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Nathan J. B. Kraft *et al.*
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Response to Comments on “Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients”

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Qian *et al.* and Tuomisto and Ruokolainen critique our analyses of elevational and latitudinal variation in tree diversity. We address their points by reanalyzing different subsets of our data and by clarifying certain misconceptions, and reiterate that gradients in β diversity can be explained in the elevational and latitudinal tree data sets by variation in the size of species pools.

Both Qian *et al.* (1) and Tuomisto and Ruokolainen (2) critique the Gentry data sets. Qian *et al.* state that β diversity among Gentry subplots is not comparable across locations because the spatial orientation of the subplots varies among locations. Subplot spatial orientation varies haphazardly across sites, and no systematic trends in spatial orientation exist. Therefore, gradients in Gentry plot β diversity are neither biased nor invalid. Qian *et al.* also assert that because the Gentry subplots tend to be located to minimize coarse environmental variability among subplots at a location, they cannot be used to study the ecological processes determin-

ing species composition. We originally stressed that the Gentry data are not appropriate for testing how coarse-grained environmental heterogeneity structures communities among subplots within a location (3). We disagree, however, that the scale of the Gentry plots makes them inappropriate for studying the myriad processes that structure community composition. Indeed, considerable β diversity exists within each location in the Gentry data estimated by the β partition either before [figure 1C in (3)] or after [figure 3C in (3)] implementing our sampling-based null model. This second point is a misunderstanding shared by both Qian *et al.* and Tuomisto and Ruokolainen. Specifically, after conditioning the observed β diversity within each location on location-level γ diversity, we still find extensive and substantial nonrandom patterns of species turnover at all points along both latitudinal and elevational gradients [i.e., the β deviation was >0 for almost all points in figure 3C and for all points in figure 3D in (1)]. Our key result, therefore, is not that species co-occurrence patterns can be explained by a null model, as Tuomisto and Ruokolainen state. Instead, we find that the β partition shows no trend with latitude or elevation after accounting for γ diversity with an appropriate null model. Although broader-scale sampling at each location might capture β diversity driven by coarser-grained environmental factors, there is pervasive, nonrandom β diversity at the spatial scale measured by the Gentry data. Our paper does not state that “latitudinal trends in β diversity...lack ecological relevance,” as Tuomisto and Ruokolainen suggest. Nonrandom patterns in the smaller-scale turnover that we documented are both real and ecologically relevant.

Qian *et al.* critique our use of latitude instead of temperature and suggest a correction to latitude that accounts for plot elevation as a proxy for mean temperature (1). We question the va-

lidity of this simple correction, given that many factors besides mean temperature differ among locations. Nevertheless, when we apply this adjustment to the full 197-location data set, the results agree with those of our previous analysis (3). Specifically, we find that the negative correlation between latitude and β diversity can be explained by our null model in the original data [Fig. 1, A and B, after (3)] and after adjusting latitude for elevation in the manner proposed (Fig. 1, C and D). We reach the same conclusion when we remove high-elevation sites from the analysis [Fig. 1, E and F; defining high elevation as >1000 m after figure 2 in (1)].

Qian *et al.* examined whether β -diversity patterns in one particular subset of the Gentry data differ from patterns seen in the entire data set. We disagree that any nonrandom subset of a larger data set would be expected to show the same pattern as the entire data set. Nevertheless, if we restrict our analysis to include only the Gentry plots from the New World (158 out of 197 locations), our original conclusions are upheld, regardless of whether we adjust latitude for elevation following (1) or remove high-elevation sites (Fig. 2). However, if we reduce the data set further, as Qian *et al.* have done, to include only the 72 South American locations south of the equator (37% of the full data set, thereby excluding $>50\%$ of the New World data and 33% of the South American data), a statistically significant relationship between the β deviation and latitude emerges. What is surprising is that the pattern is the opposite of what is expected. Specifically, although β diversity for South America south of the equator is highest at the equator ($R^2 = 0.38$) [figure 1B in (1)], after correcting for variation in γ diversity, the β deviation is highest in southern South America ($R^2 = 0.11$) [figure 1C in (1)], effectively reversing the gradient. Our global analysis demonstrated how differences in β diversity across a broad gradient can be explained by differences in γ diversity, resulting in no gradient in β diversity across latitude. By focusing on a nonrandom subset of the data, Qian *et al.* show that the effect of γ diversity can be so strong that, once it is accounted for, the pattern along the latitudinal gradient is actually reversed. This gives further strong evidence for the importance of the null-model-based approach that we have developed for analyzing β -diversity trends (3).

We fully support attempts to apply our null-model approach to other data sets, as Qian *et al.* attempt to do with a new North American tree data set. Importantly, however, our null-model approach requires data on individual abundances within subplots, because it operates by randomizing individuals among samples. The additional data set does not include abundance information, so unfortunately cannot be analyzed using our null-model approach. Qian *et al.* propose to instead account for γ diversity using least-squares multiple regression. This approach fails to properly

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account for the differences in γ diversity among transects [supporting online material (SOM) S2], and their implementation suffers from important

statistical errors (SOM S3), making their approach unsuitable for analyzing the effect of γ diversity on β diversity.

Furthermore, we question the interpretation of results offered by Qian *et al.* from the North American tree analysis. Specifically, they estimated

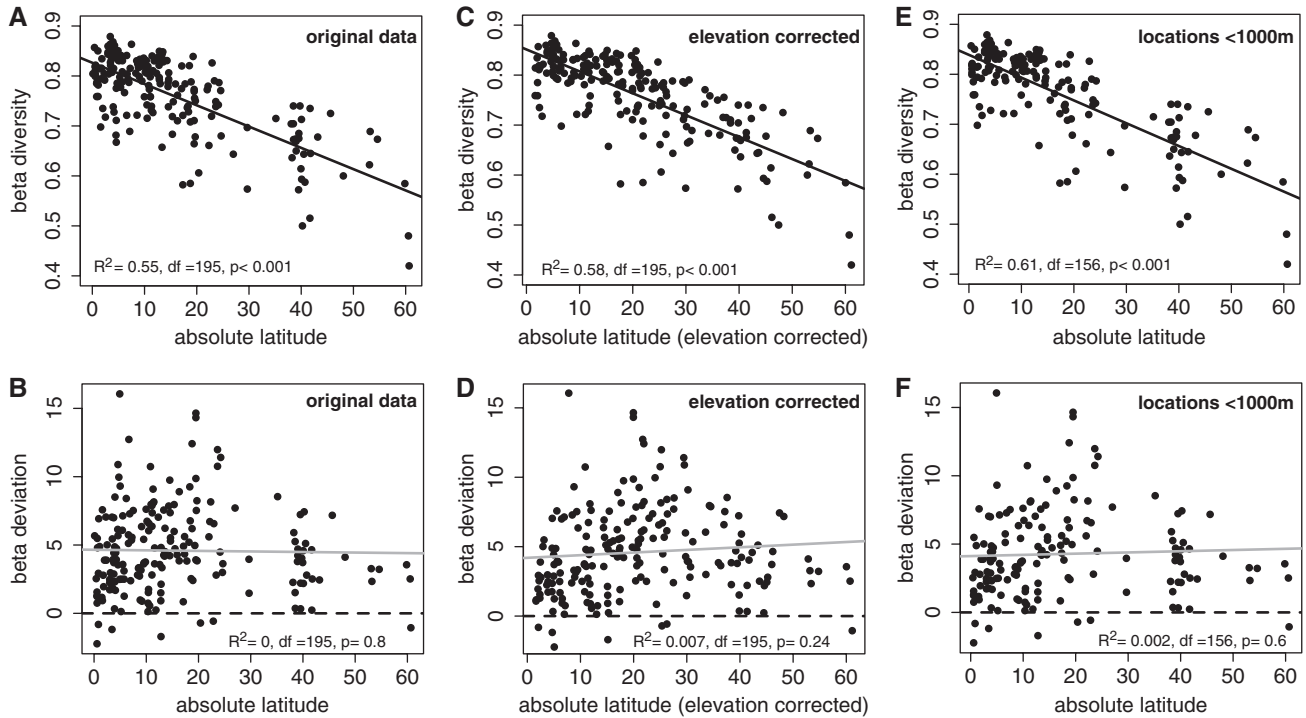


Fig. 1. Latitudinal comparison of β diversity (measured as the β partition) with the β deviation from our null model. (A) and (B) show the original results from (1), including all 197 locations across the globe. (C) and (D) adjust latitude for elevation following the correction Qian *et al.* propose. (E) and (F) remove locations above 1000 m of elevation. Dashed line indicates a β deviation of 0. Solid lines show linear relationships; black lines are significant, gray lines are nonsignificant.

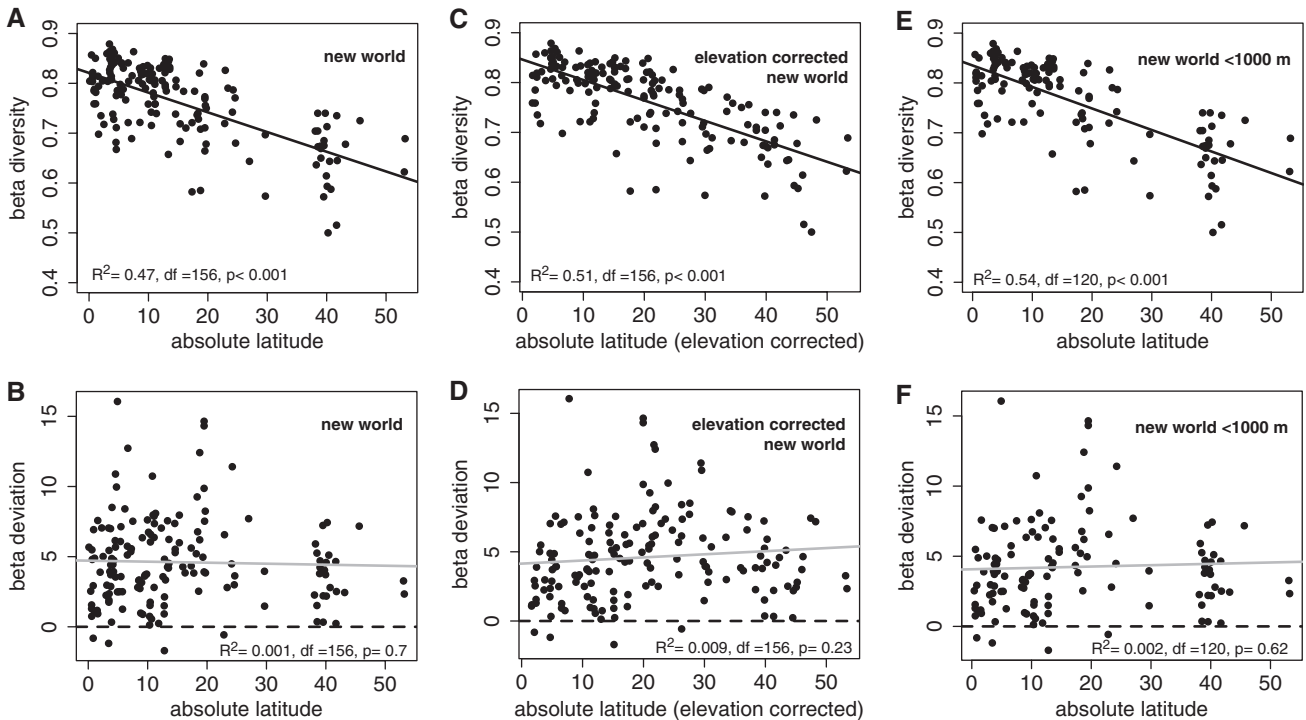


Fig. 2. Same analyses as Fig. 1, restricting data to just the New World. (A and B) β diversity and β partition versus latitude for all New World sites. (C and D) β diversity and β partition after correcting latitude for elevation using the correction Qian *et al.* propose. (E and F) β diversity and β partition after removing sites above 1000 m.

that the percentage of variance explained by latitude drops from 56.4% with β diversity measured as the β partition to just 7.3% after taking the residuals of the β - γ relationship. This is a large decrease, and although we emphasize that their method is not appropriate for their aims of accounting for the influence of γ on β , their results are nevertheless largely consistent with our main conclusion: namely, that significant variation in β diversity across large biogeographic gradients is likely to be driven by sampling effects (3).

Tuomisto and Ruokolainen question our conclusion that variation in β diversity can be driven by variation in γ diversity, claiming that our conclusion is a by-product of the fact that α diversity is not free to vary in our analyses. However, this assertion is not correct. To clarify, in our simulations, we constrained γ diversity, the number of individuals per sample, and the existing abundance distribution of the species within each location [see R code in the SOM of (3)]. Therefore, in both the simulations and the null model used to calculate the β deviation, α diversity is free to vary. Our results [e.g., figure 2A in (3)] show that increasing γ diversity does indeed drive an increase in β diversity under our random sampling null model.

Next, they propose that should the special case arise where α and γ diversity increase by exactly the same factor, β diversity would be constant with increasing γ diversity. Although this is true in their hypothetical scenario, it is clear that in both the real data sets [compare slopes in figure 1, A and B, in (3)] and in our simulations of randomly assembled communities, α and γ do not increase by the same factor. Specifically, as γ diversity increases, α diversity increases too, but by a smaller factor, yielding the increase in β diversity. Therefore, although it is theoretically possible for α and γ to increase by precisely the same factor, and it may be possible to conceive of a hypothetical scenario in which an increase in γ diversity does not increase β diversity, neither the original data sets in our analysis nor the null-model randomizations exhibited this proposed behavior of perfect scaling between α and γ , nor would we expect this to occur generally for empirical ecological systems.

Tuomisto and Ruokolainen suggest that the correlation between β and γ diversity in our data set is spurious. They show simulations indicating that α and γ depend on the number of species in the local species pool (which we define as γ diversity in our analyses) as well as the number of stems. This is exactly the point that we make in our manuscript: for example, figure 2A in (3) documents the expected relationship between α , γ , and the number of individuals in the local community under random sampling. This sampling relationship is at the core of our analyses and results (3).

Tuomisto and Ruokolainen also state that we are “undersampling” the local community and that this undersampling bias covaries with latitude in a way that drives our results. This claim seems to hinge on the idea that there is a single “best” scale at which to study ecological phenomena. We strongly disagree, as there is a long history in ecology of noting the scale-dependence of various processes (4–8). We emphasized in our paper (3) that any inferences drawn from an analysis are conditioned on the scales used in the study. As Gentry and colleagues cataloged every woody stem in each subplot, we fail to see how the data have undersampled the communities about which we draw our inferences. The solution suggested by Tuomisto and Ruokolainen to avoid this undersampling is to increase the size of local subplots until they can contain enough individuals to represent all species present in the region. This effectively requires that α and γ be measured at the same scale, but in all studies of β diversity, the scale at which α is measured is necessarily smaller than the scale at which γ is measured. Furthermore, their proposed solution would require different-sized sampling units in regions having different values for γ . This would confound sampling-scale differences with regional differences, thus making robust comparisons impossible. This also places unrealistic constraints on the spatial scale that can be considered to be a community, which in turn severely constrains the spatial scale at which one can make ecological inferences. In contrast, we have directly incorporated the sampling relationship between α and γ (in terms of the number of stems) into the null model in order to calculate the β deviation, and

this approach can be applied at any spatial scale that is of interest.

Qian *et al.* and Tuomisto and Ruokolainen suggest that the aim of our paper was to explain the effect of environmental variation on species composition. In fact, our only goal was to test the idea that the observed trends in β diversity (among subplots) with respect to either latitude or elevation could arise by random sampling from the pool of individuals at the location level. Here, we have shown that our results are robust. We welcome the application of our null-model approach to other suitable data sets, for other taxonomic groups of organisms and at other scales. As one recent example, a new global analysis of independent large-scale forest data sets implementing a similar null model to the one we developed concluded that global patterns of β diversity are largely driven by variation in γ diversity (9), much as we report (3). Proposals regarding new tests of specific mechanisms that might drive α , β , and γ diversity at a variety of scales are due to unfold but will be challenging to assess from observational data alone. A more complete understanding of what drives spatial variation in biodiversity will require, in the first instance, demonstration of the inadequacy of null models of community assembly alone to account for empirical patterns.

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SOM Text

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