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12-8-2019

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Recommended Citation

Bodie Weedop, K., Mooers, A.Ø., Tucker, C.M. and Pearse, W.D. (2019), Preserving evolutionary history with improved confidence. Anim Conserv, 22: 541-542. doi:10.1111/acv.12556

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RESPONSE

Preserving evolutionary history with improved confidence

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doi: 10.1111/acv.12556

We thank Faith (2019) and Mindell (2019) for their insightful perspectives on our study of the impact of phylogenetic imputation on the assessment of evolutionary distinctiveness (ED; Isaac et al., 2007). As Mindell highlights, the finding that ED scores for species on a phylogeny are remarkably robust despite having species missing from that phylogeny is encouraging; our results suggest that we can be confident in moving forward with prioritization of the species for which we have data. This is important because in some cases, for example, it may take considerable time to obtain samples from the missing species, resulting in further delay before the ED scores for those species already sampled can be used to inform management decisions. We cautioned, however, that the ED scores for those missing species may be imputed imprecisely, and so we gave guidelines for working with imputed species' ED scores. With this in mind, we offer some additional thoughts resulting from the commentaries of Mindell and Faith.

We agree with Mindell (2019) that our simulations use simple (homogeneous) models of diversification, and that models where diversification rates can vary within a phylogeny (heterogeneous models) may provide more realistic phylogenies. Mindell (2019) kindly mounts an argument on our behalf, pointing out that simulations based on more complex models can introduce unintended biases (and, we suggest, have less general results). Such models also have more parameters whose estimation introduces additional error, and so our approach of simulating and imputing under the same model represents a best-case scenario for successful imputation. It is true, though, that heterogeneous models are often needed to produce realistic (e.g. unbalanced; Mooers & Heard, 1997) phylogenies, with longer and more variable terminal branch lengths (on average) than phylogenies from homogeneous models. Terminal branch lengths drive ED scores (see Redding et al., 2008) and so, while we expect this would make missing species even harder to impute, we do not know whether the ED scores of known species would be resilient to missing species under such models.

We share Faith (2019) enthusiasm for the EDGE of Existence program, and are also excited by the mission of the IUCN's Phylogenetic Diversity Task Force. Our original study examines evolutionary distinctiveness, which we defined (citing Redding, 2003 and Isaac *et al.*, 2007) as partitioning total phylogenetic branch lengths among clades' subtending species. Total phylogenetic branch length is indeed Faith's PD (Faith, 1992). Readers are welcome to bear Faith's PD in mind when reading Weedop *et al.* (2019); we feel our results and arguments hold.

We focused on the evolutionary distinctiveness (ED), and not the global endangerment (GE), component of EDGE because the use of ED is what differentiates EDGE from merely conserving endangered species, and because it makes our results more general. If species' ED values cannot be precisely imputed, then other metrics and indices that also rely on phylogenetic structure should be imprecisely imputed (see Rabosky, 2015). Once an analysis incorporates GE alongside ED, it may be difficult to separate the effects of imputing missing species, particularly if the ED and GE components are not always of equal importance in empirical EDGE lists (reviewed in Isaac & Pearse, 2018).

That said, there are numerous potential extensions and alternatives to EDGE (reviewed in Isaac & Pearse, 2018). Faith (2019) discussion of using the extinction probability of close relatives and phylogenetic risk analysis is intriguing. Given that related species share responsibility for deeper branches in the tree, missing species that are safe versus not safe should have different effects on the value of species currently on the tree. We wonder if future research could consider the relative probability of species being imputed into positions that would leave them either as high-ranked species or make known species be of higher rank. If, say, such imputations were more unlikely than others, it might be possible to perform a kind of 'worst-case imputation' analysis. Mindell (2019) insightfully notes that managers are unlikely to stop imputing values for missing species, since an imprecise result might still be preferable to excluding a species altogether. Missing information is a limiting factor for conservation in general, and we foresee that imputation will be developed even further to aid managers. For example, it is becoming increasingly possible to use some combination of species' taxonomy, phylogeny, or traits to impute GE (e.g., Pelletier et al., 2018). Such imputed estimates of GE could be used in EDGE-listing as well.

While we feel that simulation studies such as ours are useful guides as we build tools in the fight to conserve biodiversity, the commentaries of Mindell (2019) and Faith (2019) remind us that we must not lose sight of our underlying purpose. We can, and must, act now to conserve the biodiversity that we value and depend upon. While our study highlights potential pitfalls in imputation, it also shows how to avoid them, so that we can confidently measure and preserve evolutionary history.

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