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LETTER

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

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**Abstract**

The role of trophic specialisation in taxonomic diversification remains unclear. Plant specialists diversify faster than omnivores and animalivores, but at shorter macroevolutionary scales this pattern sometimes reverses. Here, we estimate the effect of diet diversification on speciation rates in noctilionoid bats, controlling for tree shape, rate heterogeneity and macroevolutionary regimes. We hypothesise that niche subdivision among herbivores positively relates to speciation rates, differing between macroevolutionary regimes. We found the rate at which new herbivorous lineages originate decreases as rates of diet evolution increase. Herbivores experience higher speciation rates, but generalist herbivores and predominantly herbivorous omnivores speciate faster than specialised herbivores, omnivores and animalivores. Generalised herbivory is not a dead end. We show that analysing ecological traits and diversification requires accounting for macroevolutionary regimes and within- and between-clade variation in evolutionary rates. Our approach overcomes the high false-positive rates of other methods and illuminates the roles of herbivory and specialisation in speciation.

**Keywords**

Bayesian phylogenetic mixed models, macroevolution, Noctilionoidea, path-wise rates, specialisation, speciation, trophic level, variable-rates model.

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## INTRODUCTION

Determining the influence of abiotic forces and biotic interactions in diversification is a central task of evolutionary biology. Abiotic changes are the main causes of diversification in non-adaptive radiation, while ecological interactions drive adaptive radiation (Benton 2009). While these processes are not mutually exclusive [e.g. in West Indian *Anolis* (Losos 2009)], the term "adaptive radiation" is reserved for clades in which ecological interactions shape species and trait diversity (Schluter 2000).

Diet can reflect biotic interactions and thus test the influence of traits and ecological specialisation on diversification (Burin *et al*. 2016). For example, ecological specialisation within species is advantageous and might be retained over macroevolutionary scales under a stable environment (Futuyma & Moreno 1988). Hence, trophic specialists are expected to have higher diversification rates compared to omnivores (Schluter 2000).

Nevertheless, the relationship between trophic specialisation and taxonomic diversification has been difficult to generalise. For example, dietary specialists diversify faster than omnivorous mammals and birds (Price *et al*. 2012; Burin *et al*. 2016). At shorter macroevolutionary timescales trophic specialisation can also be associated with higher diversification rates, as in specialised frugivorous bats in the superfamily Noctilionoidea (Rojas *et al*. 2012) and in ruminants that feed on grass (Cantalapiedra *et al*. 2014). Although omnivorous noctilionoid bats diversify more slowly (Rojas *et al*. 2012), ruminants with mixed feeding habits (both browsing and grazing) have higher diversification rates (Cantalapiedra *et al*. 2014).

We hypothesise that two confounding factors could explain conflicting results. First, recent studies have used state-dependent speciation and extinction (SSE) methods (Maddison *et al*. 2007; FitzJohn 2012) and phylogenetic generalised least squares models (Grafen 1989; Pagel 1994). These methods overlook heterogeneity in speciation and extinction rates across many clades (e.g. Jetz *et al*. 2012; Rabosky *et al*. 2013; Shi & Rabosky 2015). Second, the common approach of characterising diet specialisations as guilds limits comparisons and statistical power (Davis *et al*. 2013). Usually, trophic specialisation cannot be quantified as a continuous variable, and lineages are instead defined as generalist (i.e. omnivores or mixed feeding habits), or specialists (i.e. other categories) (but see Rex *et al*. 2010; Dumont *et al*. 2012). Additionally, trait-dependent diversification analyses should focus on rates of

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trait evolution (i.e. dynamic traits) instead of trait values (i.e. static traits) (Wiens 2017). While dynamic traits can provide mechanistic explanations of diversification dynamics, the relationship between static traits and rates of taxonomic diversification may be indirect and can obscure patterns (e.g. Kozak & Wiens 2010).

To test the role of dietary specialisation on taxonomic diversification, we focus on neotropical bats of the superfamily Noctilionoidea. This clade (*c.* 244 species in five families) has outstanding ecological diversity, with adaptations in morphology, physiology and behaviour allowing different species to specialise their diet in items as different as nectar and pollen, blood or figs. A comprehensive phylogeny of the superfamily (Rojas *et al.* 2016) strongly support a single shift towards higher speciation rates, the only such shift within Chiroptera (Shi & Rabosky 2015).

Here, we quantify the effect of continuous traits on speciation using a novel approach that combines macroevolutionary methods to analyse dynamics of trait evolution and taxonomic diversification (Venditti *et al.* 2011; Rabosky 2014). We hypothesise that niche subdivision towards specialisation for herbivory is positively related to speciation rates. However, since noctilionoid bats show two macroevolutionary regimes (Rojas *et al.* 2016), and both groups have lineages with different levels of trophic specialisation, we predict this relationship should behave differently within each regime. To test these predictions, we developed a trophic level index that combines the quantity and relative importance of items in the diet of each species. Then, we accounted for variation in speciation rates and rates of trophic level evolution through time and among lineages and clades, and used Bayesian comparative models to test for linear and nonlinear relationships between evolutionary rates. We also characterised the evolutionary trend of trophic level. This framework allowed us to elucidate the relationship between trophic specialisation and speciation. We also tested the evolution of this relationship, whether under Brownian motion (BM), or shaped by different selection strengths.

## MATERIAL AND METHODS

### Trophic level data and phylogeny

Here, specialisation refers to the number of items composing the diet of a species, irrespective of the number of interactions. Thus, a species feeding on fleshy fruit-producing plants is more specialised than a species including fruit, nectar and pollen in its diet, irrespective of the number of plant species involved in each case. The relevant data and scripts are provided in Dryad.

We developed an index of trophic level by quantifying eight main items in the diet of noctilionoids – arthropods, blood, terrestrial vertebrates, fish, leaves and flower pieces, nectar and pollen, fruit and seeds – based on literature and field observations (e.g. Rojas *et al.* 2011, 2012). We classified 192 taxa as animalivores if the taxon feeds on one or more of the first four items; herbivores, if it feeds on one or more of the last four items; or omnivores, if it feeds on a combination of any of the first four and last four items. We used the following states to estimate the relative importance of these items in the diet: absent (0), complementary (1: the item is a secondary component of the diet; i.e. no more than 40%), predominant (2: the item is the most important component of the diet; i.e. no less than 60%) and strict (3: only this item is consumed) (Ferrarezzi & Gimenez 1996). All species were unambiguously assigned to these states, but future uses will have to test the sensitivity to selecting complementary or predominant when any item corresponds to 40–60% of the diet.

The trophic level was calculated as $\log_{10}\{[(1 + \sum a_i + n_a)/n_a]/[(1 + \sum h_i + n_h)/n_h]\}$, where $\sum a_i$ is the sum of the relative importance of items within the animalivory category, $\sum h_i$ the sum within herbivory, $n_a$ the number of items in the diet of the species within animalivory and $n_h$ the number of items within herbivory. The index ranges from negative to positive values; taxa specialised in plant products show the lowest values of the index, and taxa specialised in animal products show the highest values.

For comparative analyses, we used a recent phylogeny of neotropical noctilionoids (Rojas *et al.* 2016). We used the maximum clade credibility tree and 100 trees, randomly selected from the posterior distribution to estimate parameters of diversification regressed against trophic level evolution (Fig. S1).

### Trait-dependent diversification

The quantitative state speciation and extinction (QuaSSE) method could be used to examine the relationship between trophic level and diversification (FitzJohn 2010). Two independent studies identified a shift in speciation rates in Stenodermatinae – the largest subfamily within Noctilionoidea (Shi & Rabosky 2015; Rojas *et al.* 2016). As Rabosky & Goldberg (2015) demonstrated, a single shift in diversification rates can lead to spurious correlation between a binary trait and diversification. This systematic error needs to be tested with continuous traits. We simulated 100 sets of a continuous trait with no effect on speciation or extinction evolving under a diffusion process with $\sigma^2$ values from 0.0035 to 0.0125 in 0.001 increments. For each group of 100 simulated traits corresponding to each value of $\sigma^2$, we conducted two sets of analyses (R scripts provided in Dryad).

First, we fitted two QuaSSE models on the noctilionoid maximum clade credibility tree: one model with the speciation rate constant, and the other with the speciation rate varying linearly with the trait. We repeated this procedure with 100 simulated sets of a continuous trait evolving under the white noise model. Second, we partitioned the tree into two regions, based on the previously identified shift in speciation rates. We then used the 10 sets of continuous traits simulated for each $\sigma^2$ value and analysed the two partitions of the tree as if they evolved independently (split QuaSSE). We set the speciation rate to be constant in one model, while in the second model, it was set to vary linearly with time. In all cases, we set 'drift' parameters to 0 (i.e. no trend in the evolution of the trait), extinction rates were constant, and we corrected for incomplete taxon sampling. We used the Akaike Information Criterion (AIC) to measure support for each model (i.e. constant vs. linear). As the neutral trait is independent from speciation, the QuaSSE analyses should show higher average support for the constant speciation model than for the linear model, whether the tree is partitioned or not. We simulated the trait using the R library *phytools* (Revell 2012) and fitted the models using *diversitree* (FitzJohn 2012).

### Evolutionary rates

Instead of clade-averaged rates, or rates at tips (e.g. Rabosky *et al.* 2013), we propose using path-wise rates to test for trait-dependent diversification. Baker *et al.* (2015) introduced path-wise rates to study evolutionary trends of body mass in mammals. The path-wise rate for a given species is the sum of all the rates along the history of the species, from the root to the tip of the tree; it accounts for the total change the species has experienced during its evolution. Among close relatives, the variance in path-wise rates corresponds to the differences between tips, while differences between distant relatives reflect variation along many more branches. To the best of our knowledge, path-wise rates have not been associated with speciation rates, nor has the relationship between path-wise speciation rates and path-wise rates of the evolution of any trait been tested before.

We used the variable-rates model of Venditti *et al.* (2011) to analyse the evolution of trophic level in the maximum clade credibility tree of noctilionoids. The model detects significant shifts from a homogeneous BM model of evolution, without *a priori* specifications of the location of rate shifts. The model calculates a set of branch-length scalars that inform how much the underlying rate must be accelerated or decelerated in any branch to conform to BM. We conducted these analyses on BayesTraits 2.0 (Pagel *et al.* 2004). We set two independent runs using Markov chains Monte Carlo (MCMC) with 11 million iterations each and sampling every 1000 steps. After assessing convergence using the R library *coda* (Plummer *et al.* 2006), we combined the last 5000 samples from each chain and calculated the mean rate scalar for each branch.

We inferred speciation rates of noctilionoids on the phylogeny of Rojas *et al.* (2016) using BAMM 2.5.0 (Rabosky 2014). We calculated the mean rates per branch with the R library *BAMMtools* (Rabosky *et al.* 2014), and then the path-wise rates of trophic level evolution and path-wise speciation rates with *adephylo* (Jombart *et al.* 2010) (Fig. S2). We repeated the analysis using two γ values – 10 and 100 – ; γ is the mean of the prior distribution on the number of rate shifts (see Supporting Information Methods). Results were consistent for different priors (Fig. S3). Here, we report results for γ = 1.

### Statistical analyses

Based on results of SSE analyses, we partitioned the sampled trees at the stem Stenodermatinae and tested three models of trait-dependent speciation for path-wise rates of trophic level evolution in a maximum likelihood framework (split QuaSSE): (1) speciation rate is constant (i.e. no relationship with the trait) in the two partitions, (2) speciation rate is linear (i.e. there is a relationship with the trait) in the two partitions and (3) speciation rate is constant for the background and linear for the foreground. "Drift" parameters were set to 0, extinction rates were kept constant and the models were corrected for incomplete taxon sampling. We used the Akaike weight to measure the support of each model.

We used Bayesian phylogenetic mixed models (BPMM) in *MCMCglmm* (Hadfield 2010) for two sets of analyses. First, we tested the relationship between path-wise rates of speciation and trophic level evolution. Path-wise speciation rates revealed two groups: > 3.01 species/My (this includes most species of Stenodermatinae; hereafter fast-speciation group) and < 2.56 species/My (the rest of noctilionoids; hereafter slow-speciation group). Models accounted for variation between these groups – per-group slopes and intercepts – as well as among trophic strategies – herbivores, omnivores or animalivores.

Trends in the evolution of trophic level cannot be used to explain any relationship between speciation rates and rates of trophic level evolution for the fast-speciation group because this group does not include animalivory. To compare trends of trophic evolution between groups, we rescaled the trophic level index as $(y_i - y_{\min})/(y_{\max} - y_{\min})$. This placed all taxa between 0 (i.e. specialisation for herbivory) and 1 (i.e. highest marginality from herbivory or specialisation for animalivory). Hence, intermediate values correspond to an unspecialised, omnivorous trophic niche. We then tested the relationship between this marginality index and path-wise rates of trophic level evolution accounting for variation between the fast-speciation group and the slow-speciation group.

We fitted both linear and quadratic models, since the latter capture boundaries in linear relationships between variables. The BPMM approach assumes that the residuals of the models conform to a BM model of evolution, but this might not always be the case. [redacted] Finally, we used the Deviance Information Criterion (DIC) to compare the fit of models tested on the original phylogeny and the models tested on the OUMVA-tree and the OUMA-tree. Models with lower DIC are preferred to models with higher DIC.

To account for phylogenetic uncertainty, we tested the best-fitting model within each set of analyses on the sample of 100 trees, running 1 million generations sampled every 100, with a burn-in of 100 000, for a total sample of 9000 generations per tree. Runs were checked for adequate sampling and stationarity using the effective sample size of parameters estimates and visual inspection of the iterations against values sampled for each parameter. We used an inverse gamma distribution for the residuals (with shape and scale parameters = nu/2, nu = 1 and $V = 1$ in the inverse Wishart notation of *MCMCglmm*). Although commonly used in phylogenetic regressions, nu = 0.002 underestimated the residual variance. To speed up convergence and improve the mixing properties of the chain, we used a parameter-expanded prior with the parameters $V = 0.5$, nu = 1 and the prior mean and variance parameters alpha.mu = 0 and alpha.$V = 10^3$ for the random term. Results were combined to generate point estimates and 95% credible intervals from the joint posterior probability distribution. The effects of the parameters with credible intervals excluding zero were considered statistically significant. We also calculated the marginal (i.e., explained by the fixed factors) and conditional (i.e., by both the fixed and random factors) variances of the best-fitting models (Nakagawa & Schielzeth 2013).

Branches with many nodes can inflate path-wise rates through the node-density artefact (Venditti *et al.* 2006). This could yield spurious positive correlations between path-wise rates of speciation and trait evolution. We tested for node-density artefacts in path-wise rates of speciation and path-wise rates of trait evolution (δ method, http://www.evolution.reading.ac.uk/pe/index.html). If branch path lengths are significantly correlated with the number of nodes in the path (i.e. $\delta > 1$) there is support for a node-density artefact.

## RESULTS

As expected, path-wise rates of speciation and both diversification and extinction were strongly correlated (Fig. S4). We discuss speciation rates as stand-ins for net diversification rates. We acknowledge that more complex processes, such as the differential extinction of generalist lineages, cannot be estimated at this time and were not accommodated in our analyses. Although we focus on speciation, our results reflect patterns and mechanisms that can be attributed to shifts in speciation, extinction or both.

Using QuaSSE, neutral traits were associated with speciation rates for both traits simulated under BM and white noise processes. In contrast, the BM trait and speciation rates were not associated in the partitioned tree (Fig. 1). Hence, the shift in speciation rates at the base of Stenodermatinae can lead to spurious relationships between continuous traits and speciation rates when not explicitly accounted for in QuaSSE. After accounting for this shift (split QuaSSE), the model with no relationship between speciation rates and path-wise rates of trophic level evolution received the highest support (Fig. S5).

A linear model accounting for variation between the fast-speciation group and the slow-speciation group best explained the relationship between speciation and trophic level evolution path-wise rates, and the residuals followed a BM model of evolution (Fig. S6). Changes in rates of trophic level evolution explained 71% of variation in speciation rates. Speciation rate as a function of trophic level evolution changes faster in fast-speciation lineages ($0.79 \times 10^{-2}$) than in slow-speciation lineages ($0.1 \times 10^{-3}$). Higher rates of trophic level evolution correspond to lower speciation rates in the fast-speciation group (Fig. 2, Table 1). In the slow-speciation group, higher rates of trophic level evolution correspond to either lower or higher speciation rates (Fig. 2).

The relationship between marginality and rates of trophic level evolution is best explained by a quadratic model with

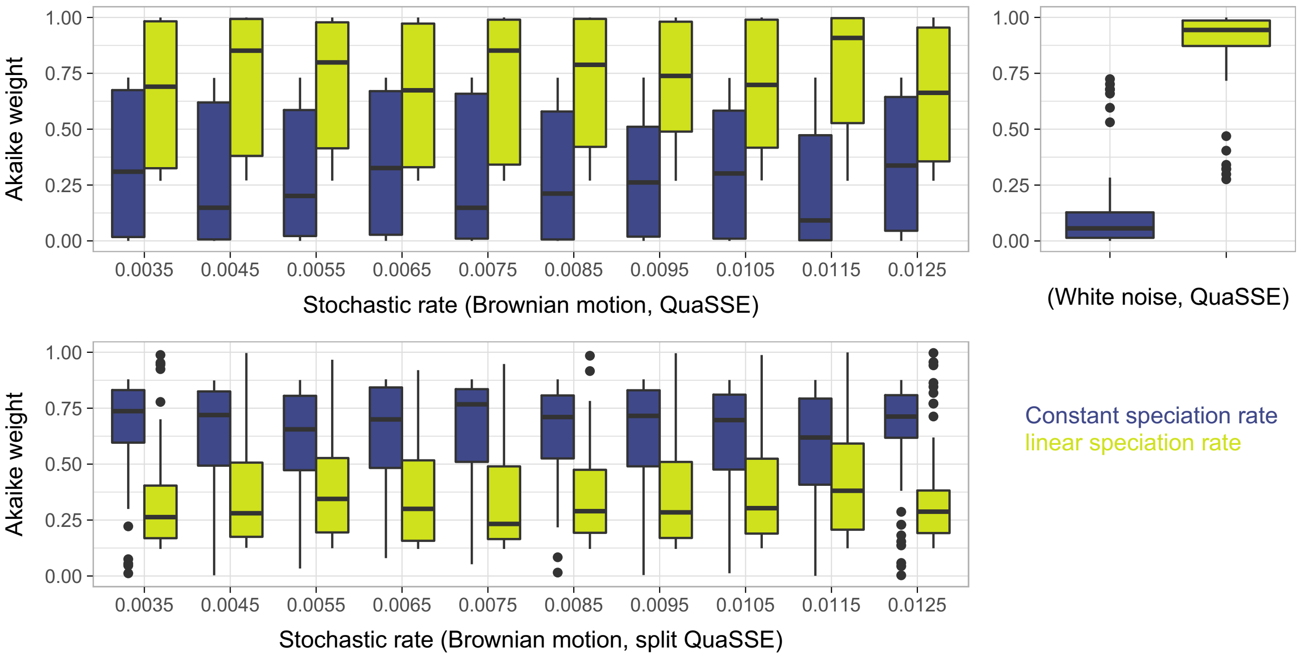

**Figure 1** Weight of evidence for two models of trait-dependent speciation. Each panel summarises results from 100 simulated data sets. Trait-dependent speciation was tested assuming constant speciation rates through time (dark grey) or speciation rates varying linearly through time (light grey). In both cases extinction rates were assumed as constant. Models were tested on a time-calibrated molecular phylogeny of 192 species of noctilionoid bats from the Neotropics (Chiroptera: Noctilionoidea), scaled to a root edge of 1.0. The R script to perform the simulations is available on Dryad.

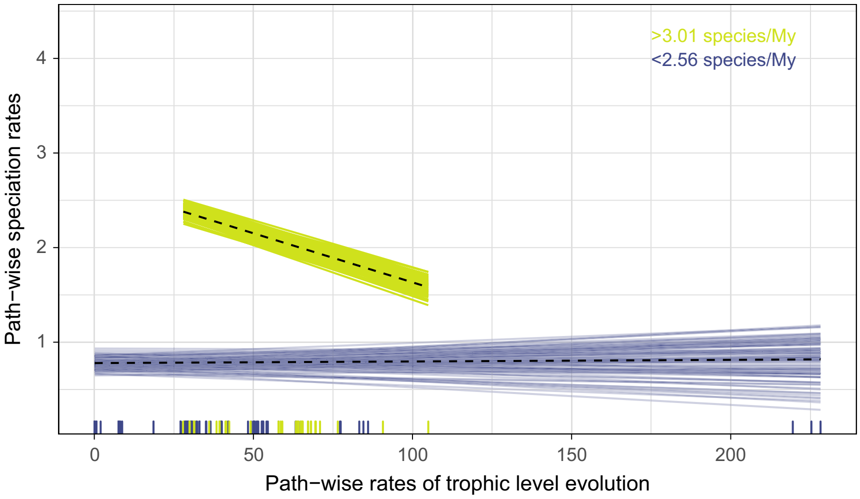

**Figure 2** Relationship between path-wise speciation rates and path-wise rates of trophic level evolution in noctilionoid bats. Regression lines were inferred on a posterior distribution of 100 trees. Dashed lines correspond to the average function in each group. Observed values are shown as ticks on the *x* axis.

**Table 1** Relationship between path-wise speciation rates and path-wise rates of trophic level evolution in noctilionoid bats (Chiroptera: Noctilionoidea)

| | Estimate | Lower CI | Upper CI |
|---|---|---|---|
| Fixed terms | | | |
| Intercept | 2.6705 | 2.1344 | 3.2162 |
| $x$ | −0.0104 | −0.0165 | −0.0043 |
| $g$[B] | −1.8913 | −2.3213 | −1.484 |
| $x$:$g$[B] | 0.0105 | 0.004 | 0.0171 |
| Random terms | | | |
| Phylogenetic variance | 0.1792 | 0.1303 | 0.2508 |
| Residual variance | 0.0263 | 0.0186 | 0.0378 |
| Marginal $r^2$ | 0.708 | 0.599 | 0.789 |
| Conditional $r^2$ | 0.965 | 0.946 | 0.975 |

The model accounts for the interaction between path-wise rates of trophic level evolution ($x$) and groups $g$. Groups are defined based on the values of the path-wise speciation rates: > 3.01 species/million year (fast-speciation group, including most lineages in the subfamily Stenodermatinae; A) or < 2.56 species/million year (slow-speciation group, including all other noctilionoids; B). Limits of the credible intervals (CI) are provided

differences between fast-speciation and slow-speciation groups (Fig. S7), and its residuals also follow a BM model of evolution. A quadratic BM model without groups (Fig. S8) received slightly higher DIC support (difference between values = 1.32), but we discuss the more complex model because there are two different regimes in Noctilionoidea and both models have almost identical explained variance. In the fast-speciation group, as path-wise rates of trophic level evolution increase, specialisation for herbivory first increases (i.e. marginality decreases) and then either increases more slowly on average, or decreases slightly in a few phylogenies (Fig. 3). The slow-speciation group shows much greater variance in rates of trophic evolution, but although mean coefficients are similar to those of the fast-speciation group, there is no relationship between these variables (Table 2).

We found no evidence of node-density artefacts for path-wise rates of either speciation, or trophic level evolution. Therefore, we interpret positive associations as emergent from macroevolutionary patterns, and not the method used to estimate rates.

## DISCUSSION

Our work extends the methods available to relate speciation (or diversification) rates to the evolution of continuous traits, provides a framework for future research across many clades and illuminates the relationship between dietary specialisation and speciation within noctilionoid bats. Additionally, by discriminating between distinct diversification regimes, our analyses account for the different ranges of trait variation. Finally, by exploring both linear and nonlinear models, along with phylogenetic structures of residuals besides those governed by BM, this new method incorporates evolutionary trends consistent with natural selection at macroevolutionary scales.

We extended the analysis for spurious correlations between speciation rates and the evolution of traits to include continuous traits and different partitions on the tree (Rabosky & Goldberg 2015). Our results confirm shifts in speciation rates can lead to false associations between speciation and continuous variables, and not just with the states of discrete traits. Therefore, all new studies using SSE methods, must test whether the relationship between speciation rates and trait states results from shifts in speciation rates in the phylogeny (Rabosky & Goldberg 2015). Our results also show that even when incorporating shifts in speciation rate (split QuaSSE), the effect of a continuous trait can be mistakenly discarded when heterogeneity in speciation rates collapses into tree partitions (Fig. S5). Accounting for as many shifts in speciation rates as can be detected on the phylogeny can make the split QuaSSE model intractable because of the large number of parameters. This highlights the importance of the approach we introduce here to examine the relationship between rates of speciation and trait evolution.

Trophic evolution is associated with speciation rates in noctilionoid bats. BPMM revealed two different relationships

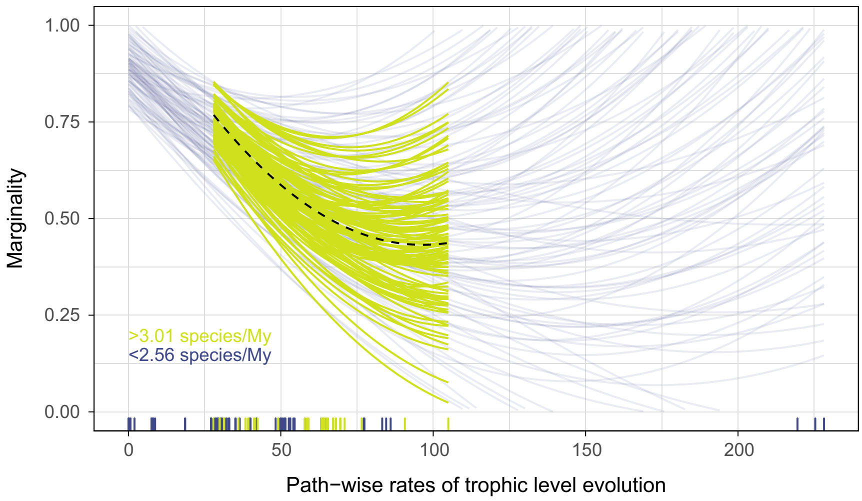

**Figure 3** Relationship between marginality and path-wise rates of trophic level evolution in noctilionoid bats. Regression lines were inferred on a posterior distribution of 100 trees. Observed values are shown as ticks on the $x$ axis. The dashed line corresponds to the average function for the fast-speciation group. Although the relationship was not significant, functions for the slow-speciation group are shown (semi-transparent) for comparison.

**Table 2** Relationship between marginality from herbivory and path-wise rates of trophic level evolution in noctilionoid bats (Chiroptera: Noctilionoidea)

| | Estimate | Lower CI | Upper CI |
|---|---|---|---|
| Fixed terms | | | |
| Intercept | 1.0982 | 0.6767 | 1.4913 |
| $x$ | −0.0138 | −0.0258 | −0.0015 |
| $x^2$ | $0.71 \times 10^{-4}$ | $-0.28 \times 10^{-5}$ | $0.18 \times 10^{-3}$ |
| $g$[B] | 0.2018 | −0.5798 | 0.1974 |
| $x$:$g$[B] | 0.0061 | −0.0067 | 0.0189 |
| $x^2$:$g$[B] | $-0.35 \times 10^{-4}$ | $-0.14 \times 10^{-3}$ | $0.67 \times 10^{-4}$ |
| Random terms | | | |
| Phylogenetic variance | 0.0342 | 0.0221 | 0.0521 |
| Residual variance | 0.0153 | 0.0118 | 0.0203 |
| Marginal $r^2$ | 0.273 | 0.113 | 0.419 |
| Conditional $r^2$ | 0.771 | 0.688 | 0.857 |

The model accounts for the interaction between path-wise rates of trophic level evolution ($x$) and groups $g$. Groups are defined as in Table 1. Limits of the credible intervals (CI) are provided.

between trophic specialisation and diversification dynamics. Compared to other lineages, most bats in Stenodermatinae, characterised by high bite forces and the ability to eat figs, experienced consistently higher rates of speciation. But the rate at which new lineages originated in stenodermatines decreased as rates of diet evolution increased, while speciation in other noctilionoid bats did not change much in association with the rate of trophic evolution (Fig. 2). Rates of trophic level evolution were generally higher among the more herbivorous of stenodermatines than among the more omnivorous stenodermatines (Fig. 3). In contrast, trends for other noctilionoids were not significant.

In both adaptive and non-adaptive radiations, specialist ancestors can diversify into both specialist and generalist descendants (e.g. Schluter 2000; Martén-Rodríguez *et al.* 2010; Givnish *et al.* 2014). But in adaptive radiation, a trend towards niche specialisation is expected if ecological opportunity results in the occupation of new adaptive zones and subsequent niche differentiation as the lineage diversifies into many species (Simpson 1953; Stroud & Losos 2016). We detected an overall trend towards specialisation for herbivory (i.e., towards lower marginality) in the fast-speciation group of noctilionoids, meeting this prediction from the ecological theory of adaptive radiation (Fig. 3). Speciation rates and marginality were (roughly) negatively related to rates of trophic level evolution. Therefore, speciation rates are positively related with marginality, or diversifying diets among most stenodermatines. This result contradicts both our original hypothesis and previous findings in insects (Wiens *et al.* 2015), mammals (Price *et al.* 2012) and birds (Burin *et al.* 2016). Those studies showed that trophic specialisation towards herbivory is associated with higher speciation. Explanations for this association include specialists undergoing more allopatric speciation than omnivores because of the fragmented distribution of specialised trophic resources (Futuyma & Moreno 1988); or speciating more than omnivores when the preferred resource is unpredictable or scarce (Wilson & Yoshimura 1994). The association between omnivory and lower speciation rates may also indicate ephemeral speciation (Rosenblum *et al.* 2012); as populations of omnivores that start to specialise experience high competition with populations of specialists, and cannot persist in time. Over larger scales, niche filling in specialised lineages would limit the occupation of new adaptive zones by omnivores.

Our results indicate that while herbivory increases speciation, too much specialisation decreases it. Further specialisation for herbivory is linked to lower speciation when it involves already low trophic levels. At shorter temporal and geographic scales, when biotic factors are hypothesised to be stronger (Benton 2009), greater specialisation results in slower speciation rates, higher extinction rates or both. In the first case, variation in specialised lineages may be insufficient for adaptation to new selective pressures (Day *et al.* 2016), as reflected in the lower variance in the rates of trophic level evolution of most stenodermatines. Similarly, and in the second case, specialisation is usually related to smaller ranges, increasing susceptibility to extinction. When stenodermatines entered a new adaptive zone in which plant items of greater hardness represent the dominant diet (Dumont *et al.* 2012), the available niche space became occupied and speciation gradually decreased (Schluter 2000; McPeek 2008). In this process, omnivorous lineages that fed mostly on plants and herbivorous lineages specialised on different plant items were favoured over herbivorous lineages specialised on a single plant item – the lowest marginality value. A more diverse diet can help cope with seasonal and spatial variation in resources in the Neotropics. For example, the two most diverse genera of Noctilionoidea, the stenodermatines *Sturnira* and *Artibeus*, can modify the composition and proportion of plants in their diet depending on latitude, altitude and ecoregion (Saldaña-Vázquez 2014). Bats in these genera, and other stenodermatines, can also include different items in their diet throughout the year, depending on resource availability (Fleming & Kress 2013). If niche differentiation explains the slowdown in speciation rates as a function of trophic diversification, diversity in stenodermatines has reached or is close to equilibrium.

In the slow-speciation group, path-wise rates of speciation barely vary as those of trophic level evolution increase, and diet diversifies towards omnivory, herbivory or animalivory. If niche filling is preventing specialised lineages from further diversifying, slow-speciation omnivores should show higher path-wise speciation rates than slow-speciation specialists, but this is not the case. The relationship between speciation rates and trophic evolution was slightly positive, and the lack of relationship between marginality and rates of trophic evolution suggests diet in this group diversified in any direction. The evolutionary role of omnivory in speciation found in the fast-speciation group is obscured in the slow-speciation group, either non-existent or reversed.

In any case, a positive effect of omnivory on speciation rates would be offset by the more important role of animal items in the diet of slow-speciation omnivores, compared to the dominance of plant items in the diet of fast-speciation omnivores. In mammals and birds, carnivorous lineages show lower speciation than herbivores (Price *et al.* 2012; Burin *et al.* 2016). Within omnivory, feeding on a higher proportion of animal items can therefore lead to slower speciation. In contrast, specialisation towards plant items allows escaping from the animalivorous space occupied by most lineages of Neotropical bats, while keeping animal items in the diet, or a more generalist herbivorous diet, provides adaptive advantages when resource abundance varies over time. This would also explain differences in speciation rates between the fast-speciation and the slow-speciation groups. Although 66% of fast-speciation lineages are omnivores compared to 73% of slow-speciation lineages, 98% of fast-speciation omnivores feed more on plant items than on animal items, while this pattern occurs in only 53% of slow-speciation omnivores. Therefore, omnivory is not a macroevolutionary sink when plants are in higher proportion in the diet than animals, at least in noctilionoid bats.

The model relating marginality and path-wise rates of trophic level evolution for all noctilionoids (Fig. S8) likely reflects the variable position of *Lonchorhina* in the phylogeny. This genus of insectivorous bats appears as sister to the predominant nectarivorous Glossophaginae and within a clade including all other lineages that feed mostly on plants. As a result, the path-wise rates of trophic level evolution recovered for *Lonchorhina* species were high. Support for this model is slightly higher than for the model assuming variation between macroevolutionary regimes (DIC: -249.17 vs. −247.85), but both models explain similar variance (conditional $r^2$: 0.26 vs. 0.27; marginal $r^2$: 0.78 vs. 0.77). The phylogenetic relationships of *Lonchorhina* with other phyllostomids has proven difficult (Rojas *et al.* 2016). When this genus is removed, we recover a significantly negative linear relationship between marginality and path-wise rates of trophic level evolution, without differences between the fast-speciation and slow-speciation groups (Fig. S9). This supports the negative association between path-wise rates of speciation and specialisation for herbivory we propose for the fast-speciation group. As more data accumulate on this genus, we will gain new insights on its role in trophic diversification of noctilionoids.

Other traits, in addition to trophic diversification, may relax stabilising selection on trophic level, allowing higher rates of evolution in this trait and affecting its relationship with speciation. Previous analyses including a subset of stenodermatines suggest mechanical advantage, a complex trait dependent on palate dimensions, could also explain taxonomic diversification of this subfamily, particularly for species feeding on hard canopy fruit (Dumont *et al.* 2014). This hypothesis cannot yet be tested with noctilionoid palates in general, as the skull architecture of the mormoopids differs radically from that of other families rendering the corresponding engineering models incomparable. The analytical framework we develop here, however, allows incorporating functional traits in phylogenetic mixed models and assessing the relative role of different factors on diversification dynamics of any clade, while testing for diversification of ecological roles and associated adaptations to explain the taxonomic diversification of a particularly lineage. Thus, these methods effectively become an empirical test of coupling variation in rates of speciation and trait evolution (Schluter 2000; Givnish 2015).

Analyses of the relationship between trophic specialisation and taxonomic diversification should explicitly consider shifts in speciation rates across the macroevolutionary dynamics of a clade. These shifts can disrupt the direction of the relationship, particularly when some groups have evolved key innovations related to feeding habits and speciation rates. We have shown whether trophic diversification or specialisation corresponds to a macroevolutionary dead end depends on the heterogeneity of the branching pattern in the phylogeny, resulting in conflicting trends even within a single radiation. Whether such adaptations are responsible for omnivory or specialisation suppressing speciation remains to be tested across other groups. The approach we introduce here can be used to that end.

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## AUTHORSHIP

DR and LMD conceived the study, collected the data and performed the analyses. All authors contributed to the discussion of the results and the writing of the manuscript.

## 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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**CORRIGENDUM**

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**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

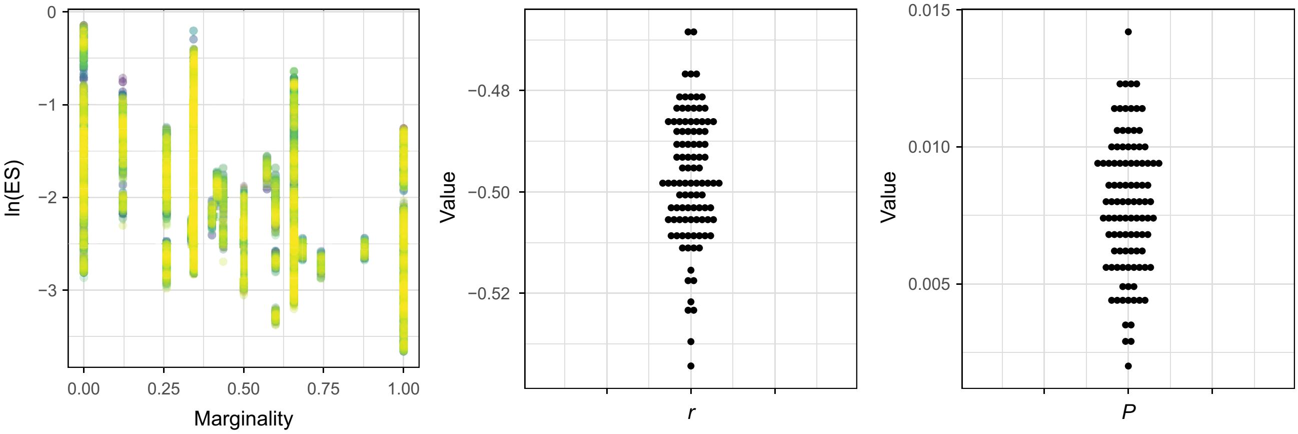

**Figure 1** Marginality-dependent speciation in noctilionoid bats, according to the ES-sim test. Left: Relationship between log-transformed inverse equal splits, ln(ES), and marginality in 100 time-calibrated molecular phylogenies of neotropical noctilionoid bats (each color represents a different tree).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

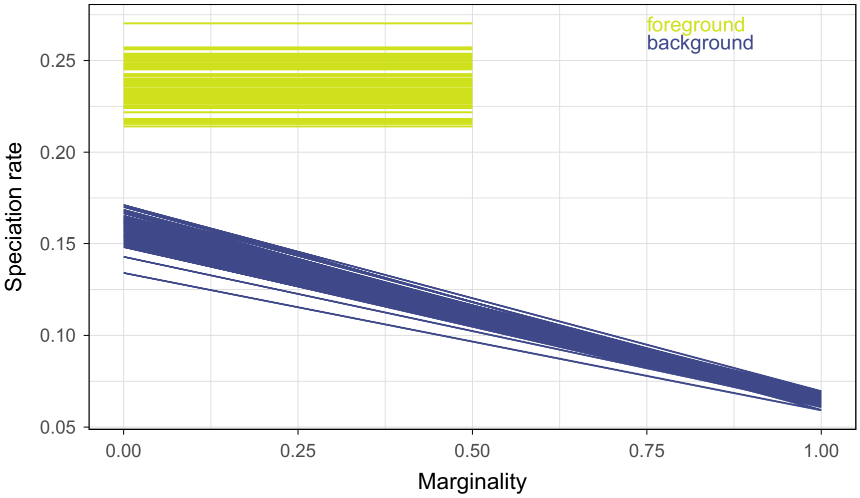

**Figure 2** Relationship between speciation rate and marginality in noctilionoid bats. Regression lines were estimated on a posterior distribution of 100 trees in a maximum likelihood framework. Foreground refers to Stenodermatinae and background to non-stenodermatines.

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 (herafter *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] × 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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