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Interpreting Past Human Diets Using Stable Isotope Mixing Models—Best Practices for Data Acquisition

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Abstract

Using stable isotope mixing models (SIMMs) to quantify past diets is becoming increasingly common in archaeology. This study highlights important field-specific difficulties encountered by archaeologists in reconstructing palaeodiets using SIMMs. Focusing on the data acquisition stage, we discuss several issues that could confound dietary quantification if not accounted for. These issues are categorized under several broad categories: diagenesis, intra-individual variability, representativeness of both the consumers and sources, and other commonly encountered field-specific problems. We summarize these issues with a flow chart to help archaeologists to select the most appropriate samples for dietary reconstruction using SIMMs, thereby decreasing the probability that the outputs of the SIMM are inaccurate. We conclude by discussing the ways in which SIMMs may not be appropriate for all archaeological contexts, highlighting those areas that are likely to be the most problematic for end users.

Keywords Stable isotopes; · Palaeodietary reconstruction; · Mixing models; · Data acquisition

Introduction

Stable isotope mixing models (SIMMs) are analytical models that can be used to determine the contribution of various sources to a mixture. In archaeology, SIMMs are primarily used to estimate dietary compositions of past communities, where the

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"mixture" typically refers to human tissue and the "sources" refer to the different dietary components. Based on the premises that (i) the dietary components in question are isotopically distinct and that (ii) the isotopic compositions of sources are incorporated into the body tissues of the consumer in a predictable way, it is possible to mathematically deduce the relative contribution of each source to a consumer's diet, with varying degrees of uncertainties. Thus, instead of providing a qualitative description such as "group X consumed a substantial amount of marine foods", with SIMMs it is possible to describe past diet quantitatively, *i.e.*, "marine foods likely contributed 50 ± 15% to group X's diet". As a result, despite some limitations in sensitivity and accuracy, numerous studies have demonstrated that SIMMs can be very useful in answering certain archaeological questions, for example quantifying differences in dietary compositions between groups (Cheung *et al.* 2017), and estimating contributions of different subsistence economic activities, such as from farming or hunting-gathering activities (Bownes *et al.* 2017). Moreover, an appealing aspect of some SIMMs is the fact that the outputs are associated with a range of possible solutions, which may more faithfully convey the uncertainty in their estimates.

Initially developed for environmental sciences, SIMMs are one of the many ecological tools that have been adopted by archaeologists. Naturally, there are fundamental differences between the two fields, and the applications of SIMMs in archaeological contexts are therefore, not entirely straightforward. A recent study discussed how different types of SIMMs (linear mixing models, simple probabilistic models, and conditional probabilistic models) can be applied to archaeological contexts (Cheung and Szpak 2020). However, a discussion of the ways in which archaeological data are different from ecological data is a crucial element that is missing from the current literature.

In this paper, we outline some of the major differences between the application of SIMMs in ecology and archaeology, and discuss several important and relevant factors that could confound palaeodietary reconstruction through SIMMs, focusing on the data acquisition stage. The data acquisition stage is the most consequential with respect to generating accurate SIMM estimates. Currently, bone collagen stable carbon and nitrogen isotope values are the most commonly used isotope systems in palaeodietary reconstruction (Szpak *et al.* 2017b). Therefore, we will primarily focus on data collection strategies as they relate to bone collagen. However, there is an increasing number of studies that incorporate isotopic measurements of other biological components such as carbonate (Ambrose *et al.* 2003; Lambert *et al.* 2012; Reitsema *et al.* 2010; Saragoça *et al.* 2016; Somerville *et al.* 2015) or individual amino acids (Cooper *et al.* 2016; Itahashi *et al.* 2014; Jaouen *et al.* 2019; Naito *et al.* 2013; Webb *et al.* 2015). The general principles discussed below should also apply to these and other analytical substrates whose isotopic compositions reflect those of the diet.

Diagenesis of Archaeological Materials

The first challenge for archaeologists is the problem of contamination and degradation of the analytical substrates. If not properly dealt with, contamination and degradation of biological tissues could influence the isotopic compositions of both the consumer (*i.e.*, humans) as well as the sources (*i.e.*, faunal and botanical remains). The possibility that

the isotopic composition of the consumer tissue has been altered in the burial environment is a major concern in archaeological contexts. These concerns also exist in modern ecosystems, but are primarily limited to the presence of lipids in proteinaceous samples such as muscle or skin (Post *et al.* 2007) or the presence of preservatives like formalin (Syväranta *et al.* 2010). Since lipids have lower $\delta^{13}C$ values relative to proteins (DeNiro and Epstein 1978), the presence of variable quantities of lipids can shift the $\delta^{13}C$ values of proteinaceous samples by several per mil (Guiry and Szpak 2020). For ancient mammalian cortical bone, lipids are not abundant enough to be a major concern when measuring the isotopic composition of collagen (Scott 2020), but the presence of humic contaminants (decayed organic matter) can have a similar effect, since these compounds are carbon-rich and primarily derived from C_3 plant matter (van Klinken and Hedges 1995). A series of quality control (QC) criteria exist for bone collagen (C:N ratio, elemental compositions, collagen yield) to eliminate samples that have isotopic compositions that have been significantly altered by contamination or degradation (van Klinken 1999), but these criteria do not account for small alterations to the original isotopic composition for samples that are near the upper or lower limits of these criteria. For instance, the most widely reported QC measure is the C:N ratio, specifically a range of 2.9 to 3.6 for atomic C:N (DeNiro 1985). The amino acid composition of bone collagen, while variable, is not characterized by a wide range in C:N ratios (Szpak 2011). Bone collagen samples with atomic C:N ratios near 3.6 are likely contaminated with either lipids or more likely humics for archaeological samples, both of which will cause the $\delta^{13}C$ values of the measured sample to be lower (Guiry and Szpak 2020). This is relevant in the context of mixing models, because a shift in the $\delta^{13}C$ value of a consumer of <1 ‰ can still significantly impact the outputs, particularly in situations where there is little isotopic separation of the sources.

A further complication when using SIMMs in archaeological contexts is the mixture of taxa and sample types being analyzed. For humans and vertebrate food sources, $\delta^{13}C$ and $\delta^{15}N$ values are generated from bone collagen, but the extent to which degradation and contamination impact the isotopic compositions of the collagen may not be equal across sample types. Fish, for example, have bones that are more prone than mammalian bone to be degraded in the burial environment due to physical and chemical differences (Szpak 2011). The high surface area relative to volume of fish bones compared to dense mammalian cortical bone may also make them more susceptible to contamination with humics in the burial environment.

Although the QC criteria for bone collagen are not perfect, abundant experimentation has shown that most of the samples that satisfied the QC criteria are likely to retain their original stable isotopic compositions (Dobberstein *et al.* 2009; Harbeck and Grupe 2009). Compared to bioapatite (Garvie-Lok *et al.* 2004), contaminants in collagen are easier to remove via rigorous sample preparation (Ambrose 1990; Brown *et al.* 1988; Budd *et al.* 2000; Jørkov *et al.* 2007; Stafford *et al.* 1988; Szpak *et al.* 2017a). Moreover, despite attempts to improve the pre-treatment (Pellegrini and Snoeck 2016; Skippington *et al.* 2019) and/or pre-screening procedures (Kontopoulos *et al.* 2018), currently no accepted QC criteria for bioapatite exist. The same is true for isotopic analyses of macrobotanical remains. Because of the heterogeneous nature of these bulk samples, the high amount of isotopic variation that may be observed among plants, and the variability in elemental compositions among plant taxa and parts, QC criteria based on elemental or isotopic compositions do not exist.

It is not the purpose of this study to provide novel solutions to deal with chemically altered archaeological materials. The growing body of literature examining these issues has, however, provided some important tools for screening samples. Within the context of bone collagen, the inclusion of data on the basis of experimentally validated QC criteria will mitigate any increased uncertainty (systematic or random) in the isotopic measurements caused by contamination or degradation. Archaeologists should, nevertheless, treat all isotopic data with due caution—especially those with unusual isotopic compositions. If the samples display clear signs of post-depositional alterations (*e.g.*, based on colour, smell, or sturdiness of sample), and the resulting outputs are at odds with other archaeological evidence, the chances are that the data may be unreliable. These data should be excluded, or that palaeodietary reconstruction (and by extension, SIMMs) based on these data should be reconsidered.

Intra-individual Differences in Biological Tissues and Components

Biological tissues also have different formation times and remodelling rates. In adults, hair and nail have a growth rate of approximately 1 cm and 1.5 to 3 mm per month, respectively (Fraser *et al*. 2006; Lehn *et al*. 2011; Meier-Augenstein and Kemp 2012). Thus, depending on the length of hair and/or nail segment(s) obtained, keratin records the diet in the most recent months for an individual. Tooth dentine and enamel does not turnover once formed and thus records the diet at the time the tissue was being laid down (Zazzo *et al*. 2006). Depending on the tooth, in humans, this could mean anywhere between several months in utero to around 20 years old (Smith 1991). Bone (collagen and bioapatite) has the slowest turnover rate among all body tissues, thus will only provide information on averaged diets over a long period of time (Gineyts *et al*. 2000). Different types of bone (trabecular vs. cortical) can have isotopic signals representing diets from a few years, up to decades in adults (Hedges *et al*. 2007; Lamb *et al*. 2014). And while bone collagen and bioapatite turnover at a slower rate than most other biological tissues, it is likely that bioapatite turns over slightly faster than bone collagen (Tykot *et al*. 1996), although the exact rate is not known.

These variable temporal windows represented by different sample types have significant implications for palaeodietary studies. For example, it is possible to monitor mobility in the form of drastically changed diets through an examination of the isotopic compositions of tissues with different turnover rates (Cheung *et al*. 2017; Cox and Sealy 1997; Lamb *et al*. 2014). However, this also means that isotope data from different elements may represent diets consumed from different timeframes, which could introduce further variables in a SIMM. Furthermore, other than dietary changes, several studies have observed that stress (*i.e.*, growth, starvation, certain pathological conditions) may introduce anomalies in isotopic compositions (Curto *et al*. 2020; Katzenberg and Lovell 1999; Kempster *et al*. 2007). Unless the condition is chronic and very severe, these anomalies are more likely to be recorded in body tissues with faster turnover rates, such as hair, than body tissues with slower turnover rates, such as bone collagen. In tissues with slower turnover rates, some of the stochastic variation that may arise in consumer isotopic compositions because of short-term variation in diet will be minimized by virtue of its long turnover time. Thus, any isotopic signal for short-term stress, or even seasonal dietary habits will be dampened due to the averaging

effect (Farnsworth *et al.* 1985). This is also true for the sources used in mixing models, since most commonly these isotopic data are derived from bone collagen from faunal remains.

Other than turnover rate, different biological components are also characterized by distinct tissue-specific isotopic discrimination factors, even if they are structurally similar. For example, even though the bioapatite in bone and enamel is the same at a chemical level (Kohn and Cerling 2002), studies have shown a larger diet to tissue spacing in enamel (Warinner and Tuross 2009; Webb *et al.* 2014). Similarly, there are also differences in the trophic discrimination factors (TDF) for keratin (hair and nail) and bone collagen (O'Connell *et al.* 2001).

Consequently, when using SIMMs, it is best to use data coming from tissues with slower turnover rates. Ideally, all measurements should come from the same element (*e.g.*, comparing ribs with ribs), or at the very least from elements that are suspected to represent relatively contemporaneous periods in the life of a consumer (Clark *et al.* 2017). This is an important consideration for both intra and inter-site comparisons, especially if data are drawn from multiple studies with different experimental designs. SIMMs already involve a high degree of uncertainty, especially in archaeological contexts, stacking additional sources of error on top could further weaken the estimates.

Representativeness of Consumer Data

Due to practical reasons such as differential preservation, funding constraints, and a desire or responsibility to preserve archaeological materials for future generations, archaeologists can almost never sample every consumer (*i.e.*, human individual) and source (*i.e.*, every distinct individual animal and plant from a given site). Instead, isotopic data from a smaller subset of the population are used to represent that population. Thus, an important consideration is the representativeness of the samples analyzed.

The "appropriate" number of consumers (humans in this case) to sample will ultimately be governed first by the availability of material, secondarily by the questions of the investigator, and lastly by the mathematical constraints imposed by both measurement sensitivity (*i.e.*, analytical error) and the natural variability of isotope compositions in the system. The second criterion is related to both the sampling techniques and the research questions: how were the samples selected? Was a cross section of the population fairly sampled? Are certain segments overrepresented? Is it possible or not to sample a large enough number of individuals to look at intrapopulation differences (e.g., male vs. female, high vs. low status)? If the ultimate goal of the study is to provide a broad-strokes estimate of the diet composition of the population, a smaller sample size would likely suffice relative to a study aimed at understanding the impacts of social inequality or gender-based differences on human diets. Even larger samples will be required if the extent of dietary variation within a population or subsets of a population is an important consideration, as capturing the central tendency (Pearson and Grove 2013) requires fewer samples than the variance (Syväranta *et al.* 2013).

The third criterion is more of a problem for applying SIMMs when sample sizes are small. Unfortunately, the archaeological record is inherently incomplete, and in some

extreme cases, isotopic data from a few individuals or even a single individual is all that is available from a site. Conducting SIMMs using data from a small number of individuals is risky, as one must assume that the isotopic composition is entirely explained by the diet. Such a proposition may sound like a straightforward assumption for any sample size, and this is true to some extent, but situations with very small sample sizes are more problematic. There are other factors that could contribute to variances in the isotope values of the consumers, such as metabolic differences and biased sampling of certain source groups (reviewed in (Cheung and Szpak 2020)). These factors, also called residual errors (Stock and Semmens 2016), are lessened when the number of consumers is large. If the sample number is too low, however, these factors may heavily sway the estimation. Furthermore, overlooking residual error can be more problematic in sites where the ranges of isotopic variability in sources are small, as a small shift in the isotope values of the consumer can potentially lead to drastically different outcomes in SIMMs. For example, assume that bone collagen $\delta^{15}N$ values can vary by ±1 ‰ due to differences in the metabolism and health of an individual. If this individual has access to foods with $\delta^{15}N$ values ranging between +4 ‰ and +8 ‰, the potential impact of those differences on the SIMM outputs will be much greater than in a situation where this individual has access to foods with $\delta^{15}N$ values ranging between +4 ‰ and +20 ‰. Thus, the results of SIMMs based on a small number of consumer data should be interpreted with great caution.

While representativeness is not a problem unique to archaeologists, it is exacerbated by the fact that archaeologists often have no analogue source group from which to draw inferences, and that there is no way to verify *a priori* whether the subsample will be representative of the whole population. For example, what is the probability that a sample of three humans sampled from a given site adequately captures the mean and central tendency of that population? Although power analysis may be useful in this regard (*e.g.*, Stevens *et al.* 2006), this approach has rarely been applied in archaeological contexts. Ultimately, the sample that is selected is a subset of a subset, since the remains that are recovered almost certainly represent only a fraction of the human population that lived at a given site. Thus, archaeologists using these approaches need to be fully aware of the biases and limitations of their methodologies, and communicate all risk factors and uncertainties to the readers in an open and transparent manner.

Representativeness of Source Data

In addition to some of the issues discussed above for consumer isotopic compositions, there are some additional considerations that may make it more or less likely that a particular set of isotopic data collected for food sources are representative of what would have been consumed. Relative to humans, most of the foods that they consume are short-lived. Many animals live only a few years or less, and annual plants like cereals grow over a single season. It is therefore reasonable to expect that these sources would be characterized by more isotopic variation than the humans that consumed them. Because, however, these humans would be consuming these foods over a period of years, this high variability should be dampened through an averaging effect (Bump *et al.* 2007), especially for bone collagen. As we explore below, the high variance in source isotopic compositions means that in order to adequately capture the true mean of

a particular source, larger samples sizes are optimal. Moreover, of all of the potential pitfalls of applying SIMMs in archaeological contexts, the extent to which the isotopic compositions of the potential sources or source groups reflect reality has the greatest potential to provide erroneous model outputs.

Detectable Threshold

Regardless of how isotopically distinctive a food source is, not all consumed foodstuffs are chemically identifiable in the tissues of a consumer. Food sources need to be consumed over a certain proportion, or detectable threshold, to be isotopically detectable. Consider a simple example in which the mean bone collagen $\delta^{13}C$ values for C_3 and C_4 source groups are –26 ‰ and –12 ‰, respectively. In this case a +1 ‰ shift equates to an increase of ~7% of C_4 resources. As the isotopic compositions of the source groups become less distinctive, greater relative changes in the amounts of food sources consumed are required to create a comparable isotopic shift. Consider another example in which pigs and cattle have $\delta^{15}N$ values of +9 ‰ and +6 ‰, respectively, but the same $\delta^{13}C$ values. Here a 7% increase in the consumption of cattle or pig would result in only a 0.2 ‰ shift in the $\delta^{15}N$ value of the consumer. Furthermore, foods consumed intensively over short periods (*e.g.*, in feasts), may not be easily identified in the isotopic composition of bone collagen. The detectable threshold for the consumption of a particular food or food group will vary among studies based on:

- The isotopic differentiation among the possible foods (as discussed above).
- The number of consumer samples analyzed, since the probability of accurately capturing the mean of a particular group increases with increasing sample size.
- The turnover rate of the material analyzed. Any short-term dietary anomalies/seasonal signals would be dampened and obscured in bone collagen (see section above). The detectable threshold for a "special" diet in bone collagen would therefore be a lot higher than that in fast growing tissues such as hair or nail.
- The level of analytical uncertainty associated with the measurements. Typically, uncertainties on $\delta^{13}C$ and $\delta^{15}N$ measurements are reported as ±0.1 to ±0.3 ‰, which creates a limit on the differences that can be meaningfully interpreted independent of the issues discussed above. As this is not a problem unique to archaeology, we will not discuss this further here. A detailed overview of this issue is outlined by Szpak *et al.* (2017b).

Missing Sources/Source Group(s)

Probably the most salient concern with the application of SIMMs in archaeology is missing sources. Theoretically, it is necessary to obtain isotopic data from every possible food source available to the consumer(s) in question; however, in practice, this is never possible. Faunal remains often do not adequately represent the full breadth of food sources consumed by humans for a number of reasons: transport bias, density-mediated attrition, the absence of ossified structures that preserve for some animal taxa, the absence of plant or animal remains from certain contexts (*e.g.*, necropolises), and difficulties in identifying species from fragmentary faunal remains (Albarella 1999;

Lyman 1994; Miksicek 1987; Minnis 1981). All these factors could contribute to underestimating (or overestimating) the contribution of a particular food source, or completely overlooking another. To mitigate this problem, archaeologists must group certain types of food sources together into more general "food groups." These groupings tend to aggregate food sources that are functionally similar and have similar isotopic compositions to one another. For example, in a situation where a range of marine and terrestrial resources were available, deer, elk, and antelope could be grouped together as "terrestrial meat" (*e.g.*, Newsome *et al.* 2004). There is still no consensus as to how food groups should be organized, but Phillips *et al.* (2005) made some recommendations. Another approach is to use cluster analysis to help determine what would be the most mathematically meaningful way to group the sources (Baumann *et al.* 2020; Bocherens *et al.* 2015; Cheung and Szpak 2020; Wißing *et al.* 2016).

To illustrate how grouping sources can help to minimize the effects of a missing source, we present an example from a simulated dataset. This dataset consists of five isotopically distinct groups of sources: C_3 plants, C_4 plants, freshwater fish, domestic herbivores, and marine fish. Each of these source groups consists of several individual sources (taxa) that are functionally and isotopically similar (see Online Resource 1). These source groups are plotted in Fig. 1 with a convex hull that represents the mixing polygon. The convex hull is the smallest convex polygon that includes all of the data points and when applied to source isotopic compositions, this area represents the mixing polygon, or the possible mixtures that can be created for a given set of sources. These source data are plotted alongside hypothetical consumers eating a mixture of these five sources. All sources have been adjusted for trophic discrimination factors (TDF). When all sources are present and accounted for, 100% of the consumer polygon overlaps with the mixing polygon (Fig. 1a). When a single source (but not an entire source group) is omitted, there is minimal change in the relative position of the source groups and the amount of overlap between the consumer and mixing polygons (Fig. 1b,c). Because each source group represents an average of several sources, the omission of a single source has a minimal impact on the size and shape of the resulting mixing polygon. The combination of single sources into groups is therefore not only necessary because quantitative models lose explanatory power with too many sources, but also because source grouping helps to mitigate the inevitable problem of missing sources in ancient systems. The overlapping areas between the mixing polygon and the consumer convex hull were calculated using the packages "raster" and "sp" (Bivand *et al.* 2013; Hijamns 2019; Pebesma and Bivand 2005). Detailed scripts for performing these calculations are provided in Online Resource 2.

A bigger problem in SIMMs is the omission of an entire source group. In archaeological contexts, this often refers to plant foods, and in some instances, aquatic resources. Whether in foraging or agricultural societies, humans have a long history of exploiting a wide range of plant foods, including cereals, nuts, legumes, vegetables, and fruits (Cordain *et al.* 2000; Mann 2007; Nestle 1999). However, remains of plant foods rarely survive in archaeological contexts, and even when they do, the recovery of these remains is highly variable among different plant taxa, types of burial environment, and excavation methods. Moreover, it is relatively rare for human palaeodiet studies to include isotopic measurements of macrobotanical remains (*e.g.*, Styring *et al.* 2018). Given that the isotopic compositions of these plant foods will typically have

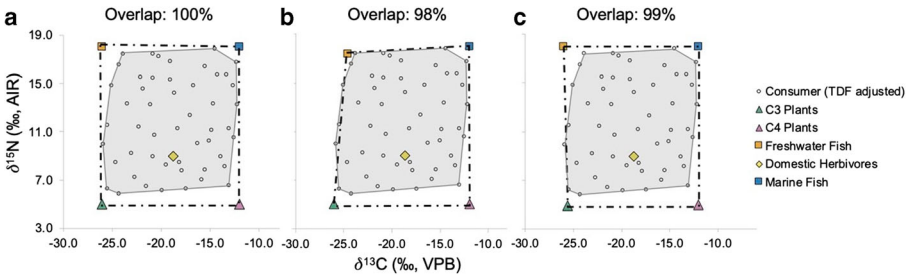

Fig. 1 Convex hulls of five source groups and consumers. In (a), all sources are present. In (b) and (c), a single source from a source group has been omitted: (b) pike (from freshwater fish) and (c) squash (from C_3 plants). The data used to generate these polygons is presented in Online Resource 1

distinct $\delta^{13}C$ and $\delta^{15}N$ values from animals within the same environment, missing this entire source group can strongly skew the results of the mixing model. The problem here is twofold: on one hand, starch-rich plants have little protein to contribute to the carbon and nitrogen in bone collagen (USDA 2019), and therefore are underrepresented when the isotopic compositions of bone collagen are measured. Thus, SIMMs will underestimate the contribution of these sources to one's diet when relying on isotopic data derived from collagen or keratin. On the other hand, some plant resources, such as legumes, are rich in protein (Phillips 1993), and have distinctively low $\delta^{15}N$ values (Kohl and Shearer 1980). Therefore, if we fail to consider legumes and/or other protein-rich plants in SIMMs, the reconstruction will be misguided. Even protein-poor plants like maize can still have a tremendous impact on bone collagen $\delta^{13}C$ values (Coltrain *et al.* 2007; Katzenberg *et al.* 1995; White *et al.* 1993), so the omission of these plants from SIMMs could also lead to erroneous interpretations despite their low protein content.

To illustrate the problem of missing source groups, an example is presented in Fig. 2, using the same simulated data as in Fig. 1. As with Fig. 1, a convex hull represents the mixing polygon for the source groups and the consumers. In Fig. 2b,c,d,e, one of the source groups is missing, causing part of the consumer convex hull to fall outside of the range of the source convex hull. If a situation such as this was encountered in an ancient context, it would be obvious that one or more source groups was missing. In Fig. 2f, one source group (domestic herbivores) is missing; however, since this group plots within the mixing polygon and does not define the shape of the hull, the omission of this source group is undetectable by a simple visual examination of the mixing and consumer polygons. This simple demonstration shows that it is not always easy to detect a missing source group isotopically. Therefore, it is of utmost importance that archaeologists sample possible sources extensively and consider other lines of evidence (*e.g.*, archaeological, historical, ethnographic) to establish a range of foods that were likely consumed.

Aquatic resources are often also missing in archaeological records. Similar to plant remains, fish bones are less likely to survive and be recovered in archaeological contexts (Nicholson 1996; Stewart and Wigen 2003; Szpak 2011), and the consumption of aquatic resources are often only inferred from secondary evidence such as the presence of fishhooks, depictions of fish, and in some cases, historical records (Højte 2006; Reinman 1967; Trakadas 2006). Even when fish bones may be absent, shells

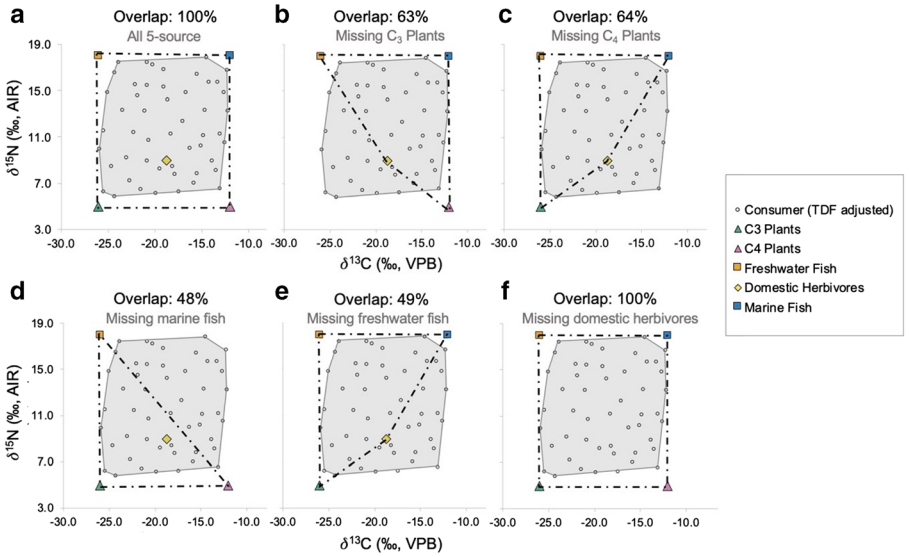

Fig. 2 Convex hulls representing consumers and mixing polygons in five different scenarios: a) all 5 source groups sampled; b) missing "C_3 plants"; c) missing "C_4 plants"; d) missing "marine fish"; e) missing "freshwater fish"; f) missing "domestic herbivores".

may be abundant, but C and N isotopic measurements of archaeological shell protein (as a proxy for the soft tissue) are rare (Black *et al.* 2017; Misarti *et al.* 2017). Because there is generally more isotopic variation in aquatic relative to terrestrial resources, the odds of missing an entire source group that significantly alters the mixing polygon is much higher in these circumstances. To counter the problem of missing sources, there are four major approaches:

- Use published isotopic data from fauna or flora from other sites in the region that may or may not be contemporaneous. For example, Fernandes *et al.* (2015) used published faunal data from Mesolithic and Neolithic sites in central and northern Europe to approximate the stable carbon and nitrogen isotopic compositions of major food groups in Neolithic Ostorf, Germany.
- Use modern faunal/floral samples as an analogue after correcting for the Suess Effect (Verburg 2007). For example, Newsome *et al.* (2004) used Suess Effect-corrected modern faunal isotope data to reconstruct diets of Early and Middle Holocene groups in Monterey Bay, California.
- Infer missing group isotopic compositions from global averages. For example, Hu *et al.* (2006) used the global averages of C_3 and C_4 plants as the two endpoints of a LMM to estimate the contribution of agricultural products (C_4 plants) in an Early Neolithic group in Jiahu, China.
- Infer missing source group isotopic compositions from other source groups (*e.g.*, inferring plant δ values from herbivore δ values). For example, Tafuri *et al.* (2009) inferred the isotopic compositions of C_3 and C_4 plants on the basis of faunal isotopic compositions in an attempt to quantify the relative importance of plant and animal protein in the diet at a Bronze Age site in Italy.

The choice of approach here will be informed by how much is known about the missing source groups. With respect to the first two approaches, at the very least, we must know which species were involved. As the saying goes, however, "you don't know what you don't know." In other words, if we knew definitively which species were consumed, we would likely have remains of those species preserved at that site, and analysing those remains would represent the most prudent strategy. It is not uncommon for human remains to yield a sufficient amount of collagen for isotopic analysis, but the same may not be true for fish from the same site, such that we know which species are present, but simply cannot generate isotopic data from the remains. This scenario is especially common when the collagen is ultrafiltered, as this processes significantly reduces yields, which frequently results in small fish bones yielding an insufficient amount of collagen for isotopic analysis (Guiry *et al*. 2016). The bigger, and unfortunately, more common problem, however, occurs when we do not know which taxa were available at the site at all. Of the four approaches listed above, the first (using archaeological data from other sites in the region) is usually the best course of action, provided all of the source groups (if not specific source taxa) can be accounted for. However, when using faunal data from other sites, it is important to ensure the two sites have comparable baseline isotopic compositions. This is a particularly important consideration as there is an implicit assumption that marine organisms, for example, have predictable $\delta^{13}C$ and $\delta^{15}N$ values across large spatial scales (Richards and Hedges 1999), when in reality this is not always the case (McMahon *et al*. 2013). For example, the $\delta^{15}N$ values of a single species of marine fauna along the coast of Chile and Peru vary by >10 ‰ (Ruiz-Cooley and Gerrodette 2012), so baseline data from one region may not be always applicable to another that is hundreds of kilometres away. An obvious problem with the second approach (using modern taxa) is that the isotopic compositions that characterize flora and fauna in the modern environment may be quite different from those in ancient environments beyond the changes caused by the Suess Effect. Nitrogen isotopic compositions of modern agricultural plants are heavily influenced by chemical fertilizers almost everywhere on the planet (Galloway and Cowling 2002), and the $\delta^{15}N$ values of marine organisms in areas near urban settlements may have shifted considerably due to eutrophication (Black *et al*. 2017; Oczkowski *et al*. 2009). The third approach (inference based on global values) should be exercised with extreme caution because it ignores the possibility of local variation in floral and faunal isotopic compositions (Amundson *et al*. 2003). This problem is likely to be the most severe in more extreme environments, where conditions deviate significantly from global averages. This strategy would never be appropriate for aquatic resources, but may be reasonable for temperate terrestrial environments dominated by C_3 plants. The fourth approach (inferring δ values based on other source groups) may be a sensible approach in some cases, however, it is not without problems. With respect to plant isotopic compositions being inferred from herbivore isotopic compositions, livestock and humans may systematically consume different plant parts, and there is systematic intra-organ variation in the $\delta^{13}C$ and $\delta^{15}N$ values within plants (Badeck *et al*. 2005; Szpak 2014). Livestock and humans may also have consumed entirely different plant taxa, and this problem may be further compounded if the cultivated plants were fertilized, but the wild plants consumed by the livestock were not. Attempting to infer the isotopic compositions of aquatic taxa in this manner is not recommended as these environments are characterized by variable, and more difficult to predict, isotopic compositions (Guiry 2019). Thus, the choice of

how best to account for missing source groups will vary from case to case, depending on the availability of appropriate data and the nature of the environment in question. In situations where source groups must be inferred from other published data, which themselves are characterized by small sample sizes and missing sources, it may be the case that there is simply too much uncertainty in the sources to effectively use a mixing model. Finally, it is of utmost importance to have all source groups included in a SIMM. Omitting a single source group in a SIMM will not only oversimplify a population's dietary structure, and cause the overestimation of the contribution of one or more other sources, but it could potentially bias the entire estimation process. If there is no way to obtain the approximate isotopic values of a missing source group, we do not recommend the use of SIMMs, and instead favour a more qualitative (calibrated eyeball) approach to interpreting the data.

Variability in Source Groups

Ideally, all source groups should have discrete, non-overlapping, and narrow isotopic ranges. However, in reality, some source groups are substantially more isotopically variable than others. For example, at the Mesolithic site of Noyen-sur-Seine, wild herbivores (n=17) have $\delta^{13}C$ values range from –23.8 to –22.3‰ (SD = 0.4‰), while those of the freshwater resources (n=10) range from –26.7 to –19.3‰ (SD = 2.1‰) (Bocherens *et al*. 2011). The variability in isotopic compositions of source groups can be influenced by many different factors, including the feeding habits of the species involved, animal husbandry practices, and local environmental conditions (Bogaard *et al*. 2007; Guiry 2019; Lightfoot et al. 2020). It is not the case that a high or low amount of variation can be assumed for a particular species, although certain groups are likely to be more variable than others. Freshwater fish in particular, are likely to be characterized by a large amount of isotopic variability (Guiry 2019), and in some cases may even require more than one source group. However, this is equally true for livestock that were managed under a variety of conditions (Pearson *et al*. 2007; Szpak *et al*. 2014). Thus, it is crucial that a larger number of source taxa be sampled in order to ensure that the central tendency and variance in those groups is accurately captured. Pearson and Grove (2013) suggested a minimum of eight samples to capture the true mean, with redundancy occurring after forty samples. Unfortunately, this threshold is rarely reached in palaeodietary studies for individual taxa, or even for many important source groups. For studies whose primary aim is to reconstruct past human diet, at the level of experimental design, a greater emphasis should be placed on characterizing the isotopic compositions of the potential foods. Doing so will ensure that the isotopic data derived from the human remains will produce the most accurate and robust interpretations with respect to diet composition.

In Fig. 3, we demonstrate the effect of different sample sizes on the probability of capturing the "true" means of populations with different levels of variability. To represent source groups of different variability, we generated three populations (n=1,000) with the same means ($\delta^{13}C$ = –15 ‰ and $\delta^{15}N$ = +10 ‰), but with standard deviations of 2 ‰, 3 ‰, and 4 ‰, respectively. From each population, we bootstrapped a subsample of 3, 5, 10, or 20 at 1000 iterations, and calculated the means of each subsample. These subsample means were then compared with the "true" mean of the population (lollipop graphs in Fig. 3), and the absolute Euclidean distance between the

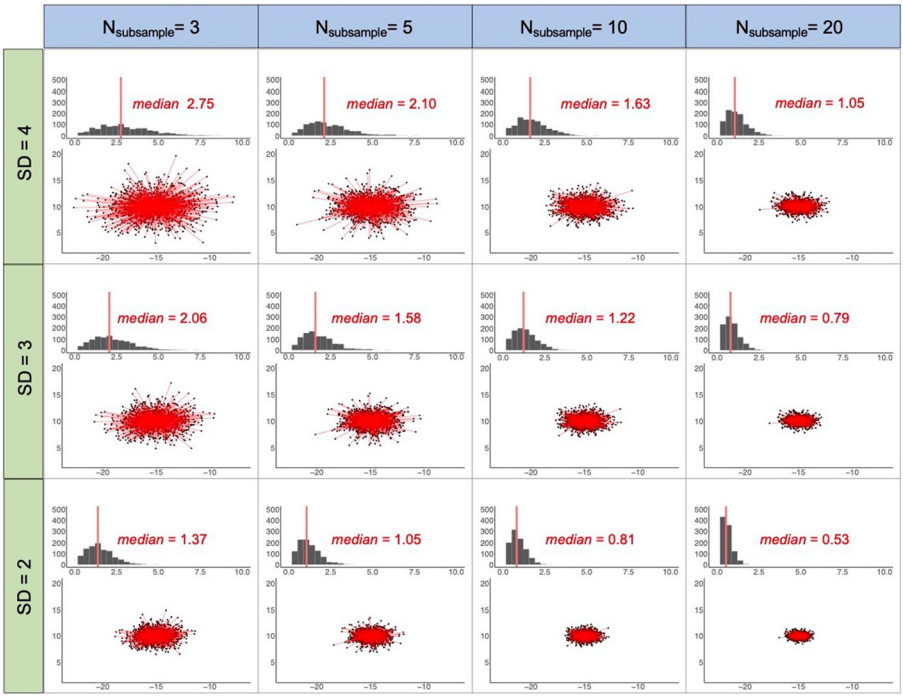

Fig. 3 Histograms and lollipop graphs showing differences in the means of subgroups of three different populations as sample size changes. For the histograms, the x-axes express the absolute difference measured between subgroup means and population means in ‰; y-axes express the total count of measurements; for the lollipop graphs, x-axes express $\delta^{13}C$ values, y-axes express $\delta^{15}N$ values. Top row: population SD = 4; second row: population SD=3, and third row: population SD=2. From left to right, subsample sizes are 3, 5, 10, and 20

two means was calculated (histograms in Fig. 3). The median distance between the true mean and the estimated mean for each bootstrapped sample is indicated as a vertical line in red on Fig. 3. As the SD of the population decreases, and more importantly, the number of subsamples increases, the probability of accurately capturing the true mean increases. This example demonstrates that for highly variable populations of consumers or sources, a subsample of 3 or 5 is unlikely to be representative of the original population (median difference between the true mean and the observed mean ranges between 1.58 and 2.75 ‰). The script to perform this calculation is provided in Online Resource 2.

A source group with high isotopic variability (*e.g.*, freshwater resources) poses two major challenges to conducting SIMMs. First, in order to truly capture the variability of such a source group, it is very important to include as many samples as possible. Failure to account for the full isotopic range will introduce error into the modelling. Secondly, even if the full isotopic range of the source group is well represented, mathematically speaking, a source group with high isotopic variability will inevitably lower the sensitivity of the model estimation. It is probable that broad categories such as “freshwater fish” or “marine mammals” likely integrate numerous taxa with distinctive isotopic compositions with no obvious way to organize them into more discrete clusters. While it may not represent the most logical or intuitive approach to divide the

source group into several tighter groups, archaeologists may have to consider this option for more accurate modelling. For example, it may be necessary to divide a highly variable group of marine resources into "benthic fish" and "pelagic fish." It may also make sense to divide isotopically distinct groups of a single taxon *a priori*. For example, the isotopic compositions for camelids from the Wari site of Conchopata clearly clustered into two groups with very low and high proportions of C_4 plants in the diet, respectively (Finucane *et al*. 2006). Using a mean value that is intermediate between the two to represent "camelids" would be inappropriate and cause inaccurate results from the SIMM. Another option is to consider using an *a posteriori* source aggregation approach using MixSIAR (Stock *et al*. 2018). This approach runs the model with a higher number of sources initially, and the sources are aggregated post hoc depending on the results. A more detailed discussion of this approach is given by Cheung and Szpak (2020).

Other Field-Specific Issues

Other than the aforementioned biological and ecological processes, human diets are further complicated by the fact that humans modify their environment and the foods that occur within that environment to a greater extent than any other species that might be studied with SIMMs. For example, certain animal husbandry practices such as different feeding regimes (foddering vs. free range) may alter the isotopic compositions of livestock (Chen *et al.* 2016; Finucane *et al.* 2006; Vaiglova *et al.* 2018). In some cases, domestic animals are given discarded parts of the crop (*e.g.*, stem, chaff, silage) as fodder (Jones 1998), which could have different isotopic compositions than the parts consumed by humans (Badeck *et al*. 2005). Provided that fauna are available for sampling, these husbandry practices should be detectable via isotopic analysis and should not create problems when using SIMMs. While the problem of shifted isotopic compositions for animal food sources is fairly easy to account for, the possibility of greatly increased isotopic variation is not. The variance in $\delta^{13}C$ and $\delta^{15}N$ values for livestock in agropastoral societies can be extremely high (Szpak *et al*. 2019) and although this can be accounted for with Bayesian SIMMs, this high level of variance should obscure the differentiation of sources. Moreover, using the central tendency for this source discounts the possibility that the isotopic variance was high because subgroups within the site (*e.g.*, families, households, ethnic groups) may have managed their livestock differently, and did not sample from the centre of the isotopic distribution.

Another issue is specific to archaeological sites where humans may have relied heavily on foodstuffs with atypical isotopic compositions to the region. For example, many migratory species such as birds, fish, marine turtles, and some mammals could have different muscle and bone isotopic compositions due to differential turnover rates and the consumption of isotopically distinct foods in different seasons (Kurle and Worthy 2002; Martínez del Rio *et al*. 2009). Thus, in groups where these migratory species were a substantial source of protein, archaeologists may be misled by the isotopic compositions of bone collagen from archaeofaunal remains, since the isotopic signature of the tissues being consumed (*e.g.*, muscle) may differ from those of the tissues being analyzed (*i.e.*, bone collagen). A similar problem may also arise when prior to slaughter, livestock are finished on a diet that is isotopically distinctive from

that which they consumed for the bulk of their life. These factors may create a situation wherein the source isotopic compositions used in a model are inaccurate. Another scenario is that humans could import isotopically distinctive foodstuffs from other places. For example, Guiry *et al.* (2012) analyzed pig bones found in fishing stations in historical Newfoundland, and discovered that imported pigs were isotopically distinctive from those raised locally, as local pigs were fed with fish, while the imported European pigs were likely fed with grain fodder. Other widely exported food in the ancient world includes grains, wine, and fish (Faust and Weiss 2005; Lowe 1997; Moreno 2007; Renfrew 2003; Van Neer *et al.* 2004). Some of these, such as the imported pigs, may leave evidence behind, but many may not, potentially biasing the interpretation in a way that is not obvious. The extent to which this is a problem depends on how heavily humans relied on these "atypical" sources, and whether or not we can identify that their isotopic compositions are, indeed, atypical. Where the extent of mismatching between analyzed and consumed tissues is very large, the application of a mixing model is probably inappropriate, and unfortunately, there is no easy way around this. If the isotopic compositions of the fauna are obviously at odds with those of the humans (*i.e.*, the human data fall outside of the mixing polygon), archaeologists should consider other ecological and anthropological explanations for such discrepancies. Generally speaking, however, the magnitude of this problem likely approximates the scenario depicted in Fig. 1 rather than the scenario depicted in Fig. 2.

Manuring can cause an increase the $\delta^{15}N$ values of crops. Studies have shown that the $\delta^{15}N$ values of intensively manured plants can show an enrichment in ^{15}N of between +2 to +8 ‰ (Bogaard *et al.* 2007; Szpak 2014), and in some extreme cases, over +30 ‰ (Szpak *et al.* 2012). The influence of manuring on crop isotopic compositions cannot be inferred without isotopic measurements of those crops. While these data have been extremely rare in palaeodietary studies (Styring *et al.* 2018), isotopic analyses of macrobotanical remains are becoming increasingly common (Fiorentino *et al.* 2015). This issue is particularly noteworthy since the possibility exists that livestock grazing on wild grasses and crops fertilized with the manure derived from those livestock may have similar $\delta^{15}N$ values. Moreover, if humans and livestock consume different plants with distinct $\delta^{15}N$ values (*i.e.*, manure crops for the former and unmanaged pasture for the latter), using faunal isotopic compositions to infer the isotopic compositions of the crops that would have been consumed by humans will produce erroneous results. Studies have shown that differential water availability can cause significant isotopic variability in plants (Austin and Vitousek 1998; Ehleringer *et al.* 1993). Thus, natural climatic conditions aside, certain water management practices can also contribute to this variation. This is especially important in complex agrarian societies, where agricultural infrastructures, such as irrigation systems were built and maintained (Harrower 2010; Netherly 1977; Zhuang *et al.* 2016). C_3 plants tend to have lower $\delta^{13}C$ values when water availability is high (Farquhar *et al.* 1989) and therefore in arid areas, irrigated crops may have lower $\delta^{13}C$ values than those that are exclusively rain-fed. As with the relationship between plant $\delta^{15}N$ values and manuring, the effects of water availability on crop $\delta^{13}C$ values cannot be inferred in the absence of isotopic measurements of macrobotanical remains. Because agricultural practices can vary strongly among sites (Styring *et al.* 2017), it is crucial that palaeodietary studies seeking to use SIMMs build isotopic analyses of macrobotanical remains into their research designs to account for this variation. Uncertainty in water

management practices is likely to approximate the problems presented in Fig. 1, with subtle shifts in $\delta^{13}C$ values. Depending on the isotopic composition of the manure and the rate of application, manuring could result in more subtle shifts (as depicted in Fig. 1) or could result in vastly altered source isotopic compositions (as depicted in Fig. 2).

SIMMs based on consumer tissues like bone collagen or hair keratin tend to underestimate contribution from food that contains little protein, such as cereals. Part of this problem is because in omnivores, the isotopic signatures of collagen, a protein, preferentially reflect those of dietary protein (Ambrose and Norr 1993; Jim *et al*. 2004). While some advanced SIMMs can take concentrations of different elements in food sources into consideration (see Cheung and Szpak (2020) for an overview), SIMMs may still underestimate contributions from plant sources under some circumstances. Consider a coastal hunter-gatherer population that consumes a large amount of protein from marine fish, and a significant portion of energy from C_3 corms and bulbs, which are protein-poor. Because these two source groups have very distinct $\delta^{13}C$, $\delta^{15}N$, %C, and %N, SIMMs incorporating concentration dependence would likely accurately reflect the diet compositions, inasmuch as is possible considering the fact that collagen's isotopic composition is still biased towards protein-rich foods. Consider an agricultural society that grows only C_3 grains and raises animals that consume only C_3 plants. Because these two sources have very different elemental but more similar isotopic compositions (relative to the previous example), SIMMs would more likely overestimate the importance of the animal products. This is because as a mathematical model, SIMMs do not automatically consider any factors beyond the isotopic and elemental compositions of the consumers and sources. They merely offer a range of possible solutions to a mixing problem in the way of proportional contributions of each source group to the consumers' diets, assuming equal accessibility to these sources. For agricultural societies this could be particularly problematic, as access to plant foods can be substantially more economical comparing to animal foods. In fact, it is estimated that during much of the historical period, European peasants consumed a largely carbohydrate-based diet that consisted of up to 90% bread or other cereals (Hanawalt 1986; Ladurie 1976). These carbohydrates-rich diets are therefore difficult to be characterized fairly by SIMMs. One possible solution to this problem is to "tell" the model to lean more heavily towards a particular source group by using hyperparameters, or priors, in Bayesian mixing models (*e.g.*, FRUITS and MixSIAR). However, ill-informed hyperparameters will strongly sway the estimations, and therefore should be used cautiously (Cheung and Szpak 2020). It is important to understand the limits of SIMMs when interpreting and reporting the results. If possible, it is always preferable to compare the outputs from a SIMM with other lines of evidence, such as zooarchaeological, archaeobotanical, or historical records. In any case, with all the uncertainties associated with the application of SIMMs in archaeological contexts, SIMM estimations should only be used as an accessory to understand palaeodietary practices, but never as a definitive confirmation.

Data Collection for SIMMs: Best Practices

First, it is important to make sure all data are reliable and have passed all relevant QC criteria. No matter how good a model is, the result will only be as good as the data

inputted into the model. Second, while most archaeologists are well aware that when it comes to sample size, bigger is better, it is not always possible to analyze as many samples as is necessary. Thus, if analytical resources are limited, when selecting members of various source groups to help establish a faunal or floral baseline, it is best to analyze more samples from highly variable source groups whenever possible (*e.g.*, prioritize freshwater fish over cattle in an exclusively C_3 environment). The variability of source groups should be inferred from pilot research or comparable sites in the region. It is best to compare the consumer and source isotopic compositions (after adjusting for TDFs) to determine if they are largely situated within the mixing polygon. If they are not, the most likely explanation is that a significant source group is missing. Finally, under most circumstances, it is best to use the same tissue/component to reconstruct past diets.

When conducting SIMMs to quantify past dietary compositions, the following conditions represent an ideal scenario:

- all samples are well preserved;
- abundant contemporaneous faunal and floral remains have been recovered and isotopically analyzed;
- the presence of all major sources consumed at the site are confirmed by other archaeological or historical evidence;
- all major sources are isotopically distinct from one another;
- all of the consumer isotopic compositions plot within the mixing polygon after adjusting for TDFs.

Unfortunately, these conditions are rarely, if ever, fully satisfied. Part of the reason for studies failing to meet these conditions may be the generally qualitative approach taken by most archaeologists in interpreting past human diets using stable isotope data. As more studies attempt to make use of SIMMs, the steps outlined in this paper should help to improve the quality of individual studies. Emphasizing the creation of more robust isotopic datasets for sources should help to provide better inputs for SIMMs when it is necessary to rely on previously published data from the study region. Figure 4 provides some guidance to optimize the performance of SIMMs given the inevitable less-than ideal scenarios that occur when working with ancient samples.

Conclusion

Our study has highlighted several important issues concerning data acquisition for SIMMs in archaeological contexts. While numerous studies have shown that when used properly, SIMMs can be immensely useful in providing quantitative assessments of past diets, few studies have pointed out the potential pitfalls of misusing SIMMs. A major advantage of SIMMs is the ability to communicate the results in terms of the relative source proportions contributing to the diet without the need for the reader to have an understanding of stable isotope ecology. As discussed in Cheung and Szpak (2020), however, many SIMM programs will provide an estimation, no matter how poorly the source and consumer data fit together. In such cases, producing a seemingly certain but erroneous estimation can do more harm than

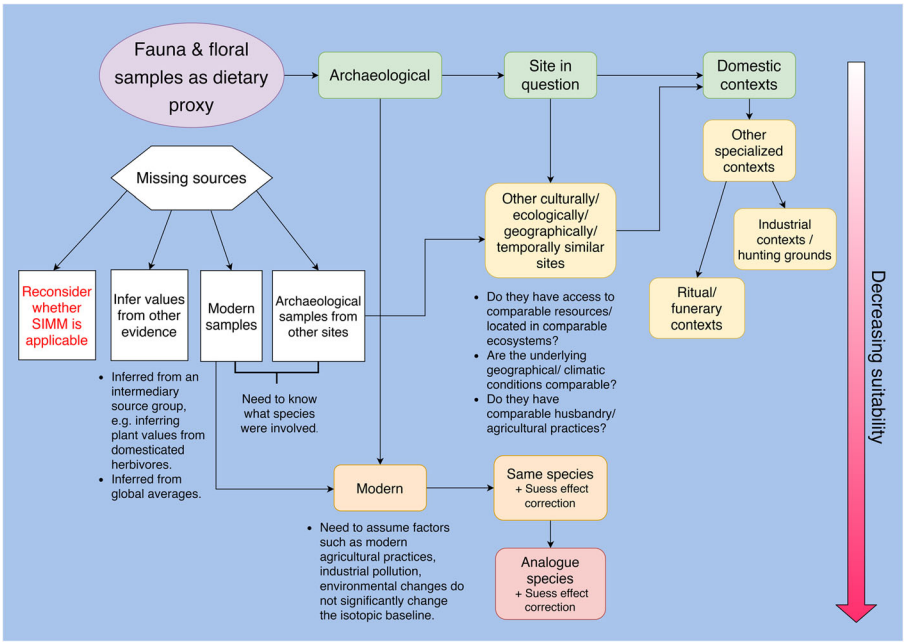

Fig. 4 Flow chart for how to decide what samples to select for SIMMs. Note that the faunal/ flora assemblage may come from different contexts

good. As archaeologists are often not informed about the uncertainties associated with SIMM estimations, blindly following a poorly made estimation could lead to misunderstanding, and worse, derail the entire study. To avoid these situations, we need to ensure that the estimations produced by SIMMs are built on a solid foundation by following the suggestions outlined in the above sections. More importantly, "SIMMs are not applicable in this study" should always be an option. The bottom line is that using SIMMs or not, inferences of past dietary practices should be based on more than just stable isotope data, and include data from as many other lines of evidence as possible.

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Data Availability All simulated data are provided in the Supplementary files.

Code Availability All codes used in this study are provided in the Supplementary files.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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