

1 **A niche for isotopic ecology**

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3 Seth D. Newsome<sup>1</sup>, Carlos Martinez del Rio<sup>2</sup>, Stuart Bearhop<sup>3</sup>, Donald L. Phillips<sup>4</sup>

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5 <sup>1</sup>Carnegie Institution of Washington, Geophysical Laboratory, 5251 Broad Branch Road NW,  
6 Washington, DC 20015, USA

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8 <sup>2</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166,  
9 USA

10

11 <sup>3</sup>Centre for Ecology & Conservation, School of Biosciences, University of Exeter, Cornwall  
12 Campus, Penryn, Cornwall TR10 9EZ, UK

13

14 <sup>4</sup>U.S. Environmental Protection Agency. National Health & Environmental Effects Research  
15 Laboratory. 200 SW 35th St. Corvallis, OR 97333, USA

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28

29 **Abstract**

30 **Fifty years ago Hutchinson defined the ecological niche as a hypervolume in n-dimensional**  
31 **space with environmental variables as axes. Ecologists have recently developed renewed**  
32 **interest in the concept. Hutchinson divided factors defining the niche into two categories:**  
33 **bionomic and scenopoetic. Technological advances now allow ecologists to use stable**  
34 **isotope analyses to quantify these niche dimensions. Analogously, we define the isotopic**  
35 **niche as an area (in  $\delta$ -space) with isotopic values ( $\delta$ -values) as coordinates. We illustrate the**  
36 **isotopic niche with two examples: the ontogenetic niche and the application of historic**  
37 **ecology to conservation biology. To make isotopic measurements comparable to other niche**  
38 **formulations we propose transforming  $\delta$ -space to p-space, where axes represent relative**  
39 **proportions of isotopically distinct resources incorporated into an animal's tissues.**  
40 **Sustaining renewed interest in the niche requires novel methods to measure variables that**  
41 **define it. Stable isotope analyses are a natural, perhaps crucial, tool in contemporary**  
42 **studies of the ecological niche.**

43  
44 **In A Nutshell**

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

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57  
58 **Introduction**

59 The term ecological niche is as fundamental to ecology as it is elusive. Niches are central to  
60 ecological thinking because they represent convenient shorthand for many of the concepts that  
61 ecologists use to approach a variety of important problems, which include resource use,  
62 geographical diversity, and many aspects of community composition and structure (McGill et al.  
63 2006). Niches are elusive for two reasons. First, there is not one, but many niche concepts, each  
64 of which emphasizes a different aspect of a species' ecological characteristics (Leibold 1995).  
65 The second reason for the elusiveness of the ecological niche is that it is difficult to measure. The

66 confusion and ambiguity that often surrounds the niche has led some ecologists to call for  
67 purging the ecological literature of niches (Hubbell 2001). Indeed, until relatively recently, the  
68 niche fell in disuse, and alternative terms replaced some of its traditional meanings (Chase and  
69 Liebold 2003).

70         Yet the niche persists and seems to be making a striking comeback. As an example, the  
71 niche was featured prominently in all the articles of a recent supplement of *Ecology* devoted to  
72 phylogenetic approaches to community ecology (*Ecology*. 2006. 87(7)). Over the last few years,  
73 niche definitions abandoned as inoperative have been renovated into relatively well-defined and  
74 functional concepts. Joseph Grinnell's (1917) "habitat" concept of the niche has reincarnated  
75 into the bioclimatic niche measured by geographical distribution area modelers (Elith et al.  
76 2006). In a similar fashion, Elton's niche concept of the role of a species in a community has  
77 morphed into Chase and Liebold's (2003) definition of the functional (or net-growth isocline,  
78 NGI) niche. Both the bioclimatic niche and the functional/NGI niche owe their existence to  
79 progress in analytical and computational methods, as well as to conceptual advances in ecology.  
80 The bioclimatic niche relies heavily on the development of effective geographical information  
81 technologies and on the ability of machines to handle large amounts of spatially explicit data  
82 analyzed by computationally intensive models (Elith et al. 2006). The functional niche is  
83 pivotally dependent on Tilman's (1988) concept of zero net growth isoclines (or ZNGIs, see  
84 Chase and Liebold 2003). The niche concept that we develop here is similarly dependent on both  
85 technological and conceptual advances.

86         We postulate the "isotopic niche" as a construct that can inform questions traditionally  
87 considered within the broad domain of the ecological niche – including the functional and  
88 bioclimatic niche concepts. We suggest that stable isotopes analyses (SIA) offer a superb tool to

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

101

## 102 **Delta spaces and the isotopic niche**

103 Almost 50 years ago, George Evelyn Hutchinson (1957) formalized the ecological niche as an  
104 abstract n-dimensional set of points in a space whose axes represent environmental variables. In  
105 subsequent elaborations of the niche, Hutchinson (1978) established a useful distinction between  
106 scenopoetic and bionomic niche axes. The scenopoetic axes are those that set the bioclimatic  
107 stage in which a species performs (Hutchinson 1978), whereas the bionomic axes are those that  
108 define the resources that animals use. After Hutchinson's original formulation, the niche has  
109 undergone many changes, but all alternative contemporary definitions retain the formalization of  
110 the niche as a multidimensional space. Isotopic ecologists have been representing the results of

111 their analyses in niche-like multivariate spaces with coordinates that are analogous to  
112 Hutchinson's scenopoetic and bionomic axes.

113         The analysis of stable isotopes has emerged as a key tool for ecologists (Fig. 1 and Table  
114 1). Stable isotopes are useful because many physicochemical (i.e., kinetic reactions) and  
115 biochemical processes (i.e., equilibrium reactions) are sensitive to differences in the dissociation  
116 energies of molecules, which often depend on the mass of the elements from which these  
117 molecules are made. Thus, the isotopic composition of many materials, including the tissues of  
118 organisms, often contains a label of the process that created it. For example, the producers at the  
119 base of food webs often imprint the biological molecules that they manufacture with distinct  
120 carbon, nitrogen, and hydrogen signatures (Farquhar 1989, Robinson 2001). Because consumers  
121 incorporate these "signatures" into their tissues, we can use  $^{13}\text{C}/^{12}\text{C}$  and  $^2\text{H}/^1\text{H}$  to identify their  
122 reliance on producers with different photosynthetic pathways –i.e.  $\text{C}_3$ ,  $\text{C}_4$ , or CAM (Wolf and  
123 Martinez del Rio 2003). We can also use a combination of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  to determine the  
124 contribution of marine and terrestrial food webs to an animal's diet or estimate trophic position  
125 (Post 2002 and references there). These are examples of the application of stable isotope  
126 analyses to the elucidation of variables along bionomic axes. Stable isotopes can also give us  
127 insight into the scenopoetic dimensions of the niche, such as environmental temperature or  
128 habitat latitude (Table 1).

129         The term "isotopic fractionation" refers to the difference in isotopic composition between  
130 the reactants and products of a physicochemical process. Isotopic fractionations can be  
131 temperature dependent (Fry 2006), so the temperature at which a fractionating process takes  
132 place is often recorded in the isotopic composition of the products. For example, the  
133 temperature-dependent fractionation of oxygen during the synthesis of calcium carbonate

134 provides a convenient isotopic thermometer that measures the temperature at which permanent  
135 carbonate-containing structures such as shells, otoliths, and bones are synthesized (Radtke et al.  
136 1996). The isotopic composition of rainwater is determined by a combination of factors, which  
137 include altitude, latitude, distance from the coast, and temperature. These factors create the  
138 broadly predictable geographical patterns in the  $\delta^{18}\text{O}$  and  $\delta\text{D}$  of precipitation (Bowen 2003).  
139 These “isoscares” have been used widely to track animal movements (Rubenstein & Hobson  
140 2004, Fig. 2). West et al. (2006) have aptly referred to stable isotopes as nature’s recorders of  
141 ecological processes. Stable isotopes represent “wireless sensors” (sensu Collins et al. 2006) for  
142 a variety of the bionomic and scenopoetic ecological variables that Hutchinson envisioned as  
143 elements of the niche.

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

151 SIA is particularly well suited to investigate the intra- and inter-individual components of  
152 niche breadth. Because different animal tissues incorporate the isotopic signatures of resources at  
153 different rates, they can integrate information over different temporal periods, which is a major  
154 advantage of SIA in comparison to traditional dietary proxies such as foraging observation or  
155 analysis of gut/scat contents (Dalerum and Angerbjörn 2005). Plasma proteins incorporate diet’s  
156 isotopic signatures very rapidly, whereas bone collagen incorporates it very slowly and therefore

157 averages the composition of assimilated diets over a much longer time (Hobson and Clark 1992).  
158 Thus, temporally segregated measurements of the same tissue in the same individual or  
159 comparing differences between isotopic measurements on different tissues with contrasting  
160 isotopic incorporation rates among individuals can reveal temporal changes in resource use  
161 (Phillips and Eldridge 2006). Bolnick et al. (2003) and Bearhop et al. (2004) suggested that  
162 variance in delta space among and within individuals may be useful proxies for niche breadth  
163 and individual and population level specialization. Comparing the isotopic composition of fast  
164 and slow tissues can also generate information about “grain size” of foraging animals (sensu  
165 MacArthur and Levins 1964). Fine-grained foragers use resources in quick succession and hence  
166 the isotopic composition of fast and slow tissues should be similar. In contrast, coarse-grained  
167 foragers specialize temporally on a single resource and hence the isotopic composition of a fast  
168 tissue should differ from that of a slow tissue, which integrates inputs over a long time scale.

169

### 170 **The limitations of the isotopic niche**

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

176 Depicting isotopic measurements in delta space is intuitively appealing and informative  
177 (Fig. 3). By plotting data of both resources and consumers in the same space, one can make  
178 inferences about a) the potential contribution of each source to the consumers, b) the amount of  
179 mixing of sources, and c) the contribution of variation among sources to variation in the

180 consumers' composition (Phillips and Gregg 2003 and references within), assuming that all the  
181 relevant food sources have been characterized. Although one can learn much about an  
182 organism's niche from the hypervolume that it occupies in delta space, isotopic niches have two  
183 limitations: 1) they can be myopic, and 2) they can give deceptive estimates of niche width.  
184 These limitations are worth recognizing.

185         Isotopic niches can be myopic for two reasons. The first one is that isotopic  
186 measurements can only distinguish among resources with contrasting isotopic compositions and  
187 blur the distinction among sources with similar compositions. Stable isotopes can tell us much  
188 about the physiological pathways and status of resources (Dawson et al. 2002), but it is not  
189 always possible to determine the specific taxonomic identity to sources. The myopic nature of  
190 isotopic measurements can apply to both bionomic and scenopoetic axes. Wunder et al. (2005)  
191 have emphasized the difficulties one faces when attempting to assign migrating birds to a precise  
192 geographical breeding area. Stable isotopes are effective tools to study animal movements, but  
193 they can have low accuracy (Rubenstein and Hobson 2004).

194         The second reason for the isotopic niche's myopic nature stems from the inconsistency of  
195 isotopic incorporation. Macromolecules (i.e., carbohydrates, proteins, lipids) derived from diet,  
196 and the elements from which they are constructed, undergo recombination and sorting during  
197 digestion, metabolism, and tissue synthesis (reviewed by Martínez del Rio and Wolf 2005). The  
198 inconsistency of isotopic incorporation, however, can be useful. The difference in  $\delta^{15}\text{N}$  between  
199 a consumer's tissues and its diet (denoted by  $\Delta^{15}\text{N}$ ) has been very widely used to diagnose  
200 trophic level (reviewed by Post 2002). The logic of this application is that if one knows the  $\delta^{15}\text{N}$   
201 of primary producers and one assumes that  $\Delta^{15}\text{N}$  is constant across each trophic level, then, one  
202 can estimate an animal's trophic level from its  $\delta^{15}\text{N}$  composition, which is a fundamental variable



203 in defining an animal's niche (Post 2002). While there is little doubt that consumers' tissues are  
204 enriched  $^{15}\text{N}$  relative to resources, trophic enrichment can vary depending on physiology and  
205 environmental factors (McCutchan et al. 2003). Until we have a better understanding of the  
206 factors that determine the magnitude of  $\Delta^{15}\text{N}$  (see Robbins et al. 2005, Martínez del Rio and  
207 Wolf 2005), the use of the  $\delta^{15}\text{N}$  axis of the isotopic niche will not provide an absolute measure of  
208 trophic level, but is still useful in determining the relative trophic position of species within a  
209 community.

210 Niche-theorists have proposed the dispersion in the distribution of points in niche space  
211 as an estimate of niche width (Bolnick et al. 2002). It is natural (albeit misleading) to assume that  
212 similar dispersion of points in delta space is evidence of a broad niche (Matthews and Mazumder  
213 2004). For example, Bolnick et al. (2003) interpret "unexpectedly large isotopic differences  
214 between individuals" as evidence of a high inter-individual component to niche width. This  
215 interpretation is problematic because the processes that create variation in the isotopic  
216 composition of producers can lead to widely divergent values. Dispersion in delta space is  
217 dependent on the distance between the isotopic values of the alternative producers. Animals that  
218 feed on two resources with widely divergent isotopic compositions will always be found to have  
219 broader niches than animals that feed on food sources with less divergent delta values (Fig. 4),  
220 but this may not always accurately reflect the true niche breadth. In the final section we will  
221 describe how a metric of niche width that does not depend on the distance between the isotopic  
222 values of producers can be constructed.

223

224 **Applications of the isotopic niche**

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

235         The identification of niche shifts, ontogenetic or otherwise, by SIA can also have  
236 important conservation implications. For example, SIA demonstrated that loggerhead turtles  
237 (*Caretta caretta*) use of productive, nearshore oceanic habitats not only increases juvenile  
238 growth rates but may also increase by-catch risk (Snover 2002). Ecologists have also used  
239 isotopes to document subtle niche shifts in lake trout (*Salvelinus namaycush*), which were  
240 otherwise undetectable, following the invasion of two exotic bass species (Vander Zanden et al.  
241 1999). SIA-derived scenopoetic and/or bionomic niche information can also be coupled with  
242 toxicological data and satellite tracking technologies to identify the sources and vectors of  
243 contaminants that threaten population viability (Finkelstein et al. 2006). Furthermore, SIA-  
244 derived information on habitat preference(s) and connectivity within and among populations  
245 could be combined with epidemiological data to identify disease vectors, especially for species

246 that have an inherently high potential for relatively fast transmission rates across spatial areas of  
247 epidemic proportion (i.e., West Nile virus; Marra et al. 2004).

248 A third area of research where SIA-derived niche information continues to inform  
249 conservation biology is in historic ecology, which aims to determine the true range of ecological  
250 flexibility of species that may have experienced significant truncations in behavior due to direct  
251 or indirect human disturbance (i.e., hunting, habitat loss). For example, SIA has been used to  
252 identify differences in the use of coastal versus inland habitats by modern and ancient California  
253 condor (*Gymnogyps californianus*) populations (Fig. 3B; Chamberlain et al. 2005, Fox-Dobbs et  
254 al. 2006). These studies contend that conservation goals should emphasize the reintroduction of  
255 condors (obligate scavengers) to coastal areas where populations would have access to stranded  
256 marine mammal carcasses. Another study found a difference in the trophic level of historic  
257 versus contemporary marbled murrelets (*Brachyramphus marmoratus*) in central California,  
258 suggesting that recent decreases in large, energetically superior prey populations due to  
259 overfishing is contributing to poor murrelet reproduction and recent population declines (Becker  
260 and Beissinger 2006). The continual use of SIA to identify past versus present differences in  
261 biogenic or scenopoetic niche space provides a means of describing the natural history of  
262 species on ecologically and evolutionarily-relevant timescales, thus providing a means of  
263 evaluating the significance of current ecological trends that is vital for the success of long-term  
264 conservation and management strategies.

265

### 266 **Transforming from $\delta$ -space to p-space**

267 The degree of specialization and generalization in individuals and populations can inform  
268 problems as diverse as the evolution of resource use (Bolnick 2003), the success of invading

269 exotics (Holt et al. 2005), and the processes that shape the composition of ecological  
270 communities (Wiens and Graham 2005). Ecologists have devised a variety of metrics to assess  
271 niche variation and the relative contribution of individual variation to these metrics (reviewed by  
272 Bolnick et al. 2002). One can assess variation in the isotopic niche, but in a previous section we  
273 identified one of the problems of isotopic niches as depicted in delta spaces. The variation within  
274 and among individuals in isotopic composition is strongly dependent on how different the  
275 isotopic signatures of the food sources are. An alternative to using  $\delta$ -values *per se* to define  
276 isotopic niches is to use mixing models to transform them into dietary proportions (p) of  
277 different isotopic sources. Briefly, if one measures the isotopic composition of n elements, one  
278 can determine the contribution of n+1 isotopically distinct sources by solving a system of n+1  
279 linear equations (Fig. 5; see Phillips and Gregg 2001 for details). This transformation from  $\delta$ -  
280 space to p-space resolves the scaling discrepancies in  $\delta$ -space discussed above, and permits using  
281 the niche-width metrics most commonly used by ecologists (see Bolnick 2002). We hasten to  
282 point out that depictions of the isotopic niche in  $\delta$ -space and p-space are complementary rather  
283 than alternative. By transforming data from delta-space to p-space, we gain the ability to  
284 construct metrics of variation that are independent of the absolute value of isotopic signatures  
285 and that are comparable to those of other niche formulations. However, we lose the insights on  
286 the types of resources and locations in isoscapes that are revealed by  $\delta$ -spaces.

287         Because mixing models are central tools in the analysis of isotopic niches, it is important  
288 to pay attention to their assumptions and potential limitations. Both the isotopic composition of  
289 isotopic sources and that of animal tissues are measured with variation. Consequently, the  
290 numerical manipulations required to transform from  $\delta$ -values to p-values involves error

291 propagation. Phillips and Gregg (2001) provide formulas for calculating variances, standard  
292 errors (SE), and confidence intervals for p values. Using correct tissue-to-diet discrimination  
293 factors is also important when estimating p values (Phillips and Gregg 2001). Finally, recall that  
294 a mixing model resolves  $n+1$  distinct sources if one measures  $n$  isotopes. Thus, a particular set of  
295  $\delta$ -values may not define a point in p-space unless the number of distinct isotopic sources is  
296 limited to one more than the number of  $\delta$ -values measured. Phillips and Gregg (2003) have  
297 devised a method that relaxes this requirement and makes it possible to determine the minimum  
298 and maximum utilization of each source that is consistent with isotopic mass balance even when  
299 one measures  $n$  isotopes and the number of resources exceeds  $n+1$ . However, the degree of  
300 utilization within these bounds cannot be determined exactly but only as a range of possible  
301 values (Phillips and Gregg 2003). In such cases, mixing models may only transform a  $\delta$ -space  
302 into a blurry p-space.

303

#### 304 **Concluding remarks**

305 Scientific concepts sometimes lie dormant until new methodologies transform them and  
306 revitalize them. Systems biology received intense interest from biologists in the 1960s and then  
307 waned. Fertilized by the growth of the “omics” (genomics, proteonomics, metabolomics) and  
308 fueled by the power of ever-faster computers, systems biology has reincarnated into a vigorous  
309 field (Wolkenhauer 2001). In a similar fashion, the revival of the niche is the result of rapid  
310 progress in bioinformatics and in the development of new technologies. Just as researchers  
311 interested in systems biology and in tracking the evolution of biological systems rely on nucleic  
312 acids and the polymerase chain reaction (PCR), ecologists interested in measuring the fluxes of  
313 energy and materials among components of ecological systems increasingly rely on SIA (Yakir

314 2002). We predict the rapid growth of niche studies and contend that they will be stimulated by  
315 faster, cheaper, and more accurate stable isotope analyses. Isotopic ecology will become an  
316 important axis in the resurgent study of ecological niches.

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TABLE 1

Gradient	Isotope System	High $\delta$ -Values	Low $\delta$ -Values	Scenopoetic	Bionomic
Trophic Level	$\delta^{13}\text{C} / \delta^{15}\text{N}$	High Levels	Low Levels		√
C <sub>3</sub> – C <sub>4</sub> Vegetation	$\delta^{13}\text{C}$	C <sub>4</sub> Plants	C <sub>3</sub> Plants		√
Marine – Terrestrial	$\delta^{15}\text{N} / \delta^{13}\text{C} / \delta^{34}\text{S}$	Marine	Terrestrial	√	√
Latitude (Terrestrial)	$\delta^2\text{H} / \delta^{18}\text{O}$	Low Latitudes	High Latitudes	√	
Latitude (Marine)	$\delta^{13}\text{C} / \delta^{15}\text{N}$	Low Latitudes	High Latitudes	√	
Altitude	$\delta^{13}\text{C}$	High Altitudes	Low Altitudes	√	
Altitude	$\delta^2\text{H}$	Low Altitudes	High Altitudes	√	
Inshore – Offshore	$\delta^{13}\text{C}$	Inshore	Offshore	√	
Benthic – Pelagic	$\delta^{13}\text{C}$	Benthic	Pelagic	√	√
Aridity	$\delta^{13}\text{C} / \delta^{15}\text{N}$	Xeric	Mesic/Hydric	√	
Eutrophication	$\delta^{15}\text{N}$	Polluted	Pristine	√	
Temperature	$\delta^{18}\text{O}$	Cooler	Warmer	√	
Geologic Substrate	$\delta^{87}\text{Sr}$	Young Rocks	Old Rocks	√	
Oxic – Anoxic	$\delta^{15}\text{N} / \delta^{13}\text{C} / \delta^{34}\text{S}$	Oxic	Anoxic	√	
Methanogenesis	$\delta^{13}\text{C}$	Photosynthetic	Methanogenic	√	

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490 **FIGURE 1.** Isotopic ratios are typically expressed as the ratio of the heavy (H) to light (L)  
491 isotope and converted into delta notation ( $\delta$ -values) through comparison of sample isotope ratios  
492 to ratios of internationally accepted standards. Standards for common systems include Vienna-  
493 Pee Dee Belemnite limestone (V-PDB) for carbon, atmospheric N<sub>2</sub> for nitrogen, and VSMOW  
494 for hydrogen and oxygen. The units are expressed as parts per thousand or per mil (‰).

495

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

499

500 **FIGURE 3.** Two examples of how delta-space can supply information on the bionomic and  
501 scenopoetic axes of the ecological niche. In some cases, an isotopic axis can have both bionomic  
502 and scenopoetic components (panel 2), where feeding on a marine or terrestrial food web implies  
503 inhabiting a marine/terrestrial habitat. Data from Wassenaar and Hobson (2000) and  
504 Chamberlain et al. (2005).

505

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

511

512

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

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**FIGURE 1**

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Isotope Ratio	Delta ( $\delta$ ) Notation Derivation	$\delta$ -Value
$HX/LX$	$\left[ \left( \frac{HX/LX_{sample}}{HX/LX_{standard}} - 1 \right) \times 1000 \right]$	$\delta^{HX}$
$^{13}C/^{12}C$	$\left[ \left( \frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right) \times 1000 \right]$	$\delta^{13}C$

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**FIGURE 2**

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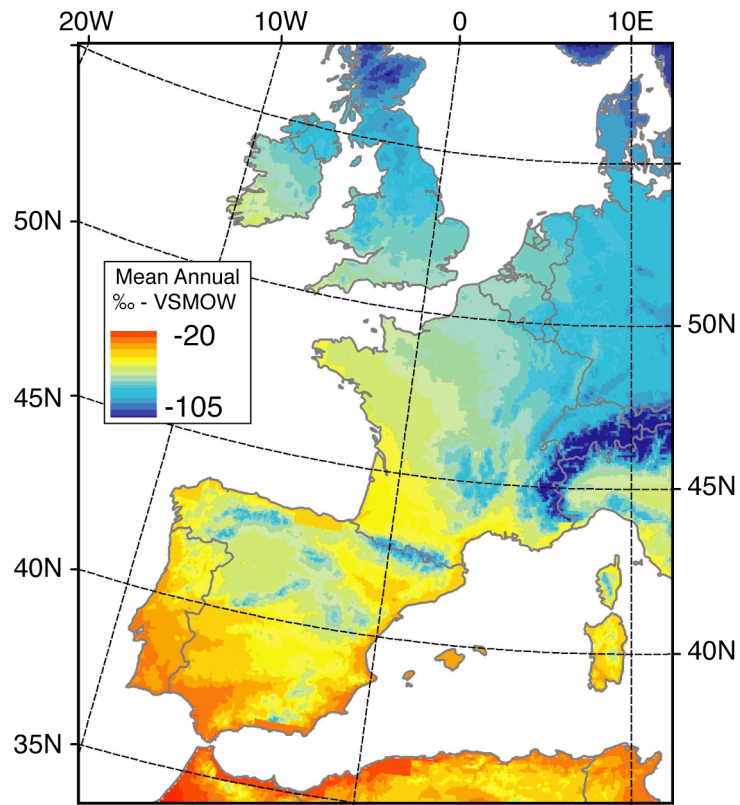
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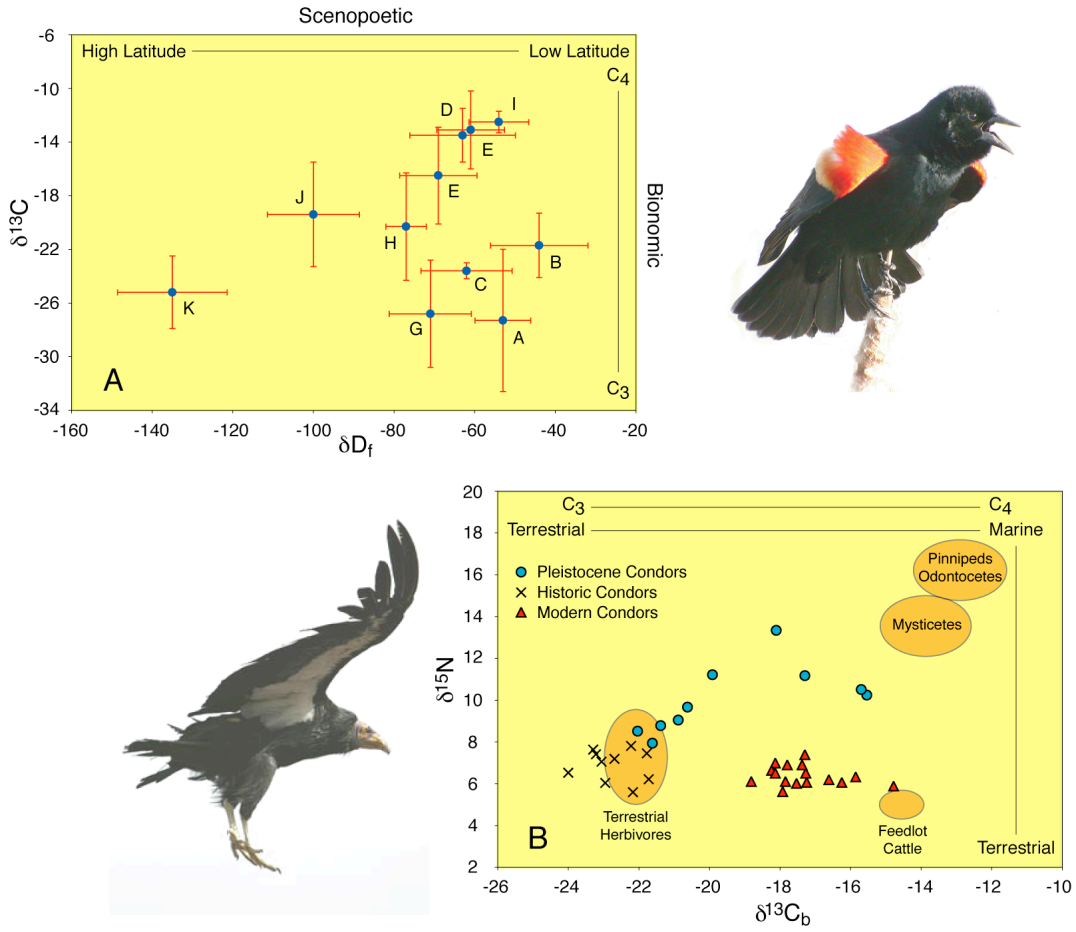
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**FIGURE 3**



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FIGURE 4

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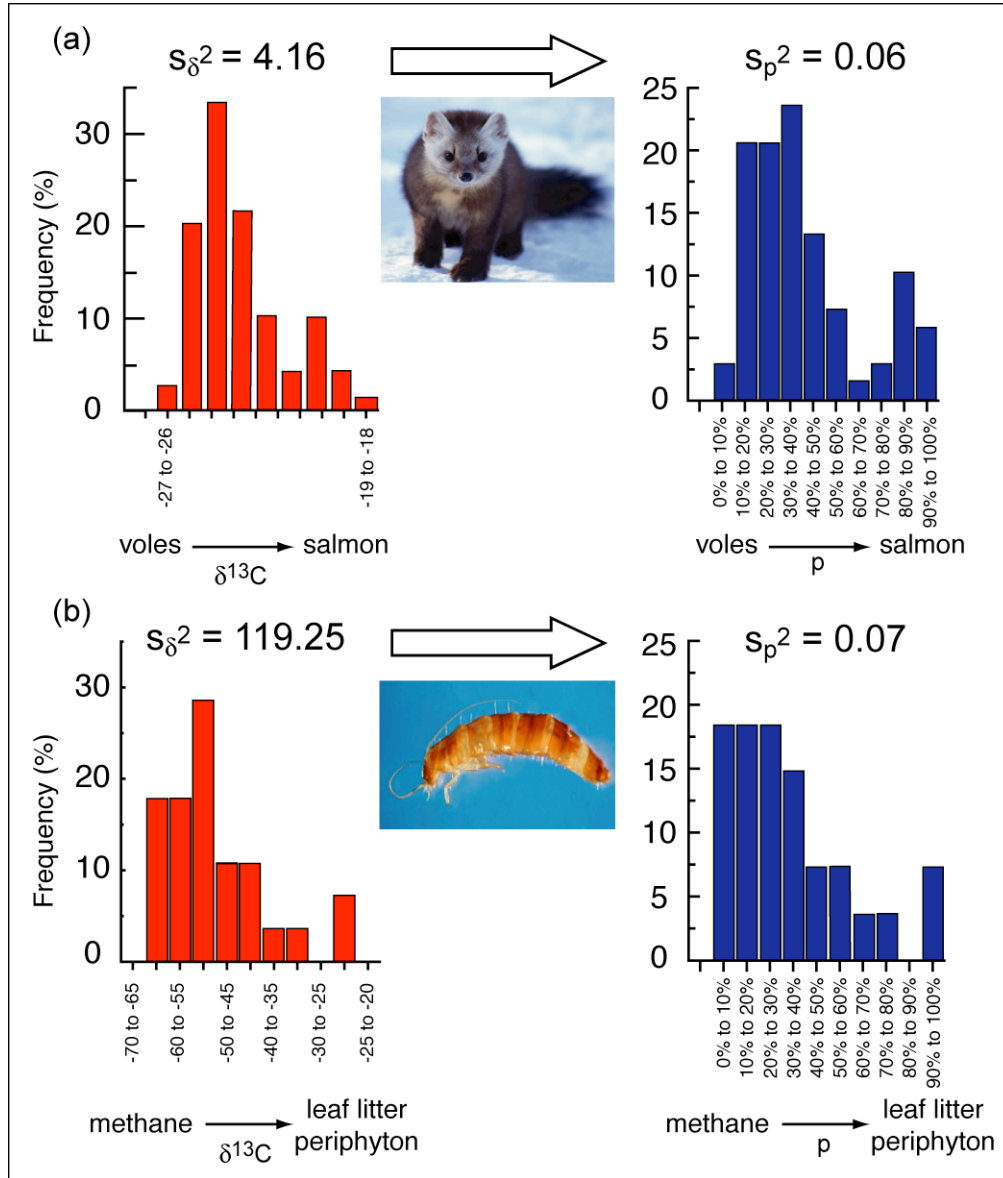
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FIGURE 5

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