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Article title: A simulation of the effect of phylogenetic missing species and their imputation on evolutionary distinctiveness scores

Running head: Evolutionary distinctiveness and missing species

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Abstract

As global extinction rates have risen, conservation biologists are increasingly focusing on how best to allocate their limited time and money to save as much diversity as possible. Increasingly, conservation effort is being allocated on the basis not just of species' endangerment, but also the evolutionary history (and so phylogenetic diversity) that they represent. Metrics such as EDGE (Evolutionary Distinct and Globally Endangered) have been successfully used to set conservation priorities for a number of taxa, such as mammals, birds, corals, and sharks. Each of these applications of EDGE has required some form of correction for species whose position within the tree of life are unknown. Perhaps the most advanced of these corrections is phylogenetic imputation, but to date there has been no systematic assessment of the impact of both missing species and imputation to correct for them. Here we perform such a systematic assessment, simulating the random loss of species from a phylogeny, the imputation of the position of those species, and measure the impact each of these processes has on the data underlying EDGE scores. We find that EDGE ranking is remarkably robust to missing species, and that phylogenetic imputation, while unbiased, is not accurate in reconstructing species' true evolutionary distinctiveness. On the basis of these results, we provide clear guidance for EDGE scoring in the face of phylogenetic uncertainty.

Keywords: conservation prioritization, evolutionary distinctiveness, EDGE, phylogenetic imputation.

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 reduce these 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, their resource allocation (Bottrill et al. 2008).

Conservation triage, like all sound decision-making, requires some metric that quantifies the urgency for conservation of 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 criteria: 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 quantified by assigning numerical values to each of the World Conservation Union (IUCN) Red List Categories. 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 (even if it does not always in practice; see Pearse et al. 2015).

The EDGE approach was never intended to be a purely academic, 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, including 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 (Faith 2008; Jensen et al. 2016). 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.

IUCN has given guidance that any available contextual data should be used to assign some threat status to species which are classified as Data Deficient (IUCN 2001; IUCN 2008). A number of studies have been done showing how to follow this guidance and assign threat categories to Data Deficient species and reduce the uncertainty in GE (Good et al. 2006; Butchart & Bird 2010; Morais et al. 2013). 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; Collen et al. 2011; Isaac et al. 2012; Jetz et al. 2014; Curnick et al. 2015; Gumbs et al. 2017; Stein et al. 2018). By using taxonomic information, researchers are able to produce fully resolved phylogenies using model-based imputation (Kuhn et al. 2011; Thomas et al. 2013). 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 need for 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 does not reliably reconstruct 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 assign Data Deficient species as threatened or otherwise based upon any available evidence, we focus solely on phylogenetic imputation. EDGE is the product of both ED and GE (Isaac et al. 2007, see), thus perfectly accurate GE values could still lead to an imperfect 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 under parameters of in the `geiger` R package (under parameters `b=1` and `d=0`; Pennell et al. 2014). 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, and fair, benchmark for a method to meet. We used `ed.calc` in the R package `caper` to calculate ED values (Orme et al. 2013). All our analysis code is available online in the supplementary materials and at `https://github.com/bweedop/edgeSims`.

The impact of missing species on EDGE scores

Our first set of simulations assessed 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 (64, 128, 256, 512, 1024, 2048, and 4096 species), removing constant fractions of tips from the tree (0%, 1%, 2%, ..., 98%, and 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). using the `sim.char` function in the `geiger` R package (Pennell et al. 2014) 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 10$^{\text{th}}$ 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 (using the `cor` function in the `stats` R package) of the species left in the tree with their original ED values, to measure the effect of species' removal on ED scores. 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. We outline our approach in figure 1a.

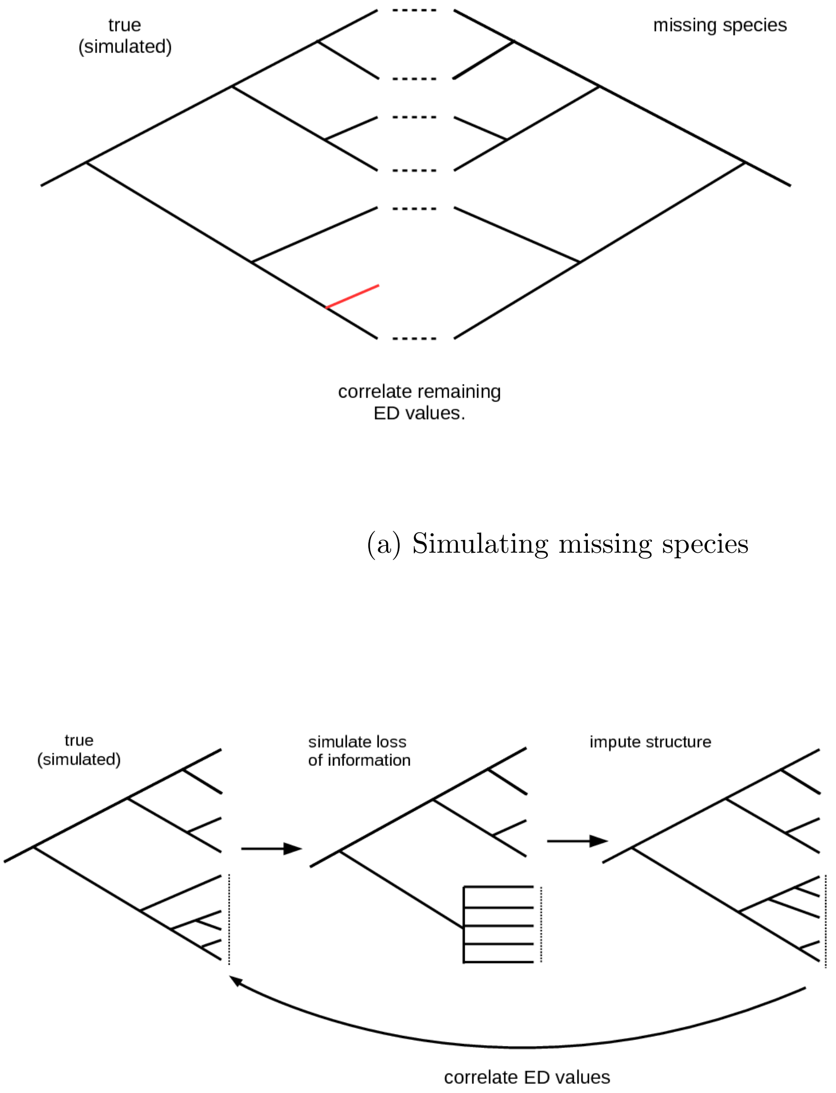
The impact of phylogenetic imputation on EDGE scores

We tested the impact of imputing missing species in relatively small clades (3, 4, ..., 31, and 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. If a newly simulated clade were so old that it was not possible to graft it into place, we discarded that clade and simulated another. 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. An overview of our approach is given in figure 1b.

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 a number of potential explanatory variables, specifically:

- The estimated speciation rate of the original phylogeny (λ, using the `yule` function in the R package `ape`; Paradis et al. 2004)
- The sum of all phylogenetic branch-lengths in the original phylogeny (essentially Faith's PD; Faith 1992)
- γ in the original phylogeny (using the `gammatest` function in the R package `phytools`; Pybus & Harvey 2000; Revell 2012),
- Colless' index of the original phylogeny (using the `as.treeshape` function in the R package `apTreeshape`; Colless 1982; Bortolussi et al. 2009)
- The kurtosis of species' ED values in the original phylogeny (using the `moments` function in the R package `kurtosis`; Komsta & Novomestky 2015)
- The skew of species' ED values in the original phylogeny (using the `skew` function in the R package `moments`; Komsta & Novomestky 2015)
- The total number of species in the original phylogeny
- The total number of species within the imputed clade

Although the expectations of many of these explanatory variables are known from theory, in each simulation they are expected to vary somewhat by chance.



(a) Simulating missing species

(b) Simulated imputed species

Figure 1: **Conceptual overview of the simulations conducted in this study.** In (a), the simulated tree on the left is the true tree prior to removal of missing species. On the right is the same tree after the removal of missing species. We correlate the ED values of the remaining species (indicated with dashed lines) to measure the impact of missing species on known species. In (b), the simulated tree on the left is the true tree prior to loss of information. To the right is each step in the process of simulating the imputation of species within the clade highlighted with the dashed line. To compare true and imputed ED values, we correlate ED values on the full phylogeny and imputed clade.

Results

Under both random and phylogenetically-patterned loss, species' ED scores are less accurate as more species are removed from the tree (table 1 and figure 2). ED values are less robust to phylogenetically-biased, rather than randomly selected, missing species: if 20% of species are missing, the average correlation between true and estimated ED is 0.88 and 0.94 for phylogenetically-biased and random missing species, respectively.

We find no support for a correlation between the imputed and true ED values for species within imputed clades (figure 3 and table 2). We could find no explanatory variables that significantly predicted variation in this trend (table 2; see also Supplementary Materials), but we do find evidence that, when imputing larger clades, the variation in correlation is lesser but remains centered on a mean of zero correlation (see Supplementary Materials). Imputed rankings of species within clades are also altered under imputation (figure 4 and table 3). This ranking error increases with the size of the imputed clade and phylogeny (table 4), and can affect ranking error within the top 100 and 250 species (see Supplementary Materials). To give an example of the magnitude of the effect, within a phylogeny of 1024 species, the members of an imputed clade of 30 species are, on average, ± 315 rankings from their true rankings.

	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).

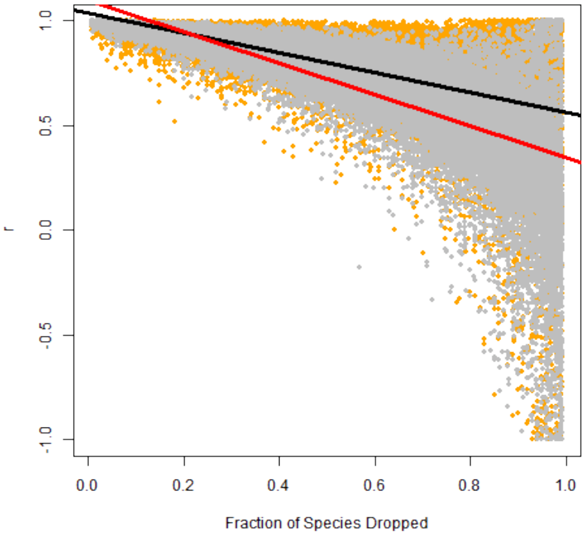


Figure 2: **R-values plotted against the fraction of species dropped at random versus clustered manner.** The color of data points denote whether species were dropped at random (orange; n = 100) or in clustered manner (grey; n = 100). The regression lines are demonstrating the relationship when species 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.

	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).

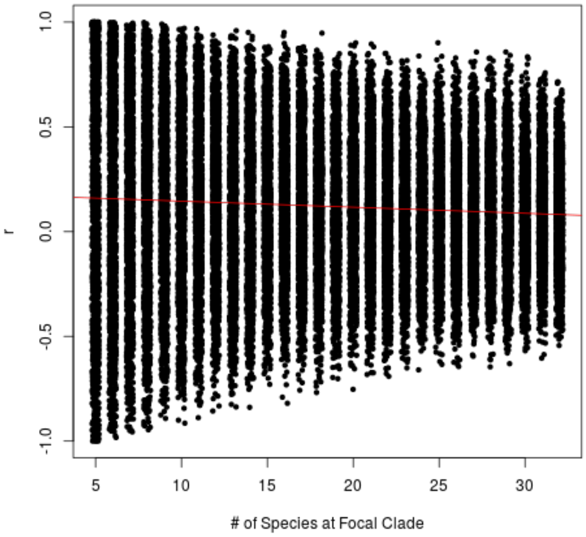


Figure 3: **R-values plotted against the number of species at focal clade.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. The regression line (red) and trend even closer to zero demonstrates the decrease in informative value of the imputed ED values. This is reinforced by the visual narrowing of r-values around zero.

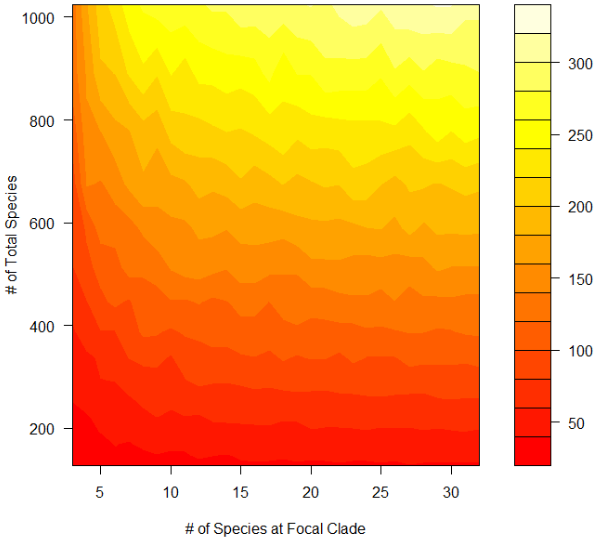


Figure 4: **Mean ranking error of species within the focal clade.** The gradient on the right demonstrates average number of positions within the full ranking that focal clade species shifted from their true rank. While controlling for the size of the full phylogeny and focal clade, species within the 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 3: **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

Phylogeny is increasingly playing a role in conservation prioritization, decision-making, and policy. A major obstacle to a more widespread adoption of phylogenetic prioritization methods such as EDGE is phylogenetic uncertainty (Collen 2015). There is a tension between the need to make decisions to preserve evolutionary history now, and the reality that we do not have complete information about the phylogenetic placement of many species of conservation concern. The intention of our study is to provide concrete information about the importance of this phylogenetic uncertainty in conservation prioritization. To address such uncertainty, we answered two key questions: (1) the extent to which species that are missing from the tree of life impact the ED scores of species for which we do have data, and (2) the extent to which phylogenetic imputation can accurately fill-in ED scores for taxa with no phylogenetic data. We found that (1) while missing species do impact the ED scores of other species, the effects are not always severe and are lesser if species are missing at random from the tree of life. (2) We found limited evidence that phylogenetic imputation can precisely reconstruct species' ED scores and rankings.

Our results are derived solely from simulations under a simple model of diversification—the Yule model. We do acknowledge that, in reality, lineages evolve in more complex ways than are captured by such a simple model. Yet it is not obvious to us that these complexities would make imputation easier, and we suggest that focusing on the simplest model of diversification makes our results more easily generalizable. Further, we focus here solely on the results from a single imputation in each simulation, despite, empirically, biologists reporting average ED scores calculated across pseudo-posterior distributions of many imputed phylogenies (Kuhn et al. 2011). Thus our simulations show that these averages are conducted across phylogenies with large degrees of uncertainty. It is well-known that such methods are not biased (indeed, this was originally shown by Kuhn et al. 2011): here we emphasize that the uncertainty they introduce is sufficiently large that they may not be as informative as has previously been thought.

ED scores are relatively robust to the loss of species

Missing species and poor phylogenetic resolution have been identified as causes of uncertainty when calculating ED (Isaac et al. 2007), but we were unable to find a quantitative assessment of how missing species might affect ED values of species which are not missing. Empirically in corals, incomplete phylogenies produced the same result as later, more complete trees (Curnick et al. 2015). Our results support this finding. Indeed, our analysis suggests that, on average (and we emphasize that there is a good amount of variation about that average; see figure 2), a phylogeny missing 20% of species at random will result in ED scores with an r of 0.94 with the true ED scores. Clearly any prioritization based around such scores will be missing information for 20% of species, but the 80% that are likely to be prioritized accurately.

We do find that the effect of missing species is somewhat greater when those species are non-randomly distributed across the phylogeny. Our simulations do not cover extreme phylogenetic patterning, such as if an entire clade were missing; this is notable because clades that are geographically restricted to difficult-to-reach regions are both difficult to sequence and not uncommon (see Arrigoni et al. 2012, for an example involving 27 coral species in the Indian Ocean). Thus we must point out that our results are somewhat conservative. We have not attempted to comprehensively simulate all of the different ways in which species could be missing from a phylogeny. We consider it sufficient to demonstrate that, if species are missing at random, the effect is not too severe, but that it can be more severe if missing species are distributed across the phylogeny in a biased fashion.

Imputation does not reconstruct the ED value of species with great precision

Our results show that imputation does not accurately recover the true ED values nor ED rank of missing species (figures 3 and 4). Thus we argue that, even though under imputation missing species are incorporated into EDGE lists, their associated EDGE scores may not accurately reflect their true scores. For example, members of an imputed clade of 25 species within a phylogeny of 850 species are, on average, imputed to have ED scores 250 ranks away from their true rank (figure 3 and table 3).

While we did not assess clades with fewer than five species (we do not consider correlations or averages to be reliable with so few data-points), we cannot think why smaller clades would necessarily be more reliable (and this would be a reversal of the trend in figure 3). Indeed, in the smallest possible clade (two species), imputation is essentially sampling a terminal branch length from an exponential distribution (Kuhn et al. 2011); such a process should still lead to a great degree of uncertainty. It is, perhaps, unsurprising that imputed ED values do not correlate with their true values (figure 3), but we were surprised at the degree of ranking error. Indeed, large phylogenies showed *greater* ranking error; we naïvely would have expected the opposite. We would have expected our upper bound on the age of the imputed clade, which ought to be relatively younger in larger phylogenies, to have somewhat controlled the range of the ranks of our imputed species. ED is known to be driven mostly by terminal branch length (Isaac et al. 2007; Steel et al. 2007); our results therefore emphasize this.

Imputation is not the only way to incorporate missing species into EDGE-like frameworks (Gumbs et al. 2017; Collen et al. 2011), but we believe it is the most common. $3,330$ of birds (˜30%; Jetz et al. 2014), 250 of mammals (˜5.6%; Collen et al. 2011), and 610 of sharks (˜49%; Stein et al. 2018) in recent EDGE lists were imputed. It is well-known that phylogenetic imputation can cause biases in other statistical problems, such as the estimation of evolutionary phylogenetic signal (Rabosky 2014). We emphasize that we are not, however, suggesting that imputation *biases* ED scores: we are, instead, suggesting that it is less precise than has previously been acknowledged. We discuss, below, the implications of this, and suggest guidelines for its use.

Guidelines for the use of imputation

The impact of imputation on EDGE scores is almost certainly lesser than its impact on ED scores, because EDGE scores are a product of both ED and IUCN status (‘GE’). This does not, however, mean that our results have any less of an impact on the calculation EDGE lists. The novelty and purpose of EDGE (and related metrics; *e.g.*, Steel et al. 2007; Faith 2008; Pearse et al. 2015; Jensen et al. 2016) is to incorporate phylogeny, and if imputed EDGE scores are driven by their GE component because of uncertainty introduced by imputation, we are essentially creating another metric of IUCN status.

Our results suggest that incomplete phylogenies can be used to estimate ED scores with remarkably high degrees of accuracy. Instead of using imputation to account for missing species, which we show has relatively mild effects, we suggest conservation biologists should focus on accounting for phylogenetic uncertainty in the species for which they have data. Evolutionary biologists frequently work with distributions of trees generated from genetic data (reviewed in Huelsenbeck et al. 2001; Bollback 2005), since even with data the precise topology and dating of a phylogeny is somewhat uncertain. This uncertainty has, indeed, already been shown to affect EDGE scores and rankings (Pearse et al. 2015). We suggest conservation biologists should focus on averaging across this uncertainty first. There is, of course, nothing stopping biologists from also using taxonomy to impute the positions of missing species within the phylogeny: being thorough is a virtue, but it is important to focus on the major sources of potential error first.

Our results suggest, however, that prioritizing species whose phylogenetic structure has been imputed should be done with extreme care, if at all. In the case that an imputed species is imputed to be below a threshold set for conservation (most EDGE studies focus on the 'top 100' species or something similar), then the path forward is clear: that species should not have conservation funds allocated to it at this time. The case where a species, on average, is above a threshold is more complex, but the theory underling imputation can give some guidance. Imputed distributions of trees essentially represent Bayesian posterior distributions (Kuhn et al. 2011), and so the 95% posterior densities of these distributions' ED values represent a range within which we can be 95% certain the true ED scores lie (if the model assumptions are met). Thus we suggest that conservation action should only be initiated for a species if there is a 95% (or 80%, or whatever confidence is deemed appropriate) probability that it is above that threshold. Thus a species whose 95% ranking was 30–300 could not, with confidence, be called a top-100 species. Our results suggest that, on average, very few imputed species meet this criterion.

Ultimately, we are currently fighting a losing battle to preserve the tree of life. Our results are good news: they suggest that we can start right away using the phylogenies we already have in-hand. We suggest that, given we do not have the resources to save everything, we should consider focusing our efforts on those species whose ED scores we can know with greater certainty: those for which we have data.

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451 A. Effect of Measures of the True, Full Phylogenies

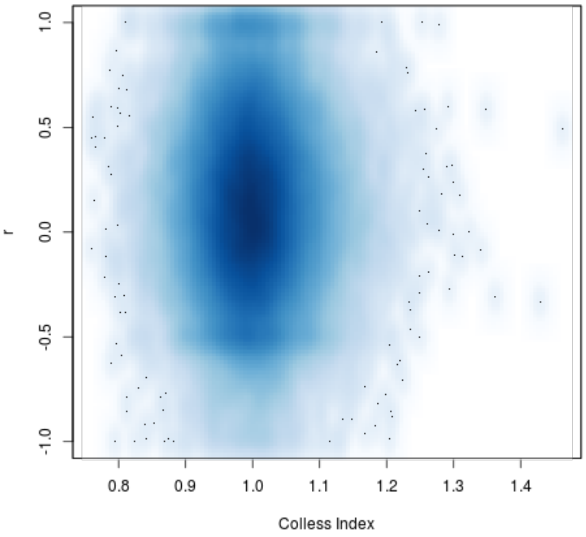

Figure 5: **Effect of the True Colless Index of Full Phylogeny.**

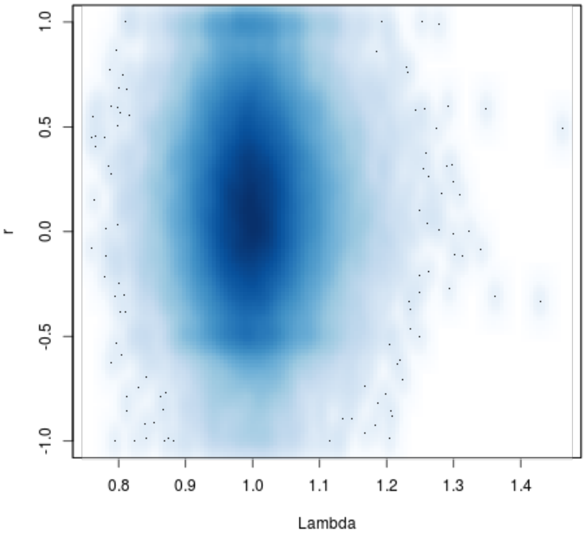

Figure 6: **Effect of the True Lambda of Full Phylogeny.**

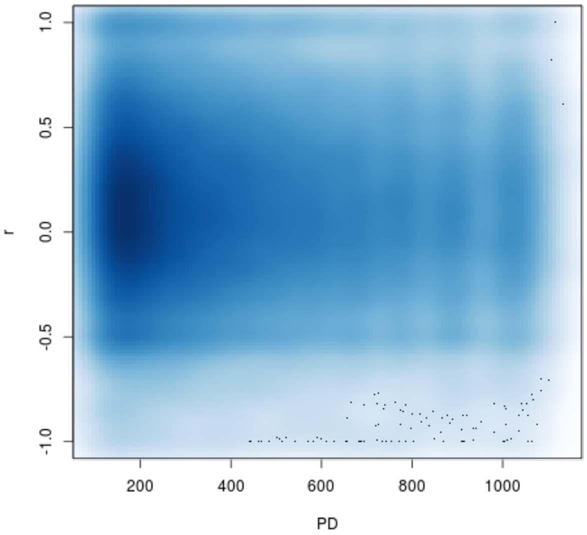

Figure 7: **Effect of True PD of Full Phylogeny.**

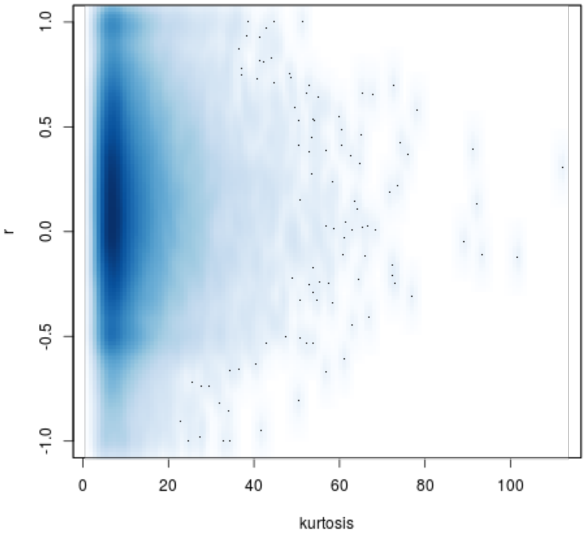

Figure 8: **Effect of the True Kurtosis of Full Phylogeny.**

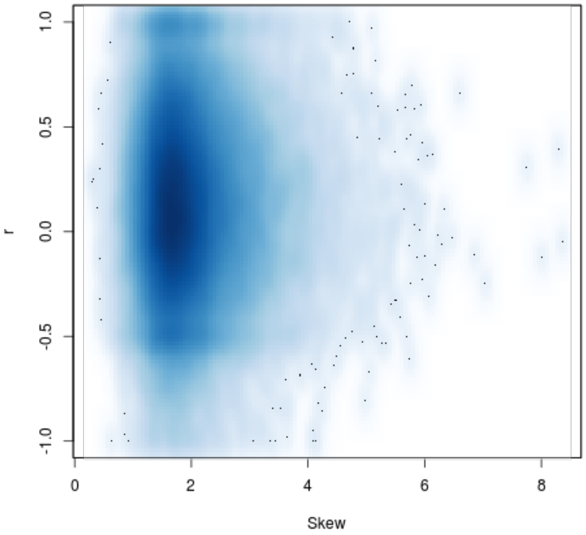

Figure 9: **Effect of the True Skew of Full Phylogeny.**

B. Error Rate in Top Rankings

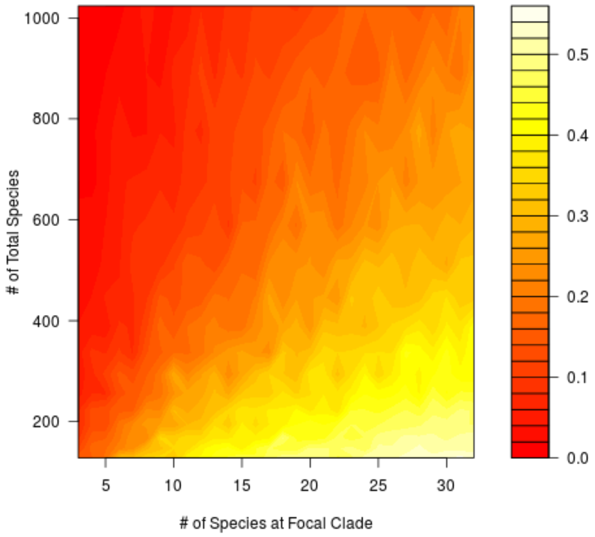

Figure 10: **Mean error rate in the ranking of top 50 species.**

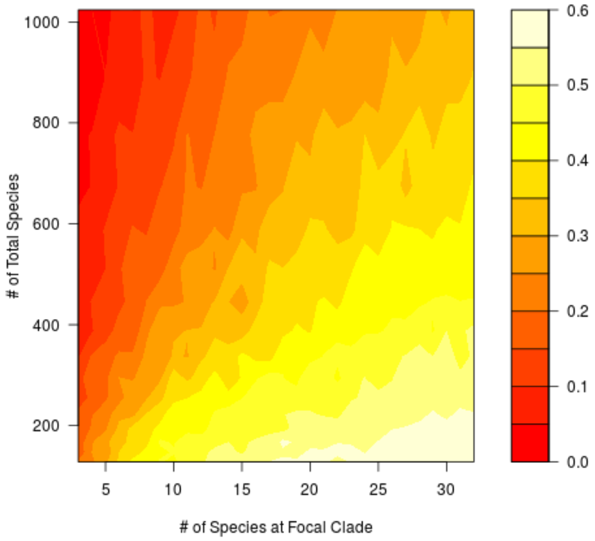

Figure 11: **Mean error rate in the ranking of top 100 species.**

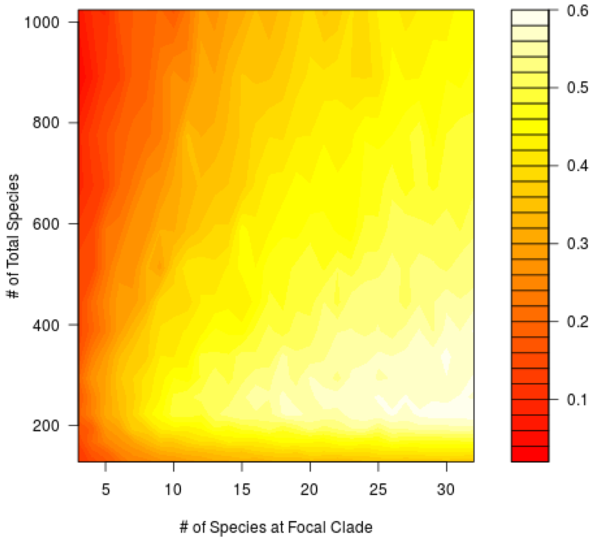

Figure 12: **Mean error rate in the ranking of top 200 species.**

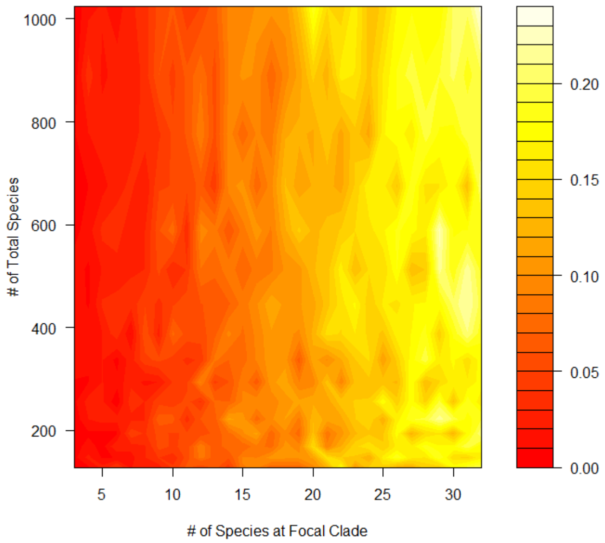

Figure 13: **Mean error rate in the ranking of top 5% of species.**

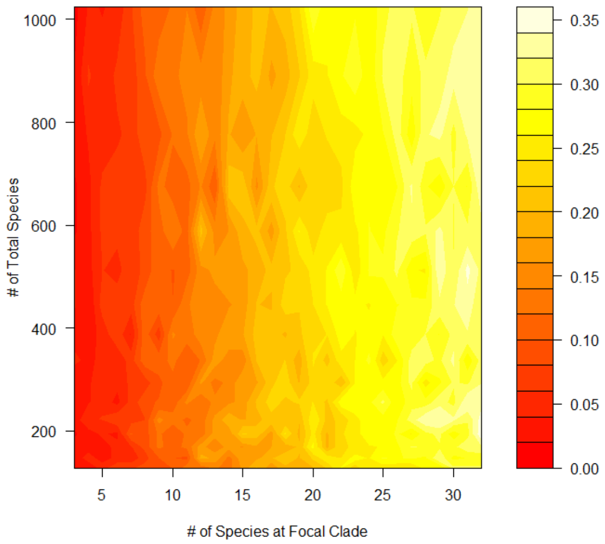

Figure 14: **Mean error rate in the ranking of top 10% of species.**

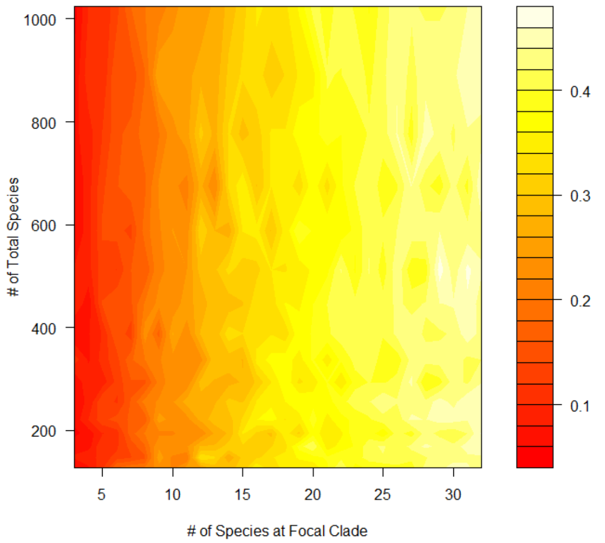

Figure 15: **Mean error rate in the ranking of top 20% of species.**

453 C: Quantile regression of imputed correlations

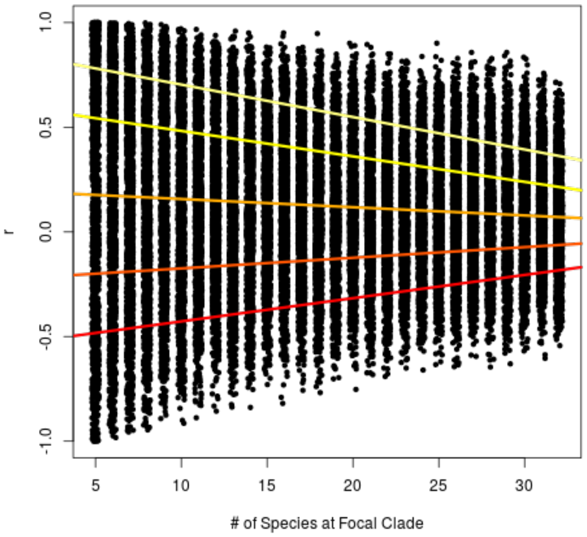

Figure 16: **Quantile regression of r-values against size of imputed clades.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. Each regression line (top to bottom) represent quantile regressions from highest to lowest, respectively. 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).