



New light on the baseline importance of temperature for the origin of geographic species richness gradients

Joaquín Hortal based on reviews by *Rafael Molina-Venegas* and 2 anonymous reviewers

A recommendation of:

Temperature predicts the maximum tree-species richness and water and frost shape the residual variation

Ricardo A. Segovia (2021), *bioRxiv*, 836338, ver. 4 peer-reviewed and recommended by Peer Community in Ecology [10.1101/836338](https://doi.org/10.1101/836338)

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Recommendation

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Whether environmental conditions –in particular energy and water availability– are sufficient to account for species richness gradients (e.g. Currie 1991), or the effects of other biotic and historical or regional factors need to be considered as well (e.g. Ricklefs 1987), was the subject of debate during the 1990s and 2000s (e.g. Francis & Currie 2003; Hawkins et al. 2003, 2006; Currie et al. 2004; Ricklefs 2004). The metabolic theory of ecology (Brown et al. 2004) provided a solid and well-rooted theoretical support for the preponderance of energy as the main driver for richness variations. As any good piece of theory, it provided testable predictions about the sign and shape (i.e. slope) of the relationship between temperature –a key aspect of ambient energy– and species richness. However, these predictions were not supported by empirical evaluations (e.g. Kreft & Jetz 2007; Algar et al. 2007; Hawkins et al. 2007a), as the effects of a myriad of other environmental gradients, regional factors and evolutionary processes result in a wide variety of richness–temperature responses across different groups and regions (Hawkins et al. 2007b; Hortal et al. 2008). So, in a textbook example of how good theoretical work helps advancing science even if proves to be (partially) wrong, the evaluation of this aspect of the metabolic theory of ecology led to current understanding that, while species richness does respond to current climatic conditions, many other ecological, evolutionary and historical factors do modify such response across scales (see, e.g., Ricklefs 2008; Hawkins 2008; D’Amen et al. 2017). And the kinetic model linking mean annual temperature and species richness (Allen et al. 2002; Brown et al. 2004) was put aside as being, perhaps, another piece of the puzzle of the origin of current diversity gradients.

Segovia (2021) puts together an elegant way of reinvigorating this part of the metabolic theory of ecology. He uses quantile regressions to model just the upper parts of the relationship between species richness and mean annual temperature, rather than

modelling its central tendency through the classical linear regression family of methods –as was done in the past. This assumes that the baseline effect of ambient energy does produce the negative linear relationship between richness and temperature predicted by the kinetic model (Allen et al. 2002), but also that this effect only poses an upper limit for species richness, and the effects of other factors may result in lower levels of species co-occurrence, thus producing a triangular rather than linear relationship. The results of Segovia’s simple and elegant analytical design show unequivocally that the predictions of the kinetic model become progressively more explanatory towards the upper quartiles of the relationship between species richness and temperature along over 10,000 tree local inventories throughout the Americas, reaching over 70% of explanatory power for the upper 5% of the relationship (i.e. the 95% quantile). This confirms to a large extent his reformulation of the predictions of the kinetic model.

Further, the neat study from Segovia (2021) also provides evidence confirming that the well-known spatial non-stationarity in the richness–temperature relationship (see Cassemiro et al. 2007) also applies to its upper-bound segment. Both the explanatory power and the slope of the relationship in the 95% upper quantile vary widely between biomes, reaching values similar to the predictions of the kinetic model only in cold temperate environments –precisely where temperature becomes more important than water availability as a constrain to plant life (O’Brien 1998; Hawkins et al. 2003). Part of these variations are indeed related with changes in water deficit and number of frost days along the XXth Century, as shown by the residuals of this paper (Segovia 2021) and a more detailed separate study (Segovia et al. 2020). This pinpoints the importance of the relative balance between water and energy as two of the main climatic factors constraining species diversity gradients, confirming the value of hypotheses that date back to Humboldt’s work (see Hawkins 2001, 2008). There is however a significant amount of unexplained variation in Segovia’s analyses, in particular in the progressive departure of the predictions of the kinetic model as we move towards the tropics, or downwards along the lower quantiles of the richness–temperature relationship. This calls for a deeper exploration of the factors that modify the baseline relationship between richness and energy, opening a new avenue for the macroecological investigation of how different forces and processes shape up geographical diversity gradients beyond the mere energetic constrains imposed by the basal limitations of multicellular life on Earth.

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Cite this recommendation as:

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Reviews

Toggle reviews

Revision round #2

2021-03-04

Author's Reply

[Download author's reply \(PDF file\)](#)

Decision round #2

Your manuscript has significantly improved, and I agree with the two reviewers of this version in that it is a fantastic work, and indeed merits recommendation. I asked a new reviewer expert in quantile regressions to take a look at the criticisms on the method raised before. S/he agrees with your arguments, but also points to a couple of simple methods to address its limitations in what refers to providing metrics of goodness-of-fit. Please follow her/his advice about this issue, and in particular the test for the deviation of the slope from -0.65; I think it will certainly strengthen your work.

Besides that, Rafael Molina-Venegas provides a number of minor comments that will be quite useful to improve this final version of the manuscript. I'm sure that, after all these revisions are done, the manuscript will be ready for my recommendation.

Thanks again for sending this beautiful work to open discussion through PCI.

Preprint DOI: <https://doi.org/10.1101/836338>

Reviewed by Rafael Molina-Venegas, 2021-01-28 12:54

I have revised the new version of the pre-print by Dr. Ricardo Segovia entitled "Temperature predicts the maximum tree-species richness and water and frost shape the residual variation", and I do think the research is simply fantastic. This piece of work clearly shows how the kinetic hypothesis of biodiversity gradients may have been largely underrated due to the use of central tendencies rather than upper bounds (i.e. quantile regressions) in previous modelling exercises, and it also illustrates on the interacting effects of other environmental factors besides mean temperature such as incidence of freezing events and water availability. The former variable is particularly interesting given that environmental information pertaining such drastic, eventual and stochastic climatic events has been comparatively less used in the macroecological literature. I also acknowledge the new cross-biome analysis, which I found largely informative. My criticism is fairly minor, and it mostly revolves around the feeling that that some of the results are perhaps loosely discussed (see comments below). It follows a few comments and suggestions that might hopefully help to lift the manuscript to its maximum informative potential. Congratulations to the author for his fine research.

Comments

The topic is introduced in an excessively sharp manner (line 2), so I would suggest rewording a bit, perhaps including a short sentence to more smoothly introduce the reader to the topic.

Line 86. Please, remove the "a" (i.e. allow for breakpoints in [...])

Line 97. I do not think you need the "actually" here

Line 99: I would suggest using "informative" instead of "robust" or alternatively "better fitted" instead of "more robust"

Line 101: I am missing half a sentence here (are not significantly different from those of the linear models)

Line 105: The active voice does not work here. Rewording suggestion: "a linear negative relationship towards the upper bound, where both models fit the better, cannot be rejected"

Figure 1 caption. It should be noted that the SIC criteria was arbitrarily subdued to the t-test when interpreting evidence for model support. As such, the linear models at 75% and 85% bounds were considered as better supported because the non-significant t-tests despite the SIC criteria suggests that the breakpoint models better fit in all cases. Therefore, and given the information the author is intending to show in Figure 1, I think it should be clarified that the breakpoint models were only considered as superior to the linear ones in case both sources of statistical evidence suggested so, and that otherwise the simplest model (i.e. linear) was considered as "best supported".

Line 126. "across biomes" instead of "by biomes"

Line 131. No need for "actually" here

Figure 2 caption. "across the main biomes [...]"

Line 179. "model that mechanistically"

Lines 213-215. I think that environment-driven diversifications are nowadays well acknowledged in the literature, so that there is consensus that diversity is not just a function of time and diversification rate. I think that the point here would be simply that previous attempts to explain spatial variation in diversification rates as a function of temperature might have failed due to the use of central tendencies instead of upper bounds. Yet, I am not sure that such contrasts have been conducted so far (i.e. using diversification rates instead of species richness as the response variable in spatial temperature-based models).

Lines 217-220. I do not get this, seems too cryptic to me.

Line 228. I am not an English native speaker, yet I think that testing a relationship "across regions" or "across biomes" actually means exploring the shape of the relationship IN every biome (i.e. the results shown in Figure 2) rather than considering all biomes/regions under the same model.

Lines 254-255. I think this idea could be expanded. For example, well-documented tropical-montane evolutionary radiations (e.g. Hughes 2015, <https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.13230>) probably blurred the macroecological signature of the kinetic hypothesis within tropical biomes.

Lines 255-259. Actually, your models show greater residual variation towards temperate, non-tropical latitudes, so I think this idea is incorrect. Perhaps the author wanted to stress that the -0.65 slope predicted by the kinetic model should only be expected in temperate regions? Besides, the expression "less environmental arrangement" is weird.

Line 265. "factors", in plural.

Lines 288-289. Rewording suggestion: "that prevents dispersion and diversification into "harsh", extra-tropical environments." Besides, recurrent disturbance (i.e. glaciations) may have also played a key role here...

Lines 296-300. This idea is loosely discussed and too cryptic.

Line 298. "dropping"

Line 304. See comment to lines 254-255

Line 308-311. I do not get this idea.

Line 322-324. In my opinion, this is a strong claim that suggests that previous studies are somewhat wrong, and I think it should be toned down. You may simply state that your contribution may serve to reevaluate the metabolic hypothesis in future latitudinal diversity gradient analyses.

Line 429. Please, describe the exact breadth of the ordered categories here and in Figure 5 caption.

Reviewed by anonymous reviewer, 2021-03-03 13:34

I liked this manuscript and I really enjoyed reading it. It is very clear and very well-written, and the topic and idea on how to address the richness- T^a relationship is nice. Upper limits instead of responses to mean values is something quite common in ecology, and it is surprising the amount of effort that has been put on analyzing mean tendencies instead of upper limits; the research topic of this manuscript is a clear example. I have also read the author's answers to the previous comments raised by the referees and I am quite happy with the arguments made by the author and the way he addressed some of the points. I have not much to say about the manuscript. The methodology is sound and robust. I understand the concerns raised by the referees and the recommender about the lack of a goodness-of-fit measure in quantile reg. similar to the R-squared, but the author is right when he explains this issue. Unfortunately, R1 does not have the same meaning as R2, and it does not inform about the explained variance. Maybe, one way that could be used to address this concern, somehow, is to check if the slope progressively decreases (or increases in absolute value) from the 5th to the 95th percentiles. This has been previously used by other authors such as:

VanDerWal, J., Shoo, L. P., Johnson, C. N., Williams, S. E. (2009). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist* 174: 282–291.

Jimenez-Valverde, A., Aragón, P., Lobo, J. M. (2021). Deconstructing the abundance-suitability relationship in species distribution modelling. *Global Ecol Biogeogr.* 2021: 30:327–338.

As a minor comment, it would be easy to check if the slopes statistically differ from -0.65.

Congratulations to the author for this enjoyable manuscript.

Revision round #1

2020-02-17

Author's Reply

[Download author's reply \(PDF file\)](#)

Decision round #1

Dear author

Sorry for the time taken to reach a decision about your preprint. Briefly, it has been difficult to find reviewers due to the holiday season, and some expected reviews have been delayed. In any case, now we do have two reviews, and both agree with my assessment that the paper may merit a recommendation in PCI, once some key problems with the current version are solved.

More precisely, for the preprint to be recommendable, you need to:

(a) provide a much better theoretical explanation linking the environmental temperature suffered by plants and mean annual temperature, as well as other descriptors of "harshness" such as Freezing Days (by the way, Humboldt first proposal of a mechanism for the latitudinal diversity gradient was precisely harshness; I think Hawkins TREE 2001 highlighted that).

(b) Assess the effects of regional variations on the richness/MAT relationship, ideally using differences between biomes and/or ecoregions, realms and glaciated/unglaciated areas.

(c) Pay special attention to the conversion of units, as it determines the slope values, and make a clearer formulation of your hypothesis about the slope that allows identifying the actual slope that is assessed. Current information in the methods is not enough so as to ascertain the exact way you may reach a comparable -0.65 slope.

(d) Provide estimates of the goodness of fit of the models. It could be argued that within an information-theory-based hypothesis testing framework goodness of fit is not needed - because you effectively assess whether/to which extent some hypotheses are informative or not. However, you use AIC for comparing between alternative models, which leaves the reader with no information about which is the power of these models to "explain" the data. If goodness-of-fit lies below, say, 5%, we are talking about massive residuals and limited explanation of the overall phenomenon of richness. If, on the contrary, such percentage goes above 30 or even 40% of variation, that is really a lot. If you account for (b) and you end up having final models that include MAT, Frost Days, CWD, biome and realm, for example, and that accounts for more than half of the variation, your results will be much more convincing that if you explain one third of richness variations, and most of it is due to regional effects.

See the reviewer's assessments for more details on these four points, and several other issues. Among these, let me highlight that you should avoid using MAT as abbreviation in the title (Mean Annual Temperature or simply Temperature would be more clear, and of course informative), and also that this manuscript desperately needs maps with richness and residual values, to allow the readers to assess your results in a wider extent.

I am looking forward to receive a revised version of the preprint, together with a detailed answer to the comments provided. I'm convinced that your research has enough quality so as to finally merit a recommendation in PCI Ecology.

All the best,

Joaquín

Preprint DOI: <https://doi.org/10.1101/836338>

Reviewed by *Rafael Molina-Venegas*, 2020-01-08 16:04

[Download the review \(PDF file\)](#)

Reviewed by *anonymous reviewer*, 2020-02-17 11:50

This is a nicely conducted, straightforward macroecological assessment of which are the actual effects of temperature on species richness. As any good macroecological work, it has the strengths and limitations of the discipline: while it makes a massive use of data – thus providing robustness, it also makes some oversimplifications – so statements about the real meaning of the relationships found need to be made with caution.

One of these oversimplifications is how you refer to temperature throughout the text (BTW, please avoid using the abbreviation in the title!). Perhaps the most worrying is in the opening paragraph, where you state that mean annual temperature would be the main driver of richness. This is not what Brown, Allen and colleagues said, for the average of the monthly averages means nothing in biological terms. This variable is a

proxy for the general temperature conditions in each place throughout the year; as such it tells a lot about the (lack of) harshness of the conditions for life in each place, but it tells nothing about the mechanisms you are talking about here. As Brown and colleagues lined them up in their Metabolic Theory, the limit to life growth (and richness) is given by the temperature of activation of enzymatic reactions, which gives the approximate slope of - 0.65. Therefore, the important factor is the temperature experienced by the cells, and more precisely for how long this temperature is available throughout the year in environmental conditions. This would be the physiological limit imposed by temperature to population growth and several aspects of diversity, including richness. In absence of such value (time with environmental temperatures suitable for enzymatic reactions), or of other a priori more adequate proxies such a Growing Degree Days, Frost Days, or the like, mean annual temperature could be used as a substitute, assuming that the higher the average temperature throughout the year, the more time with temperatures adequate for normal cell functioning, the lower the energetic costs for organic functioning, and the higher the population growth, diversification rates and the conundrum of mechanisms leading to higher species richness.

Well, I'm missing at least part of this theoretical introduction in your text. Perhaps not all of this, but at least a sharper justification for the use of mean temperatures as proxies, indicating the mechanisms linking temperature with richness, and why MAT could be a good proxy for that. In fact, to me the most important of your results (the relationship between residuals and Frost Days) would be highlighted much better if this theoretical framework was properly outlined. And so would be Water Deficit, another measure of the quantity of time available for proper biological activity.

Also, I'm missing two key papers by Hawkins et al (2007a,b) from the original evaluation of the Metabolic Theory. In the first a number of authors assessed whether the relationships between richness and temperature followed the -0.65 slope for many groups and regions (almost none of them did follow it; and in the second a subset of them provided several arguments of why this should be an expected outcome; their main argument was that even if such limit to enzymatic activity was universal, the course of evolution would lead most of biodiversity to escape from the limitations it imposes through evolving many different strategies (endothermy, cell wall structures to create microclimates, etc.) that following my argument above would lead to longer times with adequate cell functioning throughout the year, escaping from environmental temperature conditions. The fact that you find that MAT could be a limit to maximum richness and frost alters these numbers is somehow related with this realisation in Hawkins et al 2007b, although it contradicts to some extent the findings in Hawkins et al 2007a. Referring to such literature, and some other key papers on physiological limits (e.g. Peck et al. 2009, Peters et al. 2016, Brodie 2019, or some papers in a recent Phil Trans issue, see Spicer et al. 2019).

Besides that, your work is undermined by the lack of accounting for regional effects. The slope of the relationship between species richness and temperature is well known to vary in space (e.g. Cassemiro et al. 2007, Hortal et al. 2011, etc.) according to several factors such as glaciations and differences among regional communities (sensu Ricklefs 2008, 2015). So while reading it I feel constantly guessing that the alternative hypothesis that the relationship between richness and temperature varies significantly in space by factors other than frost.

To assess this, all time I'm missing a map to locate studies with their richness and another with their residual values. This paper desperately needs these two maps. But also, the robustness of your results is compromised by the lack of assessments of effect differences between different types of regions. Accounting for this could be easy by adding as cofactors biogeographic realms, biome maps, glaciated/unglaciated areas, etc. I would be really surprised to find that there are no differences between regions, biomes, ecoregions or areas that suffered glaciations or not. But if that is the case, then the importance of your paper would increase a lot.

Besides these major problems, there are several typos (e.g. in the abstract "attempts to explain (...) richness HAVE focused"), but most importantly there are a few idiomatic problems here and there, so a light English revision is needed. In particular, the following sentences need to be reworked:

- Last sentence of the abstract is confusing, it needs to be rewritten

- Lines 67-69. This sentence is also confusing ("significantly further" does not work well), rephrase and clarify. While doing so, try to relate it with the sentence in lines 90-94, which states more or less the same; right now the text feels repetitive, so it may be worth splitting the information between the two paragraphs, linking them in terms of content.
- Lines 103-104. I can't tell what does "by drop in" mean in this context, and most readers will not understand either. Please rephrase.

Brodie, J.F. (2019) Environmental limits to mammal diversity vary with latitude and global temperature. *Ecology Letters*, 22, 480-485.

Casemiro, F.A.d.S., Barreto, B.d.S., Rangel, T.F.L.V.B. & Diniz-Filho, J.A.F. (2007) Non-stationarity, diversity gradients and the metabolic theory of ecology. *Global Ecology and Biogeography*, 16, 820-822.

Hawkins, B.A., Albuquerque, F.S., Araújo, M.B., Beck, J., Bini, L.M., Cabrero-Sañudo, F.J., Castro Parga, I., Diniz-Filho, J.A.F., Ferrer-Castán, D., Field, R., Gómez, J.F., Hortal, J., Kerr, J.T., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Moreno, J.C., Olalla-Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Sanders, N.J. & Williams, P. (2007a) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, 88, 1877-1888.

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Ricklefs, R.E. (2008) Disintegration of the ecological community. *American Naturalist*, 172, 741-750.

Ricklefs, R.E. (2015) Intrinsic dynamics of the regional community. *Ecology Letters*, 18, 497-503.

Spicer, J.I., Morley, S.A. & Bozinovic, F. (2019) Physiological diversity, biodiversity patterns and global climate change: testing key hypotheses involving temperature and oxygen. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20190032.