A niche for isotopic ecology

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Abstract

Fifty years ago 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. Hutchinson divided factors defining the niche into two categories: bionomic and scenopoetic. Technological advances now allow ecologists 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. We illustrate the isotopic niche with two examples: the ontogenetic niche and the application of historic ecology to conservation biology. 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. Sustaining renewed interest in the niche requires novel methods to measure variables that define it. Stable isotope analyses are a natural, perhaps crucial, tool in contemporary studies of the ecological niche.

In A Nutshell

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

Introduction

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 that ecologists use to approach a variety of important problems, which include resource use, geographical diversity, and many aspects of community composition and structure (McGill et al. 2006). Niches are elusive for two reasons. First, there is not one, but many niche concepts, each of which emphasizes a different aspect of a species' ecological characteristics (Leibold 1995). The second reason for the elusiveness of the ecological niche is that it is difficult to measure. The confusion and ambiguity that often surrounds the niche has led some ecologists to call for purging the ecological literature of niches (Hubbell 2001). Indeed, until relatively recently, the niche fell in disuse, and alternative terms replaced some of its traditional meanings (Chase and Liebold 2003).

Yet the niche persists and seems to be making a striking comeback. As an example, the niche 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 last few years, niche definitions abandoned as inoperative have been renovated into relatively well-defined and functional concepts. Joseph Grinnell's (1917) "habitat" concept of the niche has reincarnated into the bioclimatic niche measured by geographical 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. The bioclimatic niche relies heavily on the development of effective geographical 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 (or ZNGIs, see Chase and Leibold 2003). The niche concept that we develop here is similarly dependent on both technological and conceptual advances.

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. We suggest that stable isotopes analyses (SIA) offer a superb tool to assess many of the ecological characteristics of organisms that niche research aims to investigate. In following sections we define the isotopic niche, and explain the kind of information that it can disclose. Perhaps more importantly, we also identify the limitations of isotopic niches. Then, we propose that the variation in isotopic incorporation among an animal's tissues permits characterizing the contribution of intra- and inter-individual variation to a species isotopic niche. We exemplify the utility of isotopic niches with two examples: the use of SIA to track changes in the ecological characteristics of organisms through ontogeny, and as tools in conservation biology. Finally, we describe the relationship between the isotopic niche and other niche constructs and outline the transformations of the isotopic niche space that one must perform to make the metrics of the isotopic niche comparable to those estimated in other formulations of the ecological niche. Our discussion emphasizes animals, but our approach can be modified to define botanical and microbiological isotopic niches as well.

Delta spaces and the isotopic niche

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 of the niche, Hutchinson (1978) established a useful distinction between scenopoetic and bionomic niche axes. The scenopoetic axes are those that set the bioclimatic stage in which a species performs (Hutchinson 1978), whereas the bionomic axes are those that define the resources that animals use. 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. Isotopic ecologists have been representing the results of their analyses in niche-like multivariate spaces with coordinates that are analogous to Hutchinson's scenopoetic and bionomic axes.

The analysis of stable isotopes has emerged as a key tool for ecologists (Fig. 1 and Table 1). Stable isotopes are useful because many physicochemical (i.e., kinetic reactions) and biochemical processes (i.e., 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, including the tissues of organisms, often contains a label of the process that created it. For example, the producers at the base of food webs often imprint the biological molecules that they manufacture with distinct carbon, nitrogen, and hydrogen signatures (Farquhar 1989, Robinson 2001). Because consumers incorporate these "signatures" into their tissues, we can use $^{13}C/^{12}C$ and $^{2}H/^{1}H$ to identify their reliance on producers with different photosynthetic pathways –i.e. 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 estimate trophic position (Post 2002 and references there). These are examples of the application of stable isotope analyses to the elucidation of variables along bionomic axes. Stable isotopes can also give us insight into the scenopoetic dimensions of the niche, such as environmental temperature or habitat latitude (Table 1).

The term "isotopic fractionation" refers to the difference in isotopic composition between the reactants and products of a physicochemical process. Isotopic fractionations can be temperature dependent (Fry 2006), so the temperature at which a fractionating process takes place is often recorded in the isotopic composition of the products. For example, the temperature-dependent fractionation of oxygen during the synthesis of calcium carbonate provides a convenient isotopic thermometer that measures the temperature at which permanent carbonate-containing structures such as shells, otoliths, and bones are synthesized (Radtke et al. 1996). 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 of precipitation (Bowen 2003). These "isoscapes" have been used widely to track animal movements (Rubenstein & Hobson 2004, Fig. 2). West et al. (2006) have aptly referred to stable isotopes as nature's recorders of ecological processes. Stable isotopes represent "wireless sensors" (sensu Collins et al. 2006) for a variety of the bionomic and scenopoetic ecological variables that Hutchinson envisioned as elements of the niche.

Isotopic ecologists often present their measurements as points in Cartesian spaces in which axes represent the delta (δ) values for different elements (Fig. 1 and Fig. 3). This "δ-space" is closely related to the n-dimensional space that contains what ecologists refer to as the niche. Indeed, isotopic ecologists have used delta spaces to explore questions that have been traditionally within the domain of niche theory. For example, Genner et al. (1999) and Bocher et al. (2000) used $\delta^{15}N$ and $\delta^{13}C$ values to document niche segregation in cichlids and petrels, respectively.

SIA is 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 temporal 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 diet's isotopic signatures very rapidly, whereas bone collagen incorporates it very slowly and therefore averages the composition of assimilated diets over a much longer time (Hobson and Clark 1992). Thus, temporally segregated measurements of the same tissue in the same individual or comparing differences between isotopic measurements on different tissues with contrasting isotopic incorporation rates among individuals can reveal temporal changes in resource use (Phillips and Eldridge 2006). Bolnick et al. (2003) and Bearhop et al. (2004) suggested that variance in delta space among and within individuals may be useful proxies for niche breadth and individual and population level specialization. Comparing the isotopic composition of fast and slow tissues can also generate information about "grain size" of foraging animals (sensu MacArthur and Levins 1964). Fine-grained foragers use resources in quick succession and hence the isotopic composition of fast and slow tissues should be similar. In contrast, coarse-grained foragers specialize temporally on a single resource and hence the isotopic composition of a fast tissue should differ from that of a slow tissue, which integrates inputs over a long time scale.

The limitations of the isotopic niche

In a similar fashion to Hutchinson's n-dimensional hyperspace with environmental variables as coordinates, the isotopic niche is defined by a set of isotopic composition measurements in a space with delta values as coordinates. The isotopic niche has many uses, but it also has numerous limitations. Using it to make ecological inferences demands that we recognize what we can and what we cannot infer from it.

Depicting isotopic measurements in delta space is intuitively appealing and informative (Fig. 3). By plotting data of both resources and consumers in the same space, one can make inferences about a) the potential contribution of each source to the consumers, b) the amount of mixing of sources, and c) the contribution of variation among sources to variation in the consumers' composition (Phillips and Gregg 2003 and references within), assuming that all the relevant food sources have been characterized. Although one can learn much about an organism's niche from the hypervolume that it occupies in delta space, isotopic niches have two limitations: 1) they can be myopic, and 2) they can give deceptive estimates of niche width. These limitations are worth recognizing.

Isotopic niches can be myopic for two reasons. The first one is that isotopic measurements can only distinguish among resources with contrasting isotopic compositions and blur the distinction among 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 to sources. The myopic nature of isotopic measurements can apply to both bionomic and scenopoetic axes. Wunder et al. (2005) have emphasized the difficulties one faces when attempting to assign migrating birds to a precise geographical breeding area. Stable isotopes are effective tools to study animal movements, but they can have low accuracy (Rubenstein and Hobson 2004).

The second reason for the isotopic niche's myopic nature stems from the inconsistency of isotopic incorporation. Macromolecules (i.e., carbohydrates, proteins, lipids) derived from 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 inconsistency of isotopic incorporation, however, can be useful. The difference in $\delta^{15}N$ between a consumer's tissues and its diet (denoted by $\Delta^{15}N$) has been very 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 tropic level from its $\delta^{15}N$ composition, which is a fundamental variable in defining an animal's niche (Post 2002). While there is little doubt that consumers' tissues are enriched ^{15}N relative to resources, trophic enrichment can vary depending on physiology and environmental factors (McCutchan et al. 2003). Until we have a better understanding of the factors that determine the magnitude of Δ^{15}N (see Robbins et al. 2005, Martínez del Rio and Wolf 2005), the use of the δ^{15}N axis of the isotopic niche will not provide an absolute measure of trophic level, but is still useful in determining the relative trophic position of species within a community.

Niche-theorists have proposed the dispersion in the distribution of points in niche space as an estimate of niche width (Bolnick et al. 2002). It is natural (albeit misleading) to assume that similar dispersion of points in delta space is evidence of a broad niche (Matthews and Mazumder 2004). For example, Bolnick et al. (2003) interpret "unexpectedly large isotopic differences between individuals" as evidence of a high inter-individual component to niche width. This interpretation is problematic because the processes that create variation in the isotopic composition of producers can lead to widely divergent values. Dispersion in delta space is dependent on the distance between the isotopic values of the alternative producers. Animals that feed on two resources with widely divergent isotopic compositions will always be found to have broader niches than animals that feed on food sources with less divergent delta values (Fig. 4), but this may not always accurately reflect the true niche breadth. In the final section we will describe how a metric of niche width that does not depend on the distance between the isotopic values of producers can be constructed.

Applications of the isotopic niche

Many animals experience ontogenetic niche shifts (West et al. 2003). These shifts 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 (Newsome et al. 2006 and references there). 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 utilized 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).

The identification of niche shifts, ontogenetic or otherwise, by SIA can also have important conservation implications. For example, SIA demonstrated that loggerhead turtles (*Caretta caretta)* use of productive, nearshore oceanic habitats not only increases juvenile growth rates but may also increase by-catch risk (Snover 2002). Ecologists have also used isotopes to document subtle niche shifts in lake trout (*Salvelinus namaycush*), which were otherwise undetectable, following the invasion of two exotic bass species (Vander Zanden et al. 1999). 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 spatial areas of epidemic proportion (i.e., West Nile virus; Marra et al. 2004).

A third area of research where SIA-derived niche information continues to inform conservation biology is in historic ecology, which aims to determine the true range of ecological flexibility of species that may have experienced significant truncations in behavior due to direct or indirect human disturbance (i.e., 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 (Fig. 3B; Chamberlain et al. 2005, Fox-Dobbs et al. 2006). 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 is contributing to poor murrelet reproduction and recent population declines (Becker and Beissinger 2006). The continual 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 timescales, thus providing a means of evaluating the significance of current ecological trends that is vital for the success of long-term conservation and management strategies.

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 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). One can assess variation in the isotopic niche, but in a previous section we identified one of the problems of isotopic niches as depicted in delta spaces. The variation within and among individuals in isotopic composition is strongly dependent on how different the isotopic signatures of the food sources are. An alternative to using δ-values *per se* to define isotopic niches 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 (Fig. 5; see Phillips and Gregg 2001 for details). This transformation from δ-space to p-space resolves the scaling discrepancies in δ-space discussed above, and permits using the niche-width metrics most commonly used by ecologists (see Bolnick 2002). 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 delta-space to p-space, we gain the ability to construct metrics of variation that are independent of the absolute value of isotopic signatures and that are comparable to those of other niche formulations. However, we lose the insights on the types of 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. Both the isotopic composition of isotopic sources and that of animal tissues are measured with variation. Consequently, the numerical manipulations required to transform from δ-values to p-values involves error propagation. 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, recall 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). In such cases, mixing models may only transform a δ-space into a blurry p-space.

Concluding remarks

Scientific concepts sometimes lie dormant until new methodologies transform them and revitalize them. Systems biology received intense interest from biologists in the 1960s and then waned. Fertilized by the growth of the “omics” (genomics, proteonomics, metabolomics) and fueled by the power of ever-faster computers, systems biology has 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 (PCR), 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 contend that they will be stimulated by faster, cheaper, and more accurate stable isotope analyses. Isotopic ecology will become an important axis in the resurgent study of ecological niches.

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TABLE 1

Gradient	Isotope System	High δ-Values	Low δ-Values	Scenopoetic	Bionomic
Trophic Level	$\delta^{13}C$ / $\delta^{15}N$	High Levels	Low Levels		√
C_3 – C_4 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	$\delta^{13}C$	Benthic	Pelagic	√	√
Aridity	$\delta^{13}C$ / $\delta^{15}N$	Xeric	Mesic/Hydric	√	
Eutrophication	$\delta^{15}N$	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 1. 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 VSMOW for hydrogen and oxygen. The units are expressed as parts per thousand or per mil (‰).

FIGURE 2. Geographical patterns in the δD and $\delta^{18}O$ of precipitation have been used widely to track animal movements and study population connectivity, thus supplying information on scenopoetic factors of the ecological niche.

FIGURE 3. Two examples of how delta-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 scenopetic components (panel 2), where feeding on a marine or terrestrial food web implies inhabiting a marine/terrestrial habitat. Data from Wassenaar and Hobson (2000) and Chamberlain et al. (2005).

FIGURE 4. Variance in delta-space is dependent on the isotopic composition of resources. The variance in $\delta^{13}C$ in the larvae of the marsh beetle (*Helodidae*, panel b) is 29 times greater than that of American marten (*Martes americana*, panel b. When $\delta^{13}C$ values are transformed to p values and the variances are recalculated, the values for these two species are roughly similar. Data from Kohzu et al. (2004) and Ben-David et al. (1997).

FIGURE 5. Transforming from d- to p-space requires solving a system of 3 linear equations in 3 unknowns for each point. The figure illustrates the transformation from delta- to p-space for 3 species that rely on intertidal, freshwater, and/or terrestrial food-webs. The points in p space are represented in a ternary diagram.

FIGURE 1

Isotope Ratio	Delta (δ) Notation Derivation	δ-Value
$^{H}X/^{L}X$	$\left[\left(^{H}X/^{L}X_{sample} - {}^{H}X/^{L}X_{standard}\right) - 1\right] \times 1000$	$\delta^{H}X$
$^{13}C/^{12}C$	$\left[\left(^{13}C/^{12}C_{sample} - {}^{13}C/^{12}C_{standard}\right) - 1\right] \times 1000$	$\delta^{13}C$

FIGURE 2

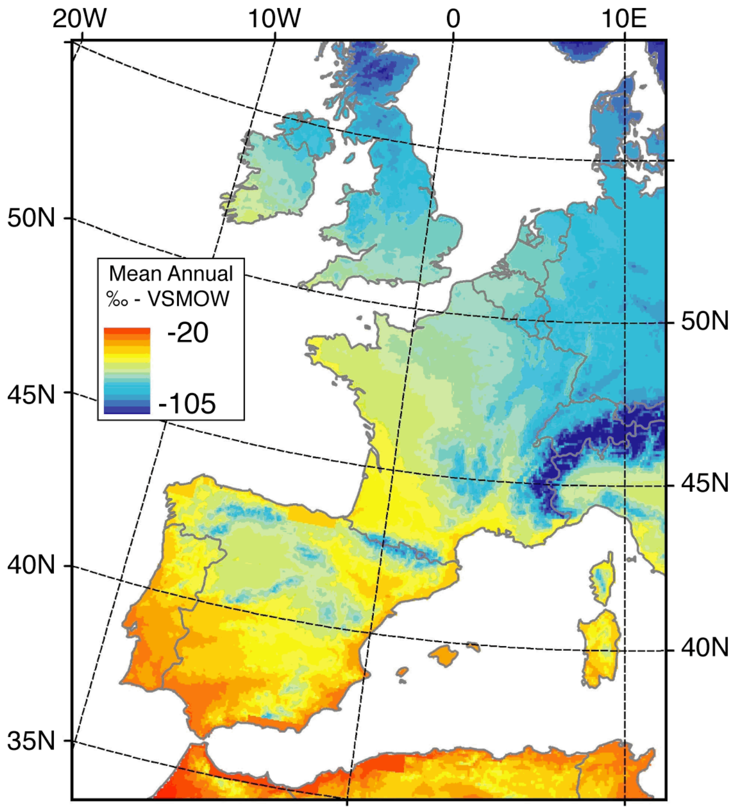

20W
10W
0
10E
50N
45N
40N
35N
Mean Annual
‰ - VSMOW
-20
-105
50N
45N
40N

FIGURE 3

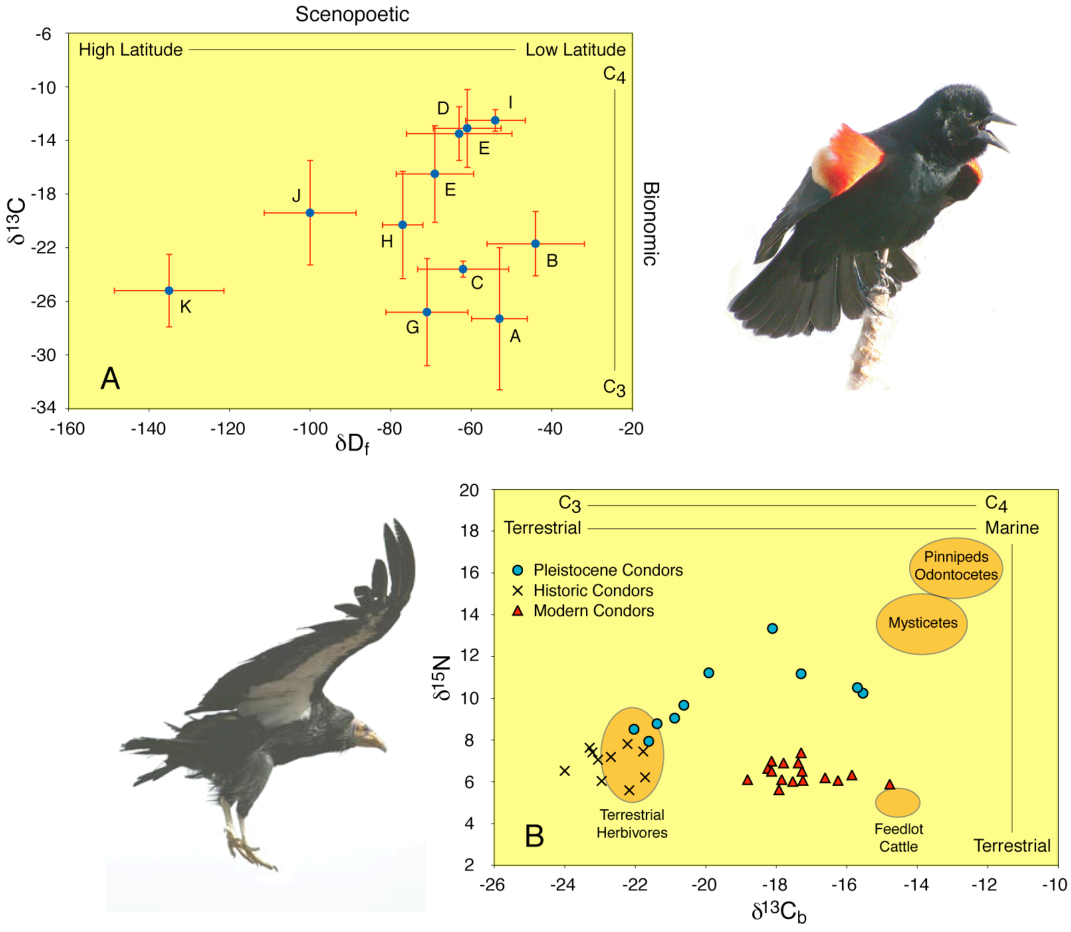

Scenopoetic
High Latitude
Low Latitude
C4
C3
Bionomic
δ13C
δDf
-6
-10
-14
-18
-22
-26
-30
-34
-160
-140
-120
-100
-80
-60
-40
-20
A
B
C
D
E
E
G
H
I
J
K
B
C3
C4
Terrestrial
Marine
Pleistocene Condors
Historic Condors
Modern Condors
Pinnipeds Odontocetes
Mysticetes
Terrestrial Herbivores
Feedlot Cattle
Terrestrial
δ15N
δ13Cb
20
18
16
14
12
10
8
6
4
2
-26
-24
-22
-20
-18
-16
-14
-12
-10

FIGURE 4

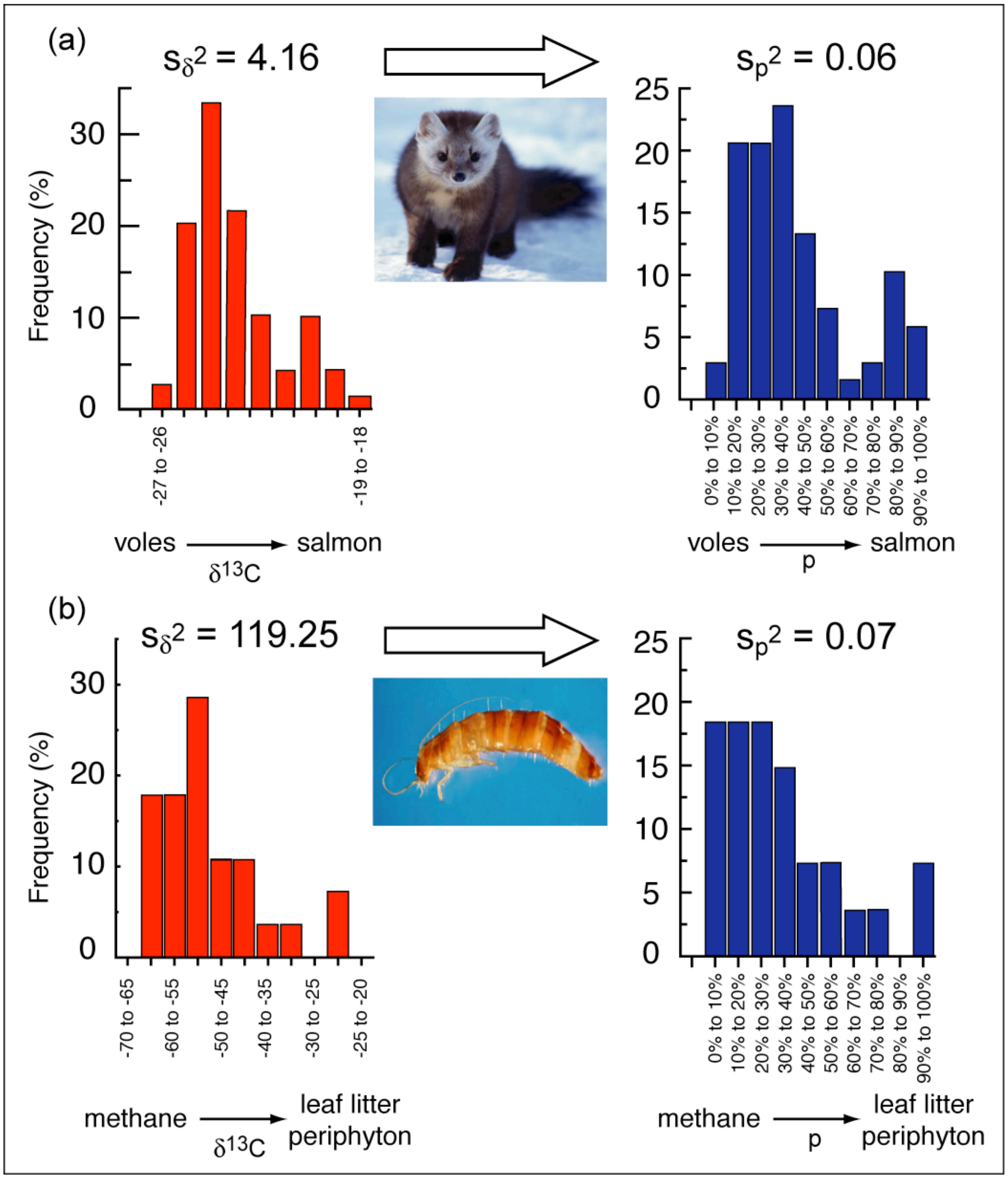
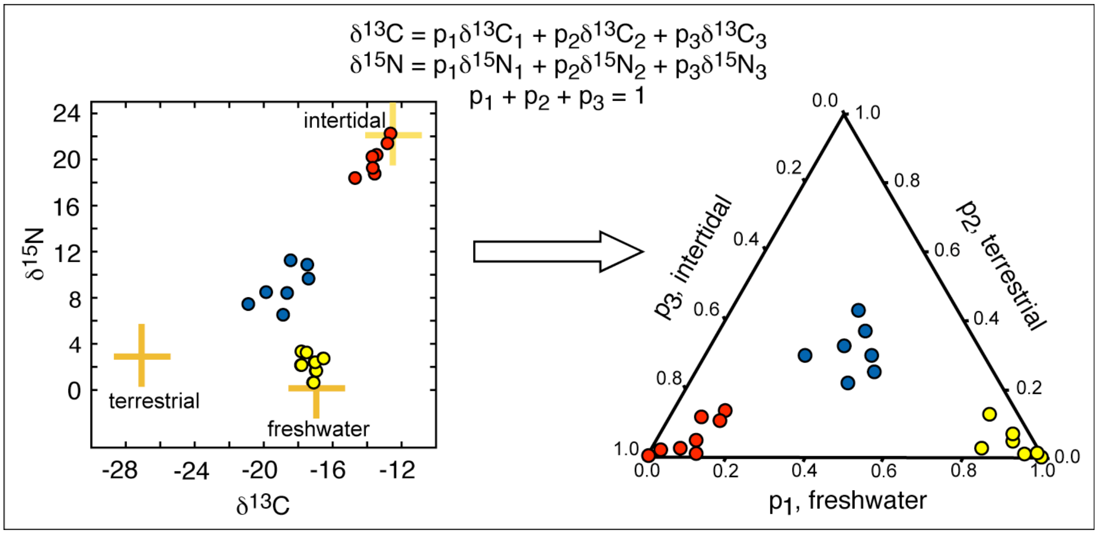

(a)
$s_\delta^2 = 4.16$
$s_p^2 = 0.06$
Frequency (%)
0
10
20
30
-27 to -26
-19 to -18
voles
salmon
$\delta^{13}C$
0
5
10
15
20
25
0% to 10%
10% to 20%
20% to 30%
30% to 40%
40% to 50%
50% to 60%
60% to 70%
70% to 80%
80% to 90%
90% to 100%
voles
p
salmon
(b)
$s_\delta^2 = 119.25$
$s_p^2 = 0.07$
Frequency (%)
0
10
20
30
-70 to -65
-60 to -55
-50 to -45
-40 to -35
-30 to -25
-25 to -20
methane
$\delta^{13}C$
leaf litter
periphyton
0
5
10
15
20
25
0% to 10%
10% to 20%
20% to 30%
30% to 40%
40% to 50%
50% to 60%
60% to 70%
70% to 80%
80% to 90%
90% to 100%
methane
p
leaf litter
periphyton

FIGURE 5



$$\delta^{13}C = p_1\delta^{13}C_1 + p_2\delta^{13}C_2 + p_3\delta^{13}C_3$$
$$\delta^{15}N = p_1\delta^{15}N_1 + p_2\delta^{15}N_2 + p_3\delta^{15}N_3$$
$$p_1 + p_2 + p_3 = 1$$