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Dr. Daniel Costa
Editor
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Dear Dr. Costa:

We have now finished the revisions for the resubmission of our manuscript "*Latitudinal gradients in biotic niche breadth vary across ecosystem types.*" for consideration in the Population and Community Ecology section of the *Proceedings of the Royal Society B*.

In your original decision, you encouraged us to resubmit a revised version of the manuscript noting that, while the Reviewers were quite positive, they and the Associate Editor had a few substantial concerns. We appreciate the comments by the Associate Editor and the Referees, and have taken care to address each one while keeping within the size limits set by *Proceedings of the Royal Society B*. We feel that the revised manuscript is both stronger and more accessible, and hope that it will please the Editors and Reviewers alike.

Thank you again for your consideration of our revised manuscript.

Reply to Associate Editor

The Associate Editor stated that both Referees found our study "very interesting", but echoed and added to their concerns. In particular, the Associate Editor requested a demonstration that our results are not "artefacts of differences in sampling effort between studies". To address this, we have taken the Associate Editor's advice and performed the extra analyses suggested by Referee 1 (described in detail below). We have also taken the Associate Editor's specific comments to heart and address each one in turn. We hope that our replies (preceded by **R:** will assuage the Associate Editor's concerns and are confident that our manuscript is strengthened as a result.

1) Title doesn't reflect our trends in freshwater communities.

Title: the current title seems to suggest that this scaling with latitude did never happen, while it was present in freshwater food webs.

R: We had originally intended to emphasize that, contrary to our expectations, scaling relationships did not vary over latitude in *most* ecosystems. We have now amended our title to "*Latitudinal gradients in biotic niche breadth vary across ecosystem types.*" in order to better capture the scaling that did occur in streams.

2) L29, L42: suggest the likely directions of effects.

L29. To help the reader, please be explicit about the direction of these 'direct relationships'.

L42. Can you make a directional prediction on how latitude is expected to affect the scaling? Otherwise, the study becomes rather exploratory presenting some phenomenological patterns not grounded in theory that need ad hoc explanations in the discussion. Similarly, can you provide a priori motivations why the relationship may differ among ecosystem types?

R: The goal of our study was to give support to one of two contrasting hypotheses (narrower niches in the tropics **?** versus broader niche space in the tropics **?**). Given the limited support available for either hypothesis, we had no *a priori* expectation that one was more likely than the other– that is, it was plausible that scaling of specialisation with species richness might be stronger towards the poles or that scaling would be unaffected by latitude. We have added to the introduction at lines 22-27 to make these two potential relationships clearer and at lines 37-42 to more explicitly frame our study as a test of these two versions of the latitude-niche breadth hypothesis. We have also followed Reviewer 2's suggestion and now provide a conceptual figure (Fig. 1) that clearly places our study within this context. We also now provide an explanation for why we included

ecosystem type as a covariate at lines 42-44.

> If the latitude-niche breadth hypothesis is correct, there should also be direct relationships between latitude and the degree of specialisation (i.e., the breadth of the Eltonian niche; **??**) of species within food webs. Specifically, narrower niches in the tropics would equate to greater specialisation (narrower niches) while constant niche sizes but greater productivity would translate to constant specialisation and niche width across latitude (Fig. 1).
>
> If the scaling of specialisation with species richness is weaker in the tropics (i.e., if species gain fewer links, predators, or prey as the size of the network increases), this will indicate narrower niches at the tropics. If, however, the scaling of specialisation with species richness does not vary over latitude, this will indicate that niches are similarly-sized worldwide but that there is a broader niche space in the tropics. Additionally, as food webs describing different ecosystem types may differ in their topology **??**, we also explored the differences in scaling relationships across ecosystem types.

3) L98-99: explain our model-selection procedure in more detail.

L98-99. According to some experts (e.g. the landmark 2002 book by Burnham and Anderson) when models differ less than 2 units in AIC, they have the same support and fit. On what theoretical grounds do you motivate the choice to select the model with the lowest AIC as the best-fit model when models have δAIC<2? To what extent does this choice affect your conclusions?

R: We are also aware of the general consensus that models where δAIC<2 are roughly equally well-supported. This is why our procedure (as stated in lines 83-86) was to first consider the set of models where δAIC<2 and select the model with the fewest degrees of freedom. We chose the smallest model where δAIC<2 in order to avoid over-fitting the models.

We only used AIC as a deciding factor where there were several models that shared the minimal degrees of freedom and all had δAIC<2. In fact, this scenario did not occur for the models presented in the previous draft (it does occur when the by-trophic-level models use counts of species rather than proportions, an analysis which we had explored in an earlier draft). To avoid confusion we have therefore removed the description of this step of our analysis from the main text.

> Simplified models were obtained by systematically removing all possible combinations of terms from the full model. The best-fitting model was

then determined to be the model with the fewest terms where ΔAIC<2, as this model is the least likely to suffer from over-fitting.

4) Move by-trophic-level analyses to appendix and/or better-explain our motivations.

L100-106. After reading the introduction, it is not clear why you 'were also interested' in this topic. I suggest following the advice of reviewer 2 and moving this part and the associated results to the appendix. Please also then explain why this is a priori interesting and relevant to investigate in the context of your study.

R: After carefully considering the Associate Editor and Reviewer's comments, we have opted to remove the by-trophic-level analyses entirely. Due to length restrictions, we were not able to both expand our description of the motivations for and implications of these analyses and accommodate the other changes suggested by the Associate Editor and Reviewers. We chose to focus on ensuring that the discussion of the species-richness results is as clear and complete as possible, and believe that our manuscript is stronger and more to-the-point after these changes.

5) L113: is there any covariance in the network properties?

L113. To what extent do the property estimates covary with each other? This may be presented in an appendix.

R: As the Associate Editor likely suspected, the property estimates are all strongly positively correlated. As generality and vulnerability describe the two components (number of prey and number of predators, respectively) of links per species, this is to be expected. We have added a brief description of these correlations to the main text (lines 122-125) as we believe it will provide some context for the very similar results for link density and vulnerability.

> Link density, generality, and vulnerability were strongly and positively correlated (R^2=0.891 for link density and generality, R^2>0.999 for link density and vulnerability, and R^2=0.890 for generality and vulnerability).

6) L116: missing supporting statistics

L116. It seems the stats to support this statement are missing.

R: We have ammended the text (lines 135-138) to support our statement.

> In stream food webs, generality increased more rapidly towards the poles ($\beta_{Latitude:Stream}$=0.007, p=0.001) while link density and vulnerabil-

ity did not vary with latitude (i.e., the interaction term $\beta_{Latitude:Stream}$ was not retained in the best-fit models).

7) L187-198: provide citations for an absence of prey-switching in communities other than streams.

L187-198. For your explanation why the scaling relationship changes with latitude in lake and stream food webs and not in the other ecosystem types to be convincing it is not enough to cite studies that high-latitude aquatic species tend to switch between different seasonally available prey, you also need to provide evidence from the literature that this is not the case in the other ecosystem types.

R: Following Reviewer 1's suggestion, we have restructured our discussion to focus more on seasonality in different ecosystem types than on prey-switching. As we are not aware of any studies explicitly comparing the frequencies of prey-switching in different ecosystem types, and do not feel qualified to conduct such a review ourselves, we hope that this revised discussion will be satisfactory.

8) Ensure layout (especially citations) matches journal specifications.

Please strictly follow the author guidelines with regard to layout (for example how to cite studies in the text).

R: We have changed all refences to the Vancouver style and have added sections for author contributions, conflicts of interest, and funding.

Reply to Reviewer 1

The Reviewer was very positive about our manuscript, calling it "an interesting paper that takes advantage of recent compilations of food webs to test basic theory with respect to latitudinal gradients in niche breadth", "exceptionally well written and presented", "sophisticated and well thought out". We thank the Reviewer for their kind words, and also for their suggestions for further improving our manuscript. We have addressed each comment below (in italics), and are confident that our responses (preceded by a **R**) have further improved the manuscript.

1) Some trends may be due to differences in sampling effort, especially due to differences between Thompson & Townsend stream food webs and other stream webs.

My concern here is how much of the pattern can be attributed to true ecological effects – as opposed to the consequences of differences in the effort used to describe different food webs... It could be explored to some extent by analysing for an effect of particular authors (e.g. the Thompson and Townsend food webs which dominate the stream dataset) but ultimately there is every chance that the results here are artefacts of differences in sampling effort between studies. Might it be possible to randomise the datasets, excluding particular food webs (or authors) to determine robustness to this effect??

R: We share the reviewer's concern that variation in sampling effort could be driving the trends we observe, as it is highly likely that the authors of all 196 webs in our dataset did not follow the same procedures. Following the reviewer's suggestion, we have performed a jackknife analysis by systematically removing each web in turn and then repeating our analysis. We also performed a similar process removing each set of food webs compiled by a common author (or set of authors where all authors worked on identical sets of food webs). We are happy to report that removing any single web had no significant effect on any model, nor did removing any set of webs compiled by a common author. We have added a description of these methods and summary of their results to the supporting information (*Appendix S3*), and we thank the reviewer for suggesting this validation of our overall results. We have also added a brief note in the main text to direct other readers with similar concerns to the supporting information (lines 111-120).

We removed webs compiled by Thompson and by Townsend separately as each author compiled one food web that the other did not. However, as 26/28 of the food webs compiled by Thompson *or* Townsend were compiled by both together, the results of both jackknife iterations were very similar (as seen in authors 7 and 6, respectively, in *Figs. S4-S6, Appendix S3*). We are particularly reassured by *Fig. S5*, where the removal of large subsets of the stream food webs had very little impact on the coefficient representing the effect of latitude on the scaling of generality with species richness in

streams.

> As a supplemental check to ensure that variation in sampling effor across food webs was not responsible for the trends we observed, we then repeated our analyses using jackknifed data sets in which we 1) sequentially removed each food web in the dataset and 2) sequentially removed sets of food webs associated with each author of the food webs in the dataset. Parameter estimates varied very little across either series of jackknifes (*Appendix S3*).

2) Emphasize our results for streams, include the possibility that they may be due to greater seasonality in stream food webs.

It is particularly interesting in that stream systems (as opposed to estuarine, marine or terrestrial food webs) are more likely to be affected by seasonal variability – and this is the mechanism evoked as underpinning the latitudinal gradient. I am surprised that the authors didn't make more of this point – to some degree the difference in habitats supports their proposed mechanism, and this could be discussed.

R: We thank the Reviewer for this suggestion, and have substantially revised our discussion (lines 182-217) to follow it. The Reviewer will note that our arguments include lakes as well as streams since both systems showed effects of latitude on scaling, and both experience severe seasonal variability as the Reviewer points out for streams. We have also added a brief note to address the potential that the New Zealand stream food webs mentioned by the Reviewer above might be affecting our results. As described below, they are grouped in a narrow band of latitude; this likely explains their minimal impact on the trends we observe. We think that our discussion is much stronger after these changes.

> That freshwater food webs supported the hypothesis of narrower niches in the tropics –while other ecosystem types did not– is noteworthy given that these ecosystems (especially streams) are known for being highly variable and that seasonal variability is one of the proposed drivers of the latitude-niche breadth hypothesis **?**. Both streams and lakes can experience severe changes in water temperature and volume (e.g., floods, drying, freezing) that remove food or other resources (notably oxygen during freezing events) **??**. These events are often linked to seasonal events such as snowmelts or summer drought **?**). Further, both temperate streams and lakes tend to experience seasonal strong pulses of allochthonous inputs (e.g., fallen leaves, terrestrial invertebrates **???**. These trends combined mean that, relative to estuarine and marine communities, freshwater food webs may experience high turnover in both community composition

and productivity **???**. Notable exceptions from the above trends are New Zealand stream communities (representing 31 of the 71 stream food webs in our dataset), which experience unpredictable flooding and drying throughout the year and do not receive seasonally pulsed subsidies **??**. However, as this subset of webs is very tightly grouped in latitude ($44.64 - 46.41°$S, within an overall range of $23-69.02°$ for stream communities), it is unlikely that they have greatly influenced our results (see also *Appendix S3*). Moreover, just as in highly-variable communities where said variation is more seasonal, New Zealand communities are dominated by ecological generalists **??** implying that they appear to fit the general pattern of streams worldwide.

Importantly, while terrestrial communities are also strongly seasonal at high latitudes and can receive significant allochthonous inputs **?**, terrestrial consumers tend to be morphologically specialised for feeding on particular prey **?**. This means that primarily gape-limited aquatic consumers tend to be more generalist across all types of aquatic habitats than terrestrial consumers **??**. The key to this explanation of the differences between freshwater and marine and estuarine ecosystems is whether the former experience more severe seasonal variation. Although we are not aware of any study explicitly comparing seasonal variation in freshwater and saltwater or brackish food webs in a similar location, we believe that freshwater ecosystems are indeed likely to experience more severe changes because of their small size. While oceans and estuaries certainly vary in terms of water temperature and nutrients over the course of a year **?**, these changes are likely to be slower and milder than in freshwaters because marine and estuarine communities are buffered by being open to the ocean rather than isolated in the midst of a terrestrial matrix. Net primary productivity in particular is much more variable over the course of a year in non-marine communities **?**, suggesting that niche breadths may also be more variable over the course of the year.

Reply to Reviewer 2

The Reviewer stated that our study is interesting and covers “a timely and important topic. The core analysis of the paper (scaling relationships of food web metrics with species richness) are convincingly presented and comprehensively discussed.” Nevertheless, the Reviewer has suggested several ways in which our manuscript could be improved. We have responded to each suggestion in turn, and believe that our replies (preceded by **R**) have further improved the manuscript.

1) Network terminology and methods might be inaccessible to researchers without network background.

the accessibility to readers outside the food-web community could be improved by a more detailed explanation of the methods, especially the applied network metrics and underlying scaling relationships; a conceptual figure visualizing the expected relationships for different communities according to the latitude-niche breadth hypothesis could be very helpful here

For readers outside the field, please explain in more detail the difference between ‘original species’ and ‘trophic species’ in food webs.

R: We thank the reviewer for their concern that our manuscript should be accessible to as wide a variety of researchers as possible, and have followed the reviewer’s suggestions in several places in the manuscript. We now include a conceptual figure to clearly and succinctly link the changes to scaling relationships we expected to these two versions of the latitude-niche breadth hypothesis (Fig. 1).

We have explained “trophic species webs" more thoroughly in lines 58-60 and added parenthetical definitions of trophic-species and orignal webs in lines 62-64. We have also added parenthetical definitions of link density, generality, and vulnerability at the begining of the results section to remind readers of the biological meaning of these measures.

> Many analyses of food-web structure attempt to reduce this variation by using food webs comprised of “trophic species” –aggregations of species with identical sets of predators and prey– rather than species *per se* **????**.
>
> We therefore analysed both original (i.e., without aggregating any species) and trophic-species (i.e., after aggregating species with identical predators and prey) versions of the dataset ...
>
> Link density (mean number of feeding links per species), generality (mean number of prey per species), and vulnerability (mean number of predators per species) were strongly and positively correlated ...

2) Reconsider by-trophic-level analysis.

the additional analyses of scaling relationships by trophic levels and latitude-species richness relationships are not well introduced. If the analysis on scaling relationships by trophic levels was maintained, then it should already be mentioned in the Introduction (including specific expectations for this analysis) and would require a more comprehensive discussion.

The abstract is incomplete. Results of the analysis on the scaling relationships by trophic levels are missing.

Please justify why you use the proportion of species within a trophic level and not the absolute number of species per trophic level; at a first glance, this would be more intuitive for me given the focus of the study on scaling relationships with species richness.

R: We appreciate the Reviewer's concerns about the integration of these results into the main text. Due to length restrictions, we were unable to explain our motivations and discuss our results more fully in the main text. Moreover, referring briefly to by-trophic-level results in the supplemental information repeated the problems with lack of justification and poor integration of the by-trophic-level results with the species-richness results. To that end we have opted to remove these results entirely. Instead, we have prioritised enriching our discussion of the species-richness results, clarifying our methods, and including the latitudinal gradient in species-richness as requested below. We hope that, on balance, this restructuring has resulted in a clearer and more well-integrated manuscript.

3) Move description of the species-richness gradient to methods and results.

Analyses of species richness along latitude should already be mentioned and described in the Methods and should be referred to in the Results section instead of the Discussion.

The start of the Discussion confused me since it presents another additional analysis. This analysis on the latitudinal gradient in species richness is interesting and important for the interpretation of the patterns, but should already be presented in Methods and Results section.

R: Given the lack of significant relationships, we had originally viewed this analysis as a very minor part of our paper, but are happy to follow the Reviewer's suggestion and integrate it in the methods and results along with our main analyses. We now describe the methods for this analysis in lines 74-86 and summarize our results in lines 125-128.

Gradients over Latitude

To put our dataset in the context of other research on latitudinal gradients in species richness, we first examined simple linear relationships between latitude and each of species richness, links per species, generality, vulnerability, and proportions of basal resources, intermediate consumers, and top predators. We fit models of the form

$$S_i = \alpha_0 + \alpha_1 L_i + \alpha_2 E_i + \alpha_3 L_i E_i + \epsilon_i, \tag{1}$$

where S_i is the species richness of web i, L_i its absolute latitude (degrees north or south regardless of direction), E_i is a categorical variable indicating the ecosystem type of network i (comprising terms for stream, marine, lake, and terrestrial networks with estuarine networks corresponding to $E_i = 0$) and ϵ_i is a residual error term. We next calculated the AIC of the maximal model as well as the AIC's of a suite of candidate simplified models identified using the R **?** function dredge from package MuMIn **?**. Simplified models were obtained by systematically removing all possible combinations of terms from the full model. The best-fitting model was then determined to be the model with the fewest terms where ΔAIC<2, as this model is the least likely to suffer from over-fitting.

Contrary to the expected latitudinal gradient, the best-fit version of equation (1) did not include a significant effect of latitude for any ecosystem type. Further, there were no significant relationships between link density, generality, or vulnerability with latitude for any ecosystem type.

4) Explain habitat categories.

Please describe in more detail why you used the chosen habitat categories and provide the number of webs per habitat type also in the main manuscript.

R: We followed the habitat categories given by the publications which aggregated the food webs. Although more detailed descriptions were also provided, we opted to use the set of five more general habitat types in order to have a greater number of food webs in each category.

We have added a brief explanation, and the number of webs in each ecosystem type, at lines 52-55:

> We grouped food web by ecosystem type (stream, N=71; lake, N=47; marine, N=28; estuarine, N=18; and terrestrial, N=31) according to their designation in previous aggregations of food webs (i.e., **???**).

5) The y-xais of Fig. 1 is unclear, top predators are unlabelled.

Please re-label the y-axis on Fig. 1 to improve clarity. The top predators are missing in this figure although they are mentioned in the legend.

R: We thank the reviewer for pointing this out and, while the inclusion of top predators specifically is moot since these results have been moved to the supplemental information, have taken care that all labels are included in all figures. We have also re-labelled the y-axes on Fig. 2 (the old Fig. 1) to improve clarity.

6) Add generality, vulnerability to Fig. 2 in main text.

I would suggest adding generality and vulnerability to Fig. 2 in the main manuscript (instead of showing them in Fig. S2 only).

R: We have followed the reviewer's suggestion.