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Investigating Isotopic Niche Space: Using rKIN for Stable Isotope Studies in Archaeology

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Abstract

Archaeological applications of stable isotope data have become increasingly prevalent, and the use of these data continues to expand rapidly. Researchers are starting to find that recovering data for multiple elements provides additional insight and quantitative data for answering questions about past human activities and behaviors. Many stable isotope studies in archaeology, however, rarely move beyond comparisons of descriptive statistics such as mean, median, and standard deviation. Over the last decade, ecologists have formalized the concept of isotopic niche space, and corresponding isotopic niche overlap, to incorporate data from two or more isotopic systems into a single analysis. Additionally, several methods for quantifying isotopic niche space and overlap are now available. Here, I describe the evolution of the isotopic niche space concept and demonstrate the usefulness of it for archaeological research through three case studies using the recently developed rKIN package that allows for a comparison of different methods of isotopic niche space and overlap estimations. Two case studies apply these new measures to previously published studies, while a third case study illustrates its applicability to exploring new hypotheses and research directions. The benefits and limitations of quantifying isotopic niche space and overlap are discussed, as well as suggestions for data reporting and transparency when using these methods. Isotopic niche space and overlap metrics will allow archaeologists to extract more nuanced information from stable isotope datasets in their drive to understand more fully the histories of the human conditions.

Keywords Isotopic niche space · Isotopic niche overlap · Minimum convex polygon · Standard ellipse area · Kernel utilization density · rKIN

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Introduction

Stable isotope studies have over a 50-year history in archaeology and have become a routinely used method in the researcher's toolkit. From the initial uses of heavy isotopes in studying ancient lead artifacts (^{206}Pb/^{204}Pb, ^{207}Pb/^{204}Pb, and ^{208}Pb/^{204}Pb) (Brill & Wampler, 1967) and the earliest uses of stable carbon isotope values (δ^{13}C) for investigating the spread of maize in the Americas (Vogel & van der Merwe, 1977; van der Merwe & Vogel, 1978), the range of topics, as well as isotopic systems analyzed, has expanded rapidly. In addition to lead and δ^{13}C, some of the more prominently studied are as follows: nitrogen stable isotope (δ^{15}N) analyses of diet and trophic levels (e.g., Schoeninger & DeNiro, 1984; Schoeninger, 1985, 1989; Ambrose, 1991), environmental and climatic conditions (e.g., Shackleton et al., 1984; Cerling et al., 1988; Sharma et al., 2004) interpreted from oxygen isotopes (δ^{18}O), and strontium isotope ratios (^{87}Sr/^{86}Sr) for migration and movement (e.g., Ericson, 1985; Sealy et al., 1991, 1995; Bentley, 2006). While many studies may focus on a single element, or consider multiple elements separately, others investigate the relationship between two elements on a scatter or bi-plot to address questions about diet or movement (e.g., DeNiro, 1987; Schoeninger & Moore, 1992; Cheung et al., 2017; Martin et al., 2020; Scaffidi et al., 2021). Even when archaeological research questions can be best addressed by considering multiple elements simultaneously, these analyses tend to remain at a descriptive level (means and standard deviations) with only recently some studies exploring the potential of calculating and interpreting isotopic niche space (e.g., Hermes et al., 2018; Loponte & Corriale, 2020).

Isotopic niche space has been proposed as a corollary of the ecological niche concept. Niches are defined as multidimensional space with axes representing resources (bionomic) and bioclimatic (scenopoetic) factors (Hutchinson, 1957). Stable isotopes, such as δ^{15}N (bionomic) and δ^{13}C (scenopoetic or bionomic), can therefore be used to quantify the niche as the chemical composition of any biological organism is related to what it consumes and its habitat. In other words, different isotopes can be used to quantitatively define the ecological niche (Newsome et al., 2007; Loponte & Corriale, 2020), although, as discussed later, some researchers have expressed concern with conflating the concept of isotopic space with trophic niches (see Hette-Tronquart, 2019). Starting with Newsome et al. (2007) development of the concept of isotopic niche space, this approach has primarily been applied to questions of niche partitioning and temporal and/or geographical differences in diet in ecological and environmental studies (e.g., Martínez del Rio et al., 2009; Newsome et al., 2012; Rossman et al., 2016; Yeakel et al., 2016). These same sorts of research topics, however, are just as relevant to humans and/or non-human fauna recovered from archaeological sites. For instance, in one of the only uses of isotopic niche space in archaeology, Hermes et al. (2018) employ this approach to identify and quantify dietary differences between nomadic and urban communities, and across different urban communities, in central Asia. Unlike descriptive analysis of δ^{13}C and δ^{15}N alone, investigating isotopic niches allowed Hermes et al. (2018) to explore questions of dietary connectivity and, perhaps, cultural differences in diet. As the isotopic niche concept has become more widely applied over the last decade, researchers have experimented with different ways of statistically comparing isotopic niche spaces in the hopes of defining different populations.

Development of the Isotopic Niche Space Concept

The earliest attempts of quantifying isotopic niche space are adopted from Layman et al. (2007) who proposed their metrics prior to (or perhaps independently at roughly the same time) the formalization of the concept by Newsome et al. (2007). In their 2007 paper, Layman *et al.* propose six different measures to investigate community differences in trophic categories, not specifically isotopic niche space. One of these — the total area of a convex hull — has been adopted for studying isotopic niche space. While Layman et al. (2007) conceptualized the convex hull as encompassing all species in order to get a sense of the total niche space occupied by a community, others (e.g., Quevedo et al., 2009) adopted this to construct convex hulls for individual species in order to compare the total area and overlaps. Use of convex hulls, however, fails to consider the variability within different species or address concerns about uneven sample sizes. In response, Jackson et al. (2011) developed the Stable Isotope Bayesian Ellipses in R (SIBER) package. SIBER accounts for these uncertainties by utilizing the standard ellipse area as opposed to the rigid convex hull. While this allows for qualitative and simple statistical comparisons (means and standard deviations) of the isotopic niche space occupied by different members of a community, SIBER was intended more to assess the overall community's isotopic niche space rather than differences of overlap among members of the community (Jackson et al., 2011).

Borrowing from spatial ecologists, Eckrich et al. (2020) expand upon the work of Jackson et al. (2011) in developing a kernel utilization density (KUD) approach to isotopic niche space called kernel isotopic niches in R (rKIN) (package originally developed by Albeke, 2017). Advantages of the kernel-based approach are that it is less sensitive to extreme values and is free of the influence of grid size or shape (i.e., fitting to an ellipse). Unlike convex hulls or SIBER, rKIN includes metrics that represent not only the niche size, but also the position of species to allow for an assessment of isotopic niche overlap. Eckrich et al. (2020) were able to demonstrate that isotopic niche overlap can be accurately calculated with only 15 samples and that even sample sizes as low as 10 provide reliable estimates of isotopic niche overlap. These are common sample size numbers in archaeological applications. In addition to sample size, kernel-based analyses require a smoothing parameter, also known as the bandwidth. Eckrich et al. (2020) find that four different bandwidths are applicable to isotopic data, although they suggest the ref bandwidth, which assumes that each kernel is normally distributed in bivariate space, as the default option. Even though kernel-based approaches appear to be an advance over previous methods, rKIN also offers the ability to calculate isotopic niche size and overlap through convex hulls (called minimum convex polygon [MCP] in rKIN) and the standard ellipse area (SEA; Albeke, 2017; Eckrich et al., 2020).

Isotopic Niche Space as a Methodological Approach

Calculating and interpreting isotopic niche space start with the familiar presentation of isotope data in bi-plots but extend this approach through the application of spatial statistics. Bi-plots alone allow for descriptive assessments of a single Hutchinsonian niche axis (i.e., quantifying the difference in δ^{15}N values revealing marine mammals to be at a higher trophic level than phytoplankton; Ambrose, 1993) or identifying visually and with means and standard deviations whether and how certain groups overlap in two-dimensional Hutchinsonian space (e.g., DeNiro, 1987; West & France, 2015). While there is nothing inherently incorrect with this approach, informal descriptions of bi-plots run the risk of overemphasizing differences or missing subtle distinctions between groups. Additionally, using measures like means to compare groups simplifies two-dimensional datasets preventing simultaneous consideration of both axes. Applying spatial statistics to these plots opens a number of fresh ways for assessing niches. Here, I focus on two — the quantification of isotopic niche space and the evaluation of niche overlap.

Isotopic niche space is defined as the total spatial area encompassing data points, providing a measure of niche width (or breadth). This is where the different models — MCP, SEA, and KUD — come into play as each deal with sample sizes and uncertainties differently. The MCP approach connects the minimum number of points in bivariate space to enclose all remaining data, but this method is necessarily sensitive to the number of samples with total area usually increasing with sample size. Outliers and extreme data points significantly influence MCP measurements by including unused areas of isotopic space. These limitations are particularly important when considering populations with different sample sizes (Layman et al., 2007; Flaherty & Ben-David, 2010). In the SEA model, ellipse construction proceeds from a pre-determined confidence level from which ellipse radii are calculated. This approach reduces the sensitivity to sample size and outliers seen in the MCP model, but the resulting niche shape is always elliptical and may include unused or exclude used areas of isotopic space. Furthermore, elliptical models assume that isotopic data are independent and normally distributed in multivariate space (Jackson et al., 2011), but many natural (and archaeological) systems are known to be prone to non-normality (Flaherty & Ben-David, 2010; Roberts et al., 2018). The KUD model developed by Eckrich et al. (2020) is generated by summing two separate kernel functions over observed data points and estimated across a regular network of equally spaced points. Total area is defined as the minimum size that includes all data points under consideration free of distributional assumptions or pre-set grid shapes, such as ellipses. Therefore, it is important to recognize that total spatial area, and, in turn, the measure of niche width will likely vary depending on the model selected. Interpreting total isotopic niche space areas and assessing larger (broader) or smaller (narrower) isotopic niche space among populations within a study is contingent on the particularities of the question at hand, although smaller niche spaces typically indicate a less diverse resource base and habitat. Narrower isotopic niche spaces may suggest specialized versus generalized feeding, but, again, this interpretation is dependent on the specific study.

For example, in their study of perch from pelagic and littoral habitats, Quevedo et al. (2009), using a MCP model, found that pelagic perch have smaller isotopic niche space area. They interpreted these results as reflecting lower prey diversity for pelagic perch, likely a result of differences in habitat and not necessarily a specialized diet compared to littoral perch. Another metric related to isotopic niche space, isotopic niche variability, can be measured within and compared among study groups by calculating the Euclidean distances among individuals from the isotopic centroid of the population in question. However, there is an unresolved debate as to whether (or how) this measure adequately represents clustering and evenness (Layman et al., 2007; Quevedo et al., 2009), and, as such, is not considered further in the current study.

In addition to isotopic niche space calculated through total area measurements, it is possible to measure the degree of overlap among different populations within a study. Overlap is defined as the size of the overlapping region between niche of population A and the niche of population B divided by the total niche size of population B. The measure can also be calculated in the reverse. The greater the percentage of overlap, the higher the inferred dietary overlap would be for bionomic axes like $\delta^{13}C$ and $\delta^{15}N$. Little or no isotopic niche overlap between co-existing species may indicate the occupation of separate niches. In a recent study of deposit-feeding polychaetes (bristle worms) in the Baltic Sea, Karlson et al. (2015) used SEA models to demonstrate that isotopic niche space of an invasive polychaete species (*Marenzelleria arctia*) did not overlap those of the three native polychaete species. These results suggest that the invasive polychaete was exploiting a vacant niche. On the other hand, the three native polychaetes were found to have highly overlapping isotopic niche spaces, up to 100%. This result suggests dietary overlap and competition for resources among the native polychaetes, although, as mentioned above, interpretations of these metrics are context dependent. For instance, while Karlson et al. (2015) state that dietary overlap and competition are likely for two of the native polychaetes; the third feeds in a deeper environment and probably does not directly compete with the other two. They also argue for the potential of overlap in driving larger isotopic niche space size as competition leads to feeding on supplemental and suboptimal resources. Issues of isotopic equifinality may also complicate interpretations of isotopic space overlap where similar dies, such as feeding on grasses that use the C_3 versus C_4 photosynthetic pathway, could lead to different isotopic values, whereas different diets, like feeding on C_3 grasses versus C_3 woody vegetation, would lead to similar isotopic values. Again, context-dependent information should be included in all interpretations of isotopic niche space and overlap.

Here, rKIN tools are applied to archaeological case studies to investigate the applicability of the isotopic niche space concept to research questions about human behavior. The case studies cover traditional uses of the isotopic niche space concept investigating diet and habitat, as well as exploring the potential of the approach for other archaeological applications outside of Hutchinsonian niche concepts. I close with a discussion of the benefits and limitations of the isotopic niche space concept to archaeology as well as suggestions for utilizing the method and reporting results.

Materials and Methods

Isotopic niche space is a relatively new concept that has only recently been used by a handful of archaeologists. A Web of Science literature search for the term "isotope niche space" as a topic returned 307 references from 2002 to 2021 with only two references from before the 2007 publications of the Layman *et al.* and Newsome *et al.* papers. Archaeology is represented by only two references and expanding out to anthropology only increases the number of publications to five (Source: Web of Science, June 2021). As such, I demonstrate the potential use of this approach through three case studies. These case studies derive from previously published datasets in order to assess what directly studying isotopic niche space may add to the results and interpretations. The first two case studies investigate more traditional dietary group studies. Case study 1 utilizes data from one of the earliest archaeological studies to combine the analysis and interpretation of δ^{13}C and δ^{15}N values — Larsen et al. (1992) study of dietary change across the transition to agriculture and European contact in the Georgia Bight. This case study is included specifically because it analyzes the two elements — carbon and nitrogen — that are investigated in most isotopic niche space analyses to date, including those in archaeology (Hermes et al., 2018). The second case study explores the dietary niche of early hominins in eastern Africa through δ^{13}C and δ^{18}O values (Sponheimer et al., 2013; Cerling et al., 2013; Wynn et al., 2013; Levin et al., 2015). Case study 3 explores the potential use of isotopic niche space outside of the more common dietary group studies by investigating the relationship between δ^{13}C and ^{87}Sr/^{86}Sr values in prehistoric southern Germany (Bentley & Knipper, 2005) in what may be referred to as a provenience study. In their study, Bentley and Knipper (2005) use pigs to identify what they call "isotope signatures" for different geographic regions in southern Germany in an attempt to provide a context for interpreting geochemical differences among Neolithic human groups.

Case Study 1: Larsen et al. (1992)

Larsen et al. (1992) analyzed δ^{13}C and δ^{15}N bone collagen values of 93 human samples from the Georgia Bight — a continental embayment on the US Atlantic coast spanning from Cape Hatteras, North Carolina to Cape Canaveral, Florida — to assess dietary trends through time. Their study was aimed at identifying changes in the importance of marine resources to the diet as well as the inclusion of maize, a C_4 photosynthetic plant, through time. δ^{13}C values reflect the isotopic composition of vegetation consumed based on differences in photosynthetic pathways (Ambrose & DeNiro, 1986; Cerling et al., 2003). C_3 plants (primarily trees, shrubs, and high-altitude grasses) have a δ^{13}C range of −36 to −22‰ with a mean of −26.4 ± 2.1‰ while C_4 plants (low-elevation tropical grasses, sedges, and shrubs of the Amaranthaceae) have a δ^{13}C mean of −11.4 ± 1.3‰ with a range of −14 to −11‰ (Cerling, 2014). While this may seem to provide a nice dichotomy, in many ways, this is an oversimplification. Succulents in dry regions and epiphytes in closed forest use the Crassulacean acid metabolism pathway and have δ^{13}C values between those of C_3 and C_4 plants. Additionally, the canopy effect — photosynthetic recycling of respired CO_2 and water, light, and temperature variability in closed canopy forests and marshes — may lead to plant $\delta^{13}C$ values outside the ranges quoted above (Diefendorf et al., 2010; Kohn, 2010). As $\delta^{13}C$ values reflect both habitat and resources consumed, it is considered a bionomic and scenopoetic factor (Newsome et al., 2007; Jackson et al., 2011). Similarly, $\delta^{15}N$ values are incorporated into animals through the plants that they consume which, in turn, incorporate nitrogen in relation to the chemical composition of the soil, the rainfall average, and the nitrogen composition of the atmosphere (DeNiro & Epstein, 1981; Hartman, 2011; Ugan & Coltrain, 2012). Unlike $\delta^{13}C$ values, $\delta^{15}N$ values become concentrated at higher trophic levels. Cool, wet ecosystems, and marine ecosystems typically have more $\delta^{15}N$ levels. The difference between marine and terrestrial in terms of trophic levels is leveraged to assess potential dietary differences among human groups (Schoeninger & DeNiro, 1984; Hedges & Reynard, 2007). In this way, $\delta^{15}N$ values primarily reflect resources consumed and are a bionomic factor (Newsome et al., 2007; Jackson et al., 2011). Age and sex, however, may influence $\delta^{15}N$ values. In particular, young individuals may appear to be in a higher trophic category than they really are due to the "carnivorous effect" of breastfeeding (Dupras et al., 2001) requiring caution in the interpretation of $\delta^{15}N$ values.

Six temporal periods are analyzed, including four prehistoric series — early preagricultural, late preagricultural, early agricultural, and late agricultural — and two historic samples — early contact and late contact. Early preagricultural spans from 1000 BC to AD 1000 and consists of 18 samples from five sites across the Refuge, Deptford, and Wilmington archaeological phases. From AD 1000 to 1150 is the late preagricultural, represented by 12 individuals from the St. Catherines phase Johns and Marys mounds. Nine individuals were sampled from the early agricultural Savannah period from the Irene burial mound (AD 1150–1300). From the Irene mortuary site dating to the late agricultural Irene phase (AD 1300–1450) are 11 samples. The early (AD 1608–1680) and late (AD 1686–1702) contact periods are represented by 22 samples from St. Catherines Island and 21 individuals from Amelia Island, respectively. Details on the archaeological and ecological information of these sites are available in the original publication (Larsen et al., 1992). Collagen samples were taken primarily from ribs and analyzed for C:N ratios with those falling between 2.7 and 3.8 included in the final study. For the purposes of the current case study, five of the six temporal periods are included representing 84 total individuals (Supplemental Dataset 1). I exclude the early agricultural period as the number of samples, nine, falls below the cutoff of 10 samples reported by Eckrich et al. (2020) as providing reliable estimates of isotopic niche space and overlap with rKIN.

Case Study 2: Early Hominin Dietary Ecology in Eastern Africa

A key question in paleoanthropology and Paleolithic archaeology is whether australopithecines occupied different ecological niches through time and space and/or if there was a shift in dietary ecology from *Australopithecus* to *Homo* (e.g., Sponheimer et al., 2013; Robinson et al., 2017; Patterson et al., 2019; Wynn et al., 2020). As the purpose of the current paper is to explore how the concept of isotopic niche space can add to anthropological and archaeological research, this case study is intended to demonstrate the potential of rKIN beyond replicating previous analyses (as in case studies 1 and 3), not to definitively address questions about early hominin diets. As such, my review of this literature is restricted to the publications that provide these data. A series of articles devoted to early hominin diets were published in the *Proceedings of the National Academy of Sciences* in June of 2013. In general, these studies found that the oldest australopith, *Australopithecus anamensis* (n = 17; ~ 4.2–4.0 Ma), primarily consumed C_3 foods and consistently had the lowest $\delta^{13}C$ values while *Australopithecus afarensis* (n = 20; ~ 3.4–2.9 Ma) and *Kenyanthropus platyops* (n = 20; ~ 3.6–3.0 Ma) incorporated significantly more C_4 foods in their diets. The robust australopith, *Paranthropus boisei* (n = 27; ~ 2.0–1.5 Ma), and early *Homo* (n = 24; ~ 2.1–1.5 Ma) were found to have the highest C_4 consumption (Klein, 2013; Sponheimer et al., 2013; Cerling et al., 2013; Wynn et al., 2013). After the publication of these studies, the site of Woranso-Mille in Ethiopia's lower Awash Valley yielded hominin remains analyzed for stable isotopes as Hominini indet. (Levin et al., 2015). These samples may represent any combination of *Australopithecus anamensis*, *Australopithecus afarensis*, *Australopithecus deyiremeda*, or even a yet to be named hominin (Haile-Selassie et al., 2015, 2019). Sixteen total samples that split between ~ 3.76 Ma sediments (n = 12) and ~ 3.469 Ma sediments (n = 4; Levin et al., 2015) were analyzed. For the purposes of the current study, I refer to these samples as Woranso-Mille hominins (Supplemental Dataset 2).

$\delta^{18}O$ values are the other variable available for use in studying isotopic niche space for these hominins. In faunal and hominin tooth enamel, $\delta^{18}O$ values are thought to provide environmental or climatic information (scenopoetic factor). In many studies, $\delta^{18}O$ values are interpreted as a proxy for aridity based on the premise that the lighter isotope, ^{16}O, will be preferentially evaporated compared with the heavier isotope, ^{18}O. In this scenario, a sample would be ^{18}O-enriched resulting in higher $\delta^{18}O$ values in faunal tooth enamel during dry periods (Levin et al., 2006; Blumenthal et al., 2017). Drawing direct inferences from herbivore and hominin $\delta^{18}O$ data is complicated as $\delta^{18}O$ values are also affected by precipitation amount and temperature. Furthermore, the relationship between $\delta^{18}O$ values of enamel and meteoric water, diet, and atmospheric oxygen and how these factors controlled $\delta^{18}O$ values of herbivore body water in the past are incompletely known (Levin et al., 2009; Faith, 2018). However, general trends in $\delta^{18}O$ values reveal potentially important environmental and ecological conditions that can be further explored. It must be kept in mind though that comparing $\delta^{18}O$ values across multiple basins may reflect large-scale climatological and hydrological differences rather than divergent dietary ecologies (Robinson et al., 2017). Since two different hydrological basins — Lake Turkana in Kenya (*Australopithecus anamensis*, *Kenyanthropus platyops*, *Paranthropus boisei*, early *Homo*) and the lower Awash River Valley in Ethiopia (*Australopithecus afarensis* and the Woranso-Mille hominins) — are represented by these hominin samples, rKIN analyses will be interpreted based both on the total sample of hominins as well as on the two basins separately (Supplemental Dataset 2). Note that this does not require separate runs of analysis as rKIN treats each group — in this case, hominin taxon — independently in calculating isotopic niche space and pairwise assessments of overlap. Within each basin, we may expect δ^{18}O values to be similar among different groups of hominins as hominins are obligate drinkers unless there is a substantial climatic difference in time and/or space. For example, if *Australopithecus afarensis* and the Woranso-Mille hominins are found to have different δ^{18}O values, and, in turn, to be occupying different areas of isotopic niche space (or have less isotopic niche space overlap), it may indicate a shift in precipitation and/or temperature from ~ 3.8–3.5 to ~ 3.4–2.9 Ma in the lower Awash Valley. Similarly, differences in δ^{18}O values among the Turkana Basin hominins would suggest climatological and hydrological changes in environments and habitats through time.

Case Study 3: Bentley and Knipper (2005)

Bentley and Knipper (2005) set out to map the bioavailable ^{87}Sr/^{86}Sr, δ^{13}C, and δ^{18}O isotopic signatures of prehistoric southern Germany by using faunal — primarily pig — tooth enamel samples from archaeological sites to create a basemap for comparing ^{87}Sr/^{86}Sr and δ^{18}O values from Neolithic humans. Southern Germany is an ideal location for ^{87}Sr/^{86}Sr analysis as the granitic geology of the uplands differs substantially from the carbonates making up the lowlands. Bentley and Knipper (2005) hypothesize that there may be altitudinal differences in δ^{18}O values. They suggest that δ^{18}O values would be more negative at upland sites than those closer to the coast, in part because the δ^{18}O values of precipitation at higher altitudes in the uplands tends to be more negative than values in the lowlands. They suggest there may also be altitudinal differences in δ^{13}C values related to photosynthetic differences between low and high-altitude environs. Since the original study only found potentially important differences between the lowlands and uplands in ^{87}Sr/^{86}Sr and δ^{13}C values, and because rKIN can only handle two elements (or axes) at a time (although see further discussion of this in the “Discussion” section), only these two elements are considered. Bentley and Knipper selected pigs as their proxy because pig physiology and metabolism are similar to that of humans and these specific samples likely fed on human food refuse as they lived more or less communally with humans. In addition to pigs, one cattle tooth and one dog tooth were included in the sample. Samples were collected from 22 sites throughout southern Germany on different bedrock geologies, including loam/loess, gravel, granite, and limestone. Temporally, the samples range from the earliest Neolithic (Linearbandkeramik: ~ 5500–4500 BC) through the Roman and into the Medieval periods. In their study, Bentley and Knipper (2005) group the loam/loess and gravel sites into the lowlands and the granite and limestone sites into the uplands. Lowland sites are primarily Neolithic and Roman in age, with the upland sites dominated by Medieval sites (Supplemental Dataset 3). While Bentley and Knipper report 49 total samples, not all were sampled for all three elements. For the purposes of the current study, only those samples that offer values for ^{87}Sr/^{86}Sr and δ^{13}C are relevant. With that in mind, the total number of samples comes to 21 for the lowlands and 18 for the uplands (Supplemental Dataset 3). Sampling and isotopic characterization followed standard procedures and are described in detail in the original publication (Bentley & Knipper, 2005).

This case study is a novel application of the spatial statistics underlying the isotopic niche space concept highlighting what is and is not identifiable using stable isotope data. In provenience studies, like place of origin or residency, based on ^{87}Sr/^{86}Sr analysis, the more restricted the range of potential ^{87}Sr/^{86}Sr values for specific geographic regions and the lower the potential overlap among regions the more confident a researcher can be in their interpretations (Bentley, 2006). The inclusion of a second isotope system, in this case carbon, is an attempt to identify potentially useful isotopic "signatures" for geographic regions that may have broad and/or overlapping ^{87}Sr/^{86}Sr values. The addition of δ^{13}C values also means that these data can be analyzed with spatial statistics. A narrower isotopic niche space (or just isotopic space to avoid confusion with dietary studies) would likely indicate a more useful geographic isotopic "signature" for archaeological purposes where place of origin can be pinpointed to a specific area. Determining whether the isotopic space of different geographic regions overlap, and the degree of that overlap, allows the researcher to assess if place of origin can be determined or if there is a particular region of isotopic space that may be more useful in place of origin studies than others.

rKIN Analysis

I employ the full suite of rKIN tools — MCP, SEA, and KUD models — on all three case studies to allow for a comparison of the isotopic niche space estimates among the methods. Instead of just measuring the total area encompassed by a specific model, rKIN provides the ability to measure niche size as the area encompassed by the contours of a particular percent of data in the dataset. Contour lines are defined in relation to the Euclidean distance of each observation to the centroid in bivariate space. Researchers may use any contour interval from 1 to 99%, but here I use three commonly used contours — 50%, 75%, and 95%. Using lower contour values prevent outliers or other extreme data points from significantly influencing estimates of isotopic niche size or overlap, enhancing the results of MCP and SEA models (Eckrich et al., 2020). The current study uses each of the three methods, at three different contour levels, for each case study. This means that there are nine sets of results for each case study. All analyses use the common functions in rKIN (Albeke, 2017), and no modifications to the package code or custom code writing were required, although I provide the specific scripts for these case studies (Supplemental Material 1) to reduce barriers in the adoption of the method by making examples easily accessible. One additional consideration is that rKIN is currently only able to support axes reflecting data in the same units. This creates an issue for case study three where ^{87}Sr/^{86}Sr values are ratios and δ^{13}C values are in parts per mille. To account for this, ^{87}Sr/^{86}Sr values are multiplied by 1000 for the analyses (i.e., a value of 0.70925 would be understood by rKIN as 709.25). This is no different from scaling ^{87}Sr/^{86}Sr values for comparison to δ^{13}C or δ^{18}O values (see Bentley & Knipper, 2005; Evans et al., 2006; Wright, 2012), but does call into question the terminology of isotopic niche space, which I address further in the "Results and Discussion" section. While the package developers have built in a smallSamp() argument to allow for analyses to be run with as few as five samples, all analyses are conducted with at least 10 samples as this is the level found to provide reliable and realistic estimates of isotopic niche space and overlap (Eckrich et al., 2020).

Results and Discussion

Case Study 1: Larsen et al. (1992)

All three methods find the early preagricultural group to have the largest isotopic niche size and the late preagricultural group to have the smallest, although the exact size estimates differ among the methods (Table 1). This result indicates that the early preagricultural group had the broadest dietary niche as foragers relying on both terrestrial and marine resources, although this interpretation must also acknowledge that the early preagricultural group spans ~ 2000 years (Larsen et al., 1992). The narrower isotopic niche size for the late preagricultural group is likely a function of the beginnings of not only a shift to maize agriculture, but also a focus on marine resources as all late preagricultural samples come from St. Catherines Island. While the value of the isotopic niche size estimate for each group varies based on the specific contour interval, contour interval selection does not change which group is larger or smaller. As found by Eckrich et al. (2020), the MCP method appears to underestimate the isotopic niche size due to the model simply fitting convex polygons to the points as opposed to statistically determining the isotope space utilized. In this case, the MCP estimates are approximately three times smaller than those of the SEA or KUD methods at each contour level, likely underestimating the used isotope space.

The late preagricultural group is fully encompassed by, or is fully overlapped, by the early preagricultural group (Table 2; Figure 1). The early and late contact groups also overlap to a high degree with the overlap ~ 60–80% based on the KUD and SEA methods. The MCP method seems to underestimate the overlap (~30–50%) of the late contact group by the early contact group, but closely approximates the overlap of the early contact group by the late contact group found with the KUD and

Table 1 Comparison of estimates of isotopic niche size from minimum convex polygon (MCP), standard ellipse area (SEA), and kernel utilization density (KUD) for case study 1: Larsen et al. (1992)

Method	EP group			LP group			LA group			EC group			LA group		
	50%	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*
MCP	4.6	9.5	19.6	0.3	1.0	1.4	1.3	1.7	3.5	0.9	1.9	4.4	1.0	2.9	6.1
SEA	11.0	22.0	47.5	1.0	2.0	4.3	3.4	6.8	14.7	3.3	6.7	14.4	3.0	6.0	13.0
KUD	15.2	28.6	52.6	1.0	1.9	3.7	3.6	6.8	12.6	2.6	5.6	11.8	3.2	6.9	12.9

Abbreviations: EP, early preagricultural; LP, late preagricultural; LA, late agricultural; EC, early contact; LC, late contact

Table 2 Pairwise isotopic niche overlaps from minimum convex polygon (MCP), standard ellipse area (SEA), and kernel utilization density (KUD) for case study 1: Larsen et al. (1992)

Method	Group	EP group			LP group			LA group			EC group			LC group		
		50%	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*
MCP	**EP**	---	---	---	0.27	0.95	0.97	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00
	LP	0.02	0.10	0.07	---	---	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LA	0.00	0.00	0.08	0.00	0.00	0.00	---	---	---	0.00	0.00	0.00	0.00	0.00	0.00
	EC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	---	---	---	0.31	0.49	0.54
	LC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.72	0.74	---	---	---
SEA	**EP**	---	---	---	0.77	1.00	1.00	0.05	0.47	0.86	0.00	0.00	0.31	0.00	0.00	0.37
	LP	0.07	0.09	0.09	---	---	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LA	0.02	0.14	0.27	0.00	0.00	0.00	---	---	---	0.00	0.00	0.06	0.00	0.00	0.02
	EC	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.06	---	---	---	0.62	0.77	0.84
	LC	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.02	0.61	0.70	0.75	---	---	---
KUD	**EP**	---	---	---	0.99	1.00	1.00	0.00	0.68	0.99	0.00	0.05	0.41	0.00	0.18	0.45
	LP	0.07	0.07	0.07	---	---	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LA	0.00	0.16	0.24	0.00	0.00	0.00	---	---	---	0.00	0.00	0.15	0.00	0.00	0.05
	EC	0.00	0.01	0.09	0.00	0.00	0.00	0.00	0.00	0.14	---	---	---	0.62	0.63	0.64
	LC	0.00	0.04	0.11	0.00	0.00	0.00	0.00	0.00	0.05	0.76	0.78	0.70	---	---	---

Abbreviations: EP, early preagricultural; LP, late preagricultural; LA, late agricultural; EC, early contact; LC, late contact

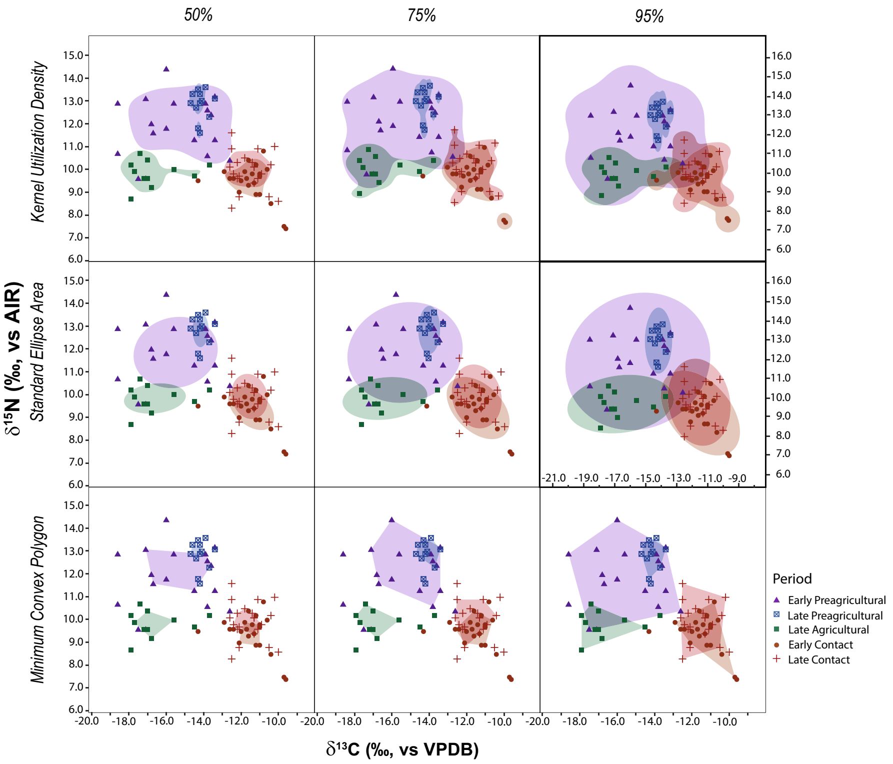

Fig. 1 Niche size and overlap for case study 1 based on data from Larsen et al. (1992). Rows represent different estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA], and kernel utilization density [KUD]). Columns display results at commonly selected contour levels — 50%, 75%, and 95%. In order to ensure that all plots present with equal proportions, the scales for the SEA and KUD methods at 95% differ. This is indicated by the thicker weight of the box boarder for these plots. VPDB, Vienna Pee Dee Belemnite

SEA models at the 75% and 95% contour levels (Table 2). Contour interval selection does have an effect on interpreting overlap among groups. Only at the 95% contour interval does the early preagricultural group overlap either the early or late contact groups with the SEA method (~ 35–45%), and the late agricultural group does not overlap the early or late contact groups at any contour level (Table 2). If a lower contour interval is selected, perhaps due to concerns about potential outliers or extreme values in the early preagricultural group because of its long temporal span, one may interpret the results as indicating that the preagricultural and contact groups had entirely different diets and occupied different dietary niches. Continuing this same example, the KUD method reveals some overlap (~ 5–20%) of the early and late contact groups by the early preagricultural group at the 75% contour interval (Table 2). Selecting between the SEA and KUD models, therefore, likely would lead to slightly different interpretations. As assessing whether data in the Larsen et al. (1992) are normally distributed is complicated by mixing of different archaeological sites, the

KUD model is the more appropriate choice. Overall, the results indicate that the general preagricultural diet differs from the late agricultural group and both contact groups. The two contact period groups' diets not only are similar to one another, but also differ from the late agricultural group (Table 2; Figure 1).

In comparison to the original study, the rKIN analyses corroborate the narrower dietary ecology (based on $\delta^{13}C$ values) of the late preagricultural period compared to the early preagricultural period, but do not support the contention of higher $\delta^{15}N$ values as the late preagricultural isotopic niche space is entirely encompassed within that of the early preagricultural period (Larsen et al., 1992). While Larsen and colleagues go on to describe how individual sites may account for the differences between the two preagricultural periods, that is beyond the scope of this paper as sample sizes for individual sites are below 10. The rKIN analyses also add nuance to the Larsen et al. (1992) results of the late agricultural period having lower $\delta^{13}C$ and $\delta^{15}N$ values than the preagricultural periods. In the new analyses, the late agricultural period has no isotopic niche space overlap with the late preagricultural period but overlaps quite a bit with the early preagricultural period at the 75% and 95% contours (Table 2; Figure 1).

Case Study 2: Early Hominin Dietary Ecology in Eastern Africa

Isotopic niche space is the largest for the Ethiopian hominins — *Australopithecus afarensis* from Hadar and the Woranso-Mille hominins — with *Australopithecus afarensis* estimated to occupy approximate twice the isotopic niche space as the Woranso-Mille hominins (Table 3; Figure 2). Here, the context of the study is important to interpreting the large isotopic niche space. As mentioned earlier, the Woranso-Mille hominin group may include more than one taxon. The larger isotopic niche spaces for these Ethiopian hominins may simply reflect the mixing of the diets and habitats of multiple species. The broad isotopic niche space for *Australopithecus afarensis* does not suffer from this concern. Compared with the Woranso-Mille hominins, the larger area of isotopic space occupied by *Australopithecus afarensis* is a result of several samples having much lower $\delta^{18}O$ values (Figure 3). The isotopic niche space of *Australopithecus afarensis* is found to overlap that of the Woranso-Mille hominins at all contour intervals utilizing all methods by > 60%, with most in the 80–100% overlap range. Despite general agreement among models of a high level of overlap, values shift, and invert based on contour interval selection. Most striking is in the MCP model where the 50% and 95% contour intervals result in an overlap of ~ 90%, but the 75% interval only shows an overlap of ~ 60%. Like the discussion of case study 1, this is a result of the MCP model connecting the closest 75% of data points as opposed to considering the distribution of data. Neither the SEA nor the KUD model have issues with inverted estimates of overlap, but the contour interval results reveal other differences. In the SEA model where the assumption is that these data are normally distributed and can be fitted to an ellipse, the overlap values are very similar, from 90 to 100%, but in the KUD model where no assumptions are placed on data the 50% contour interval only finds ~ 65% overlap. The 75% and 95% contour intervals of the KUD model calculate the overlap

Table 3 Comparison of estimates of isotopic niche size from minimum convex polygon (MCP), standard ellipse area (SEA) and kernel utilization density (KUD) for case study 2: early hominin dietary ecology in eastern Africa

Method	Turkana Basin — Kenya												Lower Awash Valley — Ethiopia					
	Au. anamensis			*K. platyops*			*P. boisei*			*Homo* sp.			*Au. afarensis*			Woranso-Mille		
	50%	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*
MCP	1.7	3.3	4.6	9.2	16.7	29.5	3.5	5.0	10.4	10.5	19.6	31.0	21.4	43.6	84.4	9.1	22.7	38.4
SEA	2.9	5.9	12.7	17.3	34.7	74.9	6.2	12.4	26.8	18.0	36.0	77.9	49.5	98.9	213.8	24.1	48.2	104.1
KUD	4.4	8.4	15.1	23.8	44.5	81.1	7.9	15.5	30.7	23.2	45.8	85.0	59.9	119.2	238.4	34.4	66.1	124.1

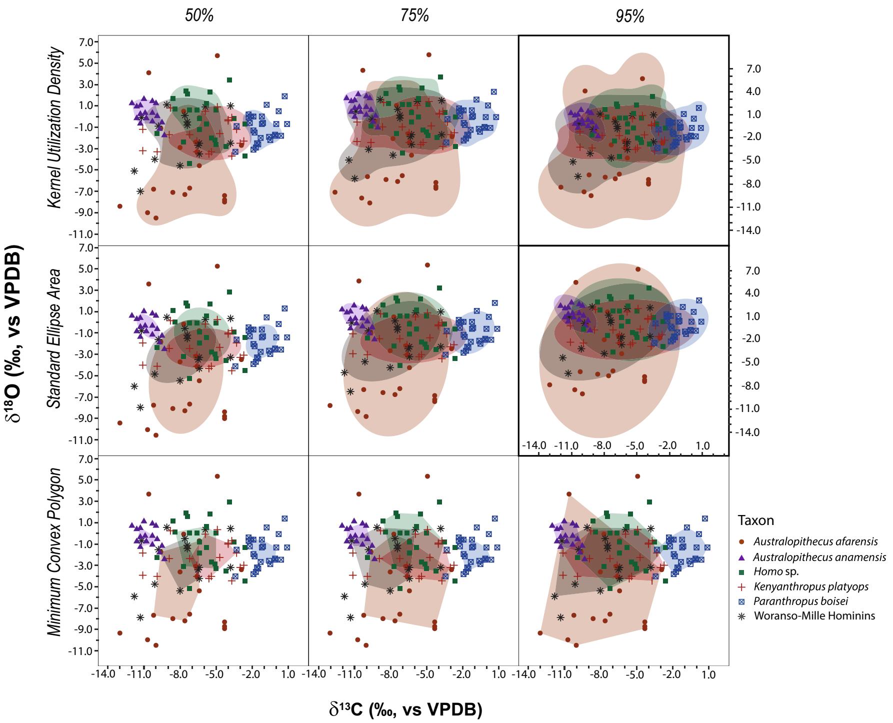

Fig. 2 Niche size and overlap for all eastern African hominins in case study 2 based on data from Cerling et al. (2013), Wynn et al. (2013), and Levin et al. (2015). Rows represent different estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA], and kernel utilization density [KUD]). Columns display results at commonly selected contour levels — 50%, 75%, and 95%. In order to ensure that all plots present with equal proportions, the scales for the SEA and KUD methods at 95% differ. This is indicated by the thicker weight of the box boarder for these plots. VPDB, Vienna Pee Dee Belemnite

at 85–90% (Table 4). While 65% may still be interpreted as a high degree of isotopic niche space overlap, depending on the context of a study, it may be seen as substantially different from 85 to 90%. The opposite overlap — *Australopithecus afarensis* overlapped by the Woranso-Mille hominins — is also found at all contour levels with all methods, but the estimated isotopic niche space overlap is much less at ~ 30–50%. The Woranso-Mille hominins and *Australopithecus afarensis* overlap almost completely on the δ^{13}C axis, but not on the δ^{18}O axis (Table 4; Figure 3). This indicates that there was a shift in climatological and/or hydrological conditions over time in the lower Awash Valley, although the complexities of δ^{18}O values conceal the specific change.

In the Turkana Basin, *Homo* sp. and *Kenyanthropus platyops* have the highest isotopic niche space sizes, with *Paranthropus boisei* in the middle and *Australopithecus anamensis* having the smallest niche space size (Table 3; Figures 2 and 4). This reflects broader dietary niches for *Homo* sp. and *Kenyanthropus platyops*, both of which are associated with changing habitats in their respective

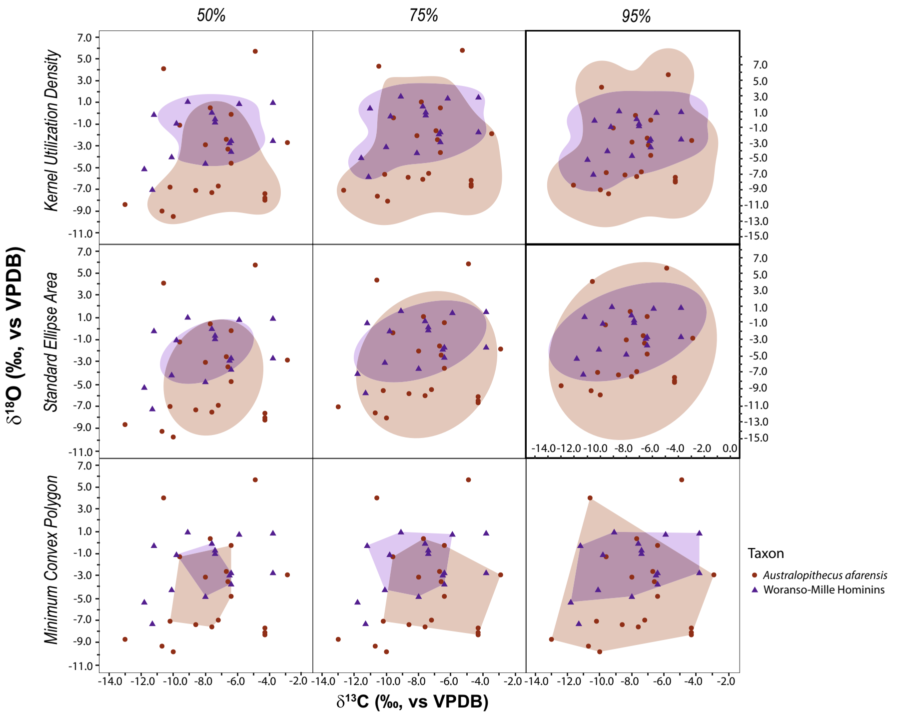

Fig. 3 Niche size and overlap for lower Awash Valley (Ethiopia) hominins in case study 2 based on data from Wynn et al. (2013) and Levin et al. (2015). Rows represent different estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA], and kernel utilization density [KUD]). Columns display results at commonly selected contour levels — 50%, 75%, and 95%. In order to ensure that all plots present with equal proportions, the scales for the SEA and KUD methods at 95% differ. This is indicated by the thicker weight of the box boarder for these plots. VPDB, Vienna Pee Dee Belemnite

time periods (Boyd et al., 2018; Patterson et al., 2019). Additionally, *Homo* sp. in the Turkana Basin is likely including meat, even if scavenged, into its diet (Sponheimer et al., 2013; Patterson et al., 2019), and *Kenyanthropus platyops* may have been the creator of the Lomekwian stone tools (Harmand et al., 2015), potentially offering new resources to exploit. The smaller isotopic niche space size for *Australopithecus anamensis* is consistent with adaptations for hard object feeding (Ward et al., 2010) and its mosaic but relatively stable and wooded habitat (Schoeninger et al., 2003). Similarly, the narrower isotopic niche space of *Paranthropus boisei* may be expected in relation to its specialized C_4 diet (Sponheimer et al., 2013; Wynn et al., 2020). *Paranthropus boisei* is found to have the least overlap in isotopic niche space with any other hominin, including those in the lower Awash Valley, with most estimates at the 50% and 75% contours < 10% regardless of method. At the 95% contour, *Kenyanthropus platyops* overlaps ~ 60–70% of the *Paranthropus boisei* isotopic niche space while *Homo* sp., *Australopithecus afarensis*, and the Woranso-Mille hominins overlap the *Paranthropus boisei* space between ~ 40 and 50% based on the KUD and SEA methods. Overlap of *Paranthropus boisei* space measured with the

Table 4 Pairwise isotopic niche overlaps from minimum convex polygon (MCP), standard ellipse area (SEA), and kernel utilization density (KUD) for case study 2: early hominin dietary ecology in eastern Africa

Method	Group	Turkana Basin — Kenya												Lower Awash Valley — Ethiopia					
		Au. anamensis			*K. platyops*			*P. boisei*			*Homo* sp.			*Au. afarensis*			Woranso-Mille		
		50%	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*
MCP	*Au. anamensis*	---	---	---	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.06	0.05
	K. platyops	0.00	0.00	0.14	---	---	---	0.00	0.00	0.00	0.47	0.57	0.74	0.06	0.27	0.29	0.08	0.23	0.68
	P. boisei	0.00	0.00	0.00	0.00	0.00	0.00	---	---	---	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
	Homo sp.	0.00	0.00	0.00	0.54	0.67	0.78	0.00	0.00	0.03	---	---	---	0.15	0.19	0.25	0.26	0.30	0.63
	Au. afarensis	0.00	0.00	0.80	0.15	0.69	0.82	0.00	0.00	0.00	0.30	0.42	0.67	---	---	---	0.89	0.63	0.87
	Woranso-Mille	0.00	0.40	0.41	0.08	0.32	0.88	0.00	0.00	0.00	0.23	0.35	0.79	0.38	0.33	0.40			
SEA	*Au. anamensis*	---	---	---	0.00	0.01	0.09	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.03	0.06	0.00	0.05	0.09
	K. platyops	0.00	0.10	0.56	---	---	---	0.00	0.24	0.69	0.59	0.68	0.75	0.27	0.30	0.33	0.47	0.54	0.60
	P. boisei	0.00	0.00	0.00	0.00	0.09	0.25	---	---	---	0.00	0.01	0.15	0.00	0.00	0.06	0.00	0.00	0.07
	Homo sp.	0.00	0.03	0.59	0.61	0.71	0.78	0.00	0.02	0.42	---	---	---	0.22	0.33	0.36	0.43	0.55	0.65
	Au. afarensis	0.00	0.44	0.96	0.76	0.87	0.93	0.00	0.00	0.50	0.61	0.92	1.0	---	---	---	0.91	0.98	1.00
	Woranso-Mille	0.00	0.37	0.76	0.65	0.75	0.83	0.00	0.00	0.23	0.58	0.74	0.87	0.44	0.48	0.49	---	---	---
KUD	*Au. anamensis*	---	---	---	0.00	0.02	0.13	0.00	0.00	0.00	0.00	0.04	0.10	0.00	0.03	0.06	0.05	0.10	0.12
	K. platyops	0.00	0.10	0.67	---	---	---	0.10	0.36	0.60	0.51	0.69	0.77	0.18	0.28	0.31	0.40	0.52	0.6
	P. boisei	0.00	0.00	0.00	0.03	0.13	0.23	---	---	---	0.00	0.03	0.17	0.00	0.00	0.06	0.00	0.00	0.10
	Homo sp.	0.00	0.19	0.59	0.50	0.71	0.81	0.00	0.10	0.46	---	---	---	0.17	0.31	0.35	0.47	0.56	0.61
	Au. afarensis	0.00	0.46	0.96	0.46	0.75	0.91	0.00	0.00	0.49	0.43	0.82	0.98	---	---	---	0.66	0.84	0.93
	Woranso-Mille	0.41	0.80	1.0	0.58	0.79	0.92	0.00	0.00	0.41	0.69	0.81	0.89	0.38	0.47	0.48	---	---	---

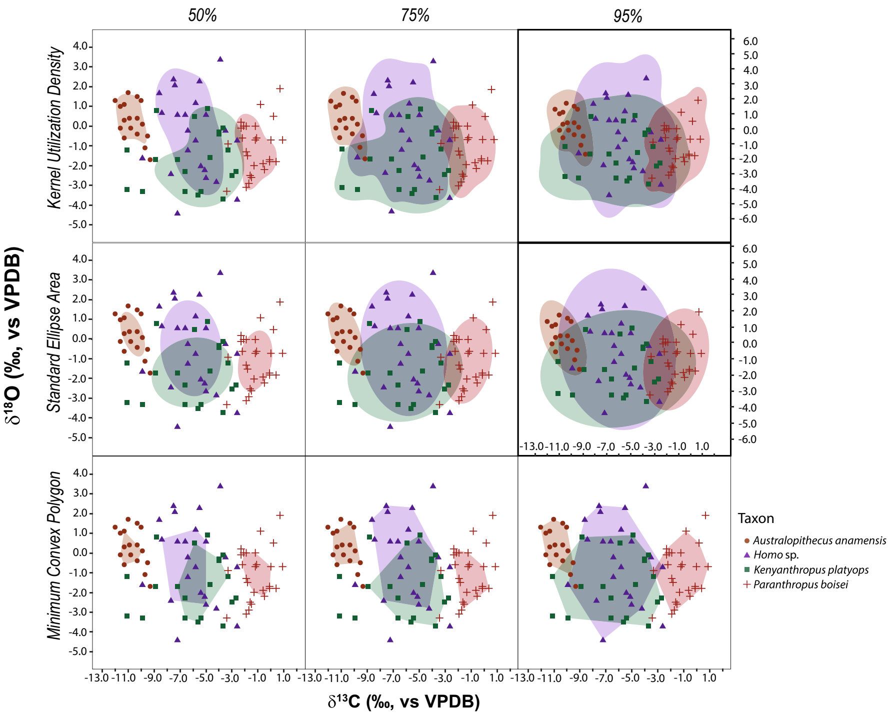

Fig. 4 Niche size and overlap for Turkana Basin (Kenya) hominins in case study 2 based on data from Cerling et al. (2013). Rows represent different estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA], and kernel utilization density [KUD]). Columns display results at commonly selected contour levels — 50%, 75%, and 95%. In order to ensure that all plots present with equal proportions, the scales for the SEA and KUD methods at 95% differ. This is indicated by the thicker weight of the box boarder for these plots. VPDB, Vienna Pee Dee Belemnite

MCP method is ~ 0–5% (Table 4). These results provide support for the argument that *Paranthropus boisei* occupied a dietary niche quite dissimilar from other hominins (Quinn & Lepre, 2021). Similarly, overlap of *Australopithecus anamensis* isotopic niche space is low at all contour levels for other Turkana Basin hominins except *Kenyanthropus platyops* at the 95% level where the overlap is ~ 50–70% in the KUD and SEA methods. Isotopic niche spaces of *Kenyanthropus platyops* and *Homo* sp. overlap each other by ~ 50% or greater at all contour levels in all methods. This degree of overlap is true regardless of whether it is measured as the overlap of *Kenyanthropus platyops* by *Homo* sp. or vice versa (Table 4; Figure 4). For both *Paranthropus boisei* and *Australopithecus anamensis*, the choice of contour interval would have a considerable effect on interpretation. If the 75% contour interval is selected as the analytical unit to avoid the inclusion of extreme values, the clear result are that these two hominins occupied dietary niches separate from any other hominins included in this study. If the 95% interval is selected, that interpretation would have to be modified or hedged by acknowledging some overlap by other hominins (Table 4). Unlike the lower Awash Valley hominins, where there is overlap of the isotopic niche space of the Turkana Basin hominins, it is primarily along the $\delta^{18}O$ axis with major differences along the $\delta^{13}C$ axis (Figure 4). This is in line with hominins being obligate drinkers and aspects of basin hydrology and climate having some control on $\delta^{18}O$ values. The Ethiopian hominins show an overlap of 40% or greater of the *Australopithecus anamensis* space at both the 75% and 95% contour levels with the KUD and SEA methods (Table 4; Figure 2). As mentioned above, however, overlap of hominin isotopic niche space across basins must consider that the $\delta^{18}O$ values likely measure factors beyond similarities or differences in dietary ecology.

A full discussion of specific dietary niches and/or potential phylogenetic relationships between the different hominins is beyond the scope of the current paper; however, there are some broad patterns revealed by the rKIN analyses. Additionally, although $\delta^{18}O$ values are reported in supplemental datasets for hominin samples, they are rarely analyzed or interpreted meaning that there are no studies to directly compare isotopic niche space results. In the current study, *Australopithecus anamensis* and *Paranthropus boisei* are found to occupy distinctive isotopic niches for hominins in the Turkana Basin whereas *Kenyanthropus platyops* and *Homo* sp. appear to have occupied a similar isotopic niche, albeit ~ 1 Ma apart. While these results are in-line with those based on $\delta^{13}C$ values alone (Sponheimer et al., 2013; Wynn et al., 2020), the rKIN analyses provide quantification and direction of overlap at different contour levels, although this depends on the contour interval choices made. The Ethiopian hominins also overlap the isotopic niche space of *Australopithecus anamensis*. Even though we must be cautious in interpreting isotopic niche space across basins, the overlap between *Australopithecus anamensis* and *Australopithecus afarensis* may provide some support for the hypothesis of an ancestor-descendant lineage (Kimbel et al., 2006; Du et al., 2020), although the isotopic niche space of *Australopithecus afarensis* is much larger (Figure 2 and see Haile-Selassie et al., 2019 for an argument against this hypothesis). Within the lower Awash Valley, the overlap reveals a wider niche space for *Australopithecus afarensis*, particularly on the $\delta^{18}O$ axis, compared with the Woranso-Mille hominins (Figure 4). The near complete overlap of the Woranso-Mille hominin isotopic niche space by *Australopithecus afarensis* may be surprising considering that multiple hominins are known to be present in the Woranso-Mille assemblage (Haile-Selassie et al., 2019). This may suggest that only representatives of *Australopithecus afarensis* at Woranso-Mille were sampled by Levin et al. (2015); that multiple hominins were occupying the same isotopic, and potentially dietary, niche at Woranso-Mille although at slightly different time periods; or that the combined isotopic space of multiple taxa at Woranso-Mille approximates the size of the isotopic niche space occupied by *Australopithecus afarensis*. Levin et al. (2015) also found the $\delta^{13}C$ values of the Woranso-Mille hominins to be indistinguishable from those of *Australopithecus afarensis* at Hadar but did not provide a comparative analysis of $\delta^{18}O$ values. Further interpretation of isotopic niche spaces of lower Awash Valley hominins awaits additional taxonomic identification of the remains from Woranso-Mille. Future work on the isotopic niche space of eastern African hominins should look to a more complete understanding of hominin $\delta^{18}O$ values, but this case study demonstrates the potential of the approach to complement other studies and reveal potentially new research directions.

Case Study 3: Bentley and Knipper (2005)

In this case study, the lowland group has the smaller isotopic niche space, but is overlapped ~ 60–80% by the upland group. This suggests that the isotopic “signature” of the lowland group will not be particularly useful in provenience or place of origin studies. It is only at lower δ^{13}C values that the upland group does not overlap the lowland group, providing a potential, but small, area of isotope space where lowland samples may be differentiated from upland samples (Figure 5). Despite this degree of overlap of the lowland group by the upland group, the lowland group only overlaps ~ 20–30% of the upland group, meaning that at higher ^{87}Sr/^{86}Sr values, it may be possible to identify upland samples from lowland samples. As with case study 1, the MCP method underestimates isotopic space size, but contour interval selection does not change which group is larger or smaller. Underestimates of

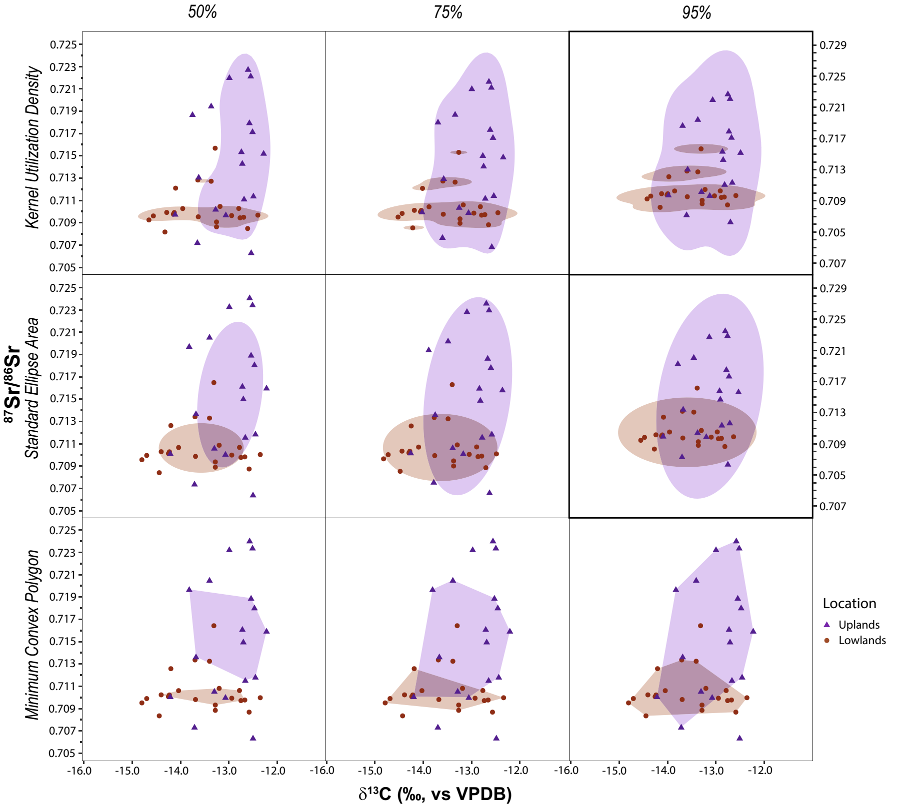

Fig. 5 Niche size and overlap for case study 3 based on data from Bentley and Knipper (2005). Rows represent different estimation methods (minimum convex polygon [MCP], standard ellipse area [SEA], and kernel utilization density [KUD]). Columns display results at commonly selected contour levels — 50%, 75%, and 95%. In order to ensure that all plots present with equal proportions, the scale of the y-axis (^{87}Sr/^{86}Sr values) for the SEA and KUD methods at 95% differ. This is indicated by the thicker weight of the box boarder for these plots. VPDB, Vienna Pee Dee Belemnite

overlaps appear to occur at the 50% contour level but are similar in the 75% and 95% levels (Table 5). Unlike in case study 1, and even with this potential underestimation of overlaps at the 50% contour, contour interval selection would not substantially change the interpretation of overlap between the upland and lowland groups with either the SEA or KUD methods.

In the original study, Bentley and Knipper (2005) found the ^{87}Sr/^{86}Sr values of lowland samples to be in a restricted range, but only after excluding several outliers that they interpret may have come from pigs traded from other regions. Using spatial statistics and the isotopic niche space concept offers two advantages for the original study's concern with traded pigs. First, isotopic space simultaneously considers both isotope systems minimizing the effect of a single or small number of outliers in one system. Second, the use of contour intervals in rKIN quickly allows for an assessment of isotope space size and overlap by excluding or including different outliers. As described above, the current study finds the lowland group to occupy a narrower isotopic space than the upland group even at the 95% contour interval with only the extreme values excluded. This is a more robust result than looking at the range of ^{87}Sr/^{86}Sr values alone. In terms of overlap, however, using contour intervals to exclude potential outliers does not appear to indicate substantially less overlap. In the scenario described by Bentley and Knipper (2005), we may be justified in utilizing the 75% contour as providing an estimate that excludes potentially traded pigs. While the degree of overlap changes moderately — ~ 75 to 65% with the SEA model or ~ 85 to 70% with the KUD model — this difference is likely not enough to justify the use of these isotopic "signatures" for provenience studies in the lowlands. On the other hand, Bentley and Knipper (2005) find the ^{87}Sr/^{86}Sr values of the upland samples generally to be higher than the lowland samples but do find lower values that overlap lowland values for some samples on volcanic bedrock. As with the Larsen et al. (1992) study above, they dive into site-by-site differences that are beyond the scope of this study due to small sample sizes. Bentley and Knipper (2005) also find the slight difference in δ^{13}C values with upland samples being 1–2‰ higher than lowland samples. This fits well with the ~ 20–30% overlap of the upland group by the lowland group found here using rKIN, meaning that these ranges may be useful measures for differentiating location of origin to the uplands. However, in the original study, Bentley and Knipper (2005) have no way to statistically assess isotopic space and, therefore, do not explore the potential of combining

Table 5 Comparison of estimates of isotopic niche size and pairwise overlap from minimum convex polygon (MCP), standard ellipse area (SEA), and kernel utilization density (KUD) for case study 3: Bentley and Knipper (2005)

Method	Lowland group			Upland group			Upland-Lowland overlap			Lowland-Upland overlap		
	50%	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*	*50%*	*75%*	*95%*
MCP	1.5	4.5	7.5	8.8	14.3	19.6	0.00	0.41	0.63	0.00	0.13	0.24
SEA	5.7	11.4	24.6	12.6	25.2	54.6	0.44	0.65	0.76	0.20	0.29	0.34
KUD	3.9	7.9	16.1	17.9	33.2	61.0	0.57	0.72	0.84	0.12	0.17	0.22

$^{87}Sr/^{86}Sr$ and $\delta^{13}C$ values for differentiating the uplands from the lowlands. This is a major shortcoming of relying on descriptions of bi-plots or reducing the interpretation of data on two axes to single measures like means. It is only with the concept of isotopic niche space and rKIN analyses that this difference in $\delta^{13}C$ values is revealed to differentiate the uplands from the lowlands even where $^{87}Sr/^{86}Sr$ values overlap. Isotopic niche space measures have the potential to improve the way we identify and justify differences between groups.

Benefits of Isotopic Niche Space and Using rKIN

The application of the isotopic niche space approach to archaeology is limited only by the various isotope systems currently in use, those that will be found to be of interests to archaeologists in the future, and the creativity of innovative research questions developed by future archaeologists. As seen in the case studies, isotopic niche space analyses more broadly, and the use of the rKIN package more specifically, are not intended to change or revise the results of previous studies, but, instead, to be an addition to qualitative comparisons and descriptive statistics (mean and standard deviation among others). In particular, isotopic niche space analyses allow for the quantification of overlap that may be a crucial parameter in hypothesis development and testing or in answering questions about the similarities and/or differences of groups in two-dimensional isotopic space. As seen in case studies 1 and 2, this approach can allow archaeologists to quantify shifts, expansions, and/or contractions in diet through time beyond what is possible with descriptive statistics alone. For paleoanthropologists or archaeologists reconstructing food webs, isotopic niche space may also allow for an interpretation of trophic category changes through time or from ecosystem to ecosystem (e.g., Jackson & Britton, 2014; Galetti et al., 2016; although see below for some limitations of this approach). While studies similar to those of case studies 1 and 2 are the way ecologists have primarily utilized the concept of a quantified isotopic niche space (Jackson et al., 2011; Eckrich et al., 2020), archaeologists can find use for this method outside of biological or dietary questions. Case study 3 shows how isotopic niche space analyses differentiate geographic regions from one another for movement and migration studies. In these studies, the use of the term “niche” may not be appropriate (see below for further discussion of this point) but quantifying the degree of overlap between regions can reveal areas of isotopic space that are (or are not) useful in identifying the source of an unknown mystery sample. All three case studies demonstrate the potential of these measures to convey information more accurately in the context of multi-isotope studies where the current methods fall short by essentially considering isotope systems separately instead of simultaneously.

There are also specific advantages of the rKIN package. rKIN is user friendly, and analyses can be customized to specific research questions or projects. Other approaches to quantifying isotopic niche space and overlap are only based on one model or method. That said, the choice of model — MCP, SEA, or KUD — should be determined by the research question and data at hand. While the MCP model was the first of these developed, most researchers today agree that the use of convex polygons fails to capture the true size and overlap of isotopic niche space (Jackson et al., 2011; Eckrich et al., 2020). This underestimate of isotope space size and overlap by the MCP model is shown throughout all three case studies here. Unless a researcher was confident that their dataset represented all possible values across two-dimensional isotope space, the use of the MCP model will likely provide underestimates as its method of simply connecting values with the straightest lines to encompass the entire dataset will exclude used isotope space. As archaeologists are typically not able to know whether their datasets represent the entire spread of data possible, caution should be applied to any interpretations of MCP results for archaeological studies. SEA and KUD models performed quite similarly across the three case studies above, although the SEA model often provides slightly higher estimates of isotopic space overlap. This difference is likely due to the spatial statistics underlying the model that assume normally distributed data for building ellipse radii (Jackson et al., 2011). Additionally, the SEA model will *always* force the data to fit an ellipse model, potentially excluding used or including unused isotope space. Since archaeological applications of stable isotope data typically result in non-normally distributed data (or it is unknown whether data are normally distributed; Roberts et al., 2018), the KUD method is probably the best option for archaeologists. In the KUD model, analyses proceed without a pre-determined grid or distribution shape allowing the isotopic space and overlap to be assessed in a free-form way (Eckrich et al., 2020). Despite potential concerns with the MCP and SEA models, rKIN easily allows for the comparison of results from all three providing the researcher with the opportunity to review results and make a post hoc decision as to the best model for their specific research question. The ability to set a contour level, regardless of method, can also be helpful. Similar to selection of a model, selection of contour interval level is driven by the research question and dataset available. While 50%, 75%, and 95% are commonly employed contour levels, a researcher can select any number from 1-99% with lower intervals including less of the original dataset in building the spatial model. Lower contour interval levels are useful if, as in case study 3, there is a concern about suspect outliers or other reasons to exclude extreme values from the model. Researchers should be aware that while contour interval level does not seem to influence which analytical group occupies the largest or smallest amount of isotopic space (although it does change the raw values of these measures), it can result in inverted estimates of the percentage of overlap as demonstrated in case study 2. Particularly when using the SEA or KUD models, removing extreme values can radically change the shape of the resulting isotopic space, and, in turn, estimate different degrees of overlap. That does not mean the calculation is incorrect if a 50% contour interval level estimates higher overlap between two groups than a 75% or 95% overlap, as long as there is a justification for only including 50% of the data in the model. Through these options, the researcher is able to tailor the analysis of isotopic niche space to their specific dataset and questions.

Limitations of Isotopic Niche Space and Using rKIN

Despite the many benefits described above, archaeologists should also be aware of the limitations of using the isotopic niche space concept and the rKIN package. One of the concerns is around how directly isotopic niche space is a proxy for ecological and trophic niche. Many ecologists have interpreted changes in isotopic niche space as indicating shifts in trophic position through time and/or space or providing insight to competition among multiple species (e.g., Jackson & Britton, 2014; Galetti et al., 2016). This direct equivalency of isotopic niche space with trophic niche has recently been criticized by Hette-Tronquart (2019) who argues that the mathematical relationship between these two variables is not as straightforward as it has been presented and requires additional conceptualization. Related to this is the terminology of isotopic niche space itself, particularly the use of the word "niche." To avoid confusion, Hette-Tronquart (2019) suggests that researchers should keep isotopic space and niche space as separate concepts. For archaeologists, this realization may be a spark of creativity as seen in case study 3. Any material from which two (or more, although see below) isotope systems have been analyzed can have their isotopic space investigated. Isotopic space studies do not have to be strictly ecological or dietary research questions. With that in mind, the word "niche" would be confusing at best, and perhaps seen as inappropriate at worst, when the concept of a quantified isotopic space is applied to questions like those in case study 3.

Other limitations are associated with the computation of isotopic space more generally, and the features of the rKIN package specifically. As with any statistical software or package, the researcher can generate quantitative results that may not be appropriate or for which an interpretive framework is lacking. For instance, while it is possible to calculate isotopic niche spaces and overlap for eastern African hominins in case study 2 using δ^{13}C and δ^{18}O values, more work is necessary to understand whether δ^{18}O values are useful as a scenopoetic axis in this context before dietary or phylogenetic interpretations can be made. The burden falls to the archaeologist to choose sound parameters for the analyses and to interpret the relevance of the results. In addition, there are four specific limitations of the rKIN package. First, as demonstrated in case study 3, rKIN is designed to calculate isotopic niche space and overlap using isotope variables on the same scale. Archaeologists frequently plot isotopic data measured on different scales, including ratios and per mille values when comparing ^{87}Sr/^{86}Sr and δ^{18}O values. Researchers need to apply similar principles that allow for the construction of these bi-plots to rKIN. Transparency about transformations carried out on datasets, such as multiplying ^{87}Sr/^{86}Sr values by 1000 in case study 3, will be crucial to ensure comparability of studies and replicability of methods. Second, rKIN provides pairwise comparisons of isotopic niche space overlap (in both directions) but is unable to offer information on the overlap of more than two groups. This can be a limiting factor if the research question is about the amount of overlap shared by three of more groups. Third, rKIN is currently only able to calculate isotopic niche space and overlap in two dimensions. Increasingly, archaeologists are conducting research where data from more than two isotopic systems help to differentiate groups. For example, Cheung et al. (2017) investigated the place of origin and time of local residence of sacrificial victims in Shang China using δ^{13}C, δ^{15}N, and sulfur (δ^{34}S) values. While there has been some discussion of how to implement models for calculating three (or more)-dimensional isotopic niche space and overlap (e.g., Swanson et al., 2015; Rossman et al., 2016), these approaches are computationally intensive to conduct from scratch and have yet to be bundled into a statistical program or package. Finally, there is no way to assess isotopic space overlap for groups where isotopic space area is calculated with different contour intervals. This capability may have been useful in case study 3 where there was concern about potential outliers in the lowland group, but not the same concerns about the upland group. A more accurate assessment of overlap may have utilized the isotopic space area of the lowland group at the 75% contour interval and the isotopic space area of the upland group at the 95% contour. In their paper presenting rKIN, Eckrich et al. (2020) state that a future direction would be to expand the capabilities of the package to higher dimensions and greater flexibility although these options are not currently available. Archaeologists should be aware of these potential complexities, the ongoing discussions in ecology on the interpretive value of isotopic niche space, and the rapid development of and updates to statistical packages when applying this concept to their own work.

Suggestions for Reporting Isotopic Niche Space Analyses and Results

Roberts et al. (2018) have recently provided one of the few comprehensive sets of guidelines for reporting on stable isotope applications in archaeology. While they offer some general suggestions for data handling and statistical analyses, here I want to supplement those with specific recommendations when conducting and reporting isotopic niche space analyses. It is important to recognize that the measurement of isotopic niche space and/or overlaps are estimates based on the model employed. Archaeologists should avoid placing too much stock in the specific values of isotopic niche space size or percent of overlap. Good practice would be reporting exact values for size and overlap in tables or supplemental datasets, but in-text discussions would be better served to round overlap values to the nearest 5% or 10% as done in the case studies here. Rounding of estimates is common with other measures based on stable isotope data, such as $\delta^{13}C$ mixing models to determine the percent of C_3 and/or C_4 resources in the diet (e.g., Chritz et al., 2015; Garrett et al., 2015; Robinson & Rowan, 2017). Furthermore, selected contour intervals should not be confused for confidence intervals or any other measure of statistical significance. As isotopic niche space and overlap are estimates, it may be helpful to report results at multiple contour levels so that readers can see if and how results change. Common contour levels are 50%, 75%, and 95% and were used in the three case studies here, although researchers can pick any set of contour intervals between 1 and 99%. Justifying the selection of contour levels beyond ones that are commonly used or explaining why a higher contour level may not be appropriate due to concerns with outliers or other reasons is critical information for assessing the usefulness of the isotopic space measure. Similarly, researchers should be clear about technique selection — MCP, SEA, or KUD — for the analyses and why as the model is directly responsible for the estimates of isotopic niche size and overlap calculated. KUD appears likely to be the best option for most archaeological purposes considering its ability to handle more easily smaller sample sizes and the lack of expectations it makes about the distribution of data, but a researcher could justify the use of the MCP and/or SEA models in addition to, or instead of, KUD. Finally, the bandwidth, or smoothing, method should be reported if using the KUD model in rKIN. If the default ref method is not used, further explanation should be given for the selection of one of the other three options. By providing information on the selected parameters for calculating isotopic niche space and overlap, archaeologists will be further promoting the transparency and standardized practices in stable isotope studies called for by Roberts et al. (2018).

Conclusion

Stable isotope datasets in archaeology have expanded rapidly over the last couple of decades, as have methods of analysis and interpretation. One particularly exciting development has been the consideration and quantification of isotopic niche space and overlap between two (or potentially more) groups when data are available on two (or potentially more) isotopic systems. Ecologists have primarily been at the forefront of developing these approaches, but archaeologists can also benefit from these methods as we ask similar questions about the dietary ecology of humans and closely associated fauna. Furthermore, as demonstrated in the case studies here, archaeologists may be able to apply the concept of isotopic space to questions outside of the realm of ecology and diet to answer interesting questions in other archaeological domains. The recently developed rKIN package is a powerful tool providing researchers many different options for analyzing and visualizing their isotopic data. Archaeologists must be aware of the benefits and limitations of both the isotopic niche space concept in general, and the capabilities of the rKIN package in particular, in order to appropriately leverage these tools. Moving beyond the descriptive statistical analyses that account for much of the archaeological use of isotopic data to more complex concepts like isotopic niche space will allow the field to push the envelope in extracting richer information from these datasets in our attempts to reconstruct past human activities and behaviors.

Availability of Data and Material All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Code Availability Data analyses were conducted using the common functions in the R package rKIN. All scripts for the analysis of the three different case studies are provided as Supplemental Material 1.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10816-021-09541-7.

Declarations

Competing Interests The author declares no competing interests.

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