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- 2 Article title: The Effect of Phylogenetic Uncertainty and Imputation on EDGE Scores
- ³ Running head: The Effect of Phylogenetic Uncertainty and Imputation on EDGE Scores
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- Word-count: 5680 (abstract, main text, acknowledgments, and references)

13 Abstract

Faced with the challenge of saving as much diversity as possible given financial and time constraints, conservation biologists are increasingly prioritizing species on the basis of their 15 overall contribution to evolutionary diversity. Metrics such as EDGE (Evolutionary Dis-16 tinct and Globally Endangered) have been successfully used to set such evolutionarily-based 17 conservation priorities for a number of taxa, such as mammals, birds, corals, amphibians, 18 and sharks. Each of these applications of EDGE has required some form of correction for 19 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 as-21 sessment of the impact of both missing species and imputation to correct for them. Here we 22 perform such a systematic assessment, simulating the random missingness of species from 23 a phylogeny, the imputation of the position of those species, and measure the impact each of these processes has on accurately estimating species' true EDGE scores. We find that 25 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.

³⁰ **Keywords**: conservation prioritization, evolutionary distinctiveness, EDGE, phylogenetic imputation.

32 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 populations than ever are declining and species face heightened danger of extinction (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 identify different ways by which to prioritize, or triage, their resource allocation (Bottrill et al. 2008).

Conservation triage, like all sound decision-making, requires an index with which to quantify
the relative urgency or importance for conservation among a set of options. This allows
scientists and policy-makers to use data to quantify need and inform conservation decisionmaking and management activities. One such triage strategy uses the EDGE metric to
identify and prioritize species that are Evolutionarily Distinct and Globally Endangered
(Isaac et al. 2007). Evolutionary Distinctiveness (ED) measures the relative contributions
to phylogenetic diversity made by each species within a particular clade, assigning each
branch length equally to all the subtending species (Isaac et al. 2007), Global Endangerment
(GE), assigns numerical values to each of the World Conservation Union (IUCN) Red List
Categories. As species become increasingly threatened and are placed into categories of
increasing concern (e.g. from Vulnerable to Endangered), the GE numerical value increases.

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).

Though originally used to prioritize global mammals, the EDGE metric has subsequently

been applied to a variety of taxonomic groups, including amphibians (Isaac et al. 2012), birds (Jetz et al. 2014), corals (Curnick et al. 2015), squamate reptiles (Tonini et al. 2016), and sharks (Stein et al. 2018). Additional related metrics have also been developed, each emphasizing subtly different things, such as the expected contribution of each species to future phylogenetic diversity (HEDGE, I-HEDGE; Steel et al. 2007; Jensen et al. 2016), our 61 uncertainty over a species' future (EDAM; Pearse et al. 2015), and the complementarity of a set of species (Faith 2008). The development and expansion of EDGE-like metrics mirrors progress in other areas 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 received attention. The EDGE index was developed explicitly with the intention of informing conservation triage, and is now the basis of the global EDGE of Existence Program (http://www.edgeofexistence.org/). The successful application of EDGE in this program highlights the potential for phylogenetic conservation prioritization metrics to provide actionable insights in the face of uncertainty about species' attributes. Nonetheless, almost every application of an EDGE-type approach has to deal with the uncertainty resulting from missing data.

Missing data can affect confidence in EDGE scores in several ways. First, the IUCN identifies some species as Data Deficient (IUCN 2001; IUCN 2008). which will affect the GE component of a species' EDGE score. Fortunately, the IUCN provides guidance for using any available contextual data to assign some threat status to such species. A number of studies illustrate how to assign threat categories to Data Deficient species, which in turn should reduce the uncertainty in GE (Good et al. 2006; Butchart & Bird 2010; Morais et al. 2013; Dulvy et al. 2014). The issue of missing phylogenetic data is arguably more complicated than that of missing threat data because not only does the focal species have no ED score, but its missingness may affect ED scores of related species. Species of conservation concern are almost by definition rare, and frequently lack sufficient DNA (or even morphological) data

to be placed with certainty on a phylogeny. For most empirical EDGE lists, taxonomic information rather than sequence data alone is used to place species in the tree of life (see Isaac et al. 2007; Collen et al. 2011; Isaac et al. 2012; Jetz et al. 2014; Curnick et al. 2015; Stein et al. 2018; Gumbs et al. 2017). 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 (Kuhn et al. 2011; Thomas et al. 2013; Rabosky 2014). Thus we do not know the fidelity of EDGE scores between imputed and non-imputed phylogenies or the magnitude of error phylogenetic imputation introduces. As the desire to use EDGE-type measures and phylogenies for conservation triage grows, the need for consensus on how to resolve cases of phylogenetic uncertainty becomes increasingly urgent.

Here we attempt to first quantify the effect of missing species on EDGE rankings and then assess the degree to which imputation overcomes the effect of missing phylogenetic data. We do so by simulating phylogenies and missing species that are distributed either at random, or with bias, across those phylogenies. By contrasting the ED scores of the species before and after the loss of other species from the phylogenies, we measure the impact of missing species on ED scores. We then assess the extent to which phylogenetic imputation can accurately estimate the EDGE scores of missing species in simulated data. We also examine the extent 100 to which such imputation affects the scores of species for which we have data. In so doing, 101 we hope to provide clear guidance as to the applicability of phylogenetic imputation as a 102 solution for species missing phylogenetic data. From our results, we argue that species' ED 103 values are remarkably robust to missing species, and that phylogenetic imputation does not 104 reliably reconstruct the true ranking of those missing species.

106 Methods

Here we use a simulation approach to test the effect of missing species (through species removal from simulated phylogenies) and imputing species on a phylogeny on species' ED (Evolutionary Distinctiveness) scores. We focus exclusively on the ED-component of the EDGE metric, since uncertainty in species GE scores has already been addressed by the IUCN's proposal to assign Data Deficient species scores (IUCN 2001; IUCN 2008). Because EDGE is the product of both ED and GE components, even perfectly accurate GE values could be associated with imperfect EDGE scores if the ED scores were inaccurate.

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 115 starting and imputed) were simulated under a pure-birth Yule model using sim.bdtree 116 in geiger (setting parameters b=1 and d=0; Pennell et al. 2014). This model was chosen 117 because it is the simplest model possible: speciation rates are constant across the entire tree 118 of life and there is no extinction. We acknowledge that more complex and/or biologically 119 realistic models of diversification could potentially improve the performance of imputation. 120 However, we suggest that imputation under a simple model that is identical to that used to 121 simulate the data is a low, and fair, benchmark for a method to meet. We used ed.calc 122 caper to calculate ED values (Orme et al. 2013). All our analysis code is available online 123 (https://github.com/bweedop/edgeSims) and in the supplementary materials. 124

The impact of missing species on EDGE scores

Our first set of simulations assess the impact of missing species data on the ED scores of remaining species, considering data missing either in a random or phylogenetically-biased fashion. We simulated phylogenies of different sizes (number of species: 64, 128, 256, ...,

2048, 4096) and then removed constant fractions of tips from the tree (0%, 1%, 2%, ..., 19%,..., 99%). To simulate species missing at random throughout the phylogeny, we used sample 130 to select the relevant fraction of species (rounded to the nearest whole number) without 131 replacement. To remove species in a phylogenetically-biased manner, we used Felsenstein 132 (2005)'s threshold model. First, we simulated a trait under a constant rate Brownian-motion 133 model (σ =0.5, starting root value = 1) using sim.char in geiger (Pennell et al. 2014). 134 Species were then removed from the tree if their simulated trait was in the upper quantile 135 matching the fraction of species to be removed. For example, if 10% of species were to be 136 removed from the tree, the species with the highest 10% of values would be removed. This 137 results in closely related species being removed more often than expected by chance. 138

To quantify the effect of these manipulations, we calculated the ED values of species that are not removed from a tree both before and after removal. We then correlated these ED scores: if missing species do not affect ED values, we would expect a strong, positive correlation between the ED scores calculated before and after species were removed from the phylogeny. Note that species removed from the phylogeny are omitted from this comparison. We outline our approach in figure 1.

The impact of phylogenetic imputation on EDGE scores

Our second set of simulations tested the impact of imputation on ED scores within an imputed clade. We used relatively small clades (5, 6, 7, ..., 30, 31, 32 species) from phylogenies
of different sizes [128 (2⁷), 147 (2^{7.2}, 168 (2^{7.4}), ..., 776 (2^{9.6}), 891 (2^{9.8}), 1024 (2¹⁰) species).
We first randomly selected a clade to be removed from the 'true' tree and then simulated
a new phylogeny of the same size as the removed clade. This newly simulated clade was
generated under the same pure-birth model as the original phylogeny. We then placed the
newly simulated clade in the full phylogeny, in the same location as the removed clade. If a

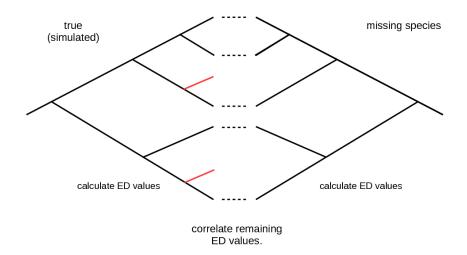


Figure 1: Example of simulated phylogenies and ED values used to compare species ED values. The simulated tree on the left is the true tree prior to removal of missing species. On the right is the same tree after missing species have been removed. Species that are removed are shown in red. We correlate the remaining ED values to compare the ED values. Dashed lines can be seen for the species which would have ED scores compared.

newly simulated clade was so old that it was not possible to graft it into place, we discarded
that clade and simulated another. In an empirical study the model of evolution under which
the clade would be simulated would have to be estimated, which is an additional source of
error not considered here. We simulated each combination of clade and total phylogeny sizes
100 times. An overview of our approach is given in 2.

To assess whether clades, once imputed, had similar ED scores, we correlated the imputed ED scores with the 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 modeled both of these metrics (the change in ranking and the correlation) as a function of a number of potential explanatory variables. Specifically, we included in our models: the estimated speciation rate

of the original phylogeny (using ape::yule; Paradis et al. 2004), the sum of all phylogenetic branch-lengths in the original phylogeny (Faith's PD; Faith 1992), the sum of all phylogenetic 165 branch-lengths in the original focal clade (Faith's PD; Faith 1992), the value of gamma in 166 the original phylogeny (using phytools::gammatest; Pybus & Harvey 2000; Revell 2012), 167 colless' index of the original phylogeny (usingapTreeshape::as.treeshape; Colless 1982; 168 Bortolussi et al. 2009), the kurtosis of species' ED values in the original phylogeny (using 169 moments::kurtosis; Komsta & Novomestky 2015), the skew of species' ED values in the 170 original phylogeny (using moments::skew; Komsta & Novomestky 2015), the total number 171 of species in the original phylogeny, the total number of species within the imputed clade, 172 and the depth (age) of the imputed clade in the phylogeny. Although the expectations of 173 many of these explanatory variables are known for Yule trees, in each simulation they are 174 expected to vary somewhat by chance. 175

Recently, there has been interest in assigning missing species the mean ED score within a clade (see Gumbs et al. 2017). To test the efficacy of such methods, , we assigned the average ED of the selected clade to each of its' species and calculated (as above) the mean change in absolute ranking under this scheme. Note that we could not correlate ED scores, as we could with the imputation method described above, since to calculate a correlation requires variation in species' scores.

182 Results

With increasing numbers of missing species, species' ED scores become less accurate (Table 1; figure 3). ED values were less robust to phylogenetically-biased missing species, as
compared to those that are randomly missing from the tree. The effect of missing species
is not necessarily severe; 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,

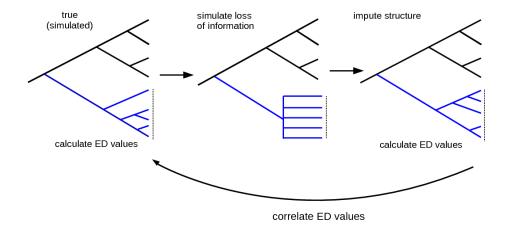


Figure 2: Conceptual overview of the simulations conducted in this study. In (a), the simulated tree on the left is the 'true tree' prior to removal of missing species. On the right is the same tree after the removal of missing species. We calculated ED values for both the true tree and the incomplete tree, and calculated the correlation between ED values for species common between these trees (indicated with dashed lines) to measure the impact of missing species on known species' scores. In (b), the simulated tree on the left is the 'true tree'. We selected a clade to treat as 'missing' (highlighted with a dashed line) by replacing it with a polytomy (middle panel), and then imputed the 'missing' species following the procedure described in the Methods to produce the imputed clade (dashed line) in the right panel. To compare true and imputed ED values within the imputed clade, we correlated ED values calculated on the true clade with those for the imputed clade.

188 respectively.

When clades were imputed on the tree, we found no average positive correlation between the imputed ED and true ED values for species within the imputed clades (figure 4, table 2). The mean correlation was 0. We also found no explanatory variables that explained significant variation in this relationship (table 2; see also Supplementary Materials). However, we did find evidence that, when imputing larger clades, the variation in the correlation between true and imputed ED scores decreases, although it remains centered around 0 (see Supplementary Materials). When considering rankings rather than raw scores, we similarly found large

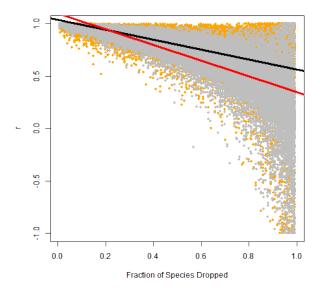


Figure 3: Correlation coefficient values plotted against the fraction of species dropped, either at random or in a clustered manner. The color of data points denote whether species were missing from the phylogeny at randomly (orange; n = 100) or in clustered manner (grey; n = 100). Lines show the relationship between correlation coefficients when species are dropped at random (red), or in a clustered manner (black). Correlations are calculated for the the ED values before and after species are dropped from the phylogeny.

effects of imputation for the imputed species (figure 5 and table 4). This ranking error increased 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, \pm 315 rankings from their true rankings. We found similar effects in ranking error when using the average ED value of clade for a missing species (see Supplementary Materials).

| | 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 missing significantly affects the remaining ED values. Species missing at random and in a clustered manner both have negative effects on the ED values of species remaining on the tree ($F_{139696,5} = 40350$, $R^2 = 0.5908$, p<0.0001).

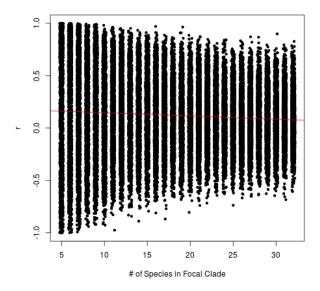


Figure 4: Correlation coefficient-values plotted against the number of species in the focal clade. Each data point represents the correlation between ED values within the focal clades where imputation has occurred, comparing ED values for the true position of species with those calculated via the imputed tree. 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) | 0.1974 | 0.0501 | 3.94 | 0.0001 |
| Size of Focal Clade | -0.0036 | 0.0005 | -7.60 | 0.0000 |
| Size of Phylogeny | 0.0001 | 0.0001 | 0.60 | 0.5497 |
| PD | -0.0001 | 0.0001 | -0.64 | 0.5241 |
| Estimated speciation rate | -0.0199 | 0.0493 | -0.40 | 0.6865 |
| Colless' Index | -0.0000 | 0.0000 | -0.08 | 0.9380 |
| Skew | 0.0022 | 0.0083 | 0.27 | 0.7885 |
| Kurtosis | -0.0001 | 0.0008 | -0.16 | 0.8736 |
| Depth of Imputed Clade | 0.0006 | 0.0005 | 1.27 | 0.2045 |

Table 2: Effect of Clade Size on Imputed ED Values. The correlation between the true and imputed values is quite low, as shown by the intercept, and declines further as the imputed clade size increases, this correlation further decreases. The remaining variables are not significant ($F_{44791,8} = 29.1$, $R^2 = 0.005$, p<0.0001).

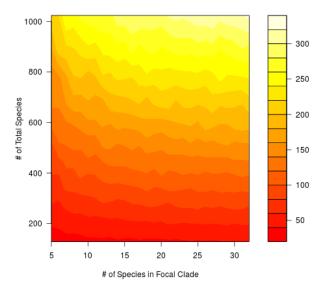


Figure 5: Mean ranking error of species within the focal clade. The gradient on the right demonstrates average number of positions within the full ranking that focal clade species shifted from their true rank. While controlling for the size of the full phylogeny and focal clade, species within the focal 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 Phylogeny Size 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 in ranking error are seen when the sizes of both the imputed clade and the full phylogeny increase ($F_{47997,2} = 77890$, $R^2 = 0.7644$, p<0.0001).

203 Discussion

Phylogenies are increasingly playing a role in conservation prioritization, decision-making, and policy (Vézquez & Gittleman 1998). A major obstacle to a more widespread adoption of 205 phylogenetic prioritization methods such as EDGE is phylogenetic uncertainty (Collen 2015). 206 There is a tension between the need to make decisions to preserve biodiversity—including 207 evolutionary history —now, and the reality that we do not have complete information about 208 the phylogenetic placement of many species of conservation concern. The intention of our 209 study is to provide concrete information about the impact of such phylogenetic uncertainty 210 on conservation prioritization. To address this uncertainty, we answered two key questions: 211 (1) the extent to which species that are missing from the tree of life impact the ED scores of 212 species for which we do have data, and (2) the extent to which phylogenetic imputation can 213 accurately fill in ED scores for taxa with no phylogenetic data. For the first question (1), 214 we found that while missing species do impact the ED scores of other species, the effects are 215 not always severe, particularly if species are missing at random from the tree of life. For the 216 second question (2), we found limited evidence that phylogenetic imputation can reconstruct 217 species' ED scores and rankings. 218

Our results are derived solely from simulations under a simple model of diversification—the 219 Yule model. We do acknowledge that, in reality, lineages evolve in more complex ways than 220 are captured by such a simple model. However, such complexities are unlikely to make impu-221 tation easier, and as they would have to be modelled and quantified, they would likely make 222 imputation more difficult. We suggest that focusing on the simplest model of diversification 223 makes our results more generalizable. Further, we focus here solely on the results from a 224 single imputation in each simulation, despite, empirically, biologists reporting average ED 225 scores calculated across pseudo-posterior distributions of many imputed phylogenies (Kuhn et al. 2011). Thus our results show that the variation within these pseuo-posterior distri-227 butions is likely very large. It is well-known that such imputation 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 be less informative than previously been thought.

ED scores are relatively robust to missing 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 for which data is available. Empirically in corals, incomplete phylogenies produced similar results 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 3), a phylogeny missing 20% of species at random will still have ED scores that are strongly correlated (r=0.94) with the true ED scores.

We did find that missing species are more problematic when those species are non-randomly distributed across the phylogeny. Our simulations do not examine 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 (as is seen with 27 coral species in the Indian Ocean; Arrigoni et al. 2012). Thus these results are likely conservative. We also do not attempt to comprehensively simulate all of the different ways in which species could be missing from a phylogeny. We simply demonstrate that, compared to a scenario in which species are missing at random, phylogenetically patterned missing species can have a greater effect on the ED scores of species for which we have data.

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 or the true ED rank of missing species (figure 4; figure 5). Thus we argue that, even though imputation allows missing species to be incorporated into EDGE lists, their associated EDGE scores may not accurately reflect their true scores. We acknowledge these are averages and may change depending on particular phylogeny, but we can find no statistically significant predictors of that variation.

While we did not assess clades with fewer than five species (we do not consider correlations 259 or averages to be reliable with so few data-points), we cannot think why smaller clades would 260 necessarily be more reliable (and this would be a reversal of the trend in figure 4). Indeed, 261 in the smallest possible clade (two species), imputation is essentially sampling a terminal 262 branch length from an exponential distribution (Kuhn et al. 2011); such a process should still lead to a great degree of uncertainty. Further, smaller sample sizes should not lead to a 264 more accurate estimate. It is, perhaps, unsurprising that imputed ED values do not correlate with their true values (see figure 4), but we were surprised at the degree of ranking error. Indeed, larger phylogenies showed greater ranking error; we naïvely would have expected the 267 opposite. We would have expected our upper bound on the age of the imputed clade, which 268 we would have expected to be relatively younger in larger phylogenies, to have somewhat 269 controlled the range of the ranks of our imputed species. ED is known to be driven mostly 270 by terminal branch length (Redding et al. 2008; Isaac et al. 2007; Steel et al. 2007); our 271 results therefore emphasize this. 272

Imputation is not the only way to incorporate missing species into EDGE-like frameworks (Gumbs et al. 2017; Collen et al. 2011), but it is likely the most common. 3,330 of the birds (~30%; Jetz et al. 2014), 250 of the mammals (~5.6%; Collen et al. 2011), and 610

of the sharks (~49%; Stein et al. 2018) in recent EDGE lists were imputed. It is wellknown that phylogenetic imputation can cause biases in other statistical methods, such as the estimation of evolutionary phylogenetic signal (Rabosky 2014). We emphasize that we are not suggesting that imputation *biases* ED scores: we are, instead, suggesting that it is less precise than has previously been acknowledged.

Guidelines for the use of imputation

The impact of imputation on EDGE scores is almost certainly less than its impact on ED scores, because EDGE scores are a product of both ED and IUCN status ('GE'). However, the goal of EDGE-like measures is to incorporate phylogeny, and if imputed EDGE scores are driven by their GE component because of uncertainty introduced by imputation, this essentially creates another metric of IUCN status.

Our results suggest that incomplete phylogenies can be used to estimate ED scores with 287 remarkably high degrees of accuracy. Instead of using imputation to account for the rela-288 tively minor impact of missing species, we suggest conservation biologists should focus on 289 accounting for phylogenetic uncertainty in the species for which they have data. While we have not explored this uncertainty here, evolutionary biologists commonly work with distri-291 butions of trees generated from genetic data (reviewed in Huelsenbeck et al. 2001; Bollback 292 2005), since the precise topology and dating of a phylogeny is almost always 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 known phylogenetic uncertainty as a priority. There is, of course, nothing stopping biologists from 296 also using taxonomy to impute the positions of missing species within the phylogeny: being 297 thorough is a virtue, but it is important to focus on the major sources of potential error 298 first.

Our results suggest that prioritizing species whose phylogenetic structure has been imputed should be done with extreme care, if it at all. In the case that an imputed species is imputed 301 to be below a threshold set for conservation (most EDGE studies focus on the 'top 100' 302 species or something similar), then the path forward is clear: that species should not have 303 conservation funds allocated to it at this time. The case where a species, on average, passes 304 a threshold is more complex, but the theory underlying imputation can give some guidance. 305 Imputed distributions of trees essentially represent Bayesian posterior distributions (Kuhn 306 et al. 2011), and so the 95% posterior densities of these distributions' ED values represent a 307 range within which we can be 95% certain the true ED scores lie (if the model assumptions 308 are met). Thus we suggest that conservation action should only be initiated for a species if 300 there is a 95% (or 80%, or whatever confidence is deemed appropriate) probability that it is 310 above that threshold. Thus a species whose ranking is estimated to have a 95% probability 311 of being between the 30th and 300th highest-ranked species could not, with confidence, be 312 called a top-100 species. Our results suggest that, on average, very few imputed species will 313 meet such a criterion. 314

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. The effect of missing species is mild enough that we often do not need costly and time-consuming imputation, and imputation rarely gives us sufficiently precise estimates of species' ED scores anyway. 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.

322 Acknowledgments

 $_{323}$ We are grateful to E. Simpson, M. Sneddon, J. Stachewicz, and XXX anonymous reviewers

for providing constructive feedback on this manuscript.

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

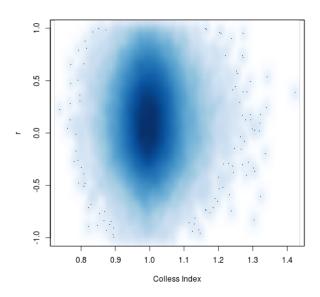


Figure 6: Effect of the True Colless Index of FullPhylogeny.

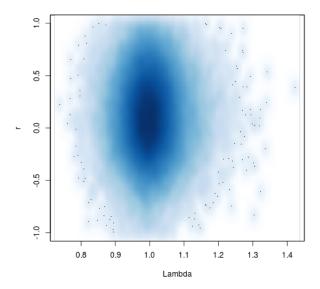


Figure 7: Effect of the True Lambda of Full Phylogeny.

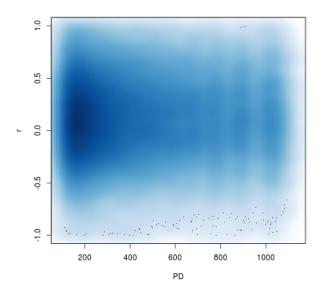


Figure 8: Effect of True PD of Full Phylogeny.

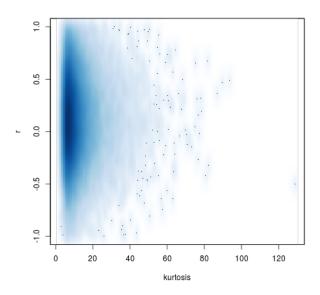


Figure 9: Effect of the True Kurtosis of Full Phylogeny.

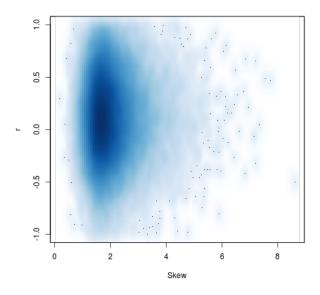


Figure 10: Effect of the True Skew of Full Phylogeny.

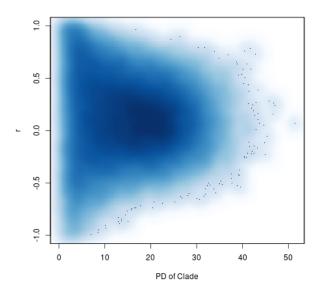


Figure 11: Effect of the True PD of The Selected Clade.

⁴⁷⁰ B. Error Rate in Top Rankings

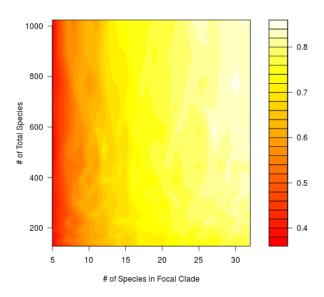


Figure 12: Mean error rate in the ranking of top 50 species.

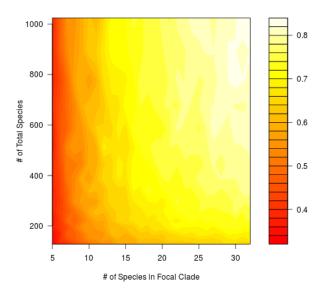


Figure 13: Mean error rate in the ranking of top 100 species.

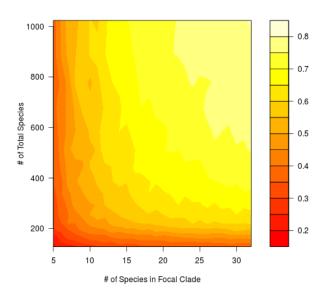


Figure 14: Mean error rate in the ranking of top 200 species.

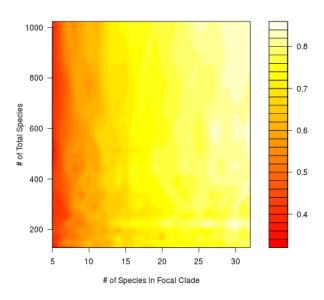


Figure 15: Mean error rate in the ranking of top 5% of species.

471 C. Ranking Error When Using Average ED Value

D. Ranking Error of Non-imputed Species

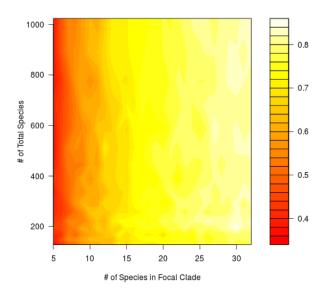


Figure 16: Mean error rate in the ranking of top 10% of species.

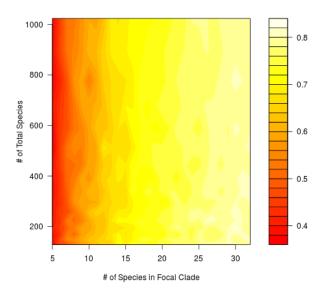


Figure 17: Mean error rate in the ranking of top 20% of species.

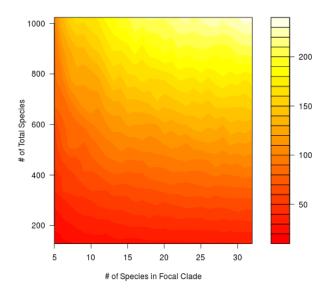


Figure 18: Mean Ranking Error of Species Assigned Average ED.

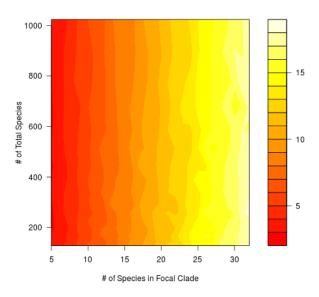


Figure 19: Ranking Error of Non-imputed Species.