A niche for isotopic ecology

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Fifty years ago, GE Hutchinson defined the ecological niche as a hypervolume in n-dimensional space with environmental variables as axes. Ecologists have recently developed renewed interest in the concept, and technological advances now allow us to use stable isotope analyses to quantify these niche dimensions. Analogously, we define the isotopic niche as an area (in δ-space) with isotopic values (δ-values) as coordinates. To make isotopic measurements comparable to other niche formulations, we propose transforming δ-space to p-space, where axes represent relative proportions of isotopically distinct resources incorporated into an animal's tissues. We illustrate the isotopic niche with two examples: the application of historic ecology to conservation biology and ontogenetic niche shifts. Sustaining renewed interest in the niche requires novel methods to measure the variables that define it. Stable isotope analyses are a natural, perhaps crucial, tool in contemporary studies of the ecological niche.

Front Ecol Environ 2007; 5(8): 429–436, doi:10.1890/060150.01

The term ecological niche is as fundamental to ecology as it is elusive. Niches are central to ecological thinking because they represent convenient shorthand for many of the concepts used by ecologists to approach a variety of important problems, including resource use, geographic diversity, and many aspects of community composition and structure (McGill *et al.* 2006). Niches are elusive for two reasons. First, there is not one niche concept but many, each of which emphasizes a different aspect of a species' ecological characteristics (Leibold 1995). Second, the ecological niche is difficult to measure. The confusion and ambiguity that often surround the niche have led some ecologists to call for purging the ecological literature of niches (Hubbell 2001). Indeed, until relatively recently, the niche had fallen into disuse, and alternative terms have replaced some of its traditional meanings (Chase and Liebold 2003).

Yet the niche persists and seems to be making a comeback. As an example, it was featured prominently in all the articles of a recent supplement of *Ecology* devoted to phylogenetic approaches to community ecology (*Ecology* 2006; **87**[7]). Over the past few years, niche definitions abandoned as inoperative have been remade into well-defined and functional concepts. Grinnell's (1917) "habitat" concept of the niche has been reincarnated into the bioclimatic niche measured by geographic distribution area modelers (Elith *et al.* 2006). In a similar fashion, Elton's niche concept of the role of a species in a community has morphed into Chase and Leibold's (2003) definition of the functional (or net-growth isocline [NGI]) niche. Both the bioclimatic niche and the functional/NGI niche owe their existence to progress in analytical and computational methods, as well as to conceptual advances in ecology (see Ackerley *et al.* [2006] for additional reincarnations of the niche). The bioclimatic niche relies heavily on the development of effective geographic information technologies and on the ability of machines to handle large amounts of spatially explicit data, analyzed by computationally intensive models (Elith *et al.* 2006). The functional niche is pivotally dependent on Tilman's (1988) concept of zero net growth isoclines (ZNGIs; see Chase and Leibold [2003]). The niche concept that we develop here is similarly dependent on both technological and conceptual advances.

Almost 50 years ago, George Evelyn Hutchinson (1957) formalized the ecological niche as an abstract n-dimensional set of points in a space whose axes represent environmental variables. In subsequent elaborations, Hutchinson (1978) established a useful distinction

In a nutshell:

- Stable isotope analysis provides quantitative information on both resource (bionomic) and habitat (scenopoetic) use commonly utilized to define ecological niche space
- Advances in isotope mixing models allow transformation of isotopic data into resource contribution values, providing a standardized means of characterizing an organism's ecological niche
- Implicit in this approach is a thorough understanding of the isotopic variation within and among resources (ie prey) available to consumers and the recognition that isotopic analysis does not typically provide information on taxon-specific resource use
- Careful implementation of stable isotope analysis will benefit studies of resource competition in community structure, and will help to characterize population-level biogeography or connectivity crucial for successful conservation of highly migratory and/or elusive species

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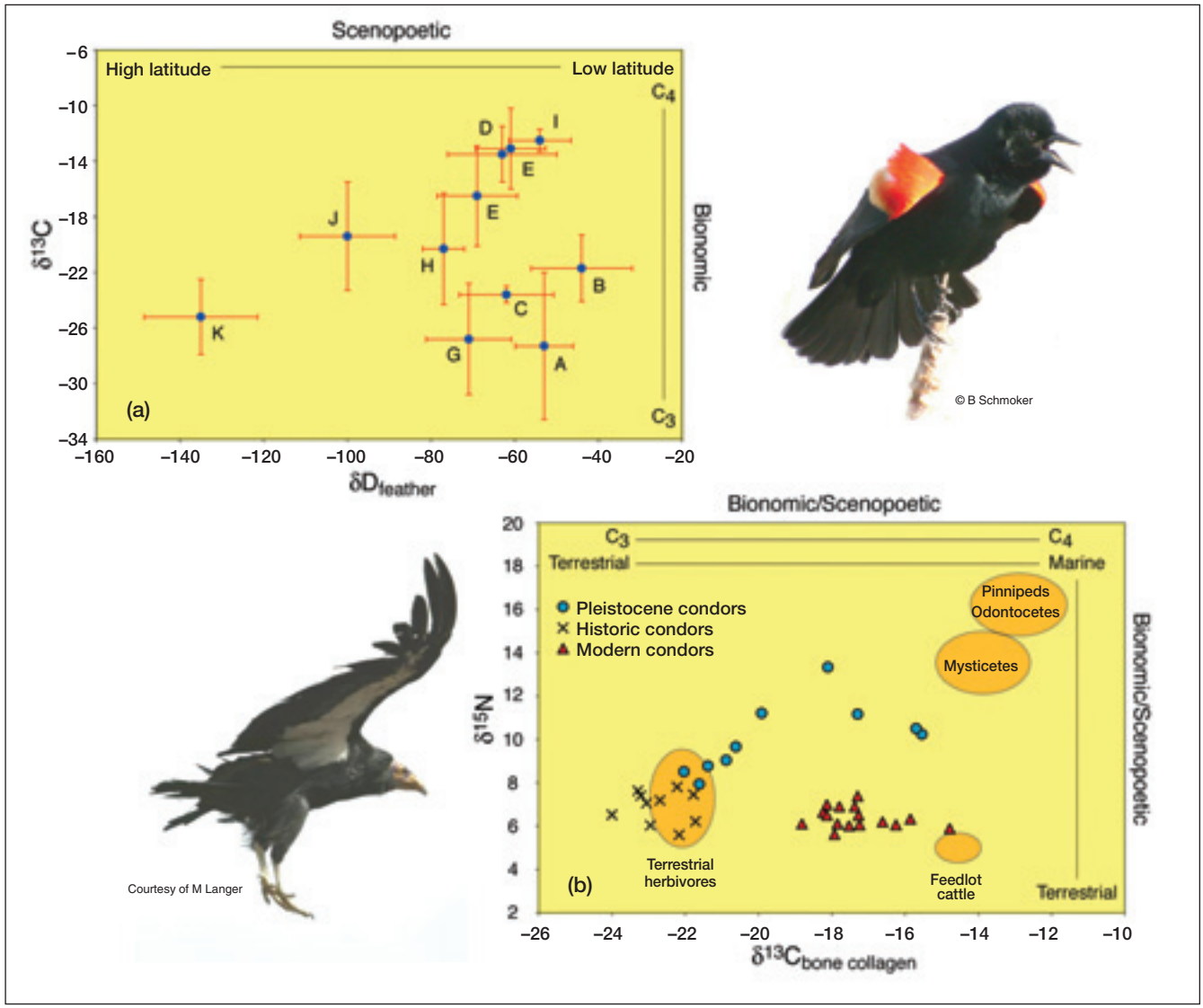

Figure 1. *Two examples of how δ-space can supply information on the bionomic and scenopoetic axes of the ecological niche. In some cases, an isotopic axis can have both bionomic and scenopoetic components, where feeding on a marine or terrestrial food web implies inhabiting a marine or terrestrial habitat. Data from Wassenaar and Hobson (2000) and Chamberlain* et al. *(2005).*

between scenopoetic and bionomic niche axes. The bionomic axes are those that define the resources that animals use, whereas the scenopoetic axes are those that set the bioclimatic stage in which a species performs (Hutchinson 1978). After Hutchinson's original formulation, the niche has undergone many changes, but all alternative contemporary definitions retain the formalization of the niche as a multidimensional space. In a similar fashion, isotopic ecologists have been representing their data in multivariate spaces (ie $\delta^{13}C$ versus $\delta^{15}N$ plot) with coordinates that record both bionomic and scenopoetic ecological information (Figure 1). This "δ-space" is comparable to the n-dimensional space that contains what ecologists refer to as the niche, because an animal's chemical composition is directly influenced by what it consumes (bionomic) as well as the habitat in which it lives (scenopoetic). Using chemistry, isotopic ecologists have used δ-spaces to explore questions that have traditionally resided within the domain of niche theory (eg Genner *et al.* 1999; Bocher *et al.* 2000).

We postulate the "isotopic niche" as a construct that can inform questions traditionally considered within the broad domain of the ecological niche, including the functional and bioclimatic niche concepts. The isotopic niche does not, by itself, solve the theoretical questions that niche theory in all its guises aims to answer. However, we suggest that stable isotope analysis (SIA) offers a superb tool to assess many of the ecological characteristics of organisms upon which niche research relies. The isotopic niche is a potentially powerful way to investigate ecological niches. We suggest that the variation in isotopic incorporation within an animal's tissues permits a characterization of the contribution of intra- and inter-individual variation to a species' isotopic niche. We highlight the transformations of the isotopic niche space that one must perform to make the metrics of the isotopic niche comparable to those esti-

mated in other formulations of the ecological niche. We then provide two examples of the utility of isotopic niches: the use of SIA to identify niche shifts relevant to conservation biology and to track changes in the ecological characteristics of organisms through ontogeny. Finally, we describe the relationship between the isotopic niche and other niche constructs and, perhaps most importantly, identify the limitations of isotopic niches. Our discussion emphasizes animals, but our approach can be modified to define botanical and microbiological isotopic niches as well.

Isotope ratio	Delta (δ) notation derivation	δ-value
$^{H}X/^{L}X$	$[(^{H}X/^{L}X_{sample} - ^{H}X/^{L}X_{standard} - 1] \times 1000$	$\delta^{H}X$
$^{13}C/^{12}C$	$[(^{13}C/^{12}C_{sample} - ^{13}C/^{12}C_{standard} - 1] \times 1000$	$\delta^{13}C$

Figure 2. *Isotopic ratios are typically expressed as the ratio of the heavy (H) to light (L) isotope and converted into delta notation (δ-values) through comparison of sample isotope ratios to ratios of internationally accepted standards. Standards for common systems include Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon, atmospheric N_2 for nitrogen, and Vienna Standard Mean Ocean Water (VSMOW) for hydrogen and oxygen. The units are expressed as parts per thousand or per mil (‰).*

■ Delta spaces and the isotopic niche

Stable isotope analysis has emerged as a key tool for ecologists (Table 1). Stable isotopes are useful because many physicochemical (ie kinetic reactions) and biochemical processes (ie equilibrium reactions) are sensitive to differences in the dissociation energies of molecules, which often depend on the mass of the elements from which these molecules are made. Thus, the isotopic composition of many materials (expressed as δ-values; Figure 2), including the tissues of organisms, often contains a label of the process that created it. For example, primary producers at the base of food webs often imprint the biological molecules that they manufacture with distinct carbon, nitrogen, and hydrogen signatures (Farquhar *et al.* 1989; Robinson 2001).

Because animals incorporate these "signatures" into their bodies via consumption and tissue synthesis, we can use isotopes to quantify bionomic elements of their niche. For example, we can use $^{13}C/^{12}C$ ratios to identify a consumers' reliance on primary producers with different photosynthetic pathways (ie C_3, C_4, or CAM; Wolf and Martinez del Rio 2003). We can also use a combination of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ to determine the contribution of marine and terrestrial food webs to an animal's diet or to estimate trophic position (Post [2002] and references therein). These are both examples of ways in which stable isotopes can help ecologists to populate the bionomic dimensions of niches. Stable isotopes can also give us insight into the scenopoetic dimensions of the niche, such as habitat latitude or environmental temperature (Table 1). For example, the isotopic composition of rainwater is determined by a combination of factors, which include altitude, latitude, distance from the coast, and temperature. These factors create the broadly predictable geographical patterns in the $\delta^{18}O$ and δD (deuterium) of precipitation (Bowen and Revenaugh 2003). These "isoscapes" have been used widely to track animal movements (Rubenstein and Hobson 2004; Figure 3). Similarly, the physicochemical sorting (ie fractionation) of oxygen isotopes during the for-

Table 1. A summary of common isotope systems and expected patterns in δ-values used to examine scenopoetic and bionomic dimensions of ecological niche space

Gradient	*Isotope system*	*High δ-values*	*Low δ-values*	*Scenopoetic*	*Bionomic*
Trophic level	$\delta^{13}C$ / $\delta^{15}N$	High levels	Low levels		✓
C3–C4 Vegetation	$\delta^{13}C$	C_4 plants	C_3 plants		✓
Marine–terrestrial	$\delta^{15}N$ / $\delta^{13}C$ / $\delta^{34}S$	Marine	Terrestrial	✓	✓
Latitude (terrestrial)	$\delta^{2}H$ / $\delta^{18}O$	Low latitudes	High latitudes	✓	
Latitude (marine)	$\delta^{13}C$ / $\delta^{15}N$	Low latitudes	High latitudes	✓	
Altitude	$\delta^{13}C$	High altitudes	Low altitudes	✓	
Altitude	$\delta^{2}H$	Low altitudes	High altitudes	✓	
Inshore–offshore	$\delta^{13}C$	Inshore	Offshore	✓	
Benthic–pelagic	$\delta^{13}C$ / $\delta^{34}S$	Benthic	Pelagic	✓	✓
Aridity	$\delta^{13}C$ / $\delta^{15}N$	Xeric	Mesic/hydric	✓	
Eutrophication	$\delta^{15}N$ / $\delta^{13}C$	Polluted	Pristine	✓	
Temperature	$\delta^{18}O$	Cooler	Warmer	✓	
Geologic substrate	$\delta^{87}Sr$	Young rocks	Old rocks	✓	
Oxic–anoxic	$\delta^{15}N$ / $\delta^{13}C$ / $\delta^{34}S$	Oxic	Anoxic	✓	
Methanogenesis	$\delta^{13}C$	Photosynthetic	Methanogenic	✓	

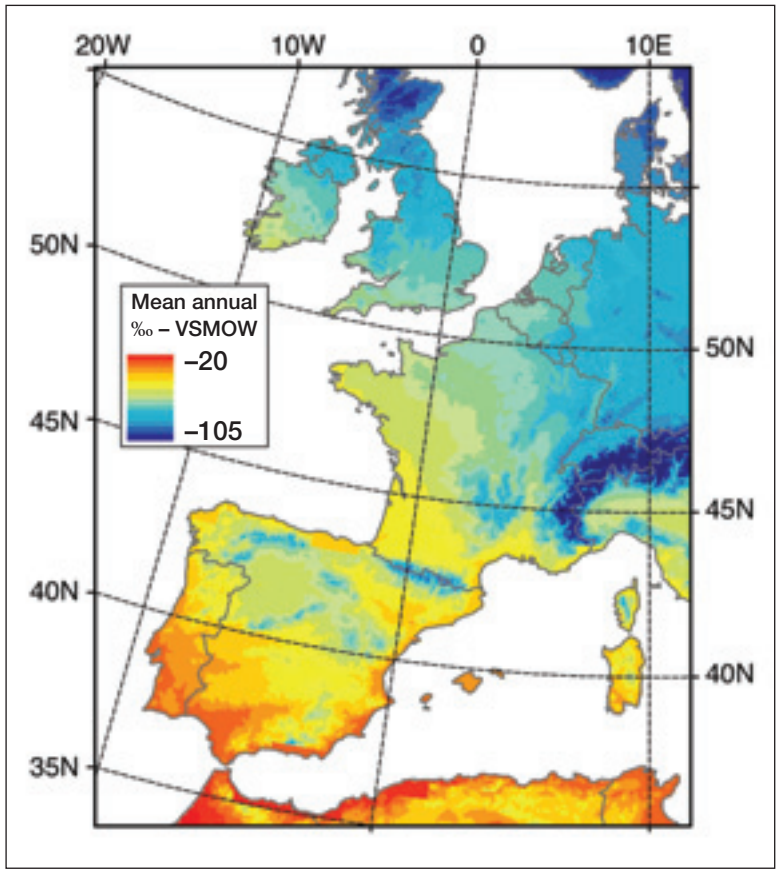

Figure 3. *Geographical patterns in the δD and $\delta^{18}O$ of precipitation have been used widely to track animal movements and study population connectivity, supplying information on scenopoetic factors of the ecological niche. Map from www.waterisotopes.org.*

mation of calcium carbonate is temperature-dependent, providing a convenient isotopic thermometer that records the temperature at which carbonate-containing structures are synthesized. Paleoecologists and paleoceanographers have been using these systematic, empirically tested fractionations for decades, by analyzing the isotopic composition of animal hard tissues (ie shells, otoliths, bones) to track changes in environmental conditions over geological timescales (Koch 1998; Zachos *et al.* 2001).

SIA is also particularly well suited to investigate the intra- and inter-individual components of niche breadth. Because different animal tissues incorporate the isotopic signatures of resources at different rates, they can integrate information over different time periods, which is a major advantage of SIA in comparison to traditional dietary proxies, such as foraging observation or analysis of gut/scat contents (Dalerum and Angerbjörn 2005). Plasma proteins incorporate the diet's isotopic signatures very rapidly, and thus provide information about the types of foods eaten by animals over a very short time scale. In contrast, bone collagen incorporates dietary signatures very slowly and therefore averages the composition of assimilated diets over a much longer time scale (Hobson and Clark 1992). Some tissues, such as feathers or apatite in teeth, are metabolically inert and therefore provide a record of the animal's position in δ-space at the time of tissue deposition. By measuring tissues deposited at different times in a single individual sampled at a single point in time, one can reveal intra-individual temporal changes in resource use (Phillips and Eldridge 2006).

Transforming from δ-space to p-space

The degree of specialization and generalization in individuals and populations can inform problems as diverse as the evolution of resource use (Bolnick *et al.* 2003), the success of invading exotics (Holt *et al.* 2005), and the processes that shape the composition of ecological communities (Wiens and Graham 2005). Ecologists have devised a variety of metrics to assess niche variation and the relative contribution of individual variation to these metrics (reviewed by Bolnick *et al.* [2002]). Bearhop *et al.* (2004) suggested that variance in δ-space among individuals may be a useful proxy for niche width. Variation of consumer values in δ-space is a problematic measure of niche width because it depends on the distance between the isotopic composition of available food sources. Thus, intra- and inter-individual variation in isotopic composition is not only dependent upon the variability of diets, but also upon the amount of isotopic variation among food sources (Matthews and Mazumder 2004). An alternative to using δ-values per se to define isotopic niches and to assess their variation is to use mixing models to transform them into dietary proportions (p) of different isotopic sources. Briefly, if one measures the isotopic composition of n elements, one can determine the contribution of n + 1 isotopically distinct sources by solving a system of n + 1 linear equations (see Phillips and Gregg [2001] for details; Figure 4). This transformation from δ-space to p-space helps to resolve some of the scaling discrepancies in δ-space (discussed in detail below), and permits the use of niche-width metrics commonly used by ecologists (see Bolnick *et al.* 2002). Thus, niche width can be estimated from p-values with the widely used Shannon–Wiener information measure (Bolnick *et al.* 2002). If a researcher is able to make isotopic measurements of tissues deposited at different times, then he or she can use the methods proposed by Bolnick *et al.* (2002) to investigate individual-level resource specialization.

We hasten to point out that depictions of the isotopic niche in δ-space and p-space are complementary rather than alternative. By transforming data from δ-space to p-space, we gain the ability to construct metrics of variation that are independent of the absolute value of isotopic signatures and are comparable to other commonly measured bionomic and scenopoetic variables used to study niche space. However, we lose the insights into the types of

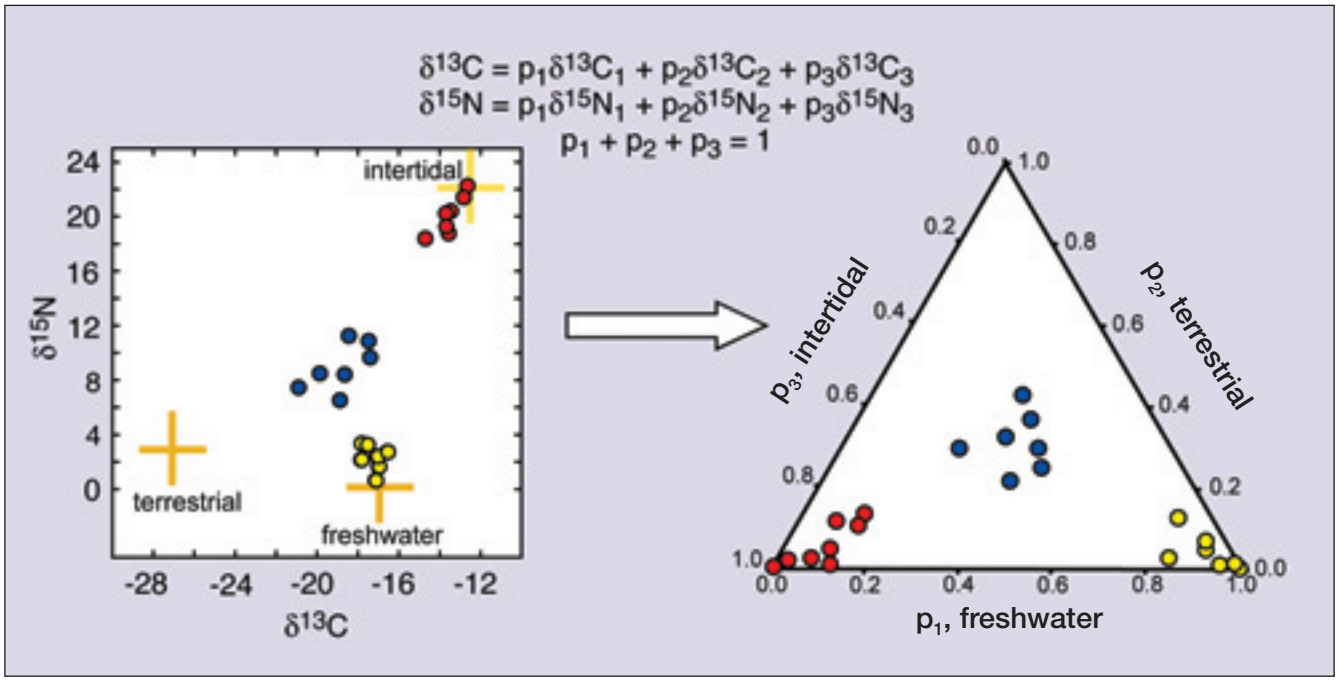

Figure 4. *Transforming from δ- to p-space requires solving a system of three linear equations in three unknowns for each point. The figure illustrates the transformation from δ- to p-space for three species that rely on intertidal, freshwater, and/or terrestrial food webs. The points in p-space are represented in a ternary diagram. Dataset provided by M Ben-David.*

resources and locations in isoscapes that are revealed by δ-spaces.

Because mixing models are central tools in the analysis of isotopic niches, it is important to pay attention to their assumptions and potential limitations. Model choice is critical and dependent on the question(s) of interest; however, users can incorporate variation in consumer and/or source isotope values, as well as differences in elemental concentrations among food sources, especially important for studies of omnivorous species (Phillips and Koch 2002). Phillips and Gregg (2001) provide formulas for calculating variances, standard errors (SE), and confidence intervals for p-values. Using correct tissue-to-diet discrimination factors is also important when estimating p-values (Phillips and Gregg 2001). Finally, remember that a mixing model resolves n + 1 distinct sources if one measures n isotopes. Thus, a particular set of δ-values may not define a point in p-space unless the number of distinct isotopic sources is limited to one more than the number of δ-values measured. Phillips and Gregg (2003) have devised a method that relaxes this requirement and makes it possible to determine the minimum and maximum utilization of each source that is consistent with isotopic mass balance, even when one measures n isotopes and the number of resources exceeds n + 1. However, the degree of utilization within these bounds cannot be determined exactly, but only as a range of possible values (Phillips and Gregg 2003). Sometimes these ranges are narrow and the results are informative, but in other cases, mixing models may only transform a δ-space into a blurry p-space in which source proportions have exceptionally large variances and may not be useful in many ecological applications.

Applications of the isotopic niche

The identification of niche shifts by SIA can have important conservation implications. For example, SIA was able to show that loggerhead turtles' (*Caretta caretta*) use of productive, nearshore oceanic habitats not only increases juvenile growth rates, but may also increase bycatch risk (Snover 2002). Ecologists have also used isotopes to document subtle niche shifts in lake trout (*Salvelinus namaycush*), following the invasion of two exotic bass species (Vander Zanden *et al.* 1999), which were otherwise undetectable. SIA-derived scenopoetic and/or bionomic niche information can also be coupled with toxicological data and satellite tracking technologies to identify the sources and vectors of contaminants that threaten population viability (Finkelstein *et al.* 2006). Furthermore, SIA-derived information on habitat preference(s) and connectivity within and among populations could be combined with epidemiological data to identify disease vectors, especially for species that have an inherently high potential for relatively fast transmission rates across geographic areas of epidemic proportion (ie West Nile virus; Marra *et al.* 2004).

A second area of research in which SIA-derived niche information continues to inform conservation biology is historic ecology, which aims to determine the true range of ecological flexibility of species that may have experienced substantial truncations in behavior, often as a result of direct or indirect human disturbance (ie hunting, habitat loss). For example, SIA has been used to identify differences in the use of coastal versus inland habitats by modern and ancient California condor (*Gymnogyps californianus*) populations (Chamberlain *et*

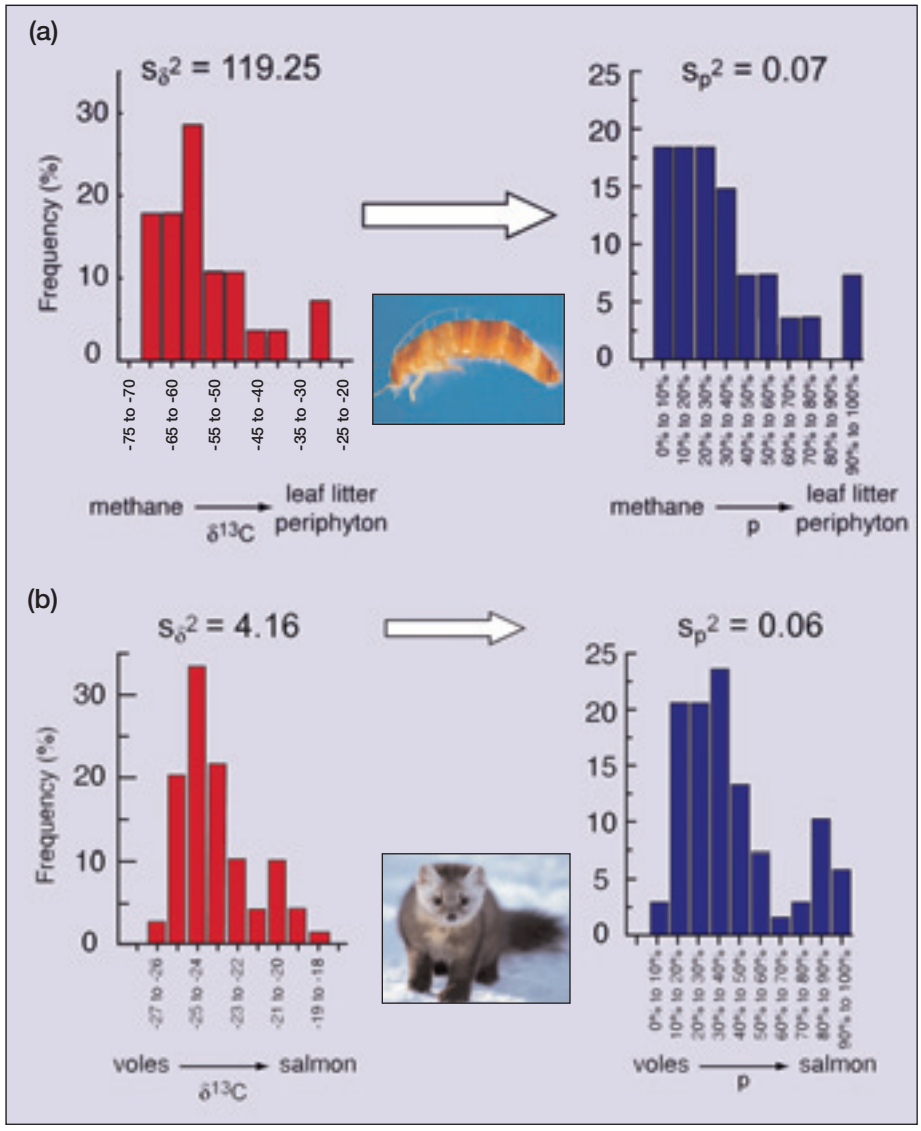

Figure 5. *Variance in δ-space, which is often assumed to be a good measure of niche width, is dependent on the isotopic composition of resources. (a) The variance in $\delta^{13}C$ in the larvae of the marsh beetle* (Helodidae *spp) is 29 times greater than (b) that of American marten* (Martes americana). *When isotopic data are transformed from δ- to p-space, we find that the niche width of the two species is very similar. Data from Kohzu* et al. *(2004) and Ben-David* et al. *(1997). (a) Courtesy of Valley City University Macro-Invertebrate Laboratory. (b) Courtesy of Habitat Education Center.*

al. 2005; Fox-Dobbs *et al.* 2006; Figure 1b). These studies contend that conservation goals should emphasize the reintroduction of condors (obligate scavengers) to coastal areas, where populations would have access to stranded marine mammal carcasses. Another study found a difference in the trophic level of historic versus contemporary marbled murrelets (*Brachyramphus marmoratus*) in central California, suggesting that recent decreases in large, energetically superior prey populations due to overfishing are contributing to poor murrelet reproductive rates and population declines (Becker and Beissinger 2006). The use of SIA to identify past versus present differences in bionomic or scenopoetic niche space provides a means of describing the natural history of species on ecologically and evolutionarily relevant time scales, vital for evaluation of current ecological trends and the success of long-term conservation and management strategies.

Finally, many animals experience ontogenetic niche shifts (West *et al.* 2003), which can be related to changes in bionomic and/or scenopoetic factors and thus can be detected by SIA. Perhaps the earliest use of SIA to study ontogenetic niche shifts was the application of $\delta^{15}N$ values to explore the biochemical effects of nursing in humans and their offspring (Fogel *et al.* 1989). This approach has now been used to assess the relative timing and nature of weaning in a growing list of mammals (see Newsome *et al.* [2006] and references therein). Other vertebrate applications include the use of SIA to examine the correlation between growth rate and diet composition in juveniles (Snover 2002; Post 2003). SIA has also been used to assess ontogenetic changes in diet type and/or quality in invertebrates, where in some cases, adult diets are nutritionally inadequate to support observed juvenile growth (Hentschel 1998).

Limitations of the isotopic niche

Depicting isotopic measurements in δ-space is intuitively appealing and informative. By plotting data on both resources and consumers in the same space (Figure 1), we can make inferences about (1) the potential contribution of each source to the consumers, (2) the amount of mixing of sources, and (3) the contribution of isotopic variation within and among food sources to variation in the consumer's composition (see Phillips and Gregg [2003] and references therein). Although one can learn much about an organism's niche from the hypervolume that it occupies in δ-space, using isotopic niches to make ecological inferences requires that we recognize its limitations. Essentially, isotopic niches have two shortcomings: (1) they can be myopic, and (2) they can give deceptive estimates of niche width.

Isotopic niches can be myopic for two reasons. First, isotopic measurements can only distinguish among

resources with contrasting isotopic compositions, and thus will blur the distinction between sources with similar compositions. Stable isotopes can tell us much about the physiological pathways and status of resources (Dawson *et al.* 2002), but it is not always possible to determine the specific taxonomic identity of sources. The myopic nature of isotopic measurements can apply to both bionomic and scenopoetic axes. Wunder *et al.* (2005) have emphasized the difficulties encountered when attempting to assign migrating birds to a precise geographical breeding area. Stable isotopes are effective tools for studying animal movements, but they can have a low level of accuracy (Rubenstein and Hobson 2004).

The second reason for the myopia is that macromolecules (ie carbohydrates, proteins, lipids) derived from the diet, and the elements from which they are constructed, undergo recombination and sorting during digestion, metabolism, and tissue synthesis (reviewed by Martínez del Rio and Wolf 2005). The difference in $\delta^{15}N$ between a consumer's tissues and its diet (denoted by $\Delta^{15}N$) has been widely used to diagnose trophic level (reviewed by Post [2002]). The logic of this application is that, if one knows the $\delta^{15}N$ of primary producers and one assumes that $\Delta^{15}N$ is constant across each trophic level, then one can estimate an animal's trophic level from its $\delta^{15}N$ composition. This is a fundamental variable in defining an animal's niche (Post 2002). While there is little doubt that consumers' tissues are enriched with ^{15}N relative to resources, trophic enrichment can vary depending on physiological and environmental factors (McCutchan *et al.* 2003). Until we have a better understanding of the factors that determine the magnitude of $\Delta^{15}N$ (see Robbins *et al.* 2005; Martínez del Rio and Wolf 2005), the use of the $\delta^{15}N$ axis of the isotopic niche will not provide a quantifiable measure of trophic level, though it is still useful in determining the relative trophic position of species or individuals within a community.

Niche theorists have proposed the dispersion in the distribution of points in niche space as an estimate of total niche width (TNW). It is natural (albeit misleading) to assume that a large dispersion of points in δ-space is also evidence of a broad TNW. However, dispersion in δ-space is dependent on the distance between the isotopic values of the available food sources. Consumers that feed on two resources with widely divergent isotopic compositions will always be found to have broader isotopic niches than animals that feed on food sources with less divergent δ-values (Matthews and Mazumder 2004; Figure 5). Differences in the dispersion of points in δ-space may not only be the result of a large spectrum of resources used, but also of the magnitude of the difference in the isotopic composition of those resources. Comparative analyses of niche width must correct for the effect of the magnitude of differences in isotopic composition of resources. This can be accomplished by transforming isotopic data from δ- to p-space. In Figure 5, the variance in $\delta^{13}C$ in the larvae of the marsh beetle (*Helodidae* spp; Figure 5a) is ~ 30 times greater than that of American marten (*Martes americana*; Figure 5b). When $\delta^{13}C$ values are transformed to p-values and the source proportions are recalculated, the variance values for these two species are similar (Ben-David *et al.* 1997; Kohzu *et al.* 2004). SIA provides a powerful tool for quantifying foraging strategies at both the individual (ie within-individual component) and population (ie between-individual component) levels; however, future studies must carefully consider the variation in the isotopic compositions of available food sources and the turnover rates of the tissues being analyzed.

Conclusions

Scientific concepts sometimes lie dormant until new methodologies transform and revitalize them. Systems biology was the focus of intense interest among biologists in the 1960s and then waned. Fertilized by the growth of the "omics" (genomics, proteonomics, metabolomics) and recent technological advances in computing, systems biology has been reincarnated into a vigorous field (Wolkenhauer 2001). In a similar fashion, the revival of the niche is the result of rapid progress in bioinformatics and in the development of new technologies. Just as researchers interested in systems biology and in tracking the evolution of biological systems rely on nucleic acids and the polymerase chain reaction, ecologists interested in measuring the fluxes of energy and materials among components of ecological systems increasingly rely on SIA (Yakir 2002). We predict the rapid growth of niche studies and project that they will be stimulated by faster, cheaper, and more accurate stable isotope analyses and that isotopic ecology will become an important axis in the resurgent study of ecological niches.

Acknowledgements

We thank M Ben-David for kindly providing data. CMR was funded by a National Science Foundation grant (IBN-0110416). The research described in this document has been funded in part by the US Environmental Protection Agency. It has been subjected to the Agency's peer and administrative review, and approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. We thank J Shannon for a constructive review of the manuscript.

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