there is no significant effect of uncertainty after a visual review), then I would recommend that you follow Dr. Calatayud's recommendations for estimating the uncertainty in the dispersal event associated to each branch of the phylogeny.

Re (b) we urge you to follow the reviewers's advice, in particular Dr. Calatayud's point #1, which I believe will improve the fairness in the presentation of your results. But importantly, we think that at the very end your manuscript may overstate the importance it has for the current configuration of the Latitudinal Diversity Gradient for the two ancient clades of turtles and crocodiles, and other tropical-adapted clades. It is not that your do not present convincing evidence that the ancient loss of tropical diversity has an imprint on the current configuration of the gradient. But the way you word things in the discussion and conclusions give the impression that current configuration is the direct result of this process, thus giving a secondary importance to all the ulterior processes niche-conservatism, post-glacial dispersal, adaptations to dryer environments, etc. This is a matter of wording, of course, but the devil is in the details. We believe that the text will be more fair to the complexity of processes and factors that give rise to the current diversity gradient if you would simply include your evidence within the framework provided by current state-of-the-art in latitudinal diversity gradients.

Such current state-of-the-art may not be clear, but it comprises a lot of different pieces of evidences and perspectives. perhaps starting with the reviews of Jansson & Dynesius (Ann Rev Ecol Evol Syst 2003) and Willig et al. (Ann Rev Ecol Evol Syst 2003), and including the outcome of, e.g., Hawkins et al. (Ecology 2003); Wiens & Donoghue (TREE 2004); Ricklefs (Ecology 2006; Am Nat 2008; Ecol Lett 2011); Mittelbach et al. (Ecol Lett 2007); Svenning & Skov (Ecol Lett 2004); Allen & Gilooly (Ecol Lett 2006); Arita & Vázquez-Domínguez (Ecol Lett 2008); or (of course) Condamine et al. (Ecol Lett 2012); and ending with the (arguably) mixed evidence provided by Hanly et al (Am Nat 2017); Rabosky et al (Nature 2018) or Rangel et al. (Science 2018), among others. Here I'm not claiming that you have to be exhaustive, but rather to reflect that there are several causes of the gradient that all are operating over the pattern we see today. This is something that can perhaps be solved tweaking a few sentences here and there and/or adding one or two more in the conclusions, perhaps without even adding any citation. But without it we believe that the text does not provide a fair account of its true importance. Note that this does not reduce its importance.

Besides these (relatively) minor concerns, we believe that your manuscripts presents an overall solid work, both conceptually and analytically, that has the potential to have a significant effect on current debate on the origin(s) of the latitudinal diversity gradient. In fact, it is not every year (or even decade) that we see a truly novel addition to the latitudinal diversity gradient debate. We are looking forward to recommend a final version of this work.

Reviewed by **Joaquin Calatayud**, 23 November 2018

This is a very interesting and conceptually and methodologically impressive study. The authors present a new hypothesis that integrates and reconciles previous ones through a time-variable framework. In agreement with comments in previous revisions, I find the contextualization of the AGE hypothesis to be excellent, including also testable predictions from other hypotheses (such as those ones presented in table 1). In my opinion, this synthesis in its own deserves credits enough as to make an important contribution to the LDG field. In this line of merits, the authors used a throughout methodological approach to test predictions from the AGE

hypothesis, including three taxa and phylogenetic (SSE models and DEC), fossil informed phylogenetic (DEC + fossils) and fossil analyses (PyRates). This provides inciting results (such as the disagreement between fossil and phylogenetic analyses), which again in its own may have an important impact on biogeographical and comparative studies. Overall, I find the study very interesting and I appreciate the outstanding synthetic and analytical effort behind it.

While I really like the manuscript as it is now, in my opinion there are few minor aspects that could be further improved. Nevertheless, it is worth noticing that I'm just a short-experience practitioner on some of the analyses used. Thus, I can not deeply evaluate the adequacy of some analyses and especially those based on fossils.

1) Perhaps the most important thing is that results in general could be presented in a more informative way. That is, while I like the figures and appreciate the effort to synthetize results from all taxa and type of analyses, I feel that important piece of information are lacking or at least difficult to access. For instance, credibility intervals in figs. 4 and 3 are difficult to visualize, especially for diversification rates. In my opinion the manuscript would benefit from presenting credibility intervals where they were computed (i.e. SSE and PyRates analyses) numerically (e.g. in Table 2). I think this is quite important to clearly demonstrate that the results support predictions from the AGE hypothesis. For instance, in fig. 4, it seems to me that the credibility intervals of diversification rates in the Holarctic and Equator datasets overlap (at least for turtles). If so, the crucial statement of lines 322-325 (i.e. "the slowing of diversification was much stronger in the Holarctic than at the equator") would be weakly supported and perhaps some rewording would be needed.

2) If I understand properly, during ancestral range estimation analyses the number of dispersal and range extinction events are calculated based on the most probable node state. While this seems to be a commonly used procedure, I think it ignores that the most probable state of a given node can still present a low probability. In others words, the uncertainty inherently associated to the model is not considered as the node state is taken as certain. As the node state probability is not provided it is difficult to evaluate whether this may influence subsequent estimations on the number of "into the equator" and "out of the equator" dispersal events. At first glance and for instance, this may be overcome by calculating the probability that such events occur for each phylogenetic branch. Then, these probabilities could be used along with any resampling technique to estimate the number of dispersal and range contraction events as well as its confidence. Please, forgive if I'm wrong and take this with caution since I'm not an expert in this sort of approaches. Alternatively, I think the state node probabilities should be provided and caution should be taken if these probabilities are low.

3) I do not understand very well why the number of dispersal events are normalized by the number of lineages. To my understanding by doing so results cannot be longer related to diversity patterns (as diversity is being controlled for).

4) From the complete ignorance, is it possible that some incongruences between phylogenetic and fossil evidence come from the different taxonomic level used (i.e. species vs genus, respectively)?

5) It seems that supplementary figures are mislabelled (e.g. those referred in lines 265-268)

6) In line 530 I think it should be "23/34".

7) In my opinion lines 604-606 should be in the results or discussion sections (right now it is only discussed for the group apparently not following the first AGE postulate, which seems unfair).

Reviewed by anonymous reviewer 2, 23 November 2018

The present manuscript by Meseguer and Condamine address and interesting and complex question using different approaches. The present version looks to be quite mature, well written and structured. Authors discussed general patterns explaining the Latitudinal Diversity Gradient in a scenario of Asymmetric Gradient of Extinction. They discussed all different results from each analysis instead choosing "the best" option to explain their hypotheses. This keep in some cases open conclusions, which is in my opinion, a positive thing considering the methodological complexity of the analyses in the manuscript and the assumptions that are implied on each one, which makes difficult to choose one alternative over the others. They also present

ancestral area reconstructions with, and without fossil records in the analyses, comparing both results, again, without choosing one over the other.

Nevertheless, I found some methodological aspects that must be, at least, discussed and better justified:

In Methods, lines 594 to 594, authors assume that "taxa inhabiting the warm Holarctic were adapted to tropical-like conditions". This assumption is supported by a reference for turtles (Testudines) but not for Squamata nor Crocodilia. You must include at least some references supporting this assumption for these two groups as in Testudines, to justify it before performing the analyses.

Additionally, authors used a DEC model for their biogeographical analyses without any specific motivation (at least it is not specified in the manuscript). Why are you using this model and no alternatives like a DIVA or BayArea-like? I would like to see some justification for the use of this model in your analyses. On the other hand, I am concerned about using fossils in a comparative study for the Holarctic and tropical regions. Fossil preservation is different in both cases due mainly to different climatic conditions. This led to a different number of occurrences (fossilization is easier to occurs in Holarctic regions), which can bias the analysis in PyRate due to lack of information in tropical regions.

Finally, in figure 7 caption, I would specify that black line corresponds to the temperature for an easier interpretation of this figure.

Evaluation round #2

Authors' reply, 05 October 2018

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Decision by **Joaquín Hortal**, **Juan Arroyo** and **Joaquín Hortal**, posted 05 October 2018

Needs a revision; see AE report

AE report on `https://doi.org/10.1101/236646`

Round 2

I apologize for the slowness of this review; as I intimated in my first report, I find this large and ambitious study difficult to evaluate. The "AGE hypothesis" that this paper offers seems to be a formalization of ideas that have been around for a long time, making it important, but its placement in the literature problematic. There is no doubt that the combination of reconstructed phylogenetic and fossil tests is novel, and offers a deep time perspective on the Latitudinal Diversity Gradient (LDG).

The authors make several claims about the process leading to the present-day LDG using several different data streams for several different taxa, sometimes keeping the data streams separate, and sometimes combining them. The main red thread seems to be that reconstructed phylogenies can capture neither (i) high extinction (leading to "negative diversification") in Holarctic regions, nor (ii) "into the tropics" dispersal and range contractions, both occurring during the transition from Greenhouse to Coldhouse conditions between ~50mya to ~23 mya. Because of this, these two processes are potentially underappreciated drivers of the LDG.

The authors present PyRate analyses of fossil genera for the three groups, considering origination and extinction of lineages in Holarctic and Equatorial realms for Greenhouse, Transition, and Coldhouse periods (so, two rates for three times for three clades, or 18 separate rates, Figure 4. To summarize, turtles show the predicted decrease in origination and increase in extinctions during the Transition phase in the Holarctic leading to negative diversification there. Crocodiles show a decrease in origination rates in both realms in the Transition phase, but an increase in extinction in *equatorial* realm during the transition phase, and *no*

change in the Holarctic; overall, there seems to be negative diversification in the Holarctic since the onset of the Transition phase. Squamates show net decreases in origination in both realms with the onset of the Transition phase, though more extreme in the *equatorial realm*, and *no change* in extinction rates in either realm during the Transition phase, and, finally, a decrease in extinction rates in the *Coldhouse* phase. These major results suggest that there are potentially strong global climate – origination and extinction links in all three groups, but only the Turtles show an overall pattern consistent with AGE. (I have italicized the contrary-to-expectation patterns in this paragraph.) My reading of the methods suggests that Figure 5 is just a reworking of Figure 4 that combines place and time in the Greenhouse phase to produce 12 rather than 18 rates.

The authors then consider range contractions and dispersals. Here I think there is a very useful message – the authors offer great examples where fossil-based constraints on ancestral lineage area of occupancy leads to very different scenarios of dispersal. As the authors succinctly put it, there is no need to formally compare model fits of ancestral occupancy and movement, since the fossils are clear evidence that a particular lineage was in fact where the fossil was. This, and the comparison of BiSSE and PyRate estimates of diversification, highlight clearly how geographically biased extinction can severely bias any sort of reconstruction on a tree – we "knew" that nonhomogeneity of process can cause all sorts of problems, but these empirical comparisons that make use of fossil data hit home. These two sets of comparisons, if presented clearly, will be read with care and interest by comparative biologists.

With regard to the fossil-based reconstructions (Figure 7), all three groups show evidence for rates of dispersal into the equator to be generally increasing through time and greater than those out of the equator, though with no discernable effect of the various temperature phases. Range extinctions show idiosyncratic patterns, again with no clear effect of the Transition or the Cold phase.

As you can see, my reading and re-reading of the paper does not have me seeing how the data are so consistent with AGE as the authors. Given PCI is a nascent and voluntary endeavor, it is likely best that this go to a journal that has expert reviewers in paleontology and comparative methods at hand to offer another opinion.

I have, however, made extensive comments and suggestions on the manuscript itself (as notes using Preview), which I hope will help the authors as they prepare the paper for submission to a major journal. I will send this file to PCI directly to pass on. Overall, the multiple comparisons among constant rate BiSSE, time-dependent BiSSE, Pyrate using both time and space and time+space = "environment" sampling, and constrained, semi-constrained and unconstrained DEC analyses for each of the three clades make for a study that risks getting lost in its many, contradictory tests. That would be a shame, as the general idea of being able to test deep time climate-driven negative diversification using some sort of combined test with trees and PyRate would be a major advance in our thinking about this "oldest pattern in ecology."

Sincerely, Arne Mooers

Reviewed by Arne Mooers, 31 July 2018

See the attached document with the recommender's comments
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Evaluation round #1

Authors' reply, 14 June 2018

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Needs a revision: all three reviews are included below, along with an AE report

Associate Editor's - Arne Mooers - Comments.

This is an intriguing study. I commend the authors for all the work they have done, and I echo the reviewers that this could be a qualitative contribution to the LDG literature. I very much liked the review and Table 1 (though I wish it had been annotated just a wee bit more).

The AGE set-up does indeed seem synthetic, but it is formalizing and extending a lot that we already knew (e.g. that the LDG is not static because equatorial conditions have waxed and waned across latitudes through deep time, and the LDG could be due to tropical forms dying out in a cooler world farther from the poles) does not come till very late in the set-up (lines 133-147). This is confusing, because it is not clear if we are being exposed to a strong or weak test of a theory or to a new theory altogether.

I am also a bit more cautious than the reviewers regarding the results. I did not see a comparison of standard BiSSE analyses (which mirror those by Rolland et al. PloS Biol. 2014) with an AGE-specific BiSSE analyses. Would this not be a relevant test of AGE? If not (perhaps because the authors feel all BiSSE analyses are suspect due to, e.g., the lack of fossil constraints on dispersal), then this needs to be clarified, and the BiSSE results recast as "unhelpful" – at the moment, I am not sure if I am to try to interpret them, or not. (And if not, does this mean I should discount the Rolland et al., results too?). The comparison of the unconstrained and constrained DEC analyses is useful to show that uninformed reconstructions may be biased, but I am not sure that this was tested (do we have a metric to evaluate bias?), nor am I convinced that reconstructions assuming the fossil record is biogeographically "complete" for these groups over these time scales (the HFC DEC) can be considered data. I would want a terrestrial vertebrate paleontologist to comment on this specifically.

I think the tests of the AGE suggested by Reviewer 2 would be very interesting, but these suggestions also highlight what may be a major issue with this manuscript – it seems to at once want to introduce a new framework and also test the predictions from that new framework, and also present a lot of very deep-time and large-bin PyRate and DEC reconstructions across three large datasets. I am not convinced one can do all this at once effectively. The fact that none of the three groups actually present patterns consistent with AGE also gives me pause (am I correct with this interpretation? – figures 6 and 7 seem the most relevant here, but the fact I have to ask should give pause).

I wonder if a paper that focused on, e.g. the Testudines as a test case might have higher impact. One could explore the AGE in detail with a view to presenting how one might properly test the AGE with these sorts of data. I leave this, and the reviewers comments, for the authors to consider as they revise and improve the paper.

This is a very nice piece, trying to provide more realistic models of the macroevolutionary processes that drive latitudinal gradients of diversity on Earth. As such, models provide a bold approach to model extinctions and dispersions between latitudinal bands, accounting for long-term climatic oscillations. The modelling part seems sound to me, although I am just a well-informed reader rather than an expert in that part. But the main hypotheses behind the models provide an incomplete coverage of Latitudinal Diversity Gradients (LDGs), and the data itself has some limitations that have not been accounted for, or at least discussed.

You state explicitly along the whole text that the Latitudinal Diversity Gradient (LDG) is universally a decrease from richer tropics to less diverse temperate and, progressively, polar regions. This is far from being an absolute truth. I can concur that such LDG stands out for many biological groups (reptiles are certainly one of these groups), but a large number of taxa and functionally-consistent groups show other LDG patterns. Besides the typical textbook examples of, say, penguins (that are just a small clade and therefore not suitable for your coarse-evolutionary extent model), there are many groups that present their maximum diversity peaks at the temperate zones, including grasses, conifers, bryophytes, many groups of freshwater invertebrates

(e.g. dive beetles, trichopterans, plecopterans, ephemeropterans, etc.; Vinson & Hawkins Ecography 2003; Boyero & Pearson J N Am Benthol Soc 2009; Morinière et al. Sci Rep 2016), parasitoid wasps, aphids (Kouli et al. Ann Zool Fennici 1994), certain families of dung beetles (but not others), among many other examples. These groups encompass a large part of terrestrial biodiversity (there are more known dung beetle species than birds and mammals altogether, for example). Patterns in the marine environment are also heterogeneous, and for many groups correlate more with the distribution of upwelling sources than with latitude. So there are many inverse LDGs due to the constraints imposed by their bauplans (see Kindlmann et al. in Scaling Biodiversity, ed. Storch et al., 2007). These basal bauplans (i.e. structural plans) are a direct consequence of the origin of each one of these major clades, that does not correspond to warm tropical periods and/or equatorial origins (e.g., the evolution of mosses in the Ordovician Ice Age, the clades originated in Laurasia during the Carboniferous, the C3/C4 transition in the Miocene and the adaptation of the major grass clades to arid and seasonal environments, etc.). Turtles show some deviation to the classic tropical-peak LDG pattern, but I miss any reference on how this affects the observed LDG for them in the context of your model.

Does this affect the validity of your alternative model? I do not think so, but questions its generality. I do think that it is has the potential to provide a nice representation (but see below) of the patterns and processes followed by many groups that currently show apparent "tropical niche conservatism" patterns. In fact, that physiological limits rather than dispersal limitations shape the patterns of diversity for many groups in the interglacials seems more than reasonable, and many groups may follow that pattern, but sometimes these patterns are mediated by other requirements, promoting peaks of diversity at higher latitudes. Compare, for example, Hortal et al. Ecol Lett 2011 with Calatayud et al. J Biogeogr 2017; I quote these because I know them well, but they show how the same processes with different basal adaptations to climate lead to contrasting latitudinal patters (within Europe in this case). In what respects to recovering the LDG, your model only applies to taxa evolved in warm-tropical environments; and it works for reptiles (which are are certainly a warm-adapted taxon). But I wonder if it could be generalized to origins in other latitudinal bands. The processes are certainly there, it may be only a matter of constructing alternative hypotheses for groups generated in cooler moments/regions, where taxa retain "memory" of the conditions where they appeared. I honestly think this would make a great paper. Should you decide not to incorporate this into the models, the partial character of the richer-in-the-tropics LDG should be acknowledged throughout the text, making clear that your models seek to represent LDGs centered around the equator.

Apart from that, I miss an assessment of whether your results are flawed by eventual biases in the fossil record. It is well known that we lack enough fossil data and adequate models to represent the tree of life, what has been termed the Darwinian shortfall (Diniz-Filho et al. TREE 2013; Hortal et al. Ann Rev Ecol Evol Syst 2015). So it is really hard to buy the assumption that the fossil record is complete; should it be unbiased, I could live with it, assuming random error and undersampling of the tree. But there is a high chance that biases in the fossil record affect the results of your paper. In this particular case, most neotropical palaeontologists advise about the strong taphonomic bias towards the Holarctic; fossils are scant in tropical regions, in part because lack of paleontological effort, and in part due to the lower adequacy for the formation of deposits in many of the old soils of tropical South America, which is the continent I know better in this aspect. I'm not so sure about other tropical regions, but my guess is that only Chinese territories hold a comparable sampling effort in tropical Asia. The problem with the comparative oversampling of the Holarctic is that it spuriously increases the probability of finding dispersions into the tropics, compared to out of the tropics (for the Holarctic branches of the tree are more populated). There may be other more sophisticated ways I'm not aware of (perhaps adding probability of fossilization as a prior), but an straightforward way to account for this would be to resample n times the fossils to obtain samples with the same number of fossils in each latitudinal band (or at least, in tropics and Holarctic), and redo the trees n times. This sensitivity analysis (or a Bayesian alternative based on an adequate prior) will provide more robust results. In any case, a fair assessment and/or statement of how the limitations of the fossil record may affect your results is needed.

Besides these two major concerns, the manuscript is nice, well-written and clear. As a minor comment, I'd

move the sentences in lines 232-236 to the paragraph starting in line 153. There are perhaps too many figures for an standard paper, but that is a matter of the journal you aim to send it to.

My own biases are obvious in this review, particularly in what respects to being picky with data quality and completeness, but generalizing current LDGs as holding a general peak of the tropics clashes with my experience, and I've seen LDGs for a fair number of groups as author, reviewer and editor, plus teaching LDGs for over ten years. So no matter whether you generalize your model or not, please avoid stating that LDG is universally centered in the equator. It undermines a really superb piece of work.

I hope this helps, Abrazos, Joaquín

Reviewed by anonymous reviewer 1, 09 January 2018

Download the review

Reviewed by Juan Arroyo ⓘ, 12 January 2018

This manuscript deals with a hot topic of long standing interest among biogeographers, macroecologists, systematists, among others, that of Latitudinal Diversity Gradient (LDG). Despite it being described long ago, it has been reluctant to exclusive hypotheses ready to be tested beyond correlation. However, this pattern has generated a renewed interest within the biogeographic and macroecological community, as modern tools for reconstructing the past of lineages and the areas where they lived, as well as information on fossils record and distribution, are increasing available.

The merits of the manuscript lie on (1) the consideration of competing hypothesis to those canonical assuming a constant through time higher diversity in the tropics; (2) the application of recent tools to explicitly disentangle the role speciation and extinction, and dispersal (although I would prefer the use of migration, just to avoid confusion with the ecological meaning of the term dispersal); (3) the use of massive data of fossil records for the former aim; and finally (4) integrate all this information in a explicit temporal hypothesis o variation according the tropical-temperate type shift.

Despite I am not an expert on the most recent analytical methods on historical biogeography, the manuscript is thought provoking and deserves to be known by the community. I feel that the hypothesis the authors are launching is falsifiable and thus a number of studies will address it, in the extent there are data set suitable for it.

My comments to specific parts of the study, some of them quite wide across the arguments, follow:

Abstract . No mention is provided to specific temporal setting of the study, despite the wide citation of specific dates throughout the main text.

I is convenient that when mentioning "We studied" (line 35) that in fact the study is widely based on existing published phylogenies, which are refined with additional data (e.g. fossils). This is also applicable to lines 147-149, at the end of Introduction.

My view about the challenge the study represents (line 43) is that in fact the authors propose a refinement of the current theories by incorporating meaningful data on temporal context with independent data (fossils), which might change in the future, when more studies on other groups are available, our views about the LDG.

Introduction

Your approach is to use different groups as to test your hypothesis (three in your study). This brings me two thoughts. One is the selection of groups. Your selection is of three groups which are related, this might limit the power of your analyses. In fact, it would be needed that you mention in the Introduction the rationale for selecting these groups, even thought you justify in detail the Methods section. The reader needs to know somewhat about this as soon as possible. The second is that, independently of the relationships among groups, it recalls about the correlative value of biodiversity patterns in groups. I mean that it should posed the question of the use the patterns in some groups as proxies for general patterns, which in fact is the ultimate aim of the study.

A serious issue throughout the manuscript is the strong bias towards the Northern Hemisphere (Holarctic is included among keywords, but see line 122). Probably this is an effect of the particular distribution of the groups selected. This is not bad at all, but a different selection of groups would have increased the prospective value of the hypothesis, particularly due to the fact that in Southern Hemisphere the climate changes were very probably smoothed due to the sea/land configuration and extension of plates. If the authors are correct, the LDG should vary not only through time, but also through hemispheres.

In table 1 and others there is not indication of the meaning of "r" in the legend. For familiar readers it is clear that this is diversification rate, but should be made explicit.

Results

Line 165. What is the meaning of "region" here? Biogeographical? Any other?

I wonder in what extent results may rely on different rates and probabilities of having reliable fossil records in particular regions (e.g., the tropics). This is central to the whole study. Traits, Ecology...