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Unifying error structures in commonly used biotracer mixing models

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Abstract. Mixing models are statistical tools that use biotracers to probabilistically estimate the contribution of multiple sources to a mixture. These biotracers may include contaminants, fatty acids, or stable isotopes, the latter of which are widely used in trophic ecology to estimate the mixed diet of consumers. Bayesian implementations of mixing models using stable isotopes (e.g., MixSIR, SIAR) are regularly used by ecologists for this purpose, but basic questions remain about when each is most appropriate. In this study, we describe the structural differences between common mixing model error formulations in terms of their assumptions about the predation process. We then introduce a new parameterization that unifies these mixing model error structures, as well as implicitly estimates the rate at which consumers sample from source populations (i.e., consumption rate). Using simulations and previously published mixing model datasets, we demonstrate that the new error parameterization outperforms existing models and provides an estimate of consumption. Our results suggest that the error structure introduced here will improve future mixing model estimates of animal diet.

Key words: Bayesian; biotracers; fatty acid; mixing model; MixSIR; SIAR; stable isotope.

Introduction

Studies in trophic ecology often require estimates of consumer diets. Typically, the diets of consumers are difficult to quantify because direct in situ observations are challenging. When direct observation is not possible, researchers have relied on a raft of techniques, including experimentation, fecal analysis, and gut content analysis (Paine 1966, Root 1967, Hyslop 1980). In recent decades, ecologists have increasingly leveraged biological tracers ("biotracers") in order to estimate consumer diet. Common biotracers include bulk stable isotopes (SI) as well as compound-specific SI and fatty acids (Boecklen et al. 2011).

Mixing models use biotracers to quantify diet by calculating source (prey) proportions to a mixture (consumer), using the principle, "you are what you eat." While they are commonly applied to diet analyses, mixing models also inform such basic ecological inquiries as animal movement, nutrient cycling, and interspecific interactions (Caut et al. 2006, Granek et al. 2009, Carlisle et al. 2012). More broadly, mixing models are employed across the natural sciences to elucidate source contributions to a mixture; for instance, to identify sediment sourcing in river systems using trace element fingerprinting (Dutton et al. 2013, Nosrati et al. 2014). Herein, we use the terms "source" proportions to a "consumer" using "tracer" data, although a given application may use fatty acids to estimate prey proportions of an animal's diet (Iverson et al. 2004, Galloway et al. 2014*a, b*), or use compound-specific SI to estimate sediment sources of a soil sample (Gibbs 2008, Blake et al. 2012).

Recent Bayesian approaches to mixing models (Moore and Semmens 2008, Semmens et al. 2009*b*, Parnell et al. 2010) have addressed many of the criticisms leveled at simpler linear mixing models (e.g., IsoSource; Phillips and Gregg 2003), such as the inability to incorporate prior information, the failure to encapsulate uncertainty in tracer data, and the assumption that all consumers in a population share the same diet proportions. For ecologists, a main advantage of Bayesian mixing models is that their flexible likelihood-based structure allows them to account for variability in consumer tracer data (hereafter, consumer variability) due to known biological processes (Appendix S1: Table S1).

The most widely used Bayesian mixing model software packages are MixSIR (Moore and Semmens 2008) and SIAR (Parnell et al. 2010), which differ in their assumptions about consumer variability (i.e., their error structures). This difference has been debated in the literature

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(Jackson et al.2009, Semmens et al. 2009*a*), but has not been resolved, with model choice likely based on software platform and familiarity rather than statistical philosophy. Since the difference between MixSIR and SIAR is subtle, the biological assumptions of these mixing models may be unclear to many ecologists. The objectives of our analysis are to unify and improve the MixSIR/SIAR framework by introducing a more process-based formulation of uncertainty in mixing models (Stock and Semmens 2013), and to evaluate how this new formulation compares to the existing models. Herein, we introduce a set of ecological process-based scenarios in order to understand the assumptions behind each error structure. We then explicitly define the model error structure equations, and finally, we evaluate model performance.

Model descriptions

Thinking of a simple hypothetical consumer-source interaction will help illustrate two ways variability in source tracer values propagates into consumer variability. Imagine a consumer population feeding exclusively on one source. After subtracting the trophic discrimination factor (TDF, difference between tracer values in consumer and source tissues), we expect the consumer tracer values to directly match those of the source. However, if we think of predation events as individual consumers sampling the source population tracer distribution, there are two reasons consumer tracer values can differ from the source mean due to the process of sampling alone:

1. Sampling error: Consumer tracer values are an average of a finite number of samples, and there will be some variability in these sample means due to chance.
2. Specialization: Individual consumers may preferentially sample above or below the source mean, resulting in some consumers enriched or depleted. For instance, larger shrimp can have higher $\delta^{13}C$ values (Fry and Arnold 1982), so larger fish preferentially eating larger shrimp would be enriched in ^{13}C relative to smaller fish.

We refer to these as "process error": variation in consumer tracer values due to the sampling process. Researchers also can include "residual error" terms in mixing models to account for other agents of consumer variability, such as individual differences in digestibility, assimilation efficiency, and metabolic rates (see Table 1 in Boecklen et al. 2011). Importantly, note one conspicuously absent driver of consumer variability—diet. If we do not include hierarchical model structures (as in Semmens et al. 2009*b*), all consumers are assumed to have the same diet. Researchers assume that deviations among consumers are due to some combination of these process and residual errors to derive mixing model error structures, which we introduce below:

Model 1: consumers as perfect specialists (MixSIR)

Consumers sample at exactly one location from each source distribution. All variability in consumer tracer values results from individual specialization and sampling error as described previously (process error, Fig. 1a). Model 1 assumes the consumer tracer values, X_{ij}, follow Eq. 1:

$$X_{ij} \sim N\left(\sum_k p_k\left(\mu_{jk}+\lambda_{jk}\right), \sum_k p_k^2\left(\omega_{jk}^2+\tau_{jk}^2\right)\right) \quad (1)$$

where:

X_{ij} = tracer value j of mixture (consumer) i,
p_k = (diet) proportion of source k (estimated by model),
μ_{jk} = source k mean for tracer j,
λ_{jk} = mean trophic discrimination factor (TDF) for tracer j on source k,
ω_{jk}^2 = source k variance for tracer j, and
τ_{jk}^2 = discrimination factor variance for tracer j on source k.

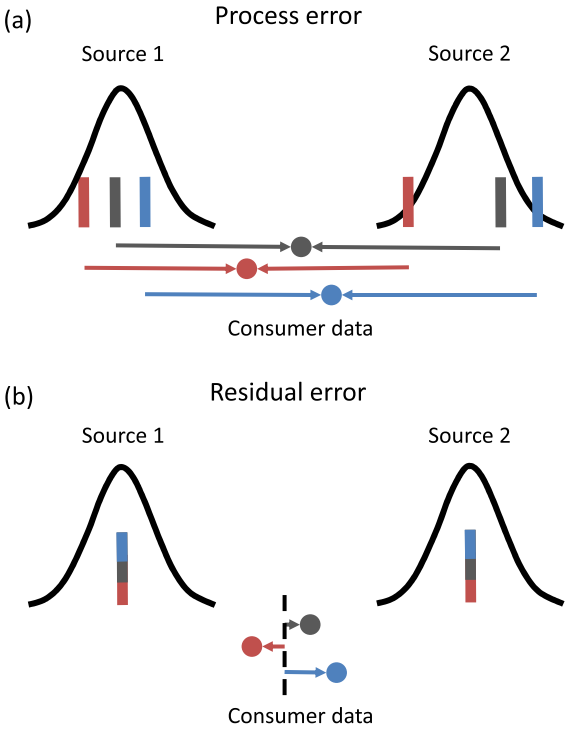

FIG. 1. Mixing model error terms. (a) Process error: consumers sample in different locations from each source distribution, and the variation in consumer tracer values is due to this sampling process. For example, the blue consumer has a higher tracer value (blue circle) than the red and grey consumers (red, grey circles) because it samples sources with higher tracer values (blue lines). (b) Residual error: all consumers sample from the source means (colored lines), and variation in consumer tracer data (circles) is due to unexplained deviations from the consumer mean (black dashed line). Potential sources of residual error include individual differences in digestibility, assimilation efficiency, and metabolic rates (see Table 1 in Boecklen et al. 2011).

The variance term in Model 1 (MixSIR, Eq. 4 in Moore and Semmens 2008) is the mathematical result obtained by adding k independent normal random variables, and defines the consumer variance as a function of the source variances (Fig. 1a). Importantly, note that no distinction is made between source variance, ω_{jk}^2, and TDF variance, τ_{jk}^2. Researchers often do not directly measure TDF means or variances for their system, yet accurate estimates of these quantities are important to mixing model results (Bond and Diamond 2011).

Model 2: consumers as perfect integrators, but with residual error

Consumers randomly sample the source distributions many times, effectively sampling the mean. The observed spread in consumer tracer values is entirely due to unexplained deviations from the mean (residual error, Fig. 1b). While this "residual error only" model appears simpler, it introduces j new parameters by adding one σ_j^2 residual error term per tracer, seen in Eq. 2:

$$X_{ij} \sim N\left(\sum_k p_k\left(\mu_{jk}+\lambda_{jk}\right), \sigma_j^2\right). \quad (2)$$

Model 3: consumers as perfect specialists, but with residual error (SIAR)

Consumers sample at exactly one location from each source distribution, which results in some consumer variability as in Model 1. Then we assume the consumer variability is higher than expected under Model 1, so we add residual error as in Model 2. This is how SIAR-based models are structured (Parnell et al. 2010). Model 3 (SIAR, Eq. 9 in Parnell et al. 2010) adds the variance terms in Models 1 and 2:

$$X_{ij} \sim N\left(\sum_k p_k\left(\mu_{jk}+\lambda_{jk}\right), \sum_k p_k^2\left(\omega_{jk}^2+\tau_{jk}^2\right)+\sigma_j^2\right). \quad (3)$$

The advantage of Model 3 is that it can fit "wide" consumer data, with more variability than that of the sources, unlike Model 1 (Fig. 2a). On the other hand, Model 3 must fit j additional parameters. Both Models 1 and 3 are unable to fit "narrow" consumer data, where the consumer variance is less than that of the sources (Fig. 2c). Yet, one may expect this to be the case in natural predator-prey systems, as each consumer repeatedly samples the prey population.

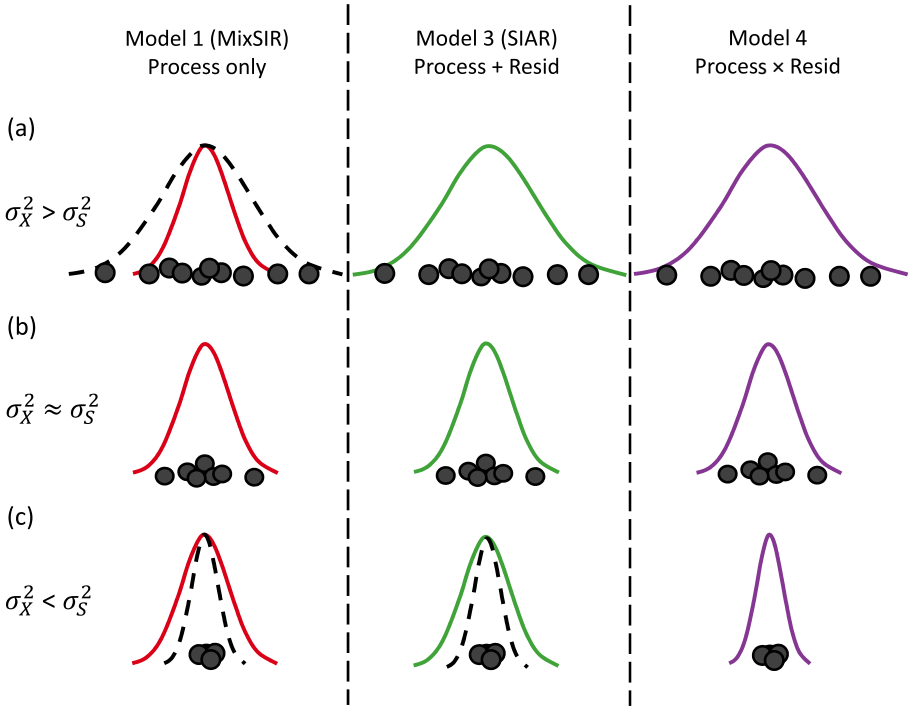

FIG. 2. 1-tracer distributions of different consumer variances, demonstrating the difference between Model 1 (process error only, MixSIR), Model 3 (process + residual error, SIAR), and Model 4 (process × residual error). Solid colored lines show each model fit to the consumer data (black points), and black dashed lines show the true consumer distribution. (a) Model 1 cannot fit wide consumer data, $\sigma_X^2 > \sigma_S^2$, because it does not have a residual error term. (b) When the consumer and source variances are roughly equal, $\sigma_X^2 \approx \sigma_S^2$, all models fit well. (c) Models 1 and 3 cannot fit narrow consumer data, $\sigma_X^2 < \sigma_S^2$, where the consumer variance is much less than the source variances. Note that all models fit the same mean.

Model 4: consumers between perfect specialists and perfect integrators

Considering these existing frameworks, it becomes clear that the ecologically most realistic scenario is missing; namely, Model 4, in which consumer populations fall somewhere between perfect specialists and perfect integrators. Model 4 multiplies the process error by a multiplicative error term, ε_j, as in Eq. 4:

$$X_{ij} \sim N\left(\sum_k p_k\left(\mu_{jk}+\lambda_{jk}\right), \sum_k p_k^2\left(\omega_{jk}^2+\tau_{jk}^2\right)\times\varepsilon_j\right). \quad (4)$$

The multiplicative error term, ε_j, allows the model to switch consumers from perfect integrators $(\varepsilon_j = 0)$ to perfect specialists $(\varepsilon_j = 1)$ to fit narrow consumer data, as well as fit wide consumer data with more variability than expected under Model 1 ($\varepsilon_j > 1$; Fig. 2a–c). A U(0,20) prior was chosen for the ε_j term because models with this prior outperformed others considered in simulation tests (Appendix S2: Figs. S1 and S2).

Model 4 has the same number of parameters as Models 2 and 3. However, in contrast to the ecologically meaningless σ_j^2 residual terms in Models 2 and 3, the ε_j term is related to the consumer consumption rate (biomass consumed per tissue turnover period). The underlying idea is that the ratio of consumer tracer variance to source variance contains information about how frequently consumers sample sources—more frequent sampling reduces consumer variance. If we assume that all consumer variability is either due to process error (Fig. 1a) or accounted for by covariates (i.e., there is no residual error), then we can solve for consumption, C, in terms of the variance, biomass, and diet proportion of the sources (for derivation see Appendix S3). The consumption of each source, C_k, is then $C_k = Cp_k$.

We hypothesize that Model 4 is generally a more appropriate model than Models 1 and 3, especially for systems with narrow consumer data $(\varepsilon_j < 1)$. We used simulated and published datasets to test the performance of all four models, calculating model selection criteria such as relative error, DIC, and credible interval width.

Methods

Simulations

We first tested the models using simulated data where the "true" diet proportions were known, across a range of consumer variability—generated by allowing consumers to sample the source distributions a variable number of times (C = 320, 160, 80, 40, 20, 10, 5) and adding residual error. We carried out all simulations for a simple case of three sources, two tracers, 10 consumer data points, and each source biomass = 1. Since mixing models assume that the correct sources have been identified a priori, we did not allow any source to contribute <5% to the true diet.

We simulated 1,000 datasets for each level of consumer variability, according to the following pseudo-code (see Appendix S9 for code):

1. Generate true proportions, p_k, for each source k ($\boldsymbol{p}$ is a K-vector, the number of sources):

$$\boldsymbol{p} \sim \text{Dirichlet}(\boldsymbol{\alpha}),\ \alpha_k = 1$$

2. Generate source means, μ_{jk}, and standard deviations, ω_{jk}, for each tracer j:

$$\mu_{jk} \sim \mathcal{N}(0, 5)$$

$$\omega_{jk} \sim \mathcal{U}(0.5, 1.5)$$

3. Each consumer i takes a sample of size Z_{ik} from source k ($\boldsymbol{Z}_i$ is a K-vector):

$$\boldsymbol{Z_i} \sim \text{Multinomial}(C, \boldsymbol{p})$$

4. Consumer i draws Z_{ik} samples from source k, resulting in sample means Y_{ijk} for each tracer j:

$$Y_{ijk} = \frac{\sum_{z=1}^{Z_{ik}} \mathcal{N}(\mu_{jk}, \omega_{jk}^2)}{Z_{ik}}$$

5. Each consumer i's tracer values, X_{ij}, are means of all source samples:

$$X_{ij} = \frac{\sum_k Y_{ijk} Z_{ik}}{C}$$

6. Add residual error from $\mathcal{N}(0, 0.1)$.

Representative simulated datasets across the range of consumer variability are shown in Appendix S4: Fig. S1.

For each dataset, we fit all four models via Markov Chain Monte Carlo (MCMC) using JAGS and R software (Plummer 2003, R Core Team 2015). We assessed model convergence with the Gelman-Rubin diagnostic, not allowing more than 50 values above 1.1 across all variables and datasets for each level of mixture variability (Gelman et al. 2004). Finally, we used the following metrics to gauge model performance (for details see Appendix S5):

1. Proportion of true p_k captured within 95% credible intervals.
2. Mean difference in DIC (ΔDIC).
3. Mean 95% credible interval width.
4. Mean absolute percent error.

Published datasets

Simulations are useful in model assessment because knowing the truth allows us to evaluate model accuracy and precision. However, simulated data may not adequately describe variation found in natural systems.

While we hypothesize that Model 4 will perform well in situations with narrow consumer data, how often is this the case?

We surveyed the recent ecological literature for published datasets from studies employing mixing models. Searching in ISI Web of Science for terms "stable isotope*" AND "mixing model*" returned 387 articles for years 2012–2014, of which thirteen had complete data—raw consumer tracer values (not means and standard deviations), source tracer values (raw, or means, standard deviations, and sample size), and discrimination values (Appendix S6). Three additional SI datasets were available online and opportunistically included (Stock and Semmens 2013). As in the simulation study, we fit the models via MCMC using JAGS and R, remaining faithful to the original mixing model analysis as performed by the authors. We included multiple mixture groups analyzed separately by the authors as one model with fixed effects in order to avoid one study dominating the results (see Appendix S10 for code). We compared models solely using ΔDIC, since estimating model accuracy without knowing the true diet is not possible.

Results

Simulations

Models 2 and 4 outperformed Models 1 and 3 (MixSIR and SIAR) across all measures of model selection for low consumer variability: lower ΔDIC (Fig. 3a), more accurate point estimates (Fig. 3b), tighter credible intervals (Fig. 3c), and lower absolute percent error (Fig. 3d). Model 4 performed similarly to Model 2 (residual error only) except a slight tradeoff between accuracy and precision for datasets with higher consumer variability (Fig. 3). As expected, Model 1 (MixSIR) was clearly the worst model for datasets

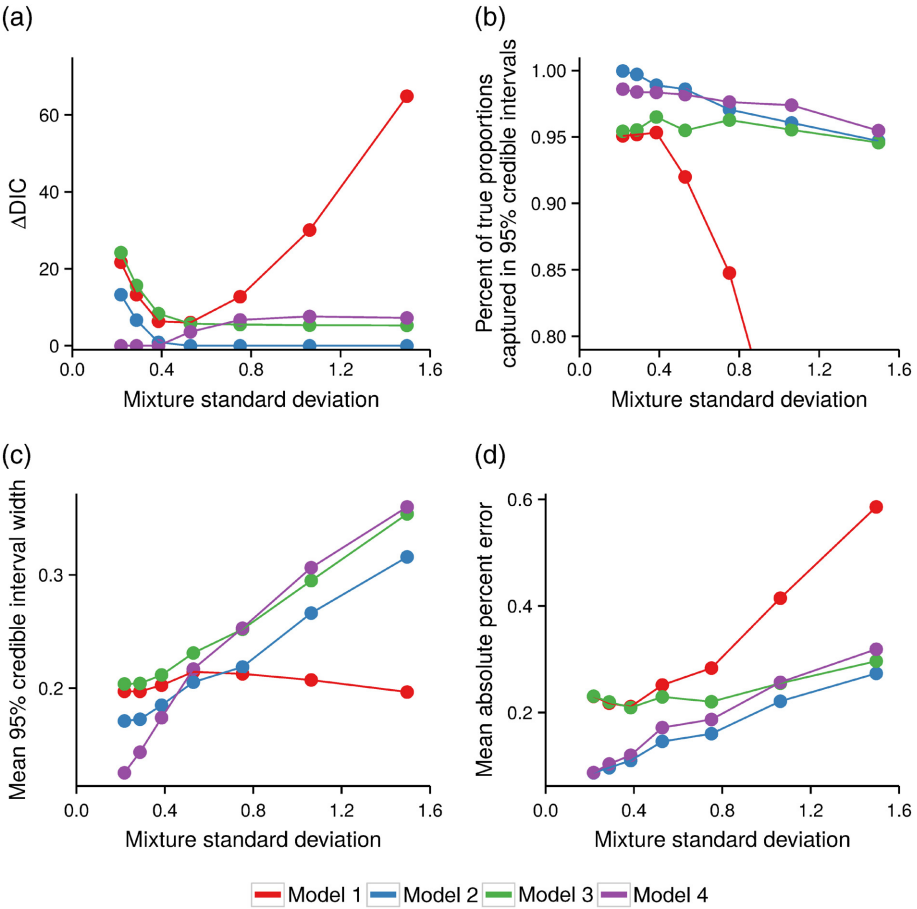

Fig. 3. Simulation results as functions of consumer variance: (a) mean ΔDIC, (b) percent of true proportions captured by 95% credible intervals, (c) mean 95% credible interval widths, and (d) mean absolute percent error (MAPE). Model 1 = process error only (MixSIR), Model 2 = residual error only, Model 3 = process + residual error (SIAR), and Model 4 = process × residual error. MAPE is calculated as $\sum \left| \frac{est.p - true.p}{true.p} \right| / 1{,}000$, where *est.p* is the proportion point estimate (median posterior density) and *true.p* is the simulated "true" proportion. Error bars (SE) are smaller than the size of points (n = 1,000 simulations).

with higher consumer variability, while the other three models performed adequately.

Published datasets

Without knowing the true proportions of the published datasets, we cannot evaluate the models' accuracy or bias directly. However, Models 2 and 4 fit the published datasets better than Models 1 and 3 overall, as evidenced by lower median ΔDIC values (Model 2 = 1.5, Model 4 = 2.7, Model 1 = 8.1, Model 4 = 9.2, Fig. 4). Model 2 had strong support for most datasets (11 out of 16 ΔDIC ≤3.2), but performed poorly in the others (five out of 16 ΔDIC ≥40). Just under half (46%) of the estimated ε_j terms in Model 4 were less than one, indicative of narrow consumer data (Appendix S7: Fig. S1). Based on the simulation results, we would expect Model 4 to outperform Models 1 and 3 for these datasets with $\varepsilon_j < 1$ (more accurate point estimates and tighter intervals). Model 4 diet estimates were quite different than those of Models 1 and 3 for some—but not all—datasets (for a typical example, Appendix S7: Fig. S2).

Consumption rate calculation

We calculated consumption rates from ε_j terms estimated by Model 4 fit to data simulated without residual error, and these agreed with the true simulated consumption rates (Appendix S3: Fig. S1). We then tested the practicality of using ε_j to estimate consumption rates using a familiar SI mixing model application to coastal wolf diet (Semmens et al. 2009*b*). Inserting the fitted ε_j values (maximum posterior densities, 0.90 and 0.38) into Eq. 4 yielded consumption rates between 3.8 and 0.3 kg per wolf per day (see Appendix S3 for calculations), which straddle other estimates of consumption for wolves primarily relying on deer (Kolenosky 1972, Person et al. 1996).

Discussion

The error structures in two commonly used Bayesian mixing models, MixSIR (Model 1) and SIAR (Model 3), were clearly outperformed by Models 2 (residual error only) and 4 (multiplicative error) in both simulations and published datasets. This is likely due to inaccurate underlying assumptions about the biological process of predation, where it is helpful to think of predation events as individual consumers sampling the source population biotracer distributions.

Models 2 and 4 performed similarly in simulation tests (Fig. 3), but Model 4 rests on more ecologically realistic assumptions. Model 2 assumes the observed variation in consumer tracer values is completely due to unexplained deviations from the mean (Fig. 1b). In contrast, Model 4 is founded on a basic biological process—consumers sample sources through predation events—linked to the consumption rate. Thus, we advise implementing multiplicative error (Model 4) as the default option in mixing models, although Models 1 and 2 are useful in some cases. For instance, Model 1 is the only option for fitting single mixture data points and may make sense when including hierarchical structures. Model 2 could be preferred in applications other than diet estimation (e.g., sediment sourcing), or where consumers essentially feed infinitely many times (e.g., filter feeders such as oysters).

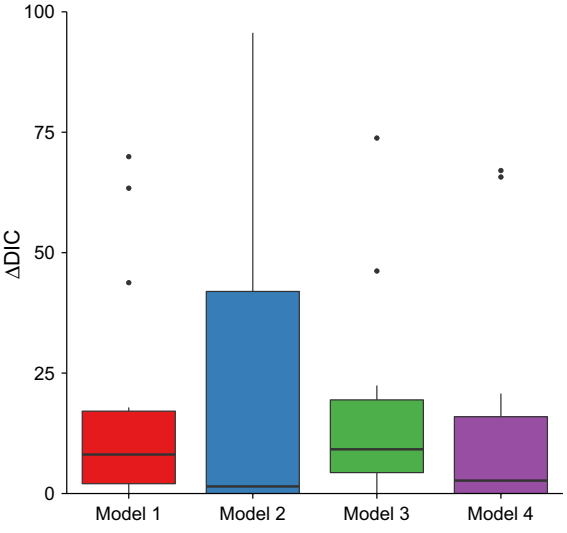

Fig. 4. Differences in DIC from the model with lowest DIC for each literature dataset. Model 2 had the lowest DIC (ΔDIC = 0) for six of the 16 datasets and lowest median ΔDIC, 1.5. Model 4 had the lowest DIC for five of the 16 datasets and next lowest median ΔDIC, 2.7. Models 1 and 3 had higher median ΔDIC: 8.1 and 9.2, respectively. DIC differences of 3–7 are significant.

If predation cannot be envisioned as occurring in discrete events, as with oysters filter feeding, the quantitative estimates of consumption from Model 4 may not make sense. In such cases, the ε_j terms should still qualitatively agree with our biological knowledge of the consumption rate (see Appendix S7: Table S1 for all ε_j estimates). For example, it is unclear what the biomass of POM that an oyster consumes in a "predation event" is, or even if it makes sense to think of "predation events" for oysters. Model 2 is probably more appropriate for oysters: assume they integrate so many source particles that they effectively "feed at the mean" of each source. Still, Model 4 estimates low ε_j (0.13 and 0.32, Appendix S7: Table S1), which is consistent with our conceptualization of how consumer sampling affects biotracer variance—oysters consume many individual particles per tissue turnover period, thus we expect their biotracer values to vary less than that of their sources.

Importantly, the relative support for Model 4 increases as biotracer variability from ecological processes is accounted for in the mixing model (Appendix S1: Table S1). As an example, consider the wolf SI dataset of Semmens et al. (2009*b*). Adding region and pack as random effects in the model explains much of the

variation in wolf isotope values. As a result, the consumer variance becomes less than the source variance, ε_j estimates decrease, and Model 4 gains more support (Appendix S8: Table S1). Researchers are increasingly building such processes into mixing models, and Model 4 should perform well in these process-based mixing models (Parnell et al. 2013, Ogle et al. 2014).

Relative support for Model 4 also depends on researchers faithfully incorporating uncertainty in trophic discrimination factor (TDF) values. Recall that mixing models do not distinguish source variance from TDF variance (ω_{jk}^2 and τ_{jk}^2 in Eqs. 1–4). Including unrealistically low estimates of τ_{jk}^2, or worse, assuming a single fixed TDF ($\tau_{jk}^2 = 0$), artificially reduces $\sum p_k^2 \left(\omega_{jk}^2 + \tau_{jk}^2\right)$ and increases ε_j in Eq. 4, weakening relative support for Model 4 over Models 1 and 3. Along with others, we consider the inclusion of uncertainty in TDFs into Bayesian mixing models a significant advance (Bond and Diamond 2011), especially given the wide range of calculated TDFs and the prevalence of borrowing literature values from different species and tissues (Caut et al. 2009). Calculating TDF variance via feeding experiments is clearly preferable, and we suspect mixing model users tend to underestimate TDF variance when using borrowed values. In such cases, including appropriate τ_{jk}^2 values would strengthen relative support for Model 4.

Including ecological processes and realistic TDF variance in mixing models not only determines relative model support, it also strongly affects the consumption rate calculation. The idea that there is information about consumption rate in the ratio of consumer to source biotracer variance is intriguing and merits further study, since consumption is fundamental to population dynamics but difficult to measure (Lotka 1925, Holling 1959). The primary limitation is that ε_j is confounded with unexplained, residual error. Thus, consumption estimates depend on accurate measures of the variability in consumer and source tracer values, as well as accounting for consumer variability from ecological processes and trophic discrimination. Additionally, the method derived here should underestimate consumption, since it assumes all of the consumer variance is due to the sampling process, when in reality some is due to residual error (i.e., ε_j are too high). Despite these limitations, this work provides a basis upon which to improve estimates of consumption via source apportionment, especially as including more (and better conserved) biotracers becomes common in ecology (e.g., fatty acids, compound-specific SI).

Finally, there has been confusion whether the models considered here—simply by virtue of being Bayesian—can solve the problem of underdetermined systems (number of sources > number of tracers + 1, Boecklen et al. 2011). We simulated determined systems (three sources, two tracers), but six of the sixteen published datasets analyzed were underdetermined (Appendix S6: Table S1). While Bayesian mixing models can fit any number of sources, they are not a panacea for underdetermined systems—as Brett (2014) demonstrates, the "uninformative" prior has more weight the less information (more uncertainty) the data contain. Including biotracers beyond bulk SI offers the opportunity to increase the number of sources while avoiding underdetermined systems. We caution, however, that the effect of an "uninformative" prior increases with the number of sources and is not only an issue in underdetermined systems—this is true even with more tracers than sources.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1517/suppinfo