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Article title: Assessing the Effects Imputation on ED Values

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Abstract

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Introduction

Evidence from the fossil record and present-day studies argue we are in the midst of, or entering, a sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015), such that more species than ever are declining and/or in danger of extinction across a range of environments (Wake & Vredenburg 2008; Thomas et al. 2004). Habitat destruction (Brooks et al. 2002), invasive species (Molnar et al. 2008), climate change (Pounds et al. 2006), and disease (Lips et al. 2006) are some of the leading causes of species declines globally. Conservation biologists seek to reverse these declines and their detrimental effects on species populations, but in reality they have limited resources with which to do so. This challenge, termed the "Noah's Ark problem" (Weitzman 1998), has driven conservation biologists to prioritize, or triage, the resource allocation (Bottrill et al. 2008).

Conservation triage, like all sound decision-making, requires some metric that quantifies the [put something here that's a bit more precise. Importance != endangerment != urgency, so pick something and go with that]~~importance and degree of endangerment urgency for a set of species~~. By using such a metric, researchers are able to avoid biasing the allocation of time and resources for conservation, and can make their conservation goals more explicit. One such triage strategies which has been widely used is the EDGE metric(Evolutionary Distinction and Globally Endangered; Isaac et al. 2007). This method prioritizes species according to two metrics: Evolutionary Distinctiveness (ED) and Global Endangerment (GE). ED measures relative contributions to phylogenetic diversity made by each species within a particular clade(Isaac et al. 2007), assigning each branch length equally to all its subtending species. GE values are assessed by assigning numerical values to each of the World Conservation Union (IUCN) Red List Categories. The precise mapping of numerical values onto each category varies, and can affect the relative rankings of EDGE species (Mooers et al. 2008). I'm not sure you need this sentence. You could, if you wish, say something more about the different kinds of rankings, or perhaps how there are different ways of doing

the ED bit (e.g., the Redding paper, which is similar but slightly different—Equal Splits)~~As species become increasingly threatened and are placed into more concerning categories (*e.g.*, from Vulnerable to Endangered), the GE numerical value increases.~~ Thus a species' EDGE score is intended to equally reflect a species' evolutionary distinctiveness and conservation status (but see Pearse et al. 2015, for discussion on this).

The EDGE approach was never intended to be a purely academic metric, and is now the basis of the global EDGE of Existence Program (`http://www.edgeofexistence.org/`). While EDGE was originally used to prioritize global mammals, it has subsequently been applied to a number of species groups.

There are now EDGE lists of amphibians (Isaac et al. 2012), birds (Jetz et al. 2014), corals (Curnick et al. 2015), and sharks (Stein et al. 2018). A number of similar metrics have been developed, each prioritizing and emphasizing subtly different things, such as the expected contribution of each species to overall phylogenetic diversity (HEDGE; Steel et al. 2007), our uncertainty over a species' future (EDAM; Pearse et al. 2015), and the complementarity of a set of species (**Faith2008**; **Jensen2016**). Thus the development of EDGE-like metrics has matched progress with other fields of conservation biology, where the likelihood of success in conservation (Wilson et al. 2007; McBride et al. 2007), relative cost of certain interventions(Naidoo et al. 2006), and complementarity of interventions(Pressey et al. 1993; Myers et al. 2000) have also been considered . Critically, EDGE has formed the basis of a successful program that quantitatively prioritizes conservation, providing actionable insights into how to focus conservation effort in the face of uncertainty about species' attributes. EDGE's success proves that phylogenetic conservation prioritization metrics can be used by conservation biologists and policy makers, and that they are popular with the public. Nonetheless, almost every application of an EDGE-like approach has had to deal with the uncertainty presented by missing species data.

The IUCN has a well-established protocol for how to deal with data-deficient species: they

are to be treated as if they were of Endangered species to ensure consistency (check this Bodie Rodrigues et al. 2006). The problem, however, is arguably more complex for species whose phylogenetic position is unknown. Species of conservation concern are almost by definition rare, and so we frequently lack sufficient DNA (or even morphological) data to place them with certainty on a phylogeny. In the face of such essentially unavoidable uncertainty, conservation biologists have worked hard to overcome data limitations. In most empirical EDGE lists, taxonomic information, rather than sequence data alone, is used to locate species in the tree of life (Isaac et al. 2007; Isaac et al. 2012; Jetz et al. 2014; Curnick et al. 2015; Stein et al. 2018).By using taxonomic information alone, researchers are able to produce fully resolved phylogenies using model-based imputation (Kuhn et al. 2011).Yet, to our knowledge, there has yet to be a systematic study of the effect of such imputation on species' EDGE scores, unlike in other aspects of comparative biology (Rabosky 2014). Indeed, there is no clear guidance as to the size of the effect of ignoring missing species on remaining species during prioritization, or the magnitude of error phylogenetic imputation introduces. As the desire to use ED and phylogenies for conservation triage grows, the importance of such tests and a consensus on how to resolve cases of phylogenetic uncertainty becomes more urgent.

Here we quantify the effect of missing species on EDGE rankings and assess whether imputing species is a defensible method for dealing with species missing phylogenetic data. We do so by simulating the removal of species from simulated trees in two ways: at random and in a phylogenetically biased manner. By doing so, we hope to provide two reasonably realistic case-studies of how species might be expected to be missing from the tree of life. We also assess the extent to which imputed species' EDGE rankings correlate with their true values. To do this, we simulate phylogenies, choose clades at random to remove, and then impute the structure of these clades, all under the same model of diversification. In so doing , we hope to provide clear guidance as to the applicability of phylogenetic imputation as a solution for species missing phylogenetic data . From our results, we argue that species' ED values are

remarkably robust to the loss of species, and that phylogenetic imputation is not reliable at reconstructing the true ranking of species.

Methods

Here we use a simulation approach to test the effect of removing and imputing species on a phylogeny on species' ED (Evolutionary Distinctiveness) scores . Since empirical studies do not (to our knowledge) impute GE (Global Endangerment) scores for species, instead relying on the IUCN's proposal to treat Data Deficient species as XXX (e.g., shark paper?), we focus solely on phylogenetic imputation . EDGE is the product of both ED and GE, thus perfectly accurate GE values could still lead to a biased EDGE score if the ED scores were imperfectly calculated.

All simulations and analyses were performed using R (version 3.4.0; R Core Team 2017), and we performed 100 replicate simulations of each parameter combination . All trees (both starting and imputed) were simulated under a pure-birth Yule model using the `sim.bdtree` function in the `geiger` R package (wrong citation; there's a newer one with Matt Pennell as the first author Harmon et al. 2007). This particular model was chosen because it is the simplest model possible: speciation rates are constant across the entire tree of life and there is no extinction. We acknowledge that it is possible that more complex and/or biologically realistic models of diversification could improve the performance of imputation. However, we suggest that imputation under a simple model that is identical to that used to simulate the data is a low benchmark for a method to surpass. We used `ed.calc` in the R package `caper` to calculate ED values (Orme 2013).

The impact of missing species on EDGE scores

Our first set of simulations assesses the impact of random and phylogenetically-biased loss of species from a phylogeny on ED scores. Both sets of simulations were carried out using phylogenies of different sizes (number of taxa: 64, 128, 256, ..., 2048, 4096), removing constant fractions of tips from the tree (0%, 1%, 2%, ..., 19%, ..., 99%). To simulate randomly missing species, we used the `sample` function in R to select the relevant percentage of species (rounded to the nearest whole number?) without replacement. Thus this randomization did not incorporate phylogenetic structure. To remove species in a phylogenetically biased manner, we used Felsenstein (2005)'s threshold model. First, we simulated a trait under a constant rate Brownian-motion model (σ^2=0.5, starting root value = 1). Species were then removed from the tree if their simulated trait was in the upper quantile of whatever fraction of species were to be dropped. For example, if 10% of species were to be dropped, species within the upper 10th quantile of character trait values were removed from the tree.

We calculated species' ED values before removal of species from the tree and afterwards. We then correlated the ED scores of the species left in the tree with their original ED values, to measure the effect of species' removal on ED scores. To see if phylogenetic structure could explain variation in the effect of removal, we also recorded, before species were removed from the tree, XXX list all the things you recorded here and give citations for them, taken from the functions' help files if you're uncertain. If missing species have no effect upon ED values, we expect a high, positive coefficient of correlation between the remaining species' ED scores before and after the other species were removed from the tree.

The impact of phylogenetic imputation on EDGE scores

We tested the impact of imputing missing species onto clades of various sizes (3, 4, 5, ..., 30, 31, 32 species) from phylogenies of different sizes (64, 128, 256, 512, and 1024 species).

We first randomly selected a clade to be removed from the original tree, simulated a new phylogeny of the same size under the same pure-birth model used to generate the phylogeny, and placed the newly simulated clade back where the original clade was removed. Thus we imputed each clade under the model used to generate it: in an empirical study this model would, itself, have to be inferred but we do not address this additional source of error here. In cases where a phylogeny was simulated without a clade of the required size (XXX cases), that particular simulation was aborted and we moved on to the next simulation. In cases where a clade could not be simulated after XXX attempts that was sufficiently young to be inserted into the phylogeny (XXX cases), that simulation was also aborted and the next simulation.

To assess whether clades, once imputed, had similar ED scores, we correlated the imputed ED scores against true ED scores. We also calculated the sum of the absolute change in ranked ED for each species, which is particularly relevant for EDGE-listing as it is often the top 100, 200, etc., species on which conservation actions are targeted. We statistically modeled both these metrics as a function of the number of total species and number of species within an imputed clade, since we might expect larger clades and/or larger phylogenies to be imputed more erroneously.

Results

Under both random and phylogenetically-patterned loss, species' ED scores are less accurate as more species are removed from the tree (Table 1; Fig. 1). What is the correlation when 10% and 20% of species are missing at random? Phylogenetically biased loss of species affects ED scores more strongly (Table 1; Fig. 1), but the effect is comparable to random loss (XXX values as you gave for random loss).
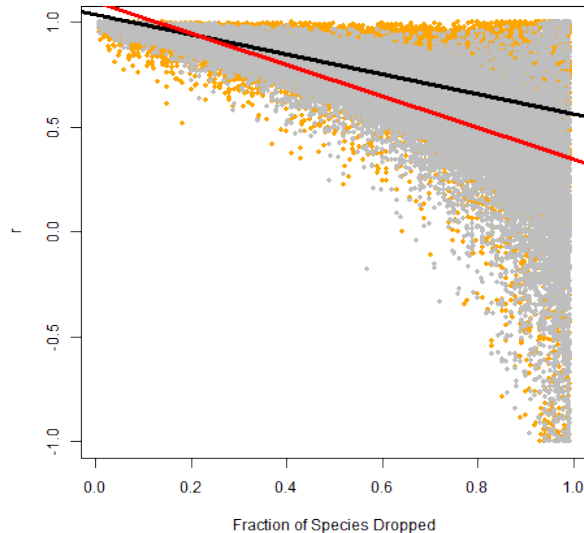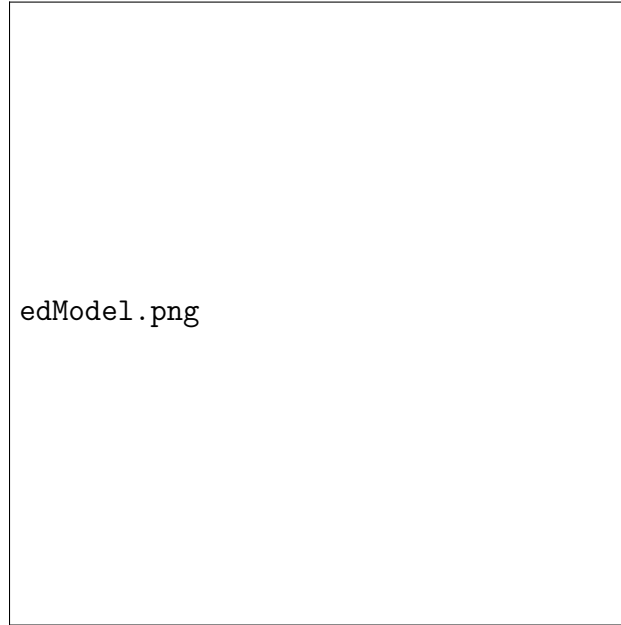
Figure 1: **R-values plotted against the fraction of species dropped at random versus clustered manner.** The color of data points denote whether species were dropped at random (orange; n = 100) or in clustered manner (grey; n = 100). The regression lines are demonstrating the relationship when species are dropped at random (red) and in a clustered manner (clustered). The correlations represent a comparison of the ED values (before and after species are dropped) of species which remain on the on the phylogeny after other species are dropped.

We find no support for a correlation between the imputed and true ED values for species within imputed clades (Fig. 2, Table 2). We found that measures of the true phylogeny such as phylogenetic diversity (PD), estimated rate of diversification $\hat{\lambda}$, Colless' Index, skew, and kurtosis do not provide any indication that imputation would negatively affect ED values (Appendix A). We do find evidence that, when imputing larger clades, the variation in the correlation is lesser (Fig. 3), but the correlation between true and imputed ED values appear to converge on zero correlation (Table 3). Imputed rankings of species within clades are also altered under imputation (Fig. 4; Table 4); quote some exemplar numbers to give an impression of the degree of problem. This ranking error increases with the size of the imputed clade and phylogeny (Table 4), and can affect ranking error within the top 100, 250, etc. species (Appendix B).

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|	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.0315	0.0013	821.39	<0.0001
Fraction of Species Dropped	-0.4696	0.0020	-233.16	<0.0001
Random Treatment	0.0630	0.0018	35.47	<0.0001
Number of Species Overall	0.0000	0.0000	7.89	<0.0001
Fraction of Species Dropped:Random Treatment	-0.2774	0.0028	-97.45	<0.0001
Random Treatment:Number of Species Overall	0.0000	0.0000	-4.38	<0.0001

Table 1: **ANCOVA model summary describing the effect of dropping species on remaining species ED Values.** The fraction of species dropped significantly affects the the remaining ED values. Dropping the fraction both at random and in clustered manner both have negative effects on the remaining ED values ($F_{139696,5} = 40350$, $R^2 = 0.5908$, p<0.0001).

Figure 2: **R-values plotted against the number of species at focal clade.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. The regression line (red) and trend even closer to zero demonstrates the decrease in informative value of the imputed ED values. This is reinforced by the visual narrowing of r-values around zero.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.1691	0.0500	3.38	0.0007
Size of Focal Clade	-0.0029	0.0002	-14.15	0.0000
Size of Phylogeny	-0.0001	0.0001	-1.01	0.3128
PD	0.0001	0.0001	0.97	0.3339
Lambda	0.0051	0.0492	0.10	0.9179
Colless' Index	0.0020	0.0021	0.96	0.3388
Skew	0.0039	0.0083	0.47	0.6409
Kurtosis	-0.0005	0.0008	-0.64	0.5247

Table 2: **Effect of Clade Size on Imputed ED Values.** The intercept describes that the correlation between the true and imputed values begins quite low. As the clade size increases, this correlation only tends toward zero. The total number of species in the full phylogeny along with measures of the true phylogenetic diversity, lambda, Colless' Index, skew, and kurtosis show no significant effect. ($F_{47992,7} = 29.38$, $R^2 = 0.005$, p<0.0001).
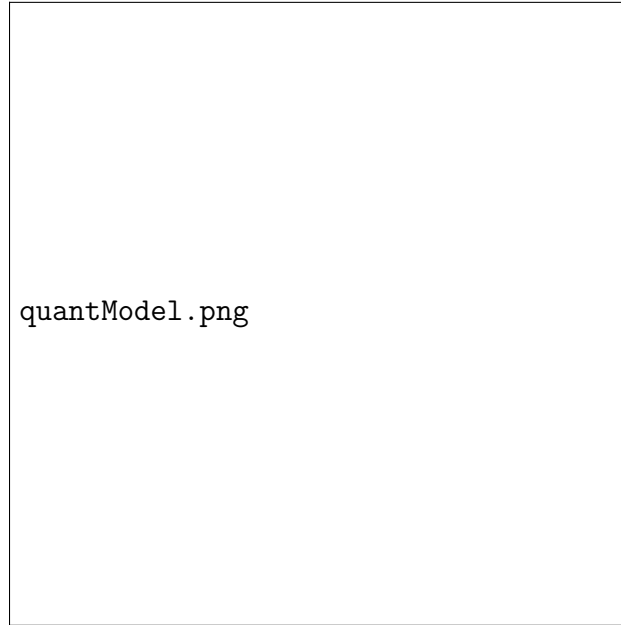
Figure 3: **Quantile regression of r-values against size of imputed clades.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. Each regression line (top to bottom) represent quantile regressions from highest to lowest, respectively. Each of the regression lines demonstrate a convergence of the variation in r-values around zero.

	$\tau = 0.10$	$\tau = 0.25$	$\tau = 0.50$	$\tau = 0.75$	$\tau = 0.90$
(Intercept)	-0.54	-0.23	0.20	0.60	0.86
Size of Focal Clade	0.01	0.01	-0.00	-0.01	-0.02

Table 3: Quantile Regression of Clade Size and Total Species on Ranking Error. Quantile regression model demonstrating the effect of clade size on the correlation between true and imputed ED values. The quantile regression estimates demonstrate statistical significance that as imputed clade size increases, variation in coefficient of correlation (r) between ED values center around zero (all p-values are <0.0001).
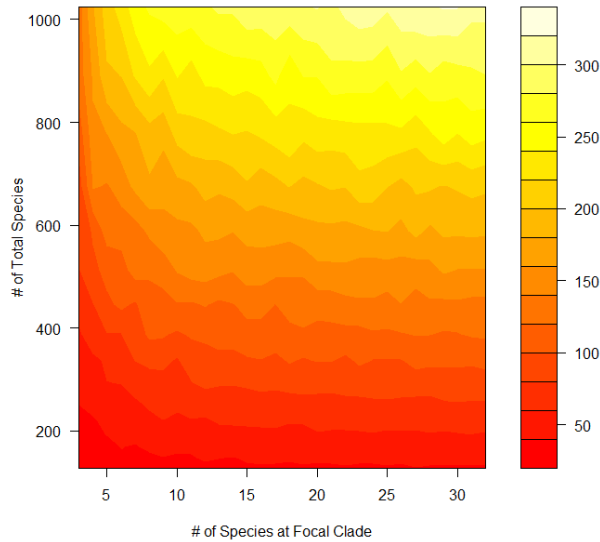
Figure 4: **Mean ranking error of species within the focal clade.** The gradient on the right demonstrates average number of positions within the full ranking that focal clade species shifted from their true rank. While controlling for the size of the full phylogeny and focal clade, species within the focal clade were, on average, ranked far from the true rank.

	Estimate	Std. Error	t value	$\Pr(>|t|)$
(Intercept)	-1.6344	0.0332	-49.29	0.0001
Size of Focal Clade	0.0900	0.0010	91.22	0.0001
Size of Phylogeny	0.5179	0.0013	383.99	0.0001

Table 4: Effect of Clade Size and Total Species on Ranking Error. Model demonstrating the relationship between focal clade species ranking error and the size of imputed clade and overall phylogeny. Square-root transformations have been applied to both ranking error and size of phylogeny. Significant increases ranking error are seen when increasing sizes of both the imputed clade and phylogeny ($F_{47997,2} = 77890$, $R^2 = 0.7644$, p<0.0001).

Discussion

Phylogenetic conservation prioritization is an emerging tool providing a much needed, objective measure for conservation decision-making and policy. However, phylogenetic uncertainty is a major obstacle for EDGE and similar metrics (Collen 2015). Uncertainty in phylogenies could mean that species in desperate need of conservation effort are overlooked. In order to address such uncertainty, we aim to determine how removing missing species from a phylogeny affects ED values for the remaining species and demonstrate how imputation affects ED values of species where imputation is performed. Our results demonstrate that missing a proportion of overall species both at random and in a phylogenetic-biased manner have different yet significant affects on remaining ED values throughout the tree and imputation does not recover the ED value or ED rank of an imputed species.

Our results are derived solely from simulations under a simple model of diversification—the Yule model. We do acknowledge that, in the real world, lineages evolve in more complex ways than are captured by such a simple model. While we do not have empirical data, imputing species under this model should be much easier given the simplicity. We have not been given any implication through this investigation that a more complex model would produce any different result. Therefore, we suggest that our results generalize from the simplest case to more complicated cases which might be seen in empirical data. However, our results demonstrate that even under a simple model imputing species lead to a misrepresentation of true ED values.

Normally, imputation and artificially, fully resolved clades are achieved by generating a pseudo-posterior distribution of numerous trees, using a birth-death model of evolution, for clades where there are unsampled species using a polytomy resolver (Kuhn et al. 2011). However, our results demonstrate that there is uncertainty in that pseudo-distribution of trees being used to set priorities (Fig. 2).

Uncertainty in imputed species

Missing species and poor phylogenetic resolution have been identified as causes of uncertainty when calculating ED (Isaac et al. 2007). Prior to our investigation, we could not find any assessment of how missing species might affect ED values of species which are not missing. In previous research, incomplete phylogenies were shown to produce nearly the same result as the later, more complete trees (Curnick et al. 2015). While demonstrating EDGE scores derived in the face of phylogenetic uncertainty still perform quite well in setting accurate priorities, they did not explicitly test the effect which missing species, nor imputing missing species, has on ED values. Our results support the finding that missing species do affect ED scores but the effect is relatively insignificant compared to percentages of species missing (Table 1).

We realize that we have provided just two ways in which species could be missing from a phylogeny and there are more that could occur. Missing species could be biased by some phylogenetic pattern other than Brownian motion evolution. Nevertheless, our investigation shows that missing species cause ED values of species remaining in the phylogeny to deviate from the true value. This effect should be considered when debating whether under other, more complex models of evolution a different effect might be seen. There could be cases where species could be missing from the phylogeny with the result that an entire clade is unsampled. This would be a case of species radiating in situ and have persisted in one, restricted area. A situation such as this is seen with corals in the Indian Ocean region (Arrigoni et al. 2012).

In the past, we have included missing species into the EDGE framework using different methods. Collen et al. assigned the mean ED score of presumed congeneric species to the missing species 2011. More frequently, missing species and poorly resolved clades have been dealt with by imputing the missing species and assigning all the species of the resolved

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clade the mean ED value obtained from all possible or numerous resolutions of the clade (**Isaac2007; Isaac2012**). This method has been adapted by others and applied where there were large percentages (30% or 3,330 species) missing (Jetz et al. 2014).

While imputation does include missing species, relying upon taxonomic information and constraints under some estimated model of evolution could become is subjective. Kuhn et al. **2011** suggests that when using their polytomy resolver, the application of the of the resolver will be biased by the model of evolution estimated. More recent research confirms, that when under the prior of a birth-death model, imputation methods consistently bias evolutionary rates and estimates of phylogenetic signal used in downstream analyses (Rabosky 2014).

When considering the analysis of ED, our results show that imputation does not recover true ED values nor ED rank of missing species (Fig. 2; Fig. 4). As the size of the imputed clade increases, ED values of imputed species do not correlate with their true values (Table 2). Even though we are including missing species into calculating ED, we are not obtaining accurate information about those species. While being uninformative, these ED values would also lead to mispriortizing species based on our results. In the event that a clade of 25 species in a phylogeny of 850 species, our results show those imputed species would be, on average, 250 ranks from their true rank (Fig. 2; Table 4). Analyzing the performance of imputation of a clade less than five species was not performed because we can't report a correlation reliably with so little data (Crawley 2012). Even still, we cannot see how the trend in our results would suddenly change such that, when imputing only one species, it improves.

Guidelines for the use of imputation

We suggest there is a straightforward synthesis of these results that should be useful in applied conservation biology. Both random and phylogenetically-patterned loss of species

affect ED values throughout the tree. However, we found that ED values of non-imputed species remain constant under imputation. Therefore, imputation could be used to avoid missing species biasing ED values of non-missing species. We have shown that imputing missing species would not provide accurate ED values for missing species. However, it would provide a method of avoiding the loss of species affecting ED values throughout the remainder of the tree. Basing conservation priorities upon the ED values of imputed species would lead to inaccurate prioritization. Nevertheless, imputation may be useful to stop missing species from biasing species easily placed on the phylogeny.

Given these results, we now present guidelines for how missing species should be dealt with and when imputation might be appropriate when calculating EDGE. Our aim is to provide a rule of thumb for the use of imputation and how imputed species should be handled. In the event of missing species, researchers should be investigating the exact amount of species that are missing and consider whether imputation is necessary. Our analyses show that even with a large proportion of species missing, ED values of remaining species are highly correlated. For some context, in our analysis we found that 30% of species missing at random or in a phylogenetic-biased manner from the phylogeny leads to a correlation coefficient of 0.8 and 0.89, respectively. Therefore if species are missing, we should verify that the amount of missing species does not exceed a percentage which we have found to provide poor ED values for remaining species. While below an acceptable percentage of missing species, EDGE should be carried out without attempting to impute the missing species. However, if a larger proportion of species are missing, imputation may be used but with some caution. ED values for species easily placed on the phylogeny are relatively unaffected and can be trusted when setting conservation priorities. Nevertheless, ED values and ranks of species which have been imputed should either be ignored or used cautiously within EDGE. Our results demonstrate that an individual species within an imputed clade of 25 species on a phylogeny of 1024 species is, on average, ranking $\pm$ 318 positions from its true rank (Fig. 4). While imputation does not affect ED values of known species, includes missing species

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in the phylogeny, it does not help understand the true ranking of an imputed species. By following these guidelines we avoid biasing species which are easily placed on the phylogeny and confounding the rankings for the sake of including missing species.

Acknowledgments

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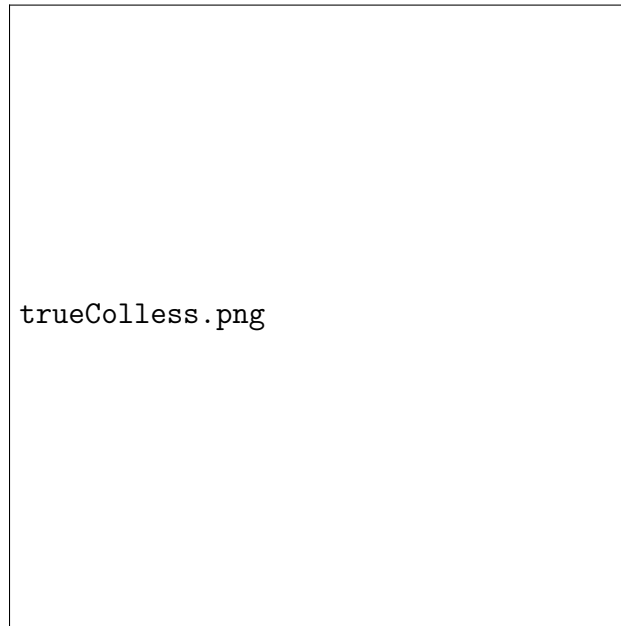
A. Effect of Measures of the True, Full Phylogenies

trueColless.png

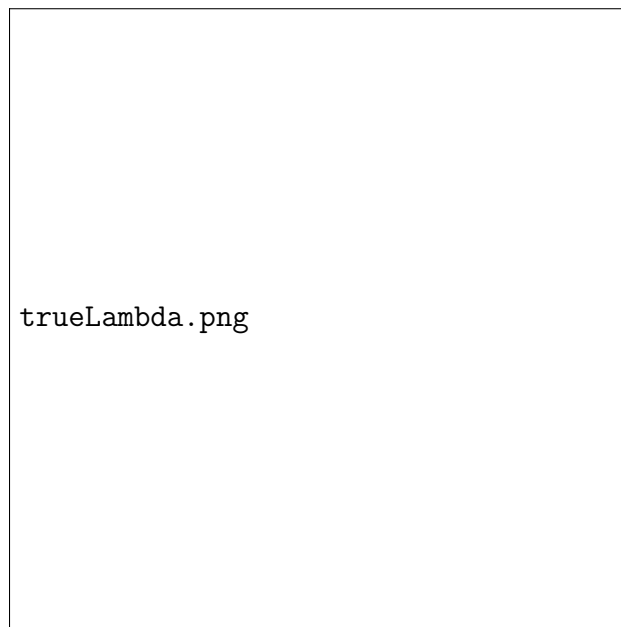Figure 5: **Effect of the True Colless Index of FullPhylogeny.**

trueLambda.png

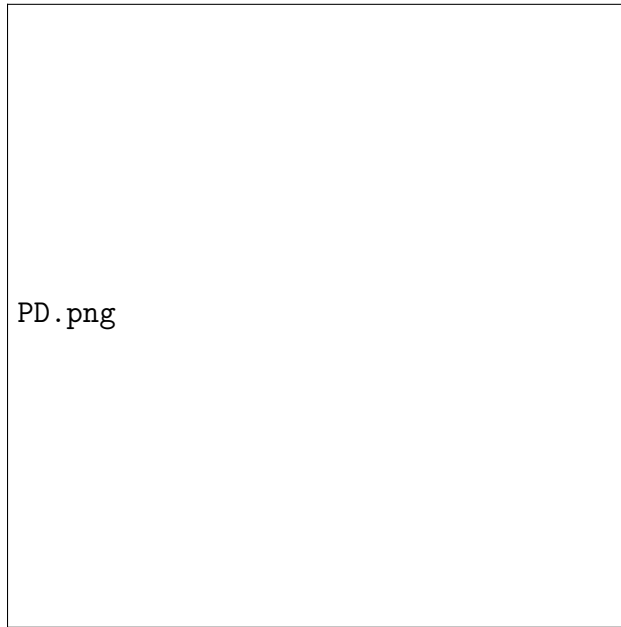Figure 6: **Effect of the True Lambda of Full Phylogeny.**
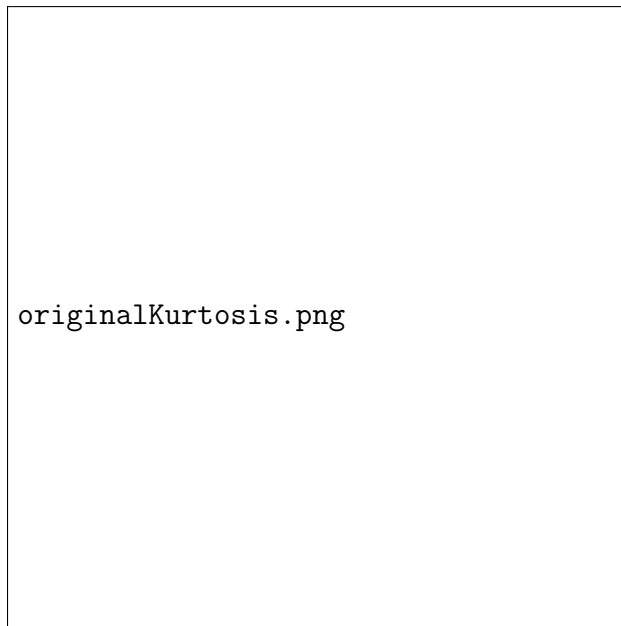
Figure 7: **Effect of True PD of Full Phylogeny.**

Figure 8: **Effect of the True Kurtosis of Full Phylogeny.**

originalSkew.png

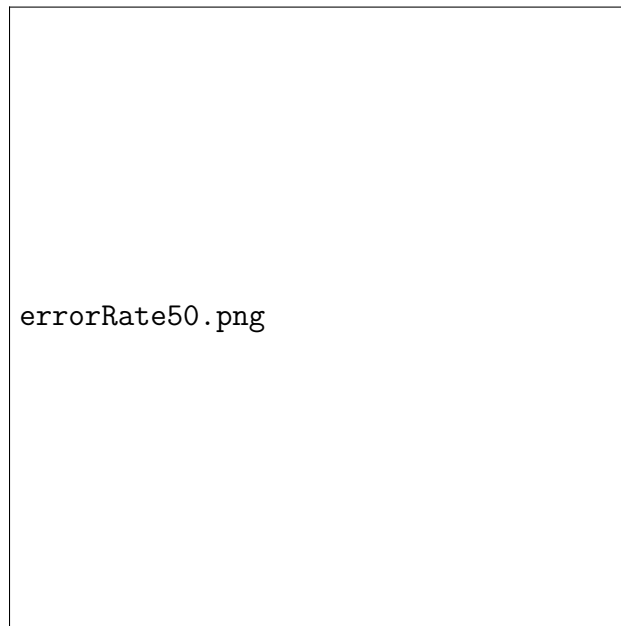Figure 9: **Effect of the True Skew of Full Phylogeny.**

B. Error Rate in Top Rankings

Figure 10: **Mean error rate in the ranking of top 50 species.**

Figure 11: **Mean error rate in the ranking of top 100 species.**
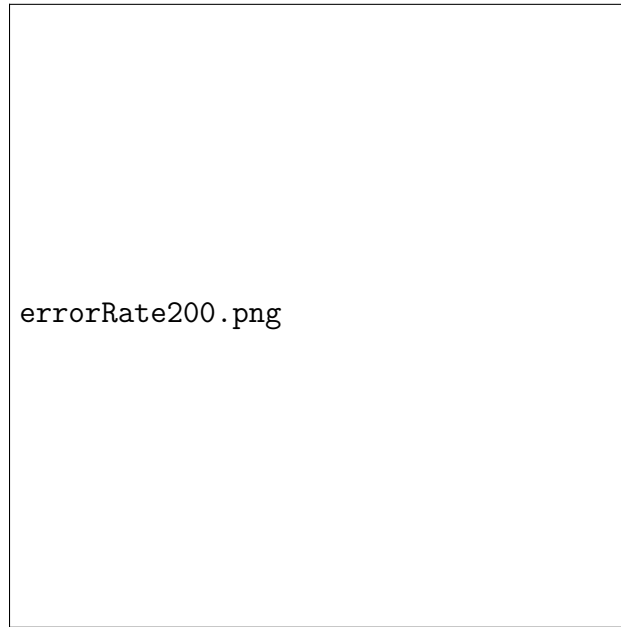
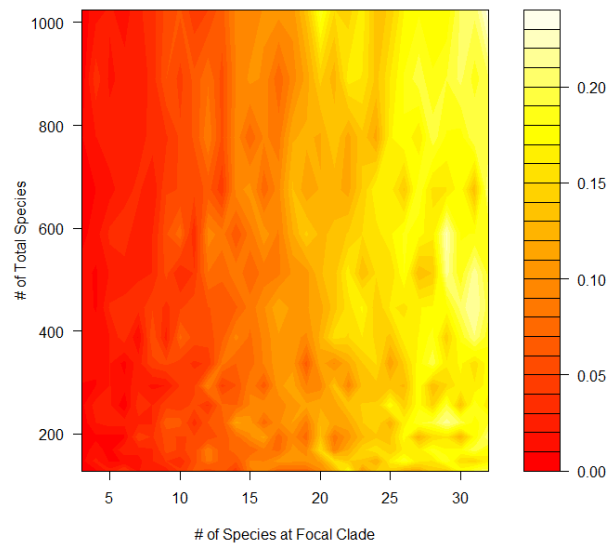Figure 12: **Mean error rate in the ranking of top 200 species.**

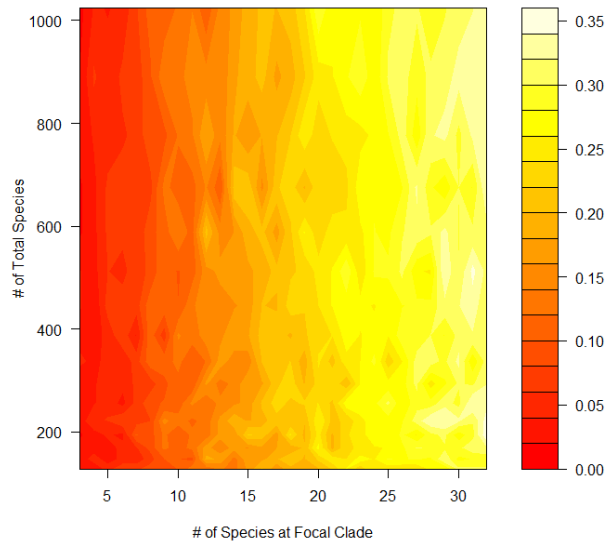Figure 13: **Mean error rate in the ranking of top 5% of species.**

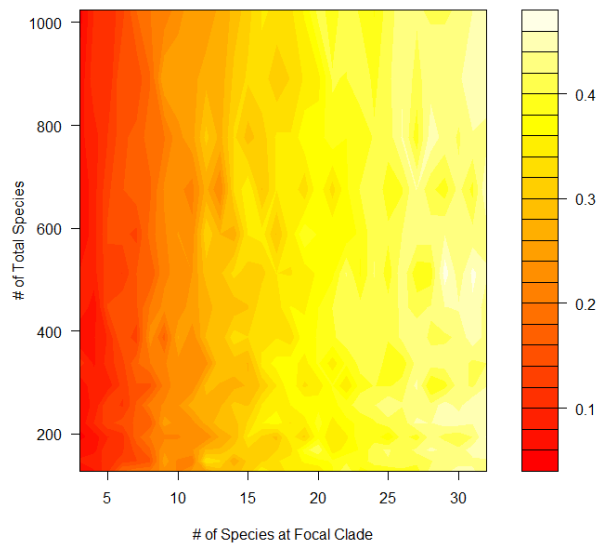Figure 14: **Mean error rate in the ranking of top 10% of species.**

Figure 15: **Mean error rate in the ranking of top 20% of species.**