Pagel's Lambda Estimates are Often Inaccurate

Abstract

{conclusion holds: interpreting the regression is not appreciably different (in terms of slopes and f values)}

Introduction

Investigating macroevolutionary patterns requires a phylogenetic approach as species are non-independent by nature of their shared ancestry. Since the first appropriate method was introduced by Felsenstein (phylogenetic independent contrasts; Felsenstein (1985)), dozens of other methods have been developed and applied to increasingly complex questions in macroevolutionary biology (e.g. Grafen (1989); Harvey and Pagel (1991); Rohlf (2001); (**???**)). A particularly useful measure in this field is phylogenetic signal, a quantification of a trait's correspondence with the clade's phylogenic history. Understanding the degree of phylogenetic signal present in a dataset is paramount and identifies the mode under which a trait has evolved; high measures of phylogenetic signal indicate a Brownian motion process, whereas lower levels of phylogenetic signal indicate natural selection or some other evolutionary force has influenced the traits evolutionary history.

Several approaches to quantify phylogenetic signal exist. For continuous data, the most common parameters used in the literature include Pagel's lambda (**???**) and Blomberg's kappa (**???**). Pagel's lambda has the advantage of being nested in the likelihood framework and thus has also been utilized to simultaneously estimate and account for phylogenetic signal while doing phylogenetic regressions or ANOVAs. At the development of these estimation methods, clear recommendations on the use and interpretation of this parameter were made based on data simulations and error evaluations (Revell 2010). However, the accuracy of the lambda estiamtion methods have not been fully evaluated, and consequently many studies have substantially misused these methods.

An earlier study (**???**), breifly addressed this topic by showing how uninformative smaller phylogenies are when estimating various evolutionary parameters, such as Pagel's lambda. However, it remains unknown the degree to which lambda estimates accurately represent degree of phylogenetic signal, and thus we fully explicate the extent to which Pagel's lambda estimation methods can and have been misused in recent macroevolutionary studies. Here we take a comprehensive approach to demonstrate the scenarios under which estimated Pagel's lambdas accurately reflect known lambdas. We then demonstrate the effect of these, at times, dubious estimation methods on significance testing when used in a PGLS framework. Finally, we perform a meta-analysis of research published in 2019 employing Pagel's lambda estimation methods to demonstrate the uses and misuses of this method in the literature. This investigation provides evidence for the circumstances under which estimating Pagel's lambda can be informative, and which interpretations or uses are misleading with the hope of moving the field towards more appropriate employment of phylogenetic

comparative methods.

Methods and Results

Simulated trait

To assess the accuracy of Pagel's lambda estimations, we simulated pure-birth phylogenies of variable size, ranging in tip number from 32 to 1024. We then scaled the simulated phylogenies by lambda values ranging from 0 to 1 (0.05 intervals; 50 trees per lambda value per tree size) with which we generated trait data with known lambdas by simulating a continuous variable on each scaled phylogeny under Brownian motion. We then estimated lambda values from these data using phylogenetic generalized least squares (PGLS) to compare against the known lambda values.

To visualize the accuracy of the lambda estimation methods, we first plotted known lambdas (input lambdas) against the estimated lambdas (Figure 1). This plot demonstrates the rampant inaccuracy of estimating lambdas on phylogenies with fewer than 200 tips, as the spread of data in the upper panels in Figure 1 is remarkably wide. We also see that the widest spread of estimated lambdas is observed near the center of each plot corresponding to intermediate values of known lambda. Lastly, we see a slight tendency for the PGLS estimation methods to underestimate lambda, especially for known lambda values below 0.5 as can be seen by the numerous data points along the x axis for the smaller phylogenies analyzed (n tips < 200).

[insert Figure 1 here]

Simulated ANOVA and Regressions

To measure the statistical performance of PGLS lambda estimation methods when applied to ANOVA and regression analyses, we used the above generated data (independent variables) to simulate a second set of trait variables (depedendent variables) across the range of correlation strengths (betas ranging from 0 to 1 at intervales of 0.25). We then used PGLS to estimate phylogenetic signal of the dependent variable and the slope coefficient for the regression between the dependent and independent variables. We also calculated F- and p-values from the regression analyses. Finally, we again fit the dependent variable to the independent variable while holding the lambda value at 0 to approximate an ordinary least squares (OLS) apprach.

3

We compared the estimated slope coefficients across variable input beta values to assess the ability of PGLS to identify significant correlations (Figure 2). All distribution groups center around the 1:1 relationship between input beta values and estimated slopes. However the variance around that mean is substantial, with estimates ranging from approximately -2 to 4 in datasets with 32 taxa and a known relationship of (beta = 1). This variance of the estimated slopes only becomes reasonable when phylogenies have over 200 tips, similarly to what we saw in the first simulation analysis in this study.

[insert Figure 2 here]

Surprisingly, the estimated lambda values of the dependent variable do not correspond with input lambda values that characterize the independent variable (Figure S1). This disconnect then resulted in no appreciable difference of slope estimates across input lambda values (Figure S2), nor do we see substantial differences in slope estimates between the PGLS and OLS analyses (results not shown). Thus, we show that phylogenetic signal present in one variable does not translate to phylogenetic signal in a second, even highly correlated, dependent variable.

Scaling and trait generation procedures for all simulation methods were repeated with symmetrical and ladder phylogenies of variable size. Results generated using these variable phylogeny shapes were consistent with the pure-birth phylogeny results presented above and can be found in the Supplemental Materials. All analyses were performed in R v3.6.0 (**???**) using the packages `geiger` (**???**) and `caper` (**???**), and the corresponding scripts can be found in the Supplemental Materials.

Meta-Analysis of Empirical Results

To understand the extent of this problematic estimation method in application, we performed a meta-analysis of studies published in 2019 that cited Pagel's 1997 manuscript (**???**). The list of manuscripts was compiled through Google Scholar on Jan 23, 2020 and totaled 341 manuscripts. For each study, we extracted any published lambda estimates, along with the size of the phylogeny used in the analysis. We also noted whether authors reported confidence intervals, significance tests assessing difference of the lambda estimate from 0 or 1, and whether authors interpreted biological meaning from the magnitude of the estimated lambda. For studies that reported more than one lambda estimate, we also noted if the authors compared the lambdas against one another, and whether that was accompanied with an appropriate statistical test between the

4

estimated lambda values.

We found 182 manuscripts from 2019 that estimated and reported Pagel's lambda values using PGLS methods. These papers averaged 8.527 lambda values, ranging from a single lambda estimate up to 71 estimated lambdas. Almost exactly half of the published lambda estimates were either below 0.05 (25.32%) or above 0.9 (24.74%; Figure 3). 73.32% of the published lambdas were estimated using phylogenies with fewer than 200 tips, and 348 lambda estimates (8.57% of all published estimates) came from phylogenies with fewer than 30 tips.

[insert Figure 3 here]

Many of the reviewed manuscripts liberally interpreted the magnitude of the estimate lambda, using phrases such as "strong" or "weak" phylogentic signal when statistically, all that was clear was a difference between the estimated lambda and 0 or 1 respectively. We estimated that about 20.49% of the manuscripts revealed some sort of biological interpretation of the magnitude of estimated phylogenetic signal that overreached the statistical findings. We also identified seven manuscripts as having inappropriately interpreted differences in lambda values, indicating that some traits had stronger or weaker signal than other traits without the appropriate statistical tests.

As is evidenced by macroevolutionary papers published in 2019 papers, Pagel's lambda estimation methods are often misused and over-interpretted. Despite the urging of Boettiger and colleagues to publish confidence intervals with all lambda parameter estimates, only 18% of papers published in 2019 do so.

Discussion

[This part is obviously not written yet]

General conclusions :Using the estimated lambda values from pgls are not useful. The questions of whether or not signal exists is appropriate, but inferring more from lambda *magnitude* is inappropriate.

More discussion paragraphs

References

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London B, Biological Sciences 326:119–157.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Revell, L. J. 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1:319–329.

Rohlf, F. J. 2001. Comparative methods for the analysis of continuous variables: Geometric interpretations. Evolution 55:2143–2160.

Figure Legends

Figure 1. Accuracy of Pagel's lambda estimations across known lambda inputs on various tree sizes. As trees increase in size, the estimates more closely resemble the input lambdas, however considerable and concerning variation is apparent in trees smaller than those with 200 tips.

Figure 2. Estimated ANOVA slopes under PGLS. Across tree sizes, the mean estimated slope matches the input slope, and as trees increase in size, the variance around this mean estimate decreases. However, for trees with fewer than 200 tips, the error around the estimated slope is considerable, where these analyses frequently estimate slopes in the opposite direction of the known pattern.

Figure 3. Frequency of estimated lambda values published in manuscripts in 2019. The majority of these values were close to 0 or 1, and from phylogenies with fewer than 200 taxa.
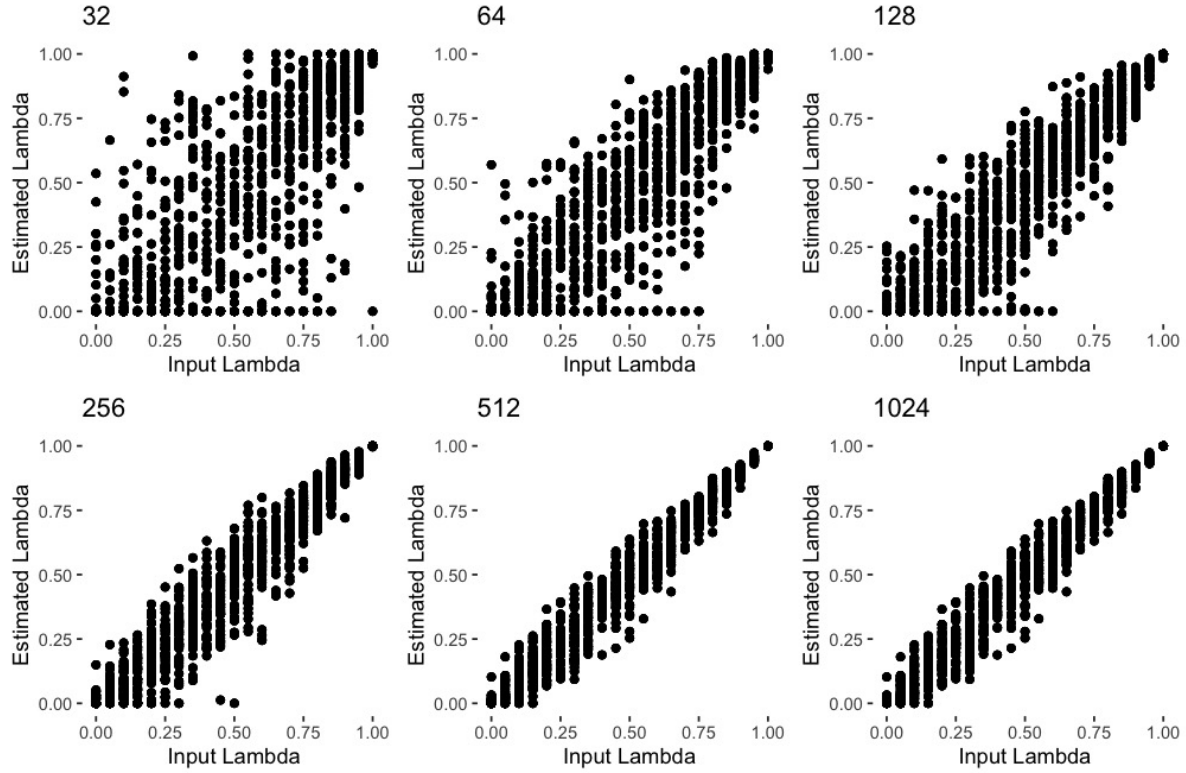
Figure 1. Accuracy of Pagel's lambda estimations across known lambda inputs on various tree sizes. As trees increase in size, the estimates more closely resemble the input lambdas, however considerable and concerning variation is apparent in trees smaller than those with 200 tips.
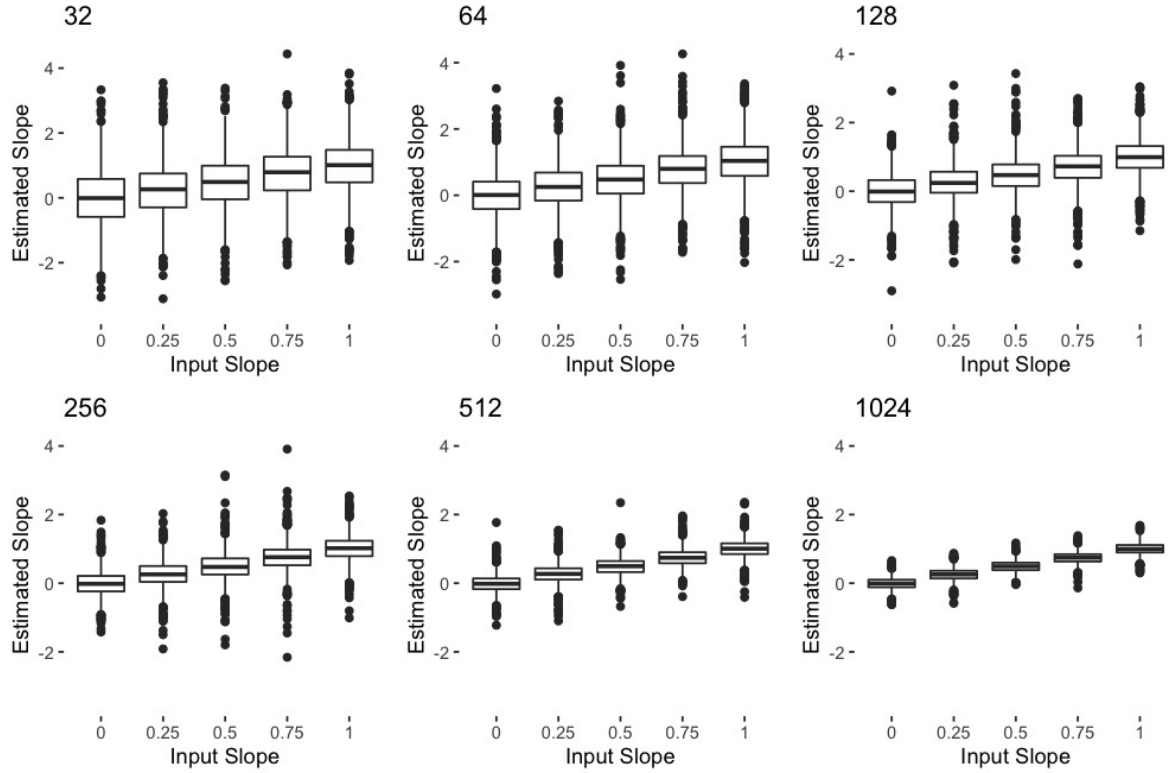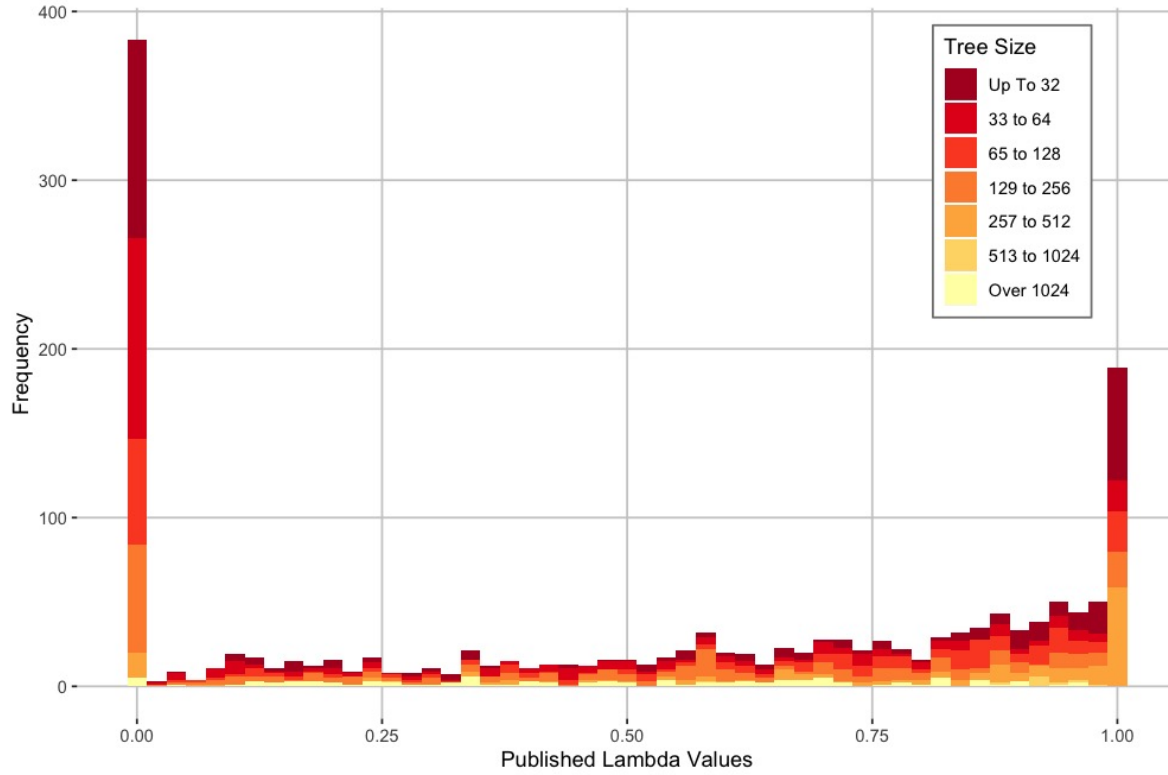
Figure 2. Estimated ANOVA slopes under PGLS. Across tree sizes, the mean estimated slope matches the input slope, and as trees increase in size, the variance around this mean estimate decreases. However, for trees with fewer than 200 tips, the error around the estimated slope is considerable, where these analyses frequently estimate slopes in the opposite direction of the known pattern.

9

Figure 3. Frequency of estimated lambda values published in manuscripts in 2019. The majority of these values were close to 0 or 1, and from phylogenies with fewer than 200 taxa.

10