Estimating trophic discrimination factors using Bayesian inference and phylogenetic, ecological and physiological data. DEsiR: Discrimination Estimation in R.

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Abstract

1. Stable isotope analysis is a widely used tool for the reconstruction and interpretation of animal diets and trophic relationships. Analytical tools have improved the robustness of inferring the relative contribution of different prey sources to an animal's diet by accounting for many of the sources of variation in isotopic data. One major source of uncertainty is Trophic Discrimination Factor (TDF), the change in isotopic signatures between consumers' tissues and their food sources. This parameter can have a profound impact on model predictions, but often, it is not feasible to estimate a species' TDF value and so researchers often use aggregated or taxon level estimates, an assumption that in turn has major implications for the interpretation of subsequent analyses.

2. We collected extensive carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) TDF data on mammals and birds from published literature. We then used a Bayesian linear modelling approach to determine if, and to what extent, variation in TDF values can be attributed to a species' ecology, physiology, phylogenetic relationships and experimental variation. Finally, we developed a Bayesian imputation approach to estimate unknown TDF values and compared the accuracy of this tool using a series of cross-validation tests.

3. Our results show that, for birds and mammals, TDF values are influenced by phylogeny, tissue type sampled, diet of consumer, isotopic signature of

food source, and the error associated with the measurement of TDF within a species. Furthermore, our cross-validation tests determined that, our tool can (i) produce accurate estimates of TDF values with a mean distance of 0.2 ‰ from observed TDF values, and (ii) provide an estimate of the precision associated with these estimates, with species presence in the data allowing for a reduced level of uncertainty.

4. By incorporating various sources of variation and reflecting the levels of uncertainty associated with TDF estimates our novel tool will contribute to more accurate and honest reconstructions and interpretations of animal diets and trophic interactions. This tool can be extended readily to include other taxa and sources of variation as data becomes available. To facilitate this, we provide a step-by-step guide and code for this tool: Discrimination Estimation in R (DEsiR)

Keywords (10): Trophic Discrimination Factor, stable isotopes, trophic enrichment factor, trophic ecology, mixing models, discrimination factor, mammals, birds, DEsiR, Bayesian Imputation.

Intro

The use of stable isotope analysis to reconstruct animal diets or determine trophic relationships has grown substantially over the previous two decades (Post 2002, Hussey, MacNeil et al. 2014). In recent years this growth has been boosted by the development of mixing models that allow for diet reconstruction in systems that often have greater than two sources more than the number of isotope ratios measured (Phillips and Gregg 2003, Moore and Semmens 2008, Parnell, Inger et al. 2010, Hopkins III and Ferguson 2012, Fernandes, Millard et al. 2014). The ability of these approaches to predict accurately the dietary proportions and hence trophic relationships depends on the relative geometry of the mixtures (usually the consumers) and their sources (their food) (Phillips and Gregg 2003, Phillips, Inger et al. 2014) in isotopic space. Furthermore, variation in these data, arising from both natural variation among samples and also through uncertainty in parameters, can together reduce both the accuracy and

precision of predictions made by these mixing models by altering the relative geometric position of consumers and their sources. One key source of variation, that can cause far more problems for users than sample-dependent variation is the parameter that describes the average change in isotopic ratios between consumers and their diets; the trophic discrimination factor (TDF).

Trophic discrimination is the change in isotopic signatures attributed to the biological and biochemical processes associated with the uptake and assimilation of food sources by consumers (DeNiro and Epstein 1981, Peterson and Fry 1987, France and Peters 1997). In the case of the commonly used elements in dietary studies (C, N, S & H), these changes in isotope ratios between sources and consumers arise usually from the preferential retention of heavier isotopes by consumers leading to a change in the ratio of heavy to light isotopes of a given element (Olive, Pinnegar et al. 2003). While TDF can typically vary from species to species, they also vary according to a range of other factors including consumer tissue type, the type of food source, the isotopic ratio of the food source, the nutritional status of both the consumer and the food source and the foraging environment of the consumer (Caut, Angulo et al. 2009). Hence, in order to accurately estimate the TDF for a given consumer-prey relationship, one must conduct an experimental study that controls for these multiple sources of variation (Greer, Horton et al. 2015).

The high costs and difficulty of performing these studies and as many species are not amenable to controlled captive environments has resulted in a relatively low coverage of species for which TDF estimates are available (Caut, Angulo et al. 2009). Hence, most stable isotope studies on dietary proportions and trophic relationships have relied on general approximately mean estimates across multiple studies, for example the addition of +3.4‰ for nitrogen and +0.4‰ for carbon (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Post 2002); estimates aggregated for certain tissue types or at high taxonomic levels (McCutchan, Lewis et al. 2003, Caut, Angulo et al. 2009); or the use of estimates from closely related species (Bodey, Ward et al. 2014). While some approaches attempt to provide general TDF values for high taxonomic levels (Caut, Angulo et

al. 2009) none of these approaches fully incorporates the true variation in TDFs associated with phylogenetic relatedness; physiology; ecology; or the error and natural individual level variation associated with the experimental measure of these values (McCutchan, Lewis et al. 2003, Del Rio and Wolf 2005, Robbins, Felicetti et al. 2005). These unaccounted sources of variation may impact the resulting analysis mainly through propagating error into the final results leading to overly conservative results (Bond and Diamond 2011), but only, we would argue, if one specifies TDFs with very small uncertainties around them (i.e. assuming overly precise estimates). In any case, by better acknowledging and accounting for these sources in TDF variation, more accurate estimates and associated errors can be calculated which in turn will yield more honest and encompassing descriptions of consumers' diets and trophic relationships.

Here we assess sources of variation in TDF and develop a tool implementing a Bayesian linear modelling approach that incorporates the variation in TDF associated with phylogeny; physiology; ecology and study measurement error. Bayesian techniques allow for the implicit imputation (i.e. estimation)of missing values, and have been developed in several fields (Fagan, Pearson et al. 2013, Swenson 2014, Jetz and Freckleton 2015, Schrodt, Kattge et al. 2015). Here we exploit this imputation approach to estimate values for species that have no current TDF values: predicted estimates will draw inference from the included explanatory variables, and will return a distribution of estimates rather than a single point-estimate. We test our approach by collecting carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) TDF values from the literature for both birds and mammals and comparing these observed values against our estimates.

Overall we show that TDF values are influenced by phylogeny, tissue type, source isotopic signature, diet type and the error associated with measurements within a species, with the importance of each source of variation dependent on the element (Nitrogen, Carbon) and taxonomic class (Aves, Mammalia). We then exploit the ability of Bayesian Inference to impute missing values in order to predict with uncertainty the TDF for un-quantified species and test these estimates using a series of cross validation tests where both individual samples,

and entire species are omitted from the model fitting process and their imputed values compared with their observed values. Finally, we provide a step-by-step guide of using the DEsiR package (https://github.com/healyke/DEsiR).

Methods

Data collection

Following the methods of (Caut, Angulo et al. 2009), we collected data on TDF of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in mammals and birds as these were the taxon with the largest amount of available data (See DEsiR package for updates that include further taxa). Our data collection covered publications from 2007 to 2015 and was supplemented by (Caut, Angulo et al. 2009) which covered the period of 1983-2007 using the same selection criteria. Only studies with isotopic ratios measured on both the tissue samples and the food source were used. For all data relating to TDF, corresponding data on diet, tissue type sampled and foraging environment were also collected. Diet was defined by the animal feed used during the study and was categorised as either omnivore, carnivore, herbivore or pellet. Tissue type was categorised as either blood, which included whole blood and all its constituents such as plasma; keratin claws; collagen; feathers; hair (including whiskers); kidney; liver; milk; and muscle (with tissues as appropriate for birds and mammals). Environment was defined based on whether a species predominantly fed primarily in a terrestrial (including freshwater) or marine environments. For full details on the methods used, including search terms and data standards, see (Caut, Angulo et al. 2009).

As common ancestry among groups can affect trait variation we included phylogenetic information for both birds and mammals in our models. Rather than basing our analyses on a single phylogenetic tree, we followed previous approaches (Healy, Guillerme et al. 2014, Healy 2015), of using a distribution of trees to incorporate the inherent uncertainty in the phylogenies. We extracted three trees from the posterior distribution of a recent bird phylogeny generated under a Bayesian inference framework (Jetz, Thomas et al. 2012), and used the mammal trees constructed by (Kuhn, Mooers et al. 2011) were each individual

tree comprises one resolution of the polytomies of a previously published supertree and these as equivalent to a Bayesian posterior distribution of trees.

Analysis of sources of variation

To estimate values of TDF we fitted models using Bayesian phylogenetic mixed models from the MCMCglmm package (Hadfield 2010). Separate models were fitted for both nitrogen and carbon and also for both Aves and Mammalia due to the use of distinct tissue types to measure TDF in both groups. We fit each model with terms known or expected to determine TDF including; food source isotopic ratio; diet type and environment type as fixed terms and tissue type and species level variation fitted as random terms. To include the non-independence between species traits due to common decent we included phylogeny as a random term using the animal term in the MCMCglmm package and run these models over a distribution of phylogenetic trees using the Multree package (Guillerme and Healy 2014). We determined the number of iterations, thinning and the burn-in period for each model run across all trees using diagnostics in the coda package (Plummer, Best et al. 2006) and we checked for convergence between model chains using the Gelman-Rubin statistic, the potential scale reduction factor (PSR), with all models required to have a PSR below 1.1 (Brooks and Gelman 1998). Following the recommendations of Hadfield (Hadfield 2010), we used an uninformative inverse-Wishart distribution (with variance, V, set to 0.5 and belief parameter, nu, set to 0.002) and a parameter expanded prior, with a half-Cauchy distribution (described by the parameters V . 0.5, nu. 1, the prior mean alpha.mu . 0, and alpha.V . 102, which represents the prior standard deviation with a scale of 10), for the random factor to improve mixing and decrease autocorrelation among iterations.

While we include isotopic ratio as a fixed effect in the main analysis, as it is found to be a strong predictor of TDF in previous studies (Caut, Angulo et al. 2009), we also run each model without the fixed terms of food source isotopic ratio as information relating to this factor is unlikely to be available outside of controlled experiments. This resulted in four models (Carbon for Aves and Mammalia and Nitrogen for Aves and Mammalia) using the full model

1. TDF ~ Fixed terms: Source isotopic ratio + Diet type + Environment
   Random terms: Phylogeny + Tissue type + Species level

and four similar models without including source isotopic ratio.

2. TDF ~ Fixed terms: Diet type + Environment
   Random terms: Phylogeny + Tissue type + Species level

Using these models, we then avail of the ability to impute missing values in a Bayesian framework by using the MCMCglmm package to estimate TDF values for new species (Hadfield 2010).

Analysis (Cross validation)

To test the accuracy of this method we compared estimates of TDF calculated using Bayesian imputations to values measured in controlled experiments. We made these comparisons by running models were an observed TDF value in the dataset was replaced with a NA coding label which is then estimated implicitly during model fitting using the imputation method described above. This was repeated for each value within the dataset so that an TDF estimate was calculated for each individual observed TDF value were that was the only missing value in the model.

To test our model for scenarios were no TDF values are present for an entire species we also sequentially replaced all values for each species in turn with the same NA coding label within the dataset. Hence in the species replacement analyses each value is estimated from a dataset that does not contain any TDF estimates for that species. All code is available as part of the FestR package (https://github.com/healyke/DEsiR).

Results

Overall our dataset includes 328 TDF values and associated data (diet type, etc) for 24 species of mammals and 24 bird species. For carbon there are 94 TDF values for 21 mammal species, and 76 TDF values across 23 bird species. For nitrogen there are 89 values across 21 mammal species and 69 TDF values across 24 bird species.

Sources of TDF variation

For both elements and taxonomic classes, the isotopic ratio of the source had a negative effect on the TDF ranging from -0.2 to -0.29 (Table. 1). For both elements in birds, but only for nitrogen isotope ratios in mammals, TDF from terrestrial habitats were found to be lower than marine habitats (Table. 1). Diet type in mammals showed significantly lower carbon TDF for pellet diets, in comparison to carnivorous diets. We also observed significantly lower nitrogen TDF for herbivores, omnivores and pellet diets in comparison to carnivore diets. In birds only omnivorous diets were found to have significantly lower nitrogen TDFs with respect to carnivorous diets.

Table 1. Summary of factors affecting TDF in Aves and Mammalia for both Carbon and Nitrogen. Estimates for effects are modal estimates with lower 5% confidence interval and higher 95% credible intervals (CI). Fixed effects estimates in bold indicate that the 95% credible interval (CI) does not contain zero.

Model Terms	Carbon					
	Aves			Mammalia		
	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Fixed Terms						
Intercept	**-3.59**	**-7.12**	**-0.167**	**-2.55**	**-4.59**	**-0.43**
Source 13C	**-0.29**	**-0.47**	**-0.11**	**-0.20**	**-0.28**	**-0.13**
Diet Type						
Herbivore	-0.28	-2.08	1.56	-0.61	-1.58	0.44
Omnivore	-1.01	-2.56	0.28	0.11	-0.71	0.99
Pellet	-0.14	-1.83	1.50	**-1.33**	**-2.41**	**-0.04**
Habitat Type						
Terrestrial	**-1.79**	**-3.42**	**-0.33**	0.58	-1.15	2.07
Random Terms						
Phylogeny	0.01	0.00	0.87	0.08	0.00	2.83
Tissue Type	0.36	0.13	3.04	0.11	0.00	1.54
Species level	0.83	0.31	2.63	0.24	0.00	1.97
Residuals	0.47	0.33	0.79	0.84	0.62	1.35

	Nitrogen					
	Aves			Mammalia		
	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Fixed Terms						
Intercept	**5.92**	**4.01**	**7.94**	**6.74**	**4.69**	**8.72**
Source 15N	**-0.24**	**-0.40**	**-0.07**	**-0.28**	**-0.40**	**-0.16**
Diet Type						
Herbivore	0.022	-2.50	2.48	**-1.81**	**-3.06**	**-0.68**
Omnivore	**-1.44**	**-3.00**	**-0.13**	**-0.90**	**-1.82**	**-0.02**
Pellet	0.44	-1.87	1.10	**-1.48**	**-2.68**	**-0.18**
Habitat Type						
Terrestrial	**-1.36**	**-2.66**	**-0.22**	**-0.50**	**-2.18**	**0.90**
Random Terms						
Phylogeny	0.19	0.00	2.02	0.26	0.00	2.55
Tissue Type	0.20	0.05	1.72	0.002	0.00	0.17
Species level	0.12	0.00	1.22	0.06	0.00	1.10
Residuals	0.31	0.22	0.53	0.68	0.50	1.01

The importance and effect of the random terms of phylogeny; tissue type; species level variation and residual variation, varied across elements and class. Phylogeny accounted for 1% and 23% of the residual variation in birds and 6% and 26% in mammals for carbon and nitrogen respectively. Tissue type was a more important term in birds accounting for 22% and 24% of the residual variation for carbon and nitrogen compared to 9% and 1% in mammals. Finally, within species level variation was found to account for as much as 19% and 50% of residual variation for carbon and 12% and 6% for nitrogen in mammals and birds (Table 1).

Model validation

The ability of our method and the associated package (DEsiR) to accurately estimate TDF values was high. Across all analyses the mode difference between estimated and observed values was found to be 0.21 for individual replacement and -0.15 for species replacement for carbon in birds (Figure 1a); -0.15 (individual) and 0.31 (species) for nitrogen in birds (Figure 1b); -0.09 (individual) and 0.09 (species) for carbon in mammals (Figure 1c); and 0.15 (individual) and 0.22 (species) nitrogen in mammals (Figures 1d).
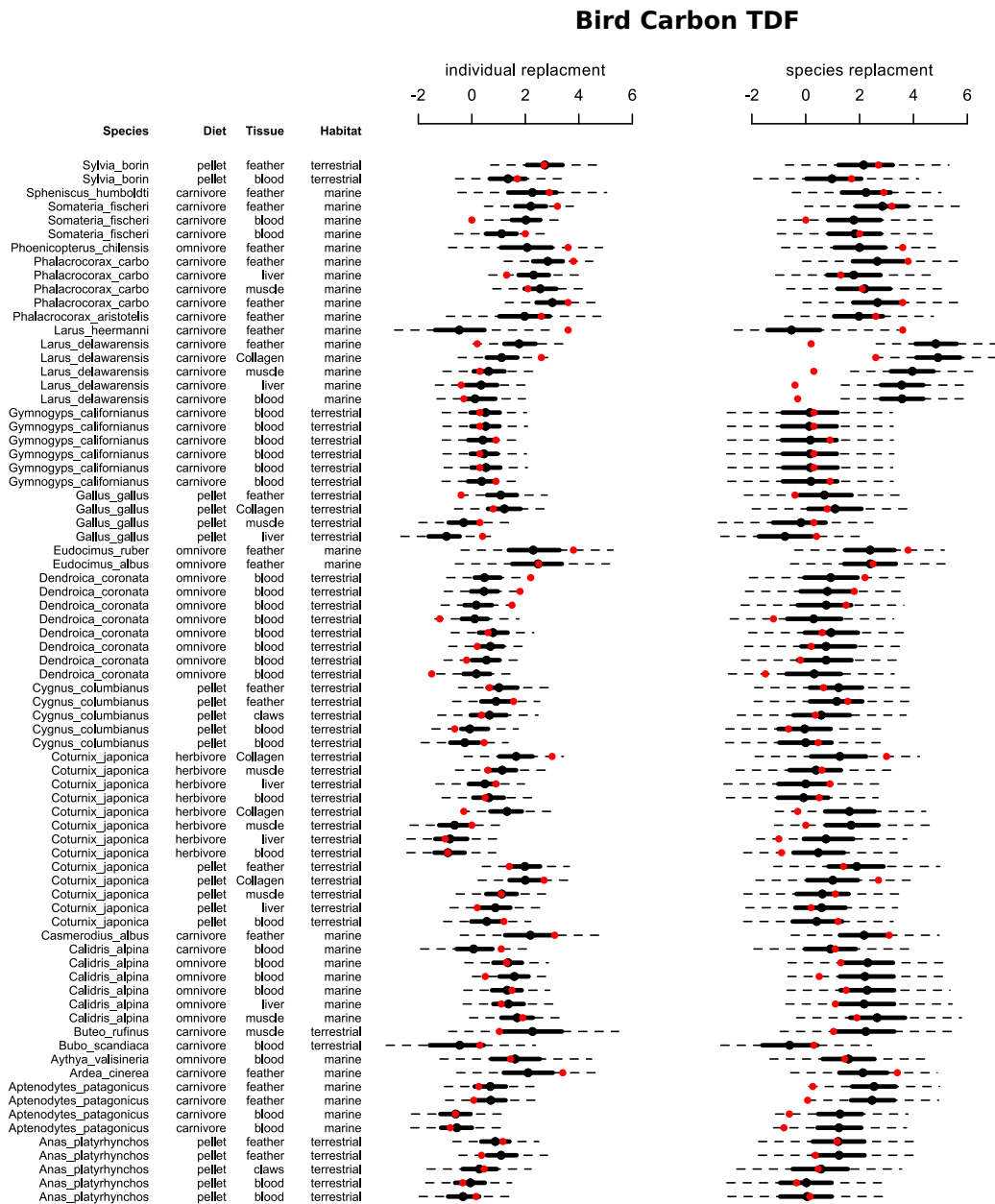
Figure 1.a TDF estimates for Carbon for birds in both individual and species replacement analyses. Black dots represent model estimates, black bars represent 50% CI and dashed bars represent 95% CI. Red dots indicate observed TDF derived from reported controlled diet experiments.
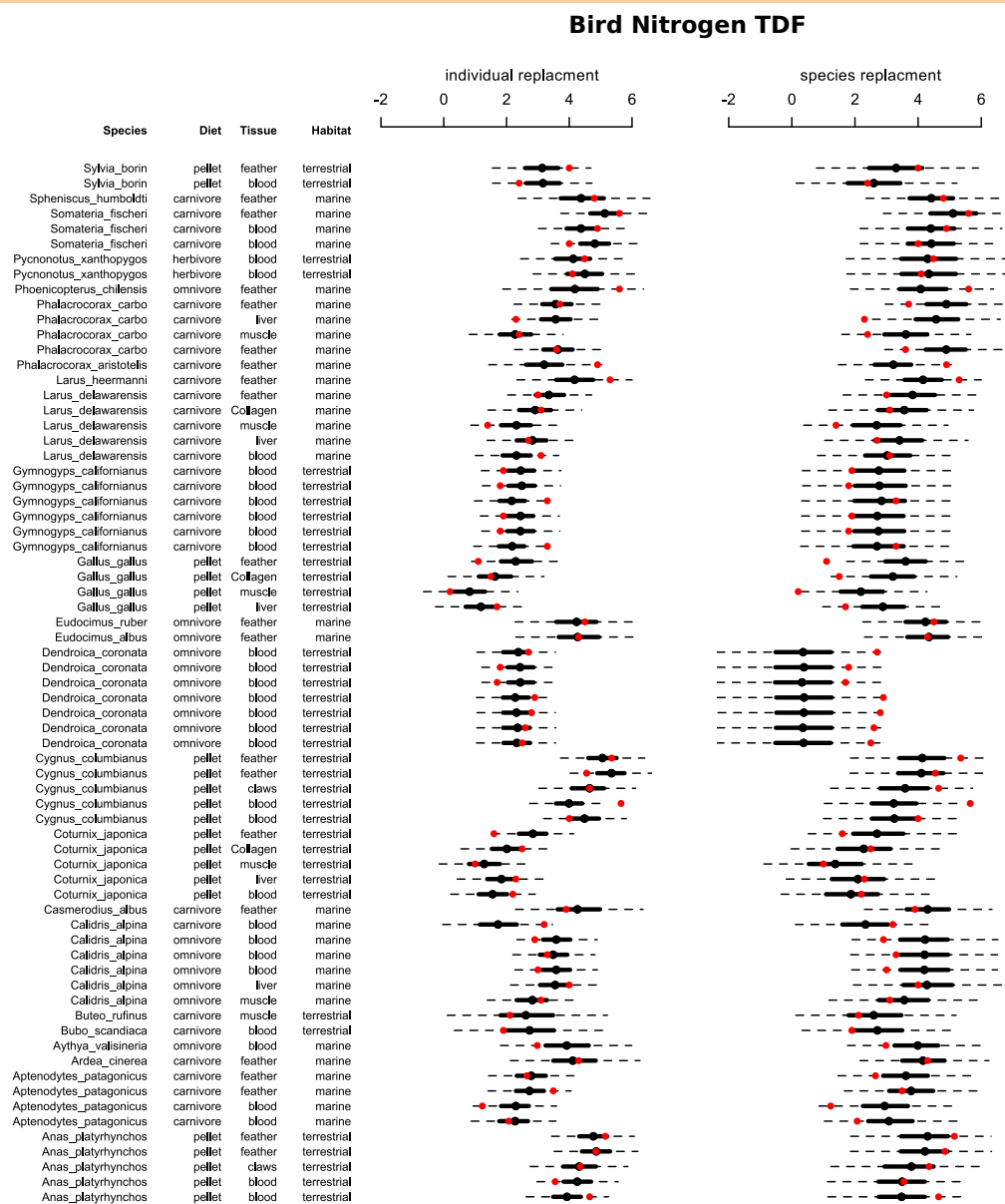
Bird Nitrogen TDF

Figure 1.b TDF estimates for nitrogen for birds in both individual and species replacement analyses. Black dots represent model estimates, black bars represent 50% CI and dashed bars represent 95% CI. Red dots indicate observed TDF derived from reported controlled diet experiments.
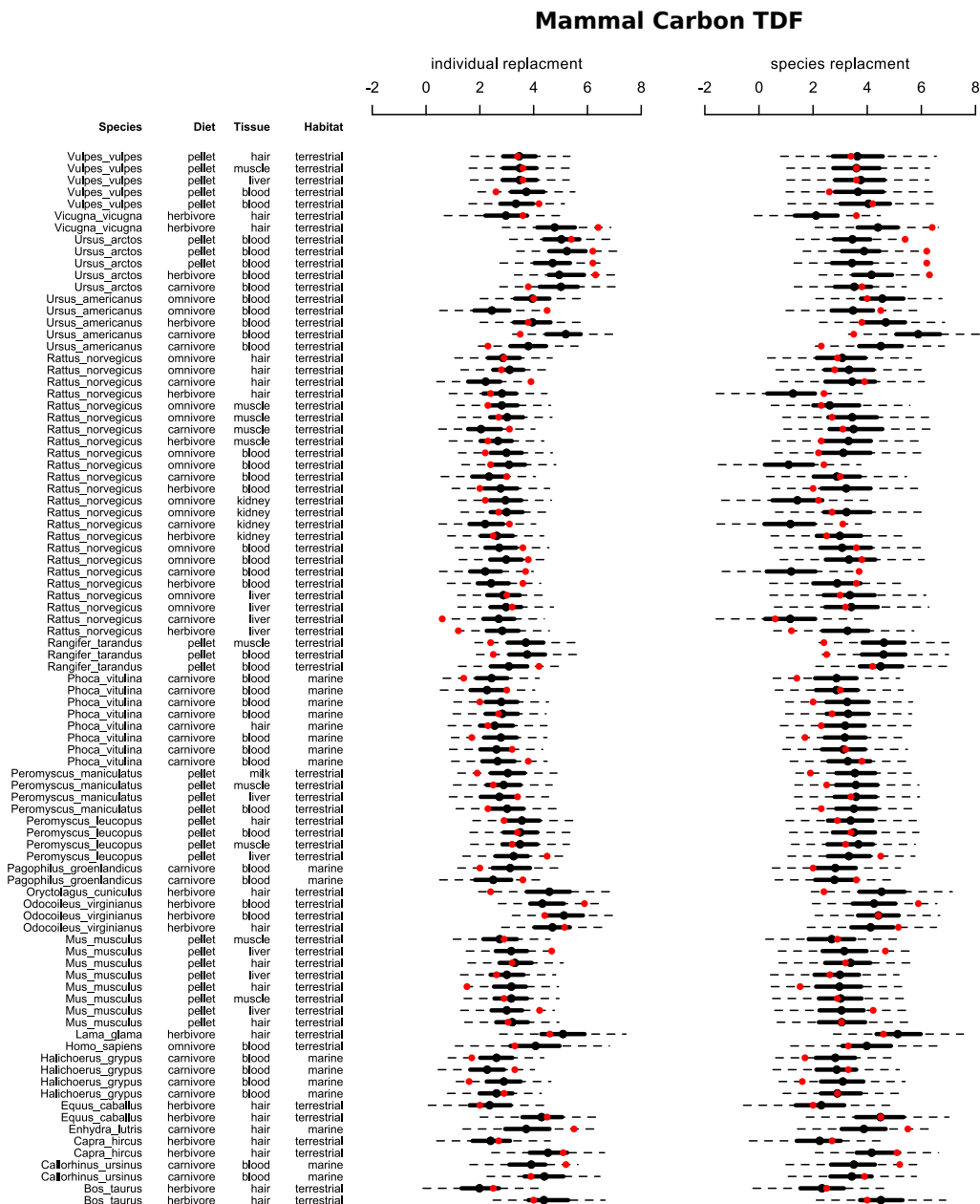
Mammal Carbon TDF

Figure 1.c TDF estimates for carbon for mammals in both individual and species replacement analyses. Black dots represent model estimates, black bars represent 50% CI and dashed bars represent 95% CI. Red dots indicate observed TDF derived from reported controlled diet experiments.
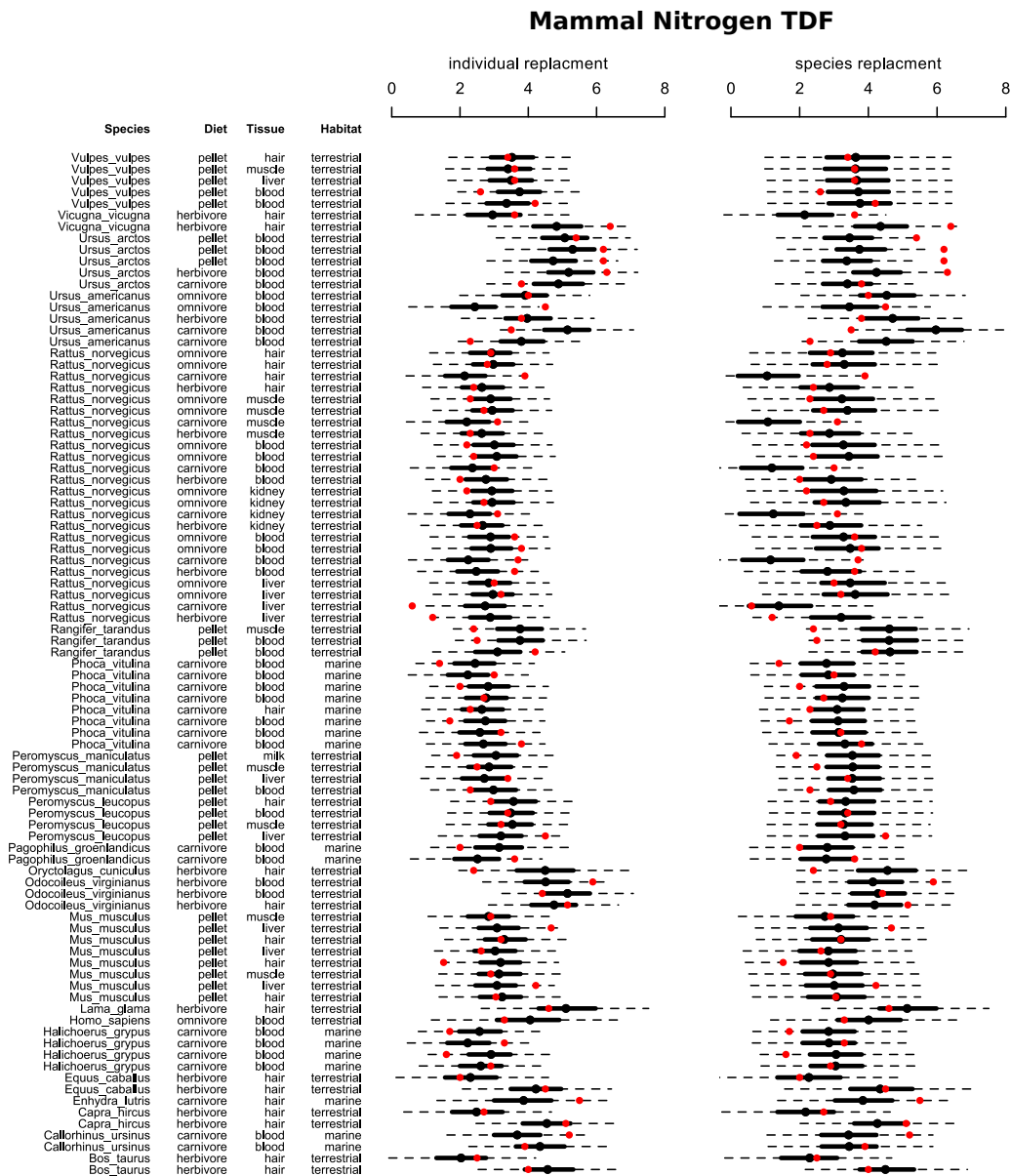
Mammal Nitrogen TDF

Figure 1.d TDF estimates for nitrogen for mammals in both individual and species replacement analyses. Black dots represent model estimates, black bars represent 50% CI and dashed bars represent 95% CI. Red dots indicate observed TDF derived from reported controlled diet experiments.

While the general accuracy of these estimates was high these estimates varied across species with underestimates as low as -4.11 in *Larus heermanni* and overestimates as high as 4.63 in *Larus delawarensis* (Figure 1a). The uncertainty associated with TDF estimates was lower in the individual replacement analysis in comparison to the species analysis with 95% of the estimates falling within

the intervals of -1.71 and 1.70 of the individual analysis and between the intervals of -2.57 and 2.65 for the species intervals (Figure 2).
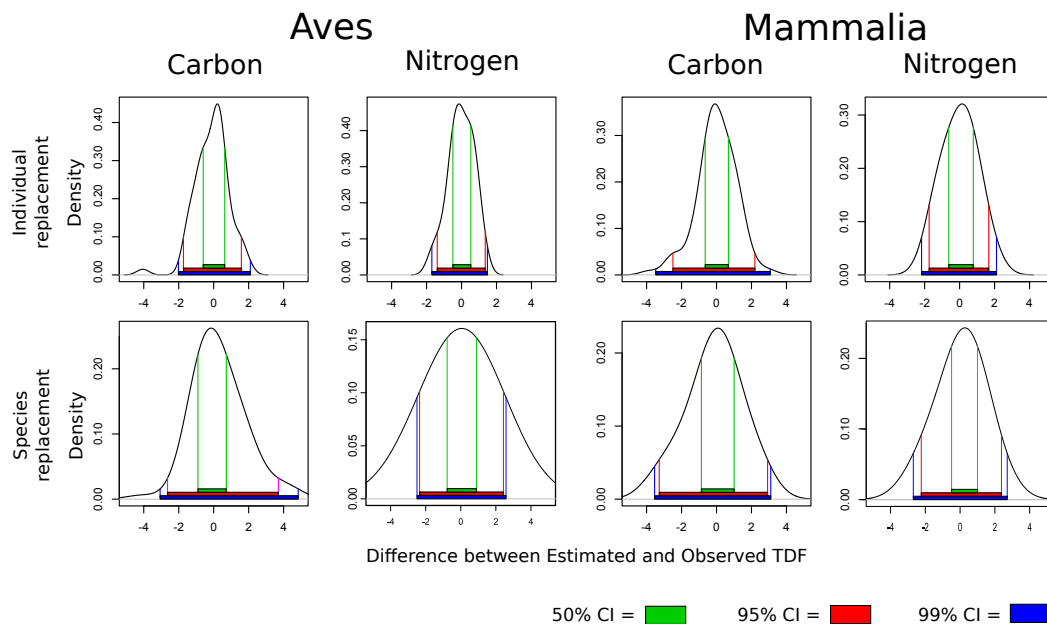

Figure 2. Density histograms of the difference between estimated values using Bayesian imputation and observed values from experimentally controlled dietary studies. The top row gives differences for estimates calculated for individual replacements for both Aves and Mammalia groups, and Carbon and Nitrogen elements. The bottom row gives differences for the species replacement analysis. Green bars represent 50%, red bars 95% and blue bars 99% confidence intervals.

The accuracy and uncertainty in models run without the inclusion of source isotopic ratio as a fixed factor with a mode difference between estimated and observed values found to be 0.19 for individual replacement and 0.05 for species replacement for carbon in birds; -0.14 (individual) and 0.16 (species) for nitrogen in birds; 0.23 (individual) and 0.01 (species) for carbon in mammals; and 0.003 (individual) and 0.42 (species) nitrogen in mammals.

Similar to the main analysis the uncertainty associated with TDF estimates in models without source isotopic ratio included was lower in the individual replacement analysis in comparison to the species analysis with 95% of the

estimates falling within the intervals of -1.96 and 1.94 of the individual analysis and between the intervals of -2.72 and 2.90 for the species intervals (Figure 3).
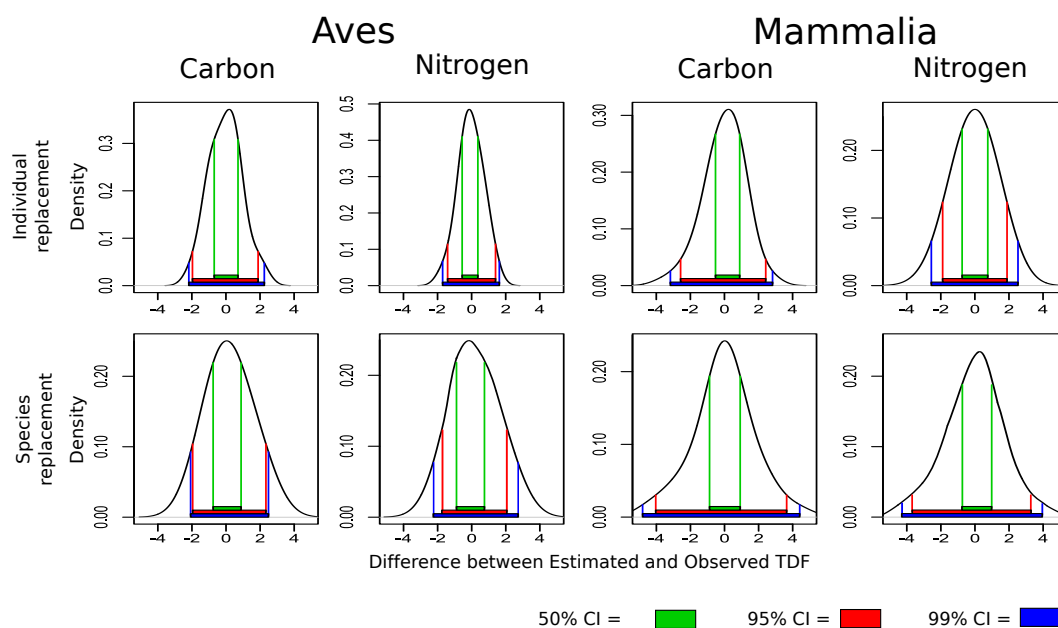

Figure 3. Density histograms of the difference between estimated values using Bayesian imputation without source isotopic ratio included and observed values from experimentally controlled dietary studies. The top row gives differences for estimates calculated for individual replacements for both Aves and Mammalia groups, and Carbon and Nitrogen elements. The bottom row gives differences for the species replacement analysis. Green bars represent 50%, red bars 95% and blue bars 99% confidence

Discussion

Here, we present DEsiR an approach for the estimation of unknown carbon and nitrogen Trophic Discrimination Factor (TDF) values in bird and mammal species. Our approach builds on previous studies that identified various sources of variation in TDF (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Caut, Angulo et al. 2009) (McCutchan, Lewis et al. 2003, Olive, Pinnegar et al. 2003) and extends them by including additional studies measuring TDF and by incorporating important additional sources of variation including phylogenetic structure and the error associated with measurements within a species. Of the additional sources of variation that we investigated, phylogeny was found to be

particularly important for nitrogen TDF for both birds and mammals but accounted for little variation for carbon TDFs. This suggests that while closely related species are likely to share a similar nitrogen TDFs, nearest-neighbour estimates are not a suitable method for estimating carbon TDFs. In contrast, a large proportion of the variation in carbon TDF estimates for birds, and to a lesser extent in mammals, was attributed to variation among tissues but also was simply left as residual error for species across studies (i.e. the error associated for a species after controlling for tissue type, diet type etc). Foraging environment was a source of significant variation for both carbon and nitrogen TDF estimates in birds, and for nitrogen estimates in mammals, with species foraging in terrestrial environments exhibiting lower TDF values than those in marine environments. While environment has been found to be a significant factor in previous studies (Caut, Angulo et al. 2009) for stable isotope ratios, these effects have not been previously recorded for nitrogen TDFs. Further data will allow for more detailed comparison of the effects of environments with the terrestrial biome, mainly freshwater environments.

In comparison to previously developed approaches for estimating TDF (Caut, Angulo et al. 2009), our models allow the phylogenetic relationship of species with available data to influence TDF estimation along with other sources of TDF variation. The accuracy of this method was validated both through leave-one-out cross validation replacement of single observations and replacement of whole species. As expected the accuracy of single observation replacement was higher than whole species replacement owing to the additional loss of information in the species removal process. However, the primary difference between the performances of the two validation models is as one would expect. If you estimate a species that is present in the dataset used to fit the model (i.e. the species removal validation) then the estimated TDF is more precise than if you estimate a species that is not present in the dataset used to fit the model (i.e. the species removal validation).

All models are but an approximation of the real world and are only as good as the data available; thus, under our approach, TDF estimates for some species are

likely to be more accurate than others. For example, in our single species replacement model, our estimates of carbon TDF for two North American gulls, *Larus delawarensis* and *L. heermanni*, are among the least accurate in the model. This may reflect peculiarities in, or a lack of detailed data relating to, the ecology and physiology of these species, such as the high level of terrestrial foraging in many gull species or the physiological process of salt excretion used by these species (Douglas 1970). Nonetheless, as more data on TDF becomes available, our approach to TDF estimation will become increasingly powerful.

Irrespective of improvements in accuracy, the ability to calculate an appropriate error associated with them can in turn be applied to current Bayesian isotope mixing models (Moore and Semmens 2008, Parnell, Inger et al. 2010), which encourage inclusion of all sources of uncertainty so as to propagate this uncertainty towards the final dietary or trophic estimates (Phillips, Inger et al. 2014) . Our approach also allows for flexibility in the model applied to estimate TDF values, which is particularly important as many of the factors influencing TDF are still debated, such as the isotopic ratio of the source itself (Phillips, Inger et al. 2014). Similarly, while our approach is currently confined to birds and mammals, it can also easily be adapted and extended to other taxonomic groups as further data on the TDF and/or phylogenetic relationships of the taxa become available and more information from controlled diet studies on both new species as well as those already included in the dataset.

We provide *R* code (https://github.com/healyke/DEsiR) for the estimation of carbon and nitrogen trophic enrichment factors for any bird or mammal species, which can easily fit into the input of current stable isotope mixing models and also be extended to other taxonomic groups in the future. By incorporating phylogeny, ecology and the error associated with TDF estimates, our approach can provide more accurate dietary proportion estimates along with a more honest representation of their precision. A key feature of our method is that it provides a framework which lends itself to refinement and improved estimates as more TDF data from experimental studies becomes available.

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