

CORRIGENDUM

Corrigendum for Rojas *et al.* (2018)

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Danny Rojas, Maria João Ramos Pereira, Carlos Fonseca, Liliana M. Dávalos

Eating down the food chain: generalism is not an evolutionary dead end for herbivores

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Rates of speciation (or diversification) estimated in BAMM, either from the tips or path-wise rates, must not be used in phylogenetic regressions in the way presented in our paper (Rojas *et al.* 2018), as we will explain in this correction. Different approaches have been recently developed to study the joint dynamics of trait evolution and species diversification across a phylogeny. These methods assume that some traits (e.g. body mass, ecological specialization, dispersal ability, among others) can explain diversification rates. Some approaches assess the correlation between tip-specific metrics of speciation and species-level trait values (e.g. STRAPP; Rabosky & Huang 2016). Another method, the quantitative state speciation and extinction approach (QuaSSE; FitzJohn 2010) tests speciation rate as different explicit functions of the trait states. Limitations of these methods have been analyzed elsewhere (e.g., Harvey & Rabosky 2017). For example, STRAPP requires large phylogenies to detect significant associations between traits and speciation rates (Rabosky & Huang 2016), while QuaSSE can lead to spurious correlations if there are different macroevolutionary regimes in the phylogeny (Rojas *et al.* 2018).

In a paper recently published in *Ecology Letters*, we examined the effect of diet diversification on speciation rates (Rojas *et al.* 2018). As part of the analyses we inferred the rates of evolution of this trait using the variable-rates model of Venditti *et al.* (2011), and calculated the path-wise rates of trait evolution (see Baker *et al.* 2015). Because our phylogeny shows two macroevolutionary regimes and not all trophic habits are equally represented in each regime, we rescaled the trophic level index between 0 (strict specialization for herbivory) and 1 (strict specialization for animalivory) and repeated the analysis with this metric (i.e. marginality from herbivory).

Similarly, we inferred speciation rates using BAMM 2.5.0 (Rabosky 2014) and calculated path-wise speciation rates therefrom. We then used Bayesian phylogenetic mixed models (BPMM) to test the relationship between path-wise rates of trophic level evolution and path-wise rates of marginality evolution with path-wise rates of speciation. In the phylogenetic

regressions we accounted for the two different evolutionary regimes as fixed factors, tested linear and quadratic models, and accounted for selection by also testing the models on Ornstein-Uhlenbeck rescaled trees. Because BAMM rates from the same macroevolutionary regime are highly correlated, the degrees of freedom of such analysis is lower than the number of different rates to the number of macroevolutionary regimes (in our case, < 2). Current phylogenetic regression methods fail to account for autocorrelation within macroevolutionary regime, even if the regimes are incorporated in the model as factors, as we did in our study (Rojas *et al.* 2018). Hence, results from such regressions are spurious as they fail to account for strong autocorrelation in the response variable (diversification or speciation rates).

Rates of trait evolution estimated with the method of Venditti *et al.* (2011) do not suffer this issue, since they represent shifts from a Brownian Motion (BM) model of evolution (i.e. how much the per-branch trait evolutionary rates must be accelerated or decelerated to conform to BM). As autocorrelation in BAMM diversification rates cannot be addressed in phylogenetic regressions, we discourage readers from using BAMM outputs in the regression approach we introduced in our paper. Other methods could be used instead. We applied some of those to our data. After doing this, the main conclusions of our paper still hold (Rojas *et al.* 2018).

To evaluate the relationship between speciation rates and trophic specialization in noctilionoid bats we used two alternative approaches to the phylogenetic regressions we used in our paper. In these analyses we focused on marginality from herbivory, since it is a standardization of the trophic level index we introduced in our paper (Rojas *et al.* 2018). Here we present the numeric results as median [interquartile range], unless otherwise stated. We used a significance level of 0.05.

Firstly, we used the ES-sim test from Harvey & Rabosky (2017) to analyze the correlation between a metric of tip-rate of speciation – the inverse equal splits (Redding & Mooers 2006) – and marginality. The ES-sim method is a semi-parametric method in which the observed correlation between the inverse equal splits and the trait is tested against a null set of associations (we used 10,000). We applied this method to the posterior distribution of 100 trees (see Methods in Rojas *et al.* 2018) to account for phylogenetic uncertainty. In all cases the Pearson correlation coefficient ($r = -0.498 [-0.505, -0.487]$) was significant ($P < 0.015$ in all cases) (Fig. 1). This indicates speciation rate increases as noctilionoid bats specialize for herbivory (i.e., as marginality decreases).

Although ES-sim is less biased towards false positives than other trait-dependent diversification methods (Harvey & Rabosky 2017), it cannot be used to analyze different macroevolutionary regimes within a tree. If we were able to

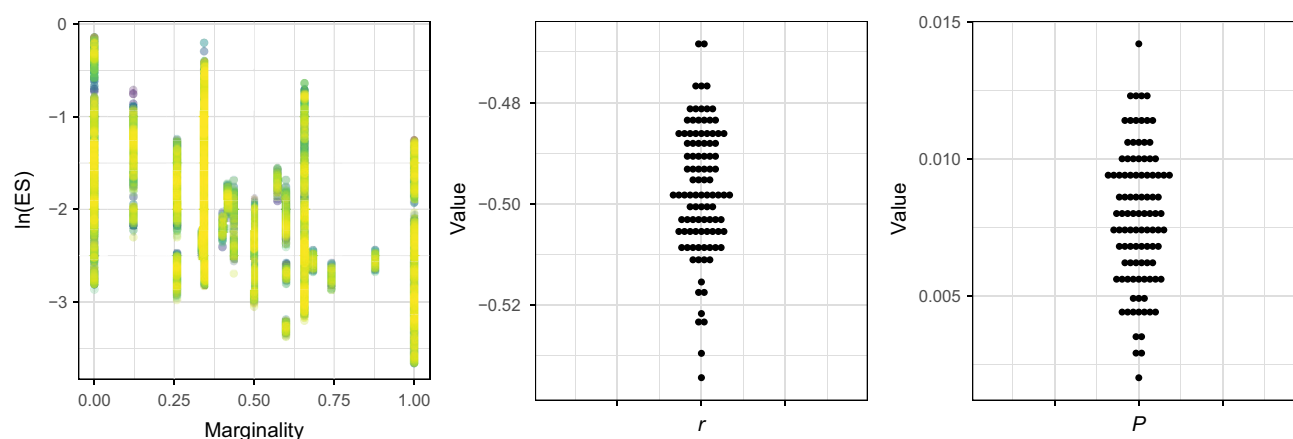


Figure 1 Marginality-dependent speciation in noctilionoid bats, according to the ES-sim test. Left: Relationship between log-transformed inverse equal splits, $\ln(ES)$, and marginality in 100 time-calibrated molecular phylogenies of neotropical noctilionoid bats (each color represents a different tree). Center and right: Pearson correlation coefficients r and P values, respectively, for this relationship on each tree.

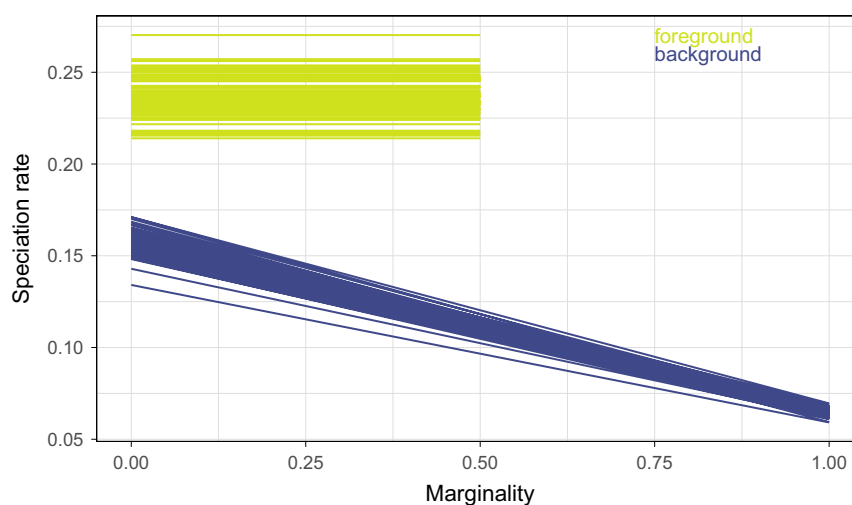


Figure 2 Relationship between speciation rate and marginality in noctilionoid bats. Regression lines were estimated on a posterior distribution of 100 trees in a maximum likelihood framework. Foreground refers to Stenodermatinae and background to non-stenodermatines.

prune the tree to generate the different subtrees that correspond to the regimes, and then perform ES-sim on each subtree for comparison, we will need more tips per subtree to achieve a high statistical power (e.g., 0.38 for 50 tips vs. 0.93 for 250 tips) (Harvey & Rabosky 2017). This is not always feasible. Partitioning the phylogeny of neotropical noctilionoid bats would yield 83- and 109-tip subtrees. This prevents us from contrasting the relationship between trophic specialization and speciation for the two macroevolutionary regimes we identified in the phylogeny of noctilionoid bats (Rojas *et al.* 2016).

To address our research question we can use the quantitative state speciation and extinction method (QuaSSE) or more specifically, split-QuaSSE. This is a variant of QuaSSE in which we can partition the tree to account for the different macroevolutionary regimes, and then test for different models of trait-dependent diversification on each partition (FitzJohn 2010). We demonstrate in our paper that unlike QuaSSE, split

QuaSSE does not lead to Type I error with the particular topology of the noctilionoid tree (although this must be evaluated for individual cases, as other trees yield higher-than-nominal error rates; Rabosky & Goldberg 2015), and thus it can be used to examine the role of trophic specialization in the diversification of these bats (Rojas *et al.* 2018).

In the original paper we partitioned the sample of 100 trees at the stem Stenodermatinae (where the shift in speciation rates was detected in BAMM) and tested three models of trait-dependent speciation for path-wise rates of trophic level evolution in a maximum likelihood framework. To reassess our results we repeated these analyses, and tested four models for marginality from herbivory: speciation rate is constant (i.e., no relationship with the trait) in the two partitions (model CC), speciation rate is linear (i.e. there is a relationship with the trait) in the two partitions (model LL), speciation rate is constant for the background and linear (model CL), and speciation rate is linear for the background and

constant for the foreground (model LC). Like in our previous paper, “drift” parameters were set to 0 in this new analysis, extinction rates were kept constant and the models were corrected for incomplete taxon sampling. We used the Akaike weight (hereafter w) to measure the support of each model.

We found higher support for the model LC ($w_{LC} = 0.672$ [0.657, 0.685]) compared to the other models ($w_{CC} = 0.07$ [0.057, 0.084]); $w_{LL} = 0.232$ [0.227, 0.239]); $w_{CL} = 0.025$ [0.02, 0.03]). Stenodermatines (foreground) – a clade that includes strictly frugivorous and predominantly frugivorous lineages that complement their diet with nectar, pollen and insects – show higher speciation rates (0.23 [0.237, 0.246] species/My) and overall lower marginality than non-stenodermatines (background), although the rates and the trait are not associated (Fig. 2). This suggests that greater specialization does not increase speciation. In non-stenodermatines – a group that includes strictly animalivorous species and omnivores –, as lineages specialize from herbivory speciation rate decreases (speciation rate = 0.155 [0.159, 0.162]–0.093 [–0.098, –0.091] $\times$ marginality). This suggests that while specializing on an animalivorous diet decreases speciation, being more omnivorous to include plants increases speciation.

Results from the new analysis using split QuaSSE are consistent with the conclusions of our paper (Rojas *et al.* 2018). As we state in that paper, split QuaSSE is a good alternative to other trait-dependent speciation methods, as long as simulations are performed first to ensure that partitioning the tree does not lead to spurious correlation between speciation and the trait. In contrast, phylogenetic regression methods using traits that were estimated in BAMM should be avoided since currently they cannot account for the high autocorrelation in these traits. We strongly recommend against using Bayesian phylogenetic mixed models coupled with BAMM diversification rates (Rojas *et al.* 2018), and instead explore alternative trait-dependent diversification methods as ES-sim for tree-wide

analysis or split-QuaSSE to account for different macroevolutionary regimes.

AUTHORSHIP

DR and LMD performed the new analyses. All authors contributed to the discussion of the results and the writing of the correction.

DATA ACCESSIBILITY STATEMENT

Data is available on Dryad (<https://doi.org/10.5061/dryad.rn5pt>) and upon request from rojasmartin.cu@gmail.com.

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