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Abstract

Global extinction rates have been increasing steadily over the recent past causing a much needed, increased focus on conservation. Conservation triage provides a decision making criteria to be effective and efficient in setting conservation priorities. EDGE, an implementation of conservation triage, has provided a successful foundation and has been applied to set conservation priorities for a number of taxa (*e.g.* mammals, birds, corals, and sharks). However, uncertainty has been an issue in each application of EDGE and remains an issue today. Phylogenetic uncertainty is one source of uncertainty yet to be properly addressed. The goal of this study was to investigate and model the effect phylogenetic uncertainty (*e.g.* missing species) and current methods to compensate for such uncertainty has on EDGE scores. We evaluate the effect that missing species has on EDGE scores and see that the removal of missing species has little effect on species remaining in the phylogeny. Further, we analyze how imputing missing species affects EDGE scores and whether it is a defensible method of including missing species. We show that imputation alters the EDGE scores and rankings for species within clades where imputation is being applied.

Keywords:

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 urgency for conservation 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 assessed 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 (Pearse et al. 2015).

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 (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 Data Deficient species (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; Isaac et al. 2012; Collen et al. 2011; Jetz et al. 2014; Curnick et al. 2015; Stein et al. 2018; Gumbs et al. 2017). By using taxonomic information alone, 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 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 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, 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 under parameters of (b=1, d=0) in the `geiger` R package (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 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

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₁₂₅ missing species, we used the `sample` function in R to select the relevant percentage of species

₁₂₆ (rounded to the nearest whole number) without replacement. Thus this randomization

₁₂₇ did not incorporate phylogenetic structure. To remove species in a phylogenetically biased

₁₂₈ manner, we used Felsenstein (2005)'s threshold model. First, we simulated a trait under a

₁₂₉ constant rate Brownian-motion model (σ^2=0.5, starting root value = 1). using the `sim.char`

₁₃₀ function in the `geiger` R package (Pennell et al. 2014) Species were then removed from the

₁₃₁ tree if their simulated trait was in the upper quantile of whatever fraction of species were

₁₃₂ to be dropped. For example, if 10% of species were to be dropped, species within the upper

₁₃₃ 10th quantile of character trait values were removed from the tree.

₁₃₄ We calculated species' ED values before removal of species from the tree and afterwards. We

₁₃₅ then correlated the ED scores (using the `cor` function in the `stats` R package) of the species

₁₃₆ left in the tree with their original ED values, to measure the effect of species' removal on ED

₁₃₇ scores (fig. 1). If missing species have no effect upon ED values, we expect a high, positive

₁₃₈ coefficient of correlation between the remaining species' ED scores before and after the other

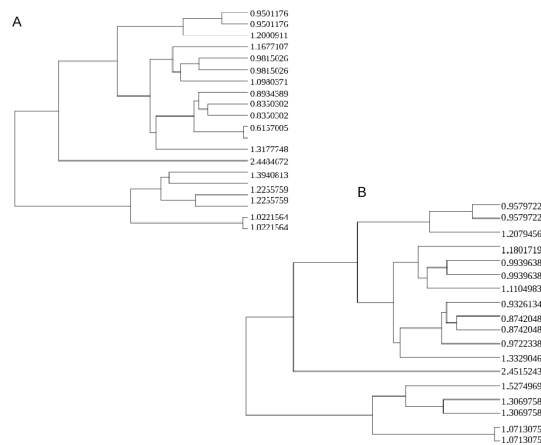₁₃₉ species were removed from the tree.

Figure 1: **Example of simulated phylogenies and ED values used to compare species ED values.** The simulated tree on the right (A) is the true tree prior to removal of missing species. On the left (B), is the same tree after missing species have been removed. Each of the ED values for species can be seen to the right of each tip. We correlate the remaining ED values to compare the ED values. In this example, one species is missing and been removed and the correlation coefficient $r = 0.976$.

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. To see if phylogenetic structure or distribution is ED values could explain variation in the effect of removal and subsequent imputation, we also recorded, before species were removed from the tree, lambda (using the `yule` function in the R package `ape` (Paradis et al. 2017)), overall branch length (by summing the branch lengths given by `sim.bdtree`), gamma (using the `gammatest` function in the R package `phytools` (Revell et al. 2017)), colless' index (using the `as.treeshape` function in the R package `apTreeshape` (Bortolussi et al. 2009)), kurtosis (using the `moments` function in the R package `kurtosis` (Komsta & Novomestky 2015)), and skew (using the `skew` function in the R package `moments` (Komsta & Novomestky 2015)). In cases where a phylogeny was simulated without a clade of the required size, that particular simulation was aborted and we moved on to the next simulation in order to obtain a clade of that size.

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.

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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. 2). Correlations between ED values before and after 10% and 20% of species are missing at random are ~0.957 and ~0.882, respectively. When missing 10% and 20% of overall species in the phylogenetically-biased manner we see the correlation coefficient is higher at ~0.985 and ~0.938.
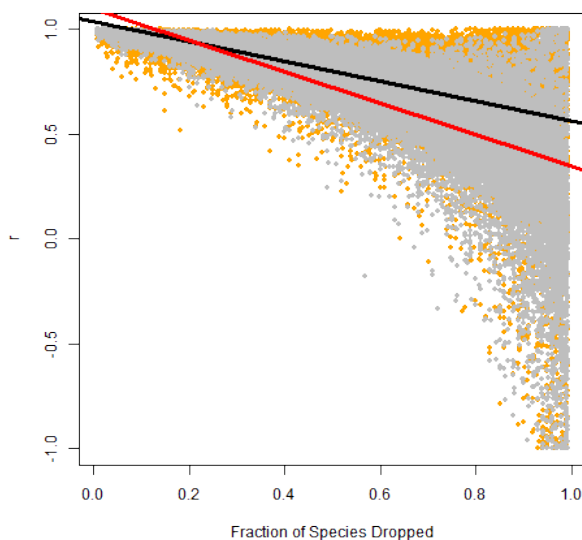

Figure 2: **R-values plotted against the fraction of species dropped at random versus clustered manner.** The color of data points denote whether species were dropped at random (orange; n = 100) or in clustered manner (grey; n = 100). The regression lines are demonstrating the relationship when species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

We find no support for a correlation between the imputed and true ED values for species within imputed clades (Fig. 3, Table 2). We found that measures of the true phylogeny such as phylogenetic diversity (PD), estimated rate of diversification $\hat{\lambda}$, Colless' Index, as well as skew and kurtosis of the distribution ED values do not provide any indication that imputation would negatively affect ED values (Appendix A). We do find evidence that, when

	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).

imputing larger clades, the variation in the correlation is lesser (Fig. 4), 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. 5; Table 4). 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). For example, within a phylogeny of 1024 species, a species within an imputed clade of 30 species is, on average, $\pm 315 rankings from its true ranking.$

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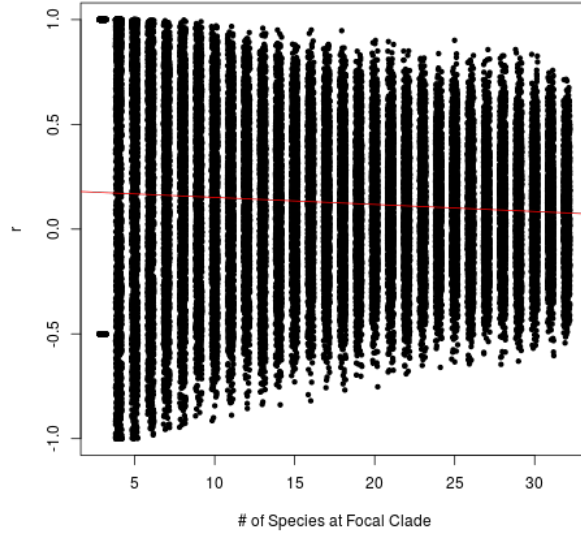
Figure 3: **R-values plotted against the number of species at focal clade.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. The regression line (red) and trend even closer to zero demonstrates the decrease in informative value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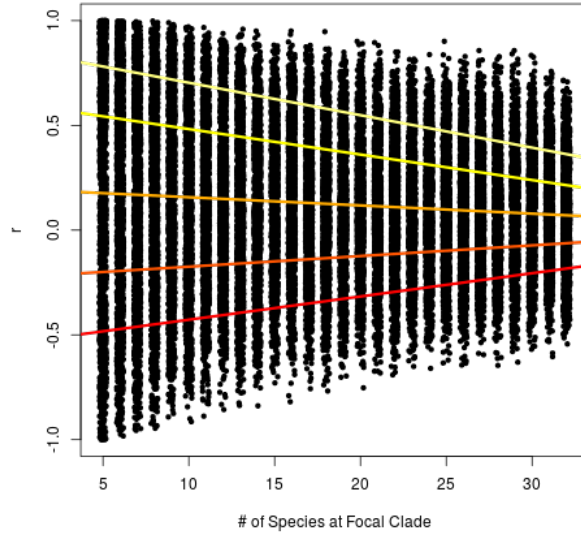

Figure 4: **Quantile regression of r-values against size of imputed clades.** Each data point denotes a correlative comparison between ED values within the focal clades where imputation has occurred. Each regression line (top to bottom) represent quantile regressions from highest to lowest, respectively. 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).
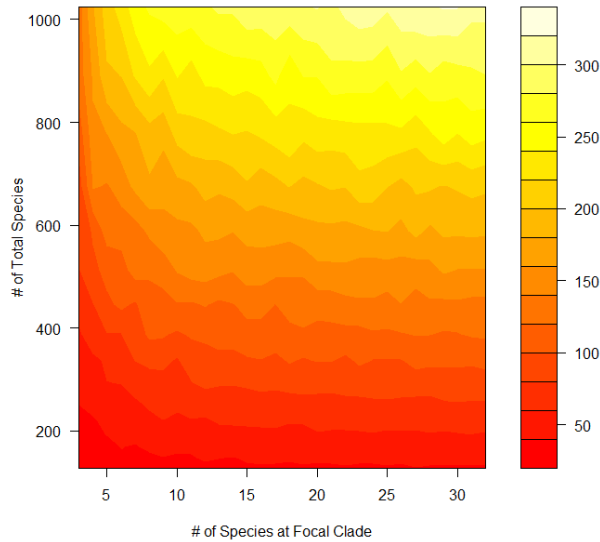
Figure 5: **Mean ranking error of species within the focal clade.** The gradient on the right demonstrates average number of positions within the full ranking that focal clade species shifted from their true rank. While controlling for the size of the full phylogeny and focal clade, species within the 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 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 obstactle to a more widespread adoption of phylogenetic prioritization methods such as EDGE is phylogenetic uncertainty (Collen 2015). We do not have phylogenetic information on all species, and without this it is difficult to allocate resources to most efficiently protect the evolutionary history of species. In order 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 tre of life. (2) We found limited evidence that phylogenetic imputation can accurately 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. Equally, we focus here solely on the results from a single imputation in each simulation. Normally, pseudo-posterior distributions of many phylogenies are creates and results reported across averages of these distributions (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. Our analysis demonstrates that, for example, missing 20% of total species, at random and in a phylogenetically-biased manner, only to a drop in r of 0.882 and 0.938, respectively (Table 1). A drop in r of only 0.118 and 0.062 between true and imputed ED values is not, in our opinion, all that concerning when assigning ED scores to remaining species.

We do find that the effect of missing species is more severe when those species are randomly distributed across the phylogeny. However, perhaps, the most extreme form could be if an entire clade were missing, and clades that are geographically restricted to difficult-to-reach regions (as is seen with 27 coral species in the Indian Ocean; Arrigoni et al. 2012) are both difficult to sequence and not uncommon. 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 (Fig. 3; Fig. 5). Thus we argue that, even though under imputation

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missing species are incorporated into EDGE lists, their associated EDGE scores may not 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 (Fig. 3; Table 4).

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 Fig. 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 (see table XXX), 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 we would have expected 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 fields: Rabosky (2014) showed that imputation consistently biases evolutionary rates and estimates of 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 acnkowledged. 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 produce of both ED and IUCN status. This does not, however, mean that phylogenetic imputation is any less of a problem. The novelty and purpose of EDGE-like metrics is to incorporate phylogeny, and if imputed EDGE scores are driven by the GE component because of the uncertainty introduced by imputation we are accidentally creating a metric based on IUCN listing alone.

We suggest there is a straightforward synthesis of our results that should be useful in applied conservation biology. Both random and phylogenetically-patterned missing species affect ED scores, albeit to differing extents. Therefore, conservation biologists should consider using imputation to mitigate such bias. We do emphasize, however, that in a phylogeny missing 30% of species at random, the mean correlation coefficient (r) of the remaining species' ED scores with their true scores was 0.81 (with variation, of course; see figure 2). Where the same proportion of species missing in a phylogenetically-biased way, the r was 0.891. The problem may not be as severe as has previously been thought, but that is not reason to try and mitigate it through imputation.

However, we suggest that prioritizing species whose phylogenetic structure has been imputed should be done with extreme care. Our simulations show that the ED rankings, and the top-scored species, are very variable under imputation. If imputed distributions of trees essentially represent Bayesian posterior distributions (Kuhn et al. 2011), then we should treat them as such: the 95% posterior densities of these distributions' ED values represent the range within which we can be 95% certain the true ED scores lie (if the model assumptions are met). Our results highlight that the ranges of these distributions are often much greater than has previously been acknowledged. If we are to avoid prioritizing the wrong species, we should consider focusing our efforts on those species whose ED scores we can know with

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271 greater certainty: those for which we have data.

Acknowledgments

References

Arrigoni, R., Stefani, F., Pichon, M., Galli, P., & Benzoni, F. (2012). Molecular phylogeny of the robust clade (Faviidae, Mussidae, Merulinidae, and Pectiniidae): an Indian Ocean perspective. *Molecular Phylogenetics and Evolution* 65.1, 183–193.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature* 471.7336, 51–57.

Bortolussi, N., Durand, E., Blum, M., & Blum, M. M. (2009). Package 'apTreeshape'.

Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., et al. (2008). Is conservation triage just smart decision making? *Trends in Ecology & Evolution* 23.12, 649–654.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology* 16.4, 909–923.

Butchart, S. H. & Bird, J. P. (2010). Data deficient birds on the IUCN Red List: what don't we know and why does it matter? *Biological Conservation* 143.1, 239–247.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science advances* 1.5, e1400253.

Collen, B. (2015). Conservation prioritization in the context of uncertainty. *Animal Conservation* 18.4, 315–317.

Collen, B., Turvey, S. T., Waterman, C., Meredith, H. M., Kuhn, T. S., Baillie, J. E., & Isaac, N. J. (2011). Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366.1578, 2611–2622.

Curnick, D., Head, C., Huang, D., Crabbe, M. J. C., Gollock, M., Hoeksema, B., Johnson, K., Jones, R., Koldewey, H., Obura, D., et al. (2015). Setting evolutionary-based conservation priorities for a phylogenetically data-poor taxonomic group (Scleractinia). *Animal Conservation* 18.4, 303–312.

Faith, D. P. (2008). Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conservation Biology* 22.6, 1461–1470.

Felsenstein, J. (2005). Using the quantitative genetic threshold model for inferences between and within species. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 360.1459, 1427–1434.

Good, T. C., Zjhra, M. L., & Kremen, C. (2006). Addressing data deficiency in classifying extinction risk: a case study of a radiation of Bignoniaceae from Madagascar. *Conservation Biology* 20.4, 1099–1110.

Gumbs, R., Gray, C. L., Wearn, O. R., & Owen, N. R. (2017). Tetrapods on the EDGE: Overcoming data limitations to identify phylogenetic conservation priorities. *bioRxiv*, 232991.

Isaac, N. J., Redding, D. W., Meredith, H. M., & Safi, K. (2012). Phylogenetically-informed priorities for amphibian conservation. *PLoS one* 7.8, e43912.

Isaac, N. J., Turvey, S. T., Collen, B., Waterman, C., & Baillie, J. E. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PloS one* 2.3, e296.

IUCN (2001). *IUCN Red List categories and criteria*. IUCN.

– (2008). Guidelines for Using the IUCN Red List Categories and Criteria, Version 7.0. *Prepared by the Standards and Petitions Working Group of the IUCN SSC Biodiversity Assessments Sub-Committee in August 2008.*

Jensen, E. L., Mooers, A. Ø., Caccone, A., & Russello, M. A. (2016). I-HEDGE: determining the optimum complementary sets of taxa for conservation using evolutionary isolation. *PeerJ* 4, e2350.

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K., & Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology* 24.9, 919–930.

Komsta, L. & Novomestky, F. (2015). Moments, cumulants, skewness, kurtosis and related tests. *R package version 0.14.*

Kuhn, T. S., Mooers, A. Ø., & Thomas, G. H. (2011). A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution* 2.5, 427–436.

Lips, K. R., Brem, F., Brenes, R., Reeve, J. D., Alford, R. A., Voyles, J., Carey, C., Livo, L., Pessier, A. P., & Collins, J. P. (2006). Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the national academy of sciences of the United States of America* 103.9, 3165–3170.

McBride, M. F., Wilson, K. A., Bode, M., & Possingham, H. P. (2007). Incorporating the effects of socioeconomic uncertainty into priority setting for conservation investment. *Conservation Biology* 21.6, 1463–1474.

Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6.9, 485–492.

Morais, A. R., Siqueira, M. N., Lemes, P., Maciel, N. M., De Marco Jr, P., & Brito, D. (2013). Unraveling the conservation status of Data Deficient species. *Biological conservation* 166, 98–102.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403.6772, 853–858.

Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006). Integrating economic costs into conservation planning. *Trends in ecology & evolution* 21.12, 681–687.

Orme, D. (2013). The caper package: comparative analysis of phylogenetics and evolution in R. *R package version 5.2*, 1–36.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., Desper, R., & Didier, G. (2017). Package 'ape'. *Analyses of phylogenetics and evolution, version*, 2–4.

Pearse, W. D., Chase, M. W., Crawley, M. J., Dolphin, K., Fay, M. F., Joseph, J. A., Powney, G., Preston, C. D., Rapacciuolo, G., Roy, D. B., et al. (2015). Beyond the EDGE with EDAM: prioritising British plant species according to evolutionary distinctiveness, and accuracy and magnitude of decline. *PloS one* 10.5, e0126524.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., Alfaro, M. E., & Harmon, L. J. (2014). geiger v2. 0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30.15, 2216–2218.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., et al. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439.7073, 161–167.

Pressey, R., Humphries, C., Margules, C. R., Vane-Wright, R., & Williams, P. (1993). Beyond opportunism: key principles for systematic reserve selection. *Trends in ecology & evolution* 8.4, 124–128.

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria.

Rabosky, D. L. (2014). No substitute for real data: phylogenies from birth-death polytomy resolvers should not be used for many downstream comparative analyses. *Xx2*, 1–23. arXiv: 1503.04978.

Revell, L. J., Revell, M. L. J., & grDevices, M. (2017). Package 'phytools'.

Steel, M., Mimoto, A., & Mooers, A. Ø. (2007). Hedging our bets: the expected contribution of species to future phylogenetic diversity. *Evolutionary bioinformatics online* 3, 237.

Stein, R. W., Mull, C. G., Kuhn, T. S., Aschliman, N. C., Davidson, L. N., Joy, J. B., Smith, G. J., Dulvy, N. K., & Mooers, A. O. (2018). Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nature Ecology & Evolution*, 1.

21

378 Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham,
379 Y. C., Erasmus, B. F., De Siqueira, M. F., Grainger, A., Hannah, L., et al. (2004). Ex-
380 tinction risk from climate change. *Nature* 427.6970, 145–148.

381 Thomas, G. H., Hartmann, K., Jetz, W., Joy, J. B., Mimoto, A., & Mooers, A. O. (2013).
382 PASTIS: an R package to facilitate phylogenetic assembly with soft taxonomic inferences.
383 *Methods in Ecology and Evolution* 4.11, 1011–1017.

384 Wake, D. B. & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction?
385 A view from the world of amphibians. *Proceedings of the National Academy of Sciences*
386 105.Supplement 1, 11466–11473.

387 Weitzman, M. L. (1998). The Noah's ark problem. *Econometrica*, 1279–1298.

388 Wilson, K. A., Underwood, E. C., Morrison, S. A., Klausmeyer, K. R., Murdoch, W. W.,
389 Reyers, B., Wardell-Johnson, G., Marquet, P. A., Rundel, P. W., McBride, M. F., et al.
390 (2007). Conserving biodiversity efficiently: what to do, where, and when. *PLOS biology*
391 5.9, e223.

A. Effect of Measures of the True, Full Phylogenies
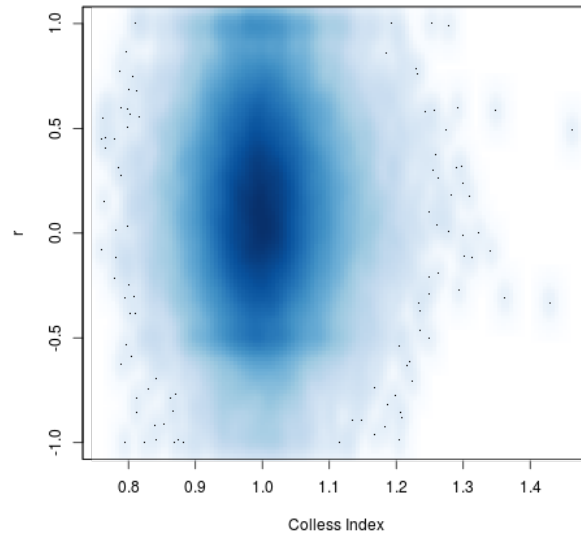
Figure 6: **Effect of the True Colless Index of FullPhylogeny.**
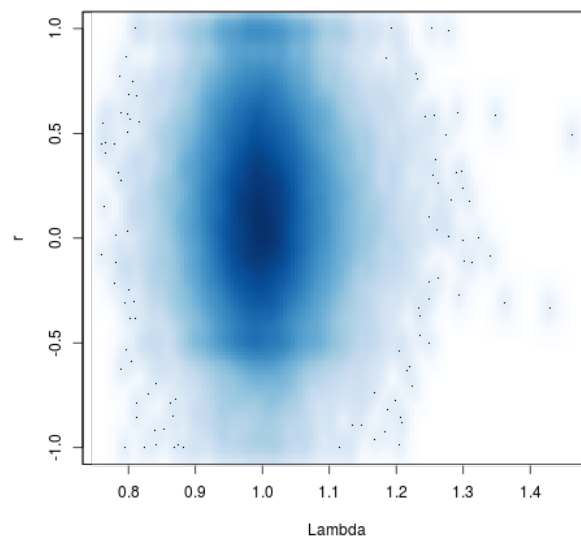
Figure 7: **Effect of the True Lambda of Full Phylogeny.**
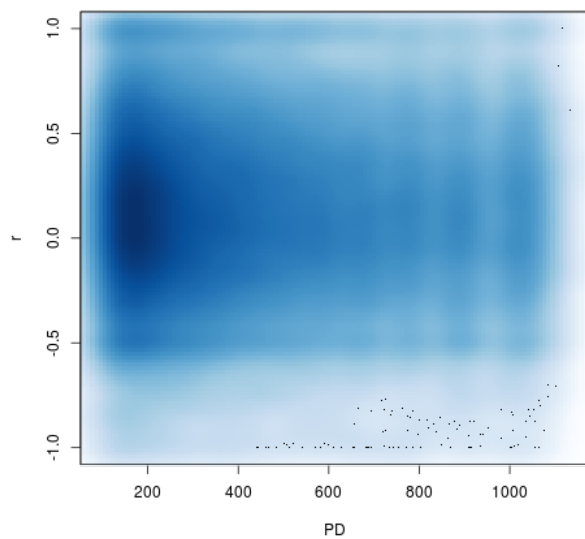
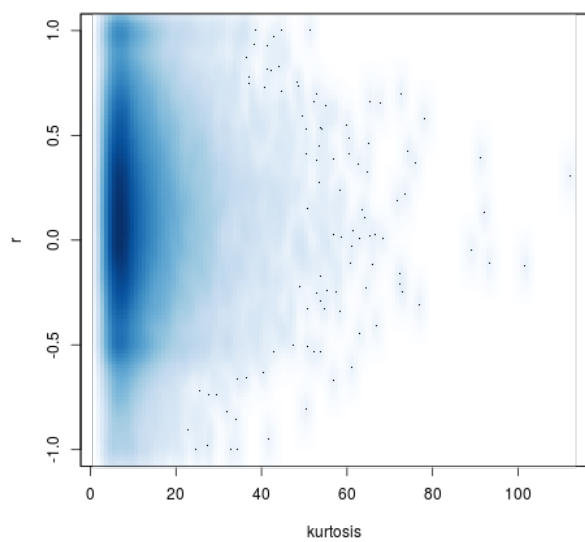Figure 8: **Effect of True PD of Full Phylogeny.**

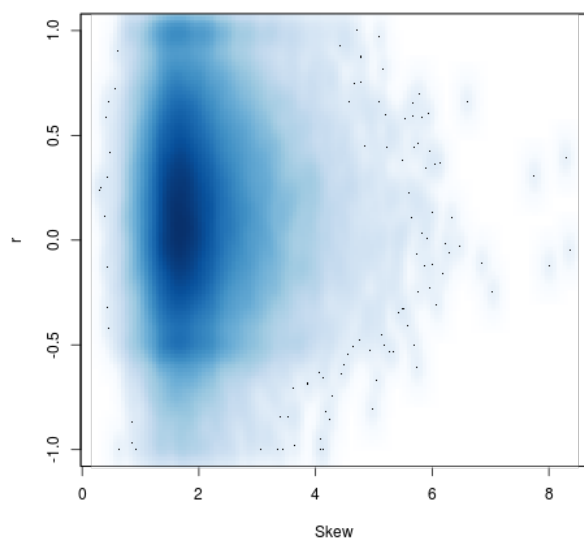Figure 9: **Effect of the True Kurtosis of Full Phylogeny.**

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Figure 10: **Effect of the True Skew of Full Phylogeny.**
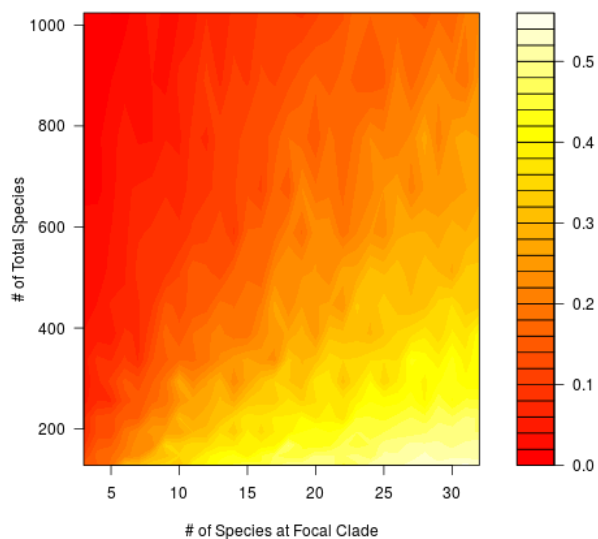
B. Error Rate in Top Rankings

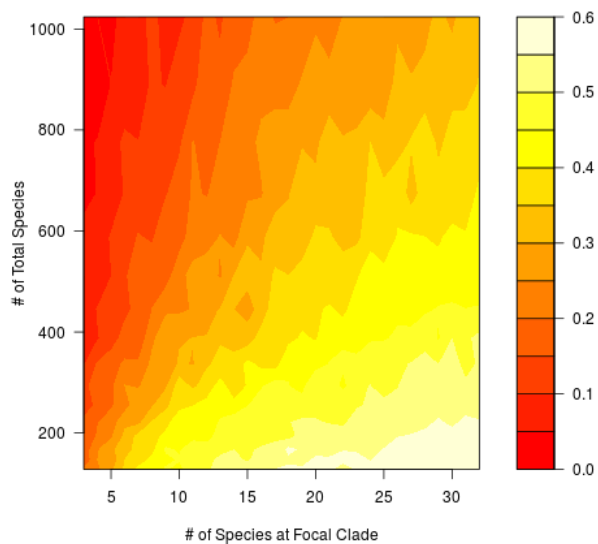Figure 11: **Mean error rate in the ranking of top 50 species.**

Figure 12: **Mean error rate in the ranking of top 100 species.**
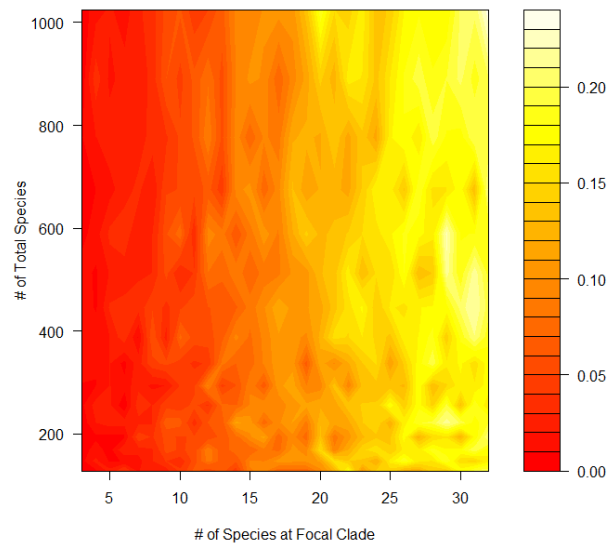
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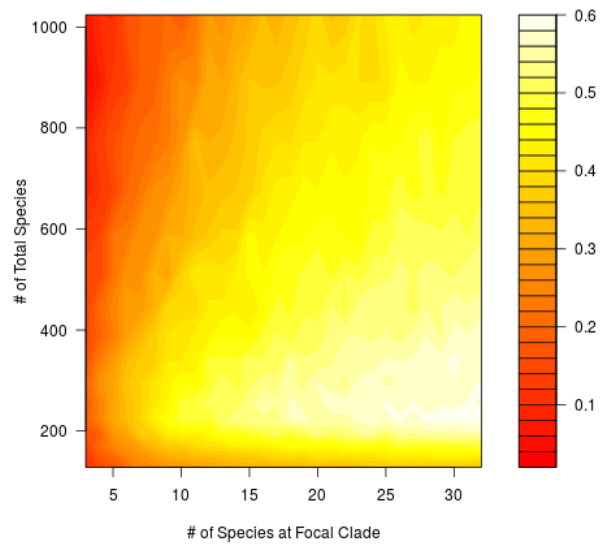
Figure 13: **Mean error rate in the ranking of top 200 species.**

Figure 14: **Mean error rate in the ranking of top 5% of species.**

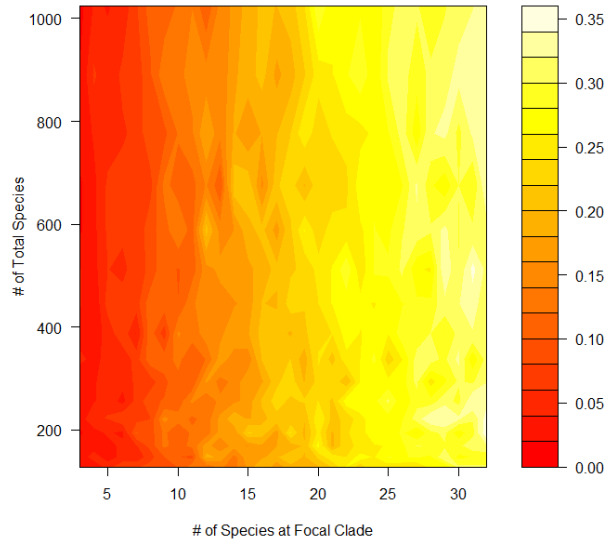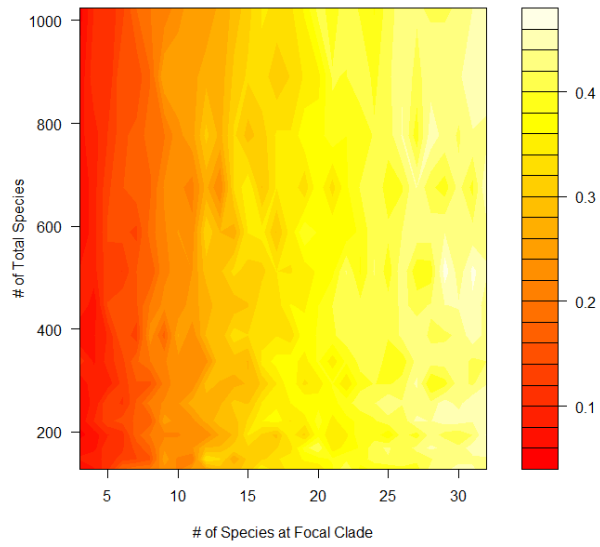Figure 15: **Mean error rate in the ranking of top 10% of species.**

Figure 16: **Mean error rate in the ranking of top 20% of species.**