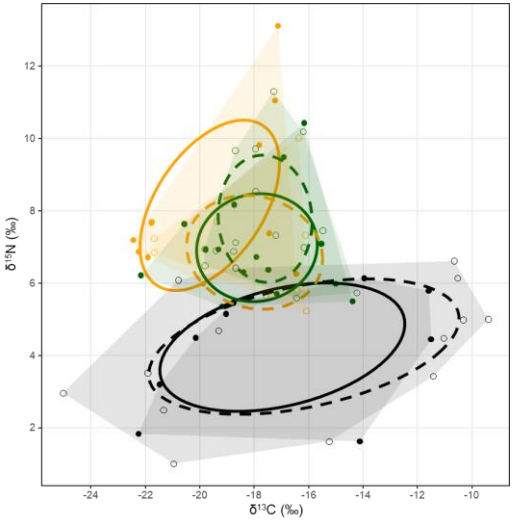
Quantifying ecological diversity: stable isotopes as realized niche proxies



Loïc MICHEL – Deep Sea lab, Ifremer Brittany

Contact: loicnmichel@gmail.com

About me

2017 – Present : Research scientist at Ifremer Brittany, Brest, France

Before that: mostly ULiège (Freshwater and OCeanic science Unit of reSearch, FOCUS)

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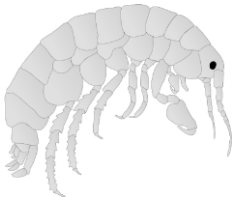
I mostly tackle those issues by using polar and deep-sea benthic invertebrates as ecological models, and by developing approaches based on trophic markers, notably stable isotopes.

What's an ecological niche?

Conceptual definition by George E. Hutchinson (1957):

A hypervolume set in an n-dimensional space where each of the axes represents an environmental parameter



Concluding Remarks

G. Evelyn Hutchinson
Yale University, New Haven, Connecticut

Cold Spring Harbor symposia on quantitative biology 22: 415-427

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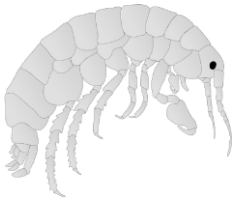

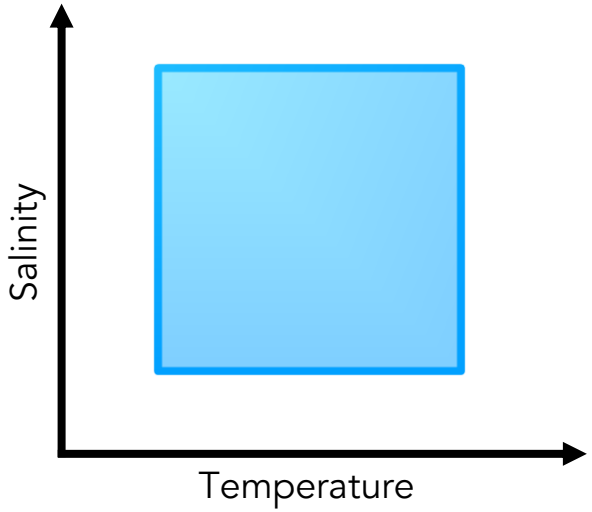

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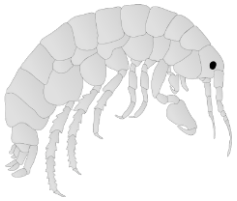

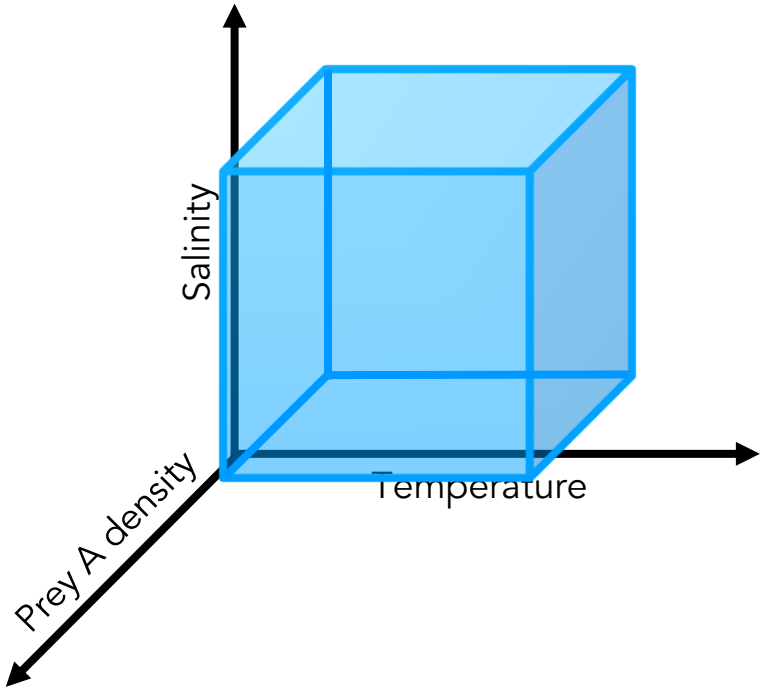

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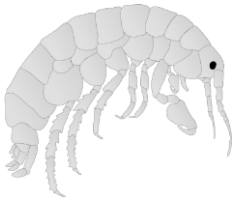

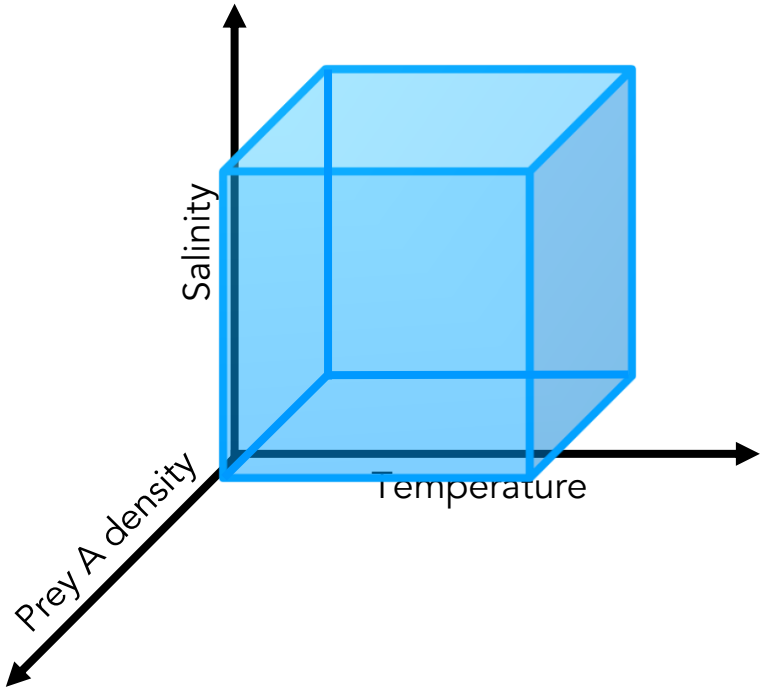

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2 categories of dimensions: habitat- and resource-related

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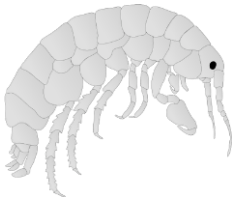

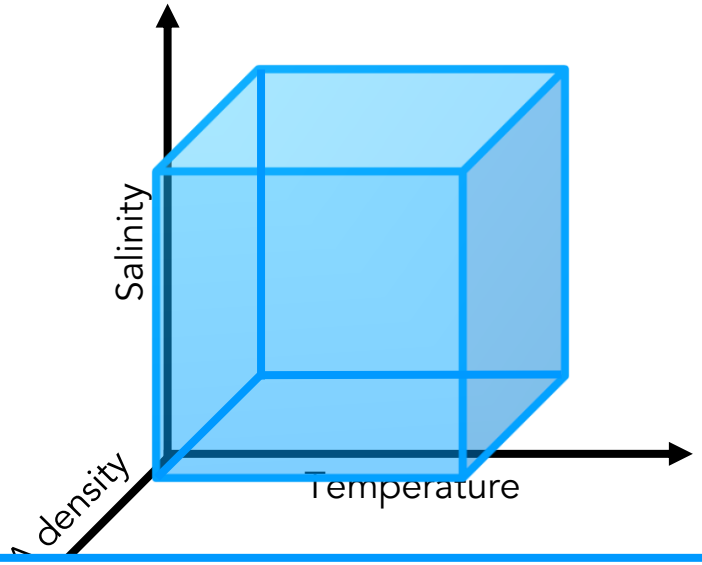

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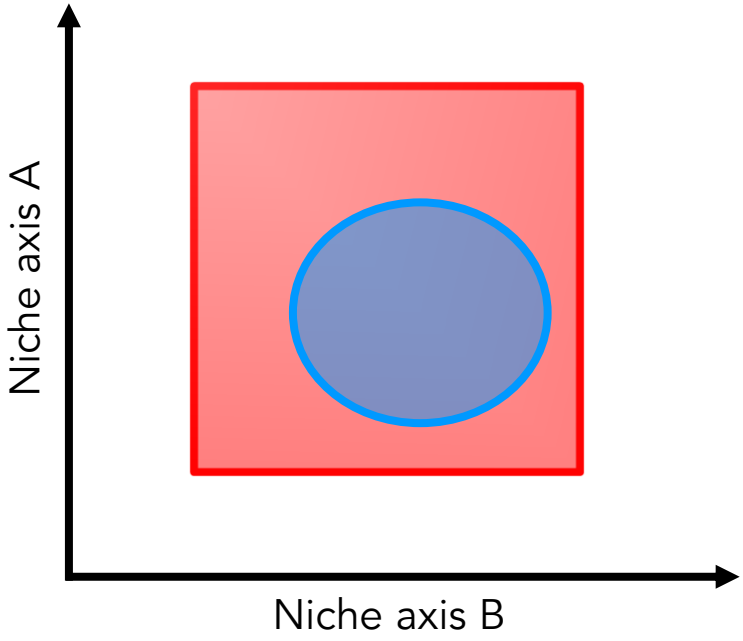
Trophic niche = part of the ecological niche built using the subset of dimensions related to trophic resources

2 categories of dimensions: habitat- and resource-related

What's an ecological niche?

Fundamental niche: full range of conditions and resources in which an organism could survive and reproduce if free of any interference

Realized niche: narrower space that an organism is "forced" to occupy as a result of interactions with other species



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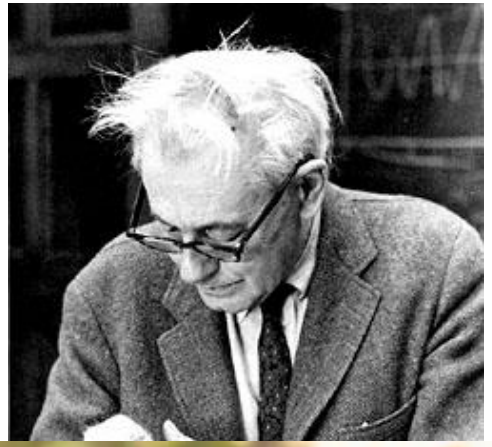
Cold Spring Harbor symposia on quantitative biology 22: 415-427

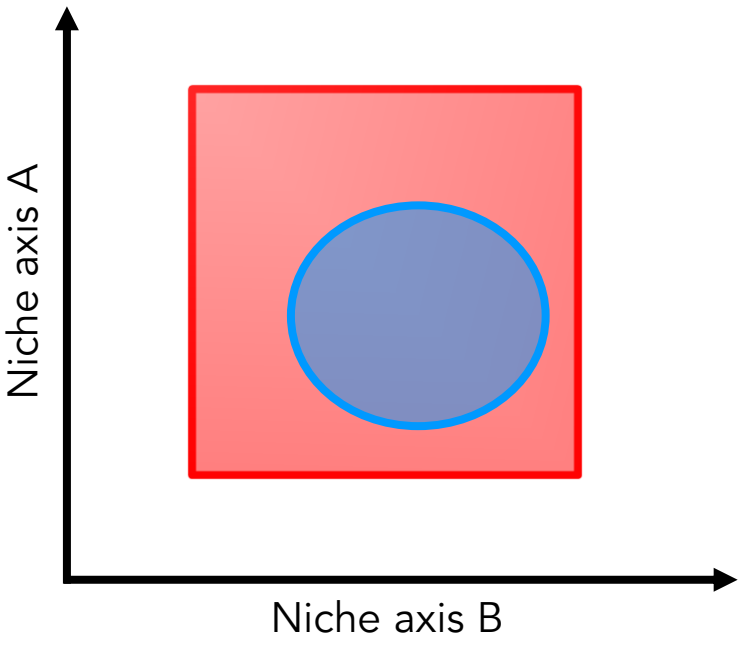
What's an ecological niche?

Fundamental niche

Realized niche

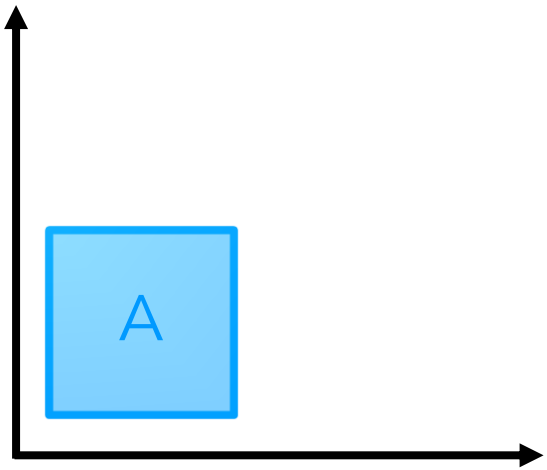
Importance of competition as a driving mechanism

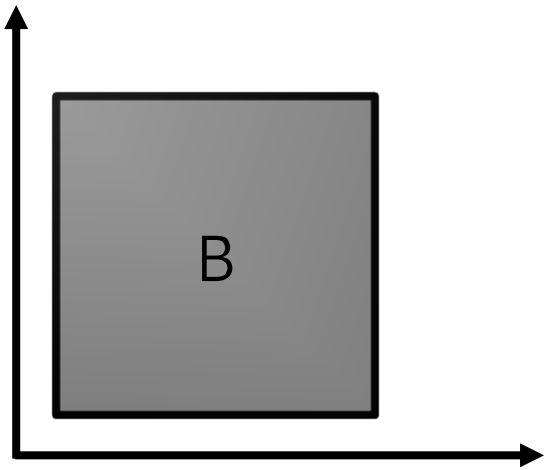




Ecological niche study: why?

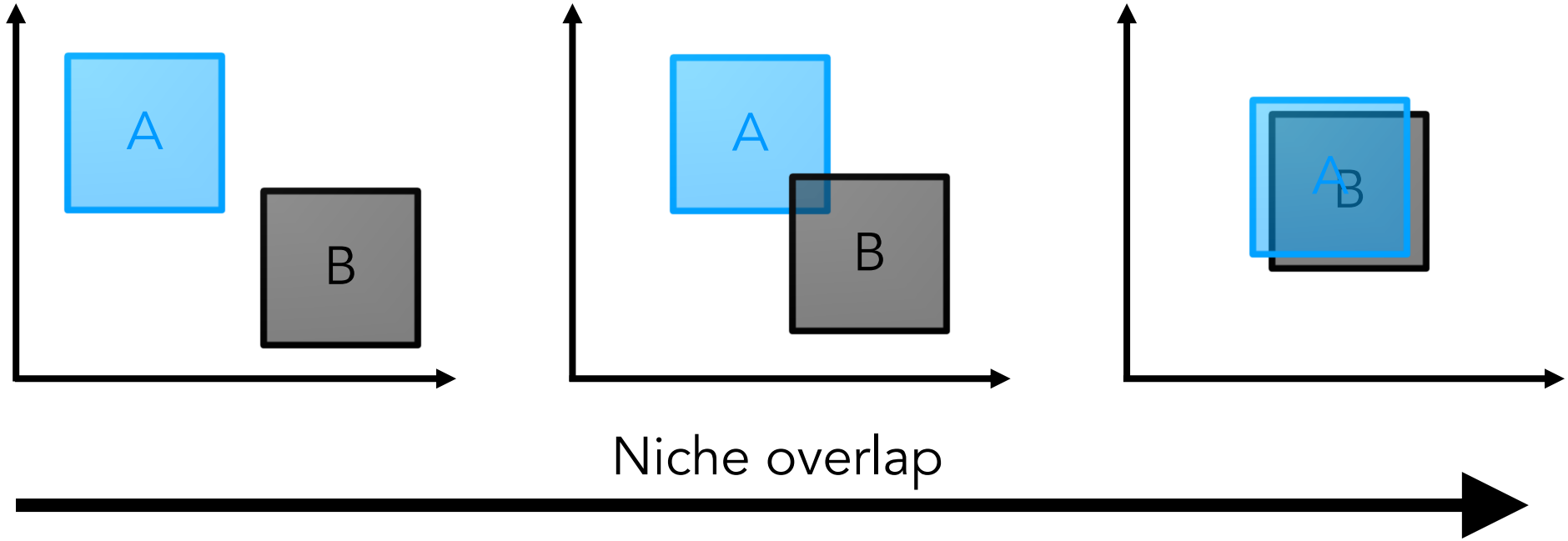
- Identify ecological strategies: amount of resources and habitats used by animals (narrow vs. wide niches)





Ecological niche study: why?

- Identify ecological strategies
- Understand how ecological interactions can affect community structure



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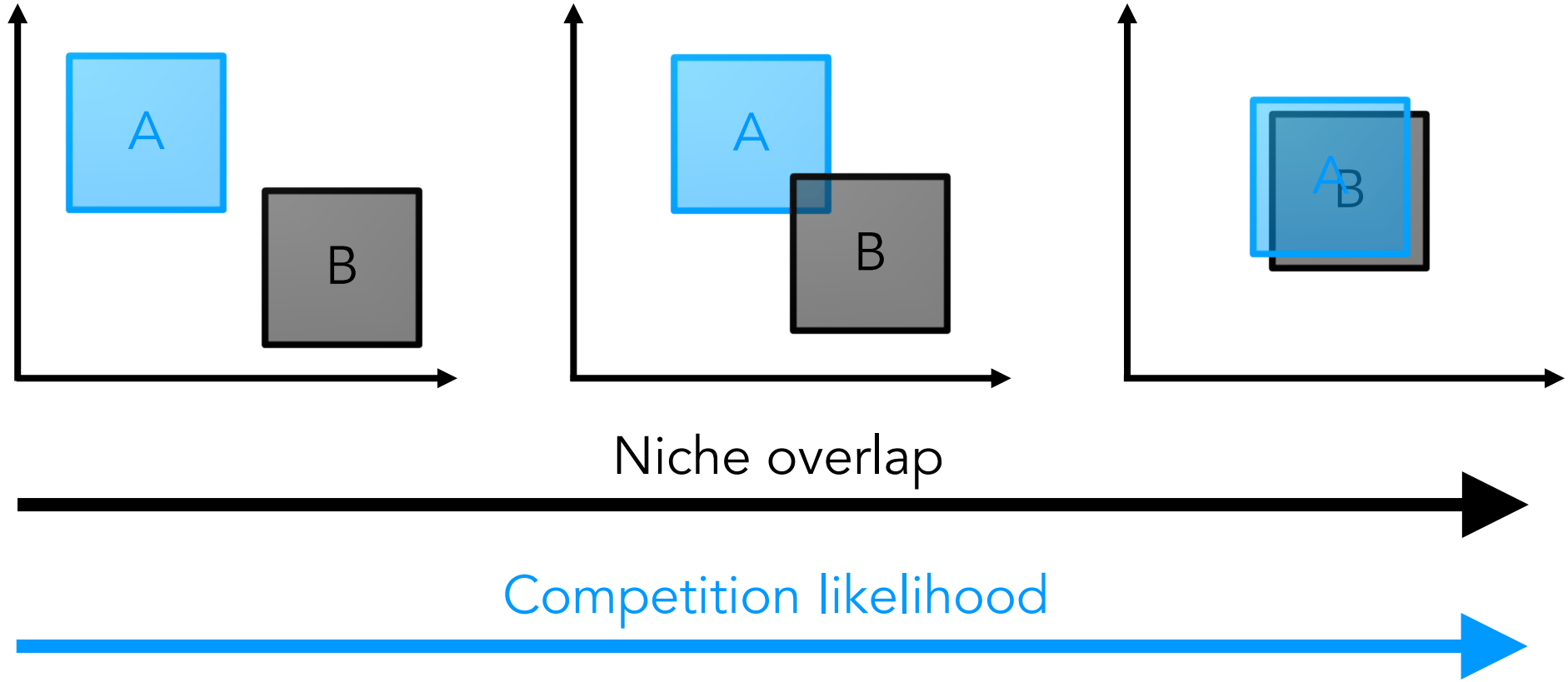
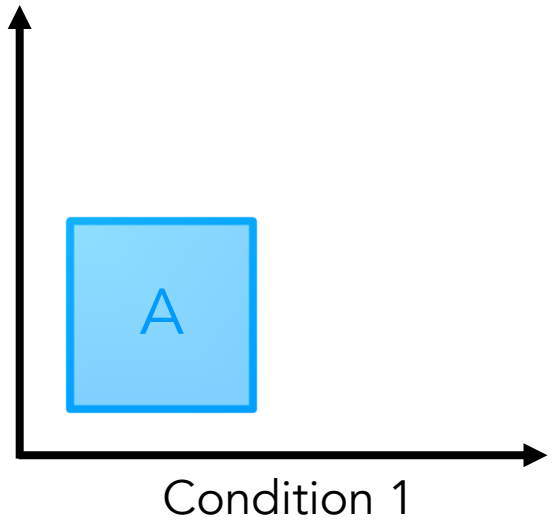
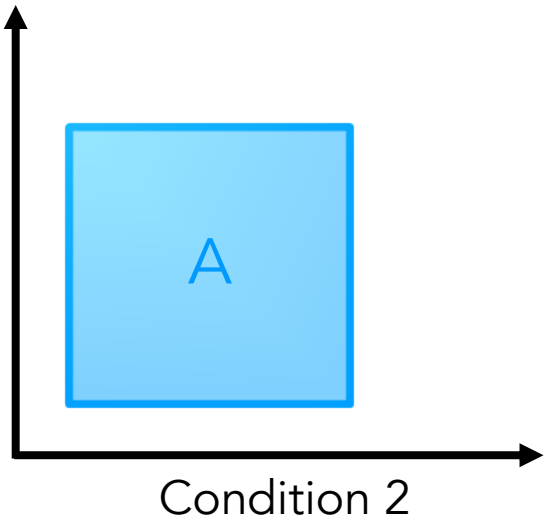
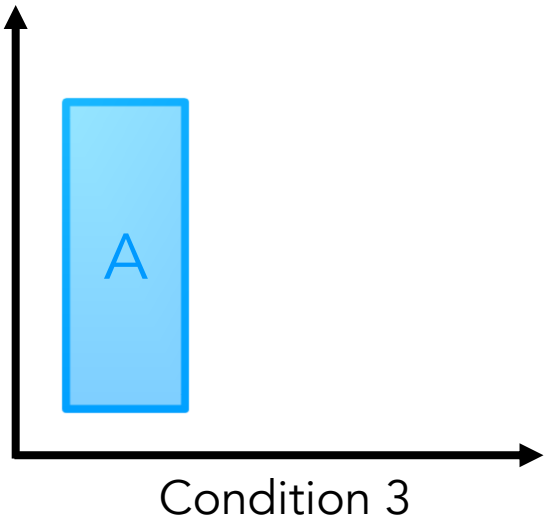


Ecological niche study: why?

- Identify ecological strategies
- Understand how ecological interactions can affect community structure
- Highlight ecological shifts and study ecological plasticity







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- The niche concept is useful to address many fundamental ecological questions
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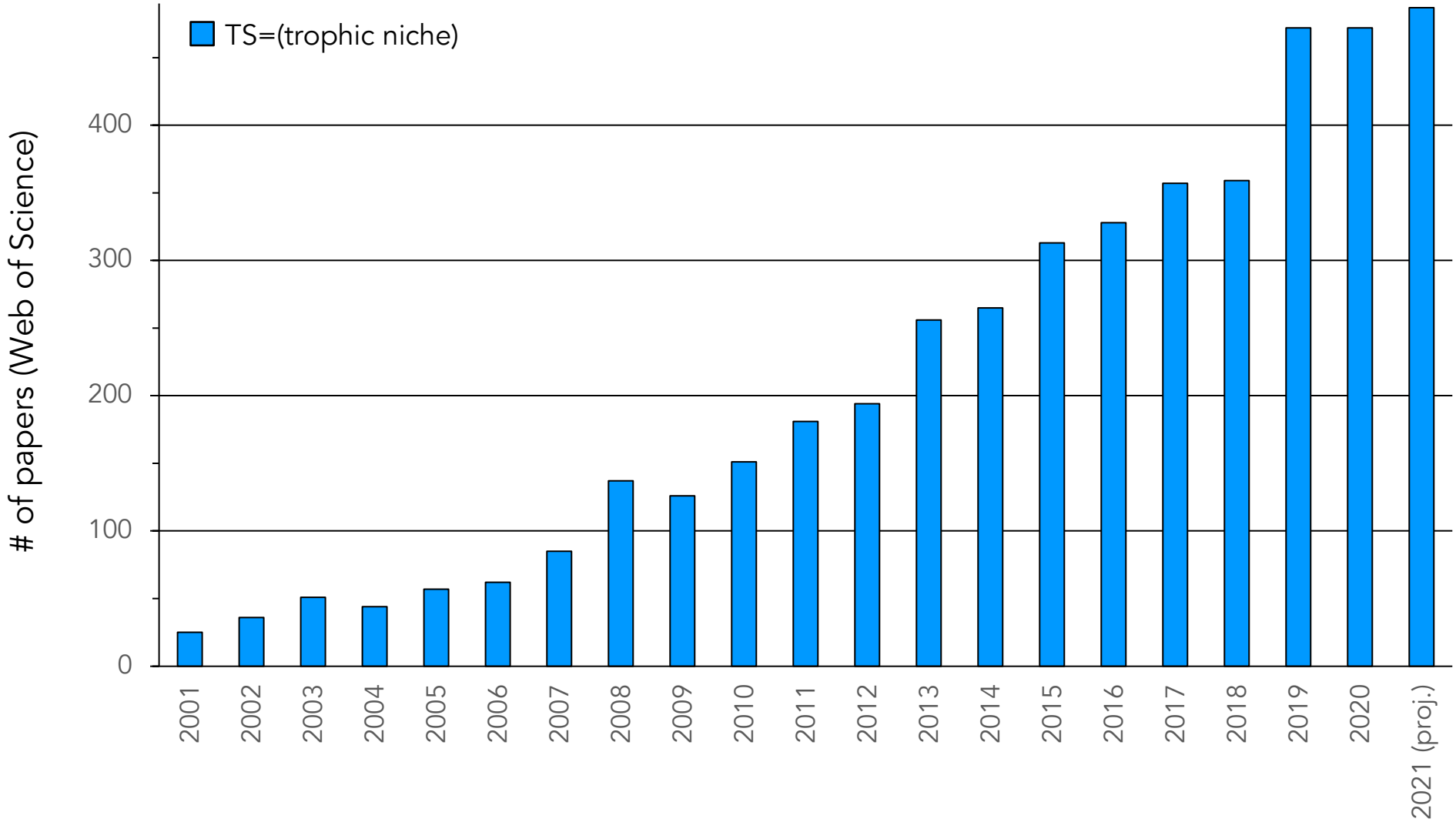

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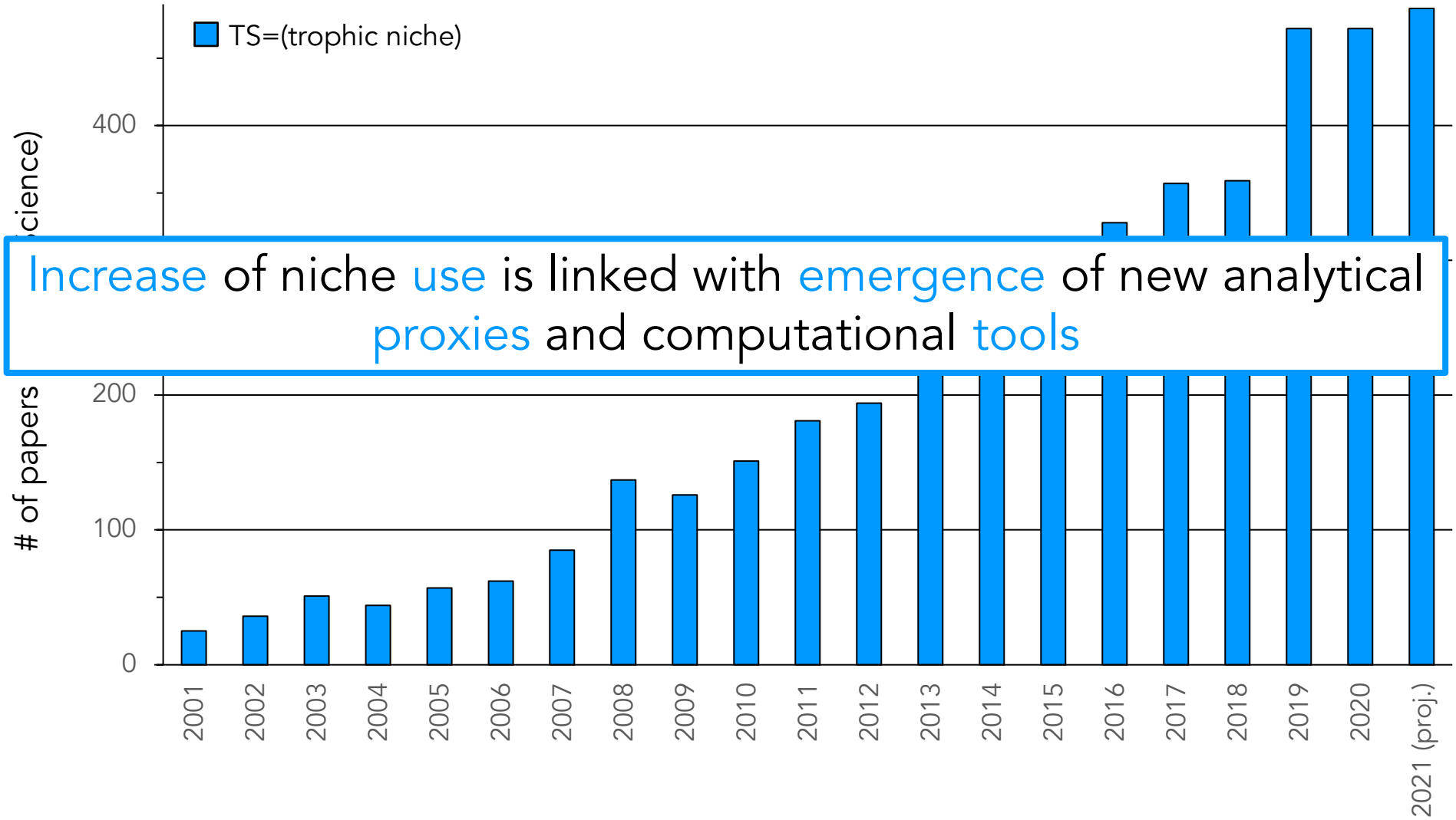

Increase of niche use is linked with emergence of new analytical proxies and computational tools

Ecological niche study: how?

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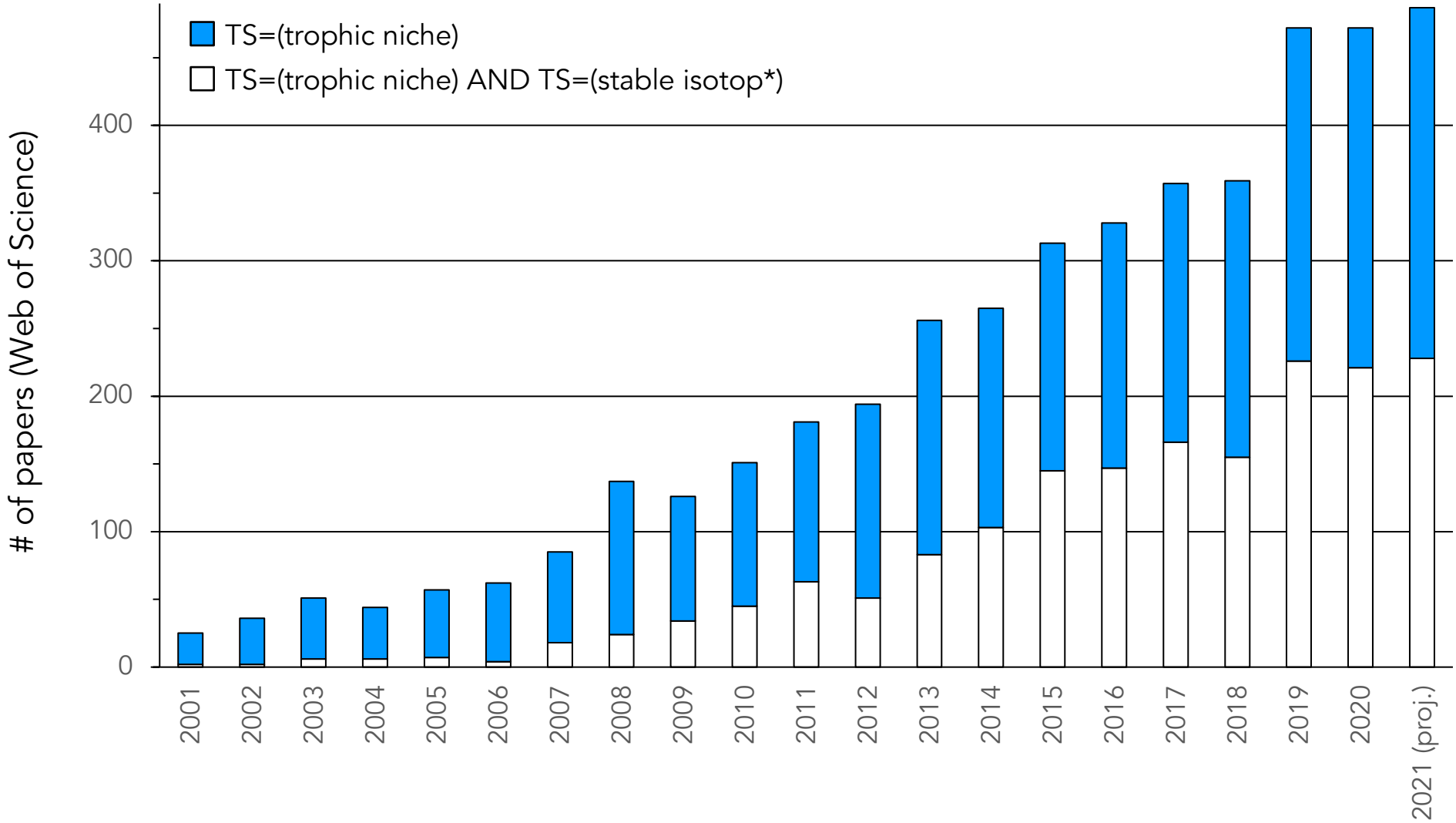
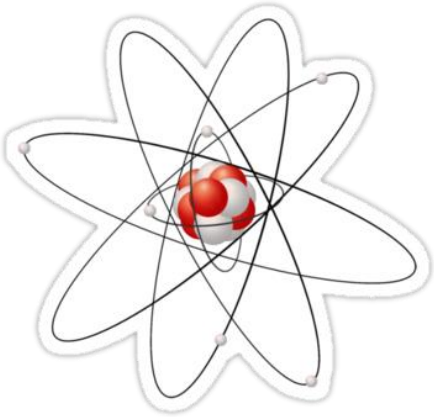
- For decades: practical issues to provide quantitative estimates of niche parameters



Stable isotopes: you are what you eat

Mixing law: stable isotope composition of an animal is a proportional mix of its food sources' isotopic composition



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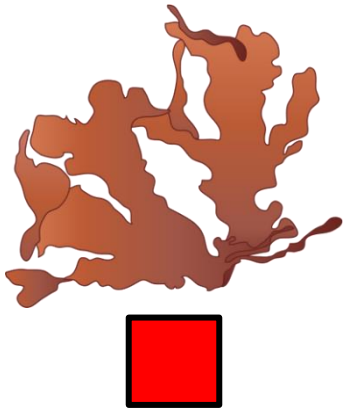

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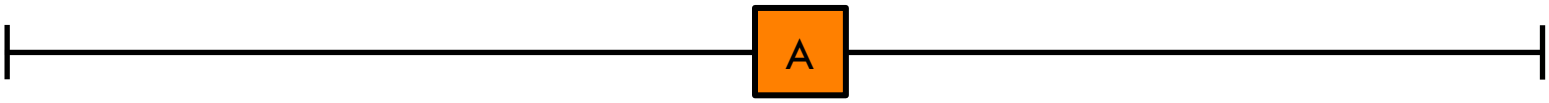

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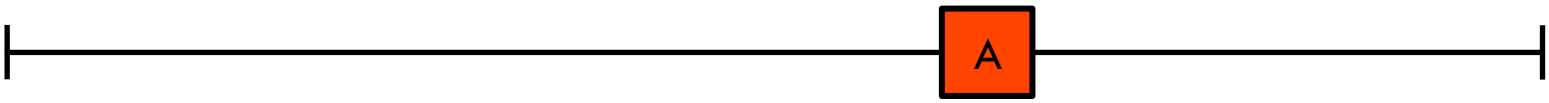

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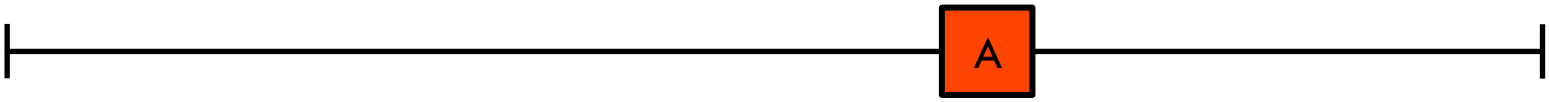
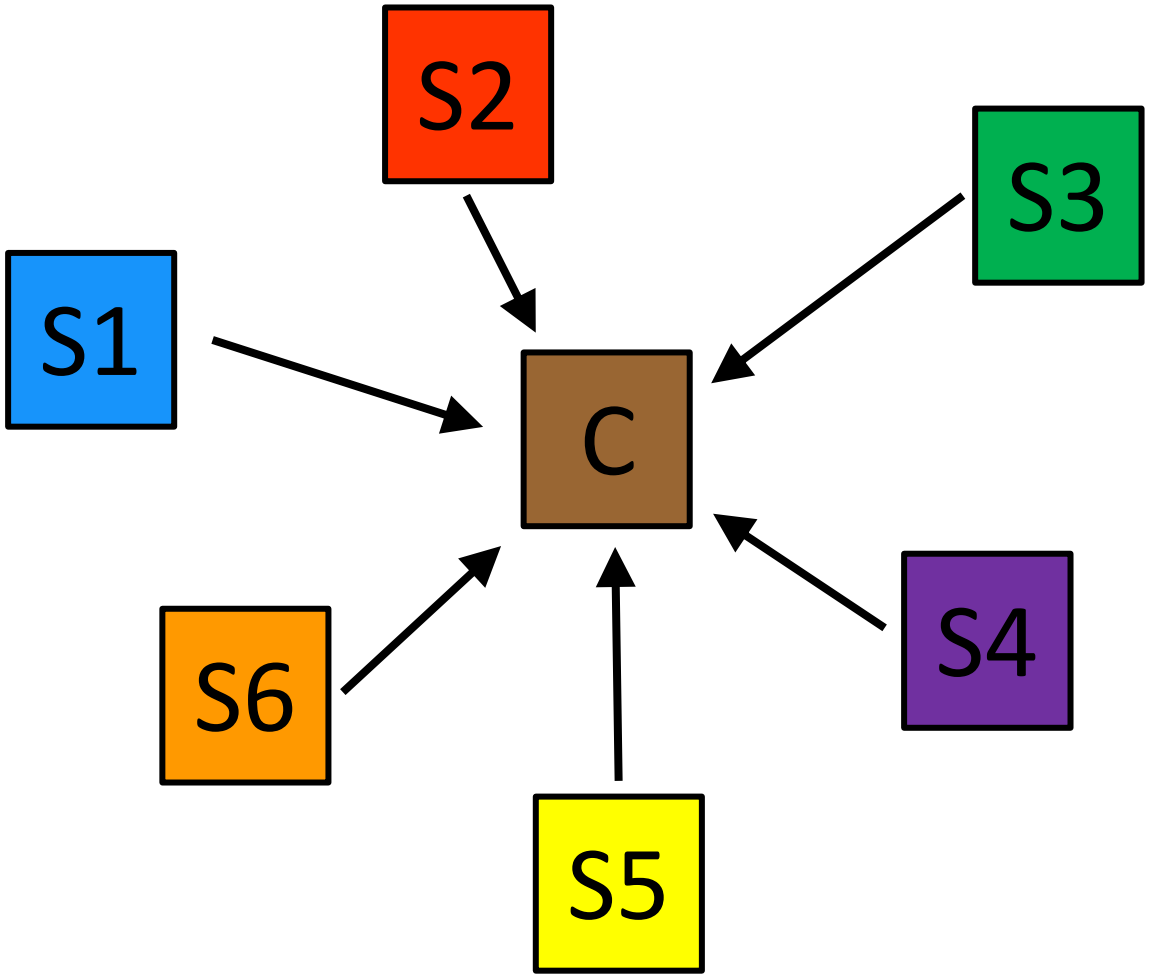


If you measure the isotopic compositions of an animal and its food item, you can calculate contributions of each food item to this animal's diet

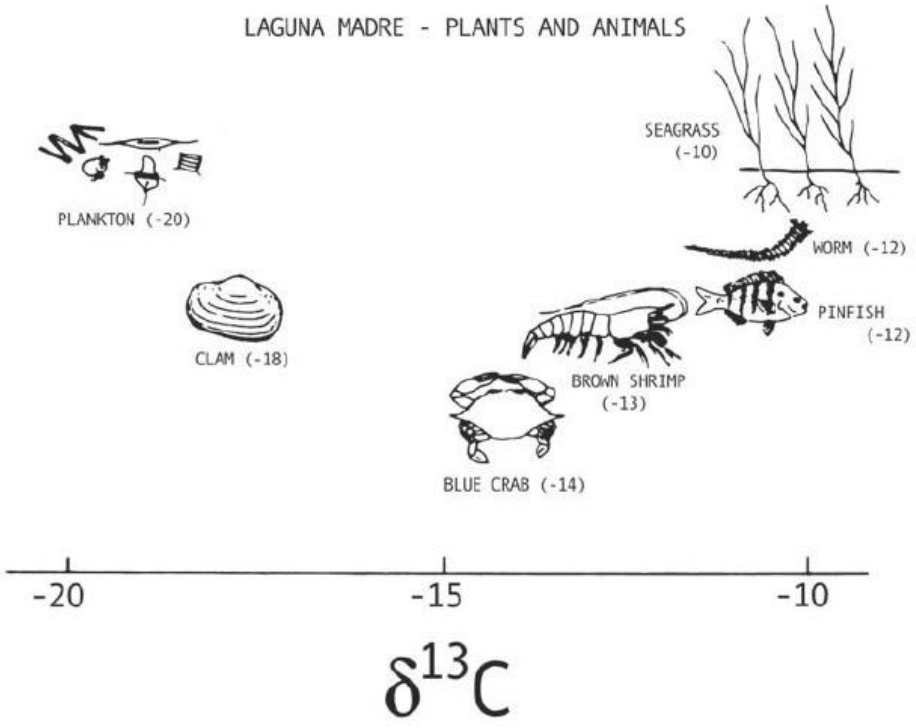
Stable isotopes: you are what you eat

Real world ecosystems: multiple potential food items

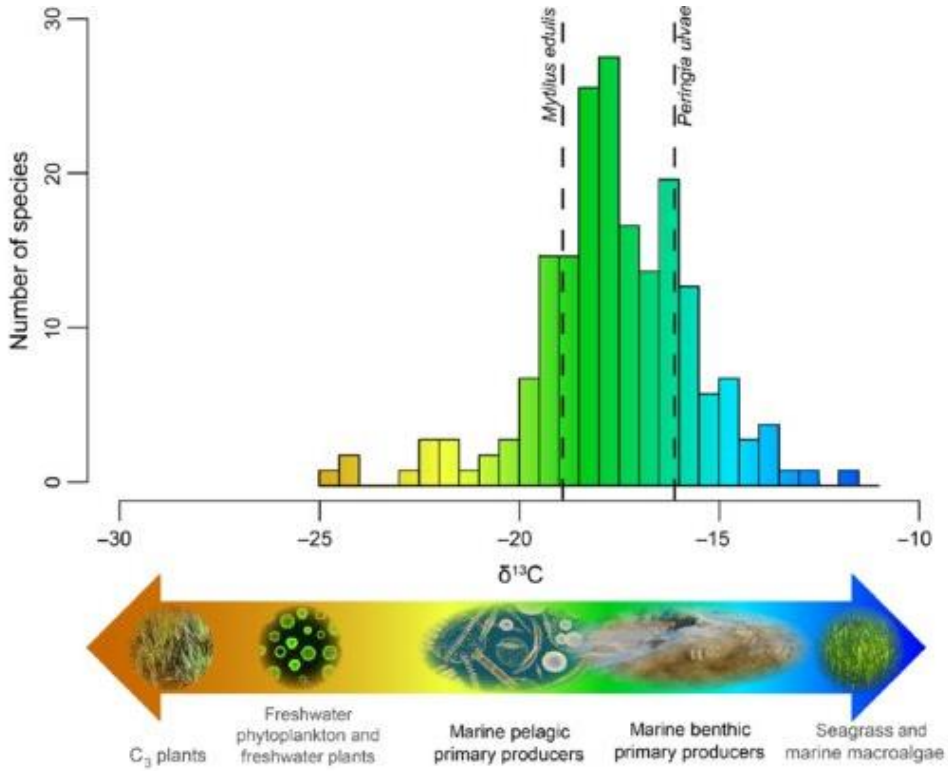


Carbon stable isotopes

Fry (2006): Stable Isotope Ecology



Christianen *et al.* 2017 Ecology 98: 1498-1512

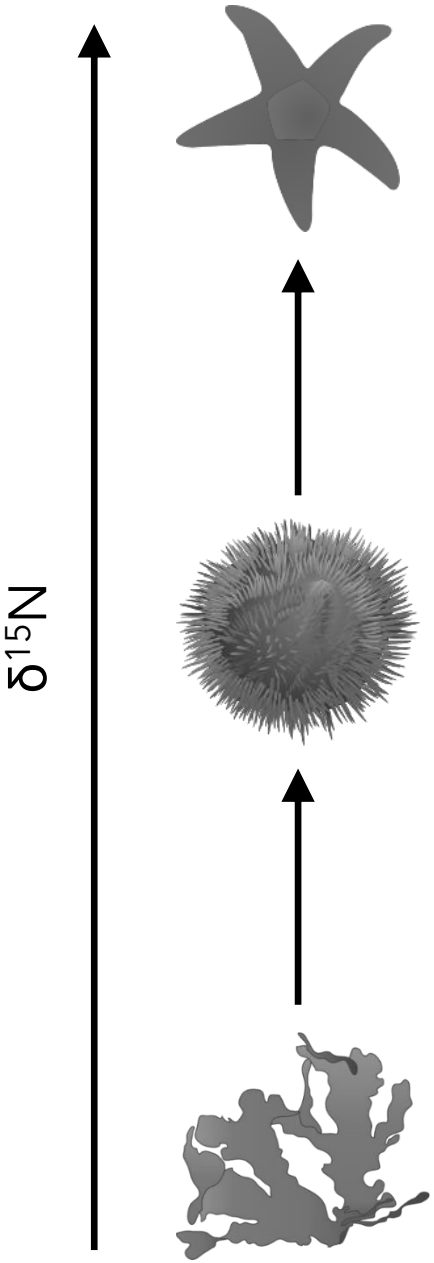


$\delta^{13}C$ of marine producers is variable

This $\delta^{13}C$ is mostly conserved throughout the food web

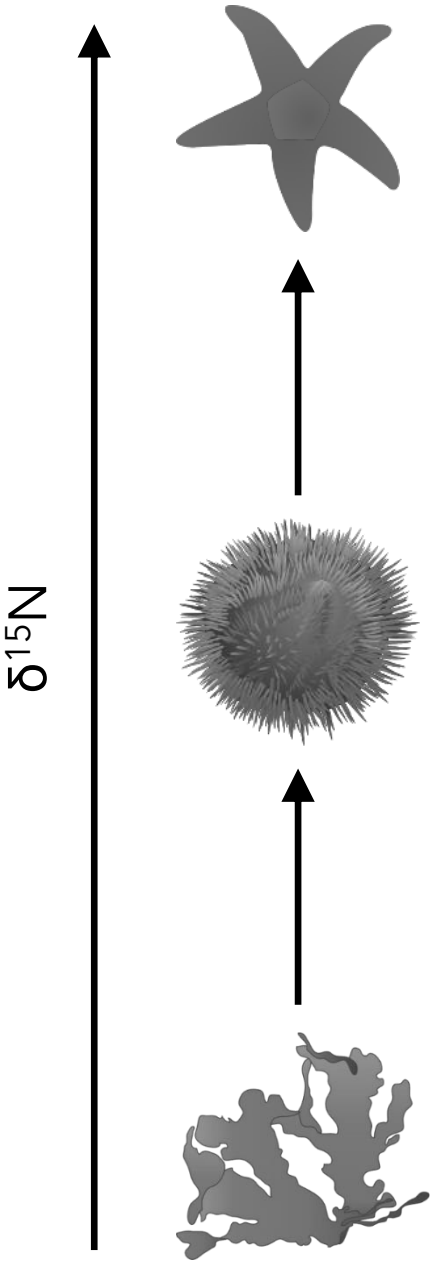
$\delta^{13}C$ can be used to identify producers supporting animal populations in marine ecosystems

Nitrogen stable isotopes



The heavy nitrogen stable isotope (^{15}N) follows a predictable stepwise enrichment pattern with increasing trophic level

Nitrogen stable isotopes



Secondary consumers
TL = 3

Primary consumers
TL = 2

Primary producers
TL = 1

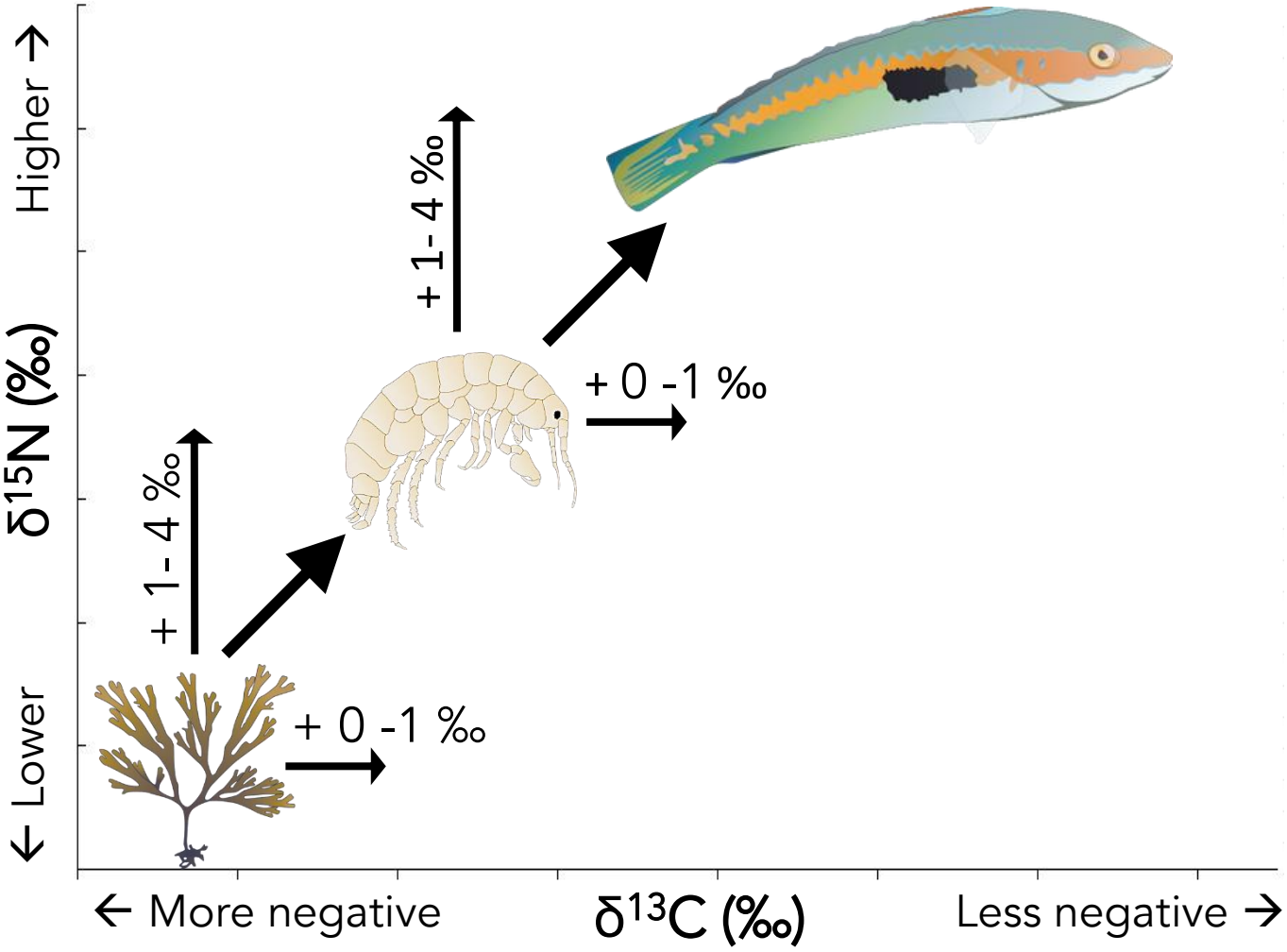
The heavy nitrogen stable isotope (^{15}N) follows a predictable stepwise enrichment pattern with increasing trophic level

Measurement of stable isotope composition of consumers and baseline items (primary producers)

Infer trophic level of animals through calculation or use of a model

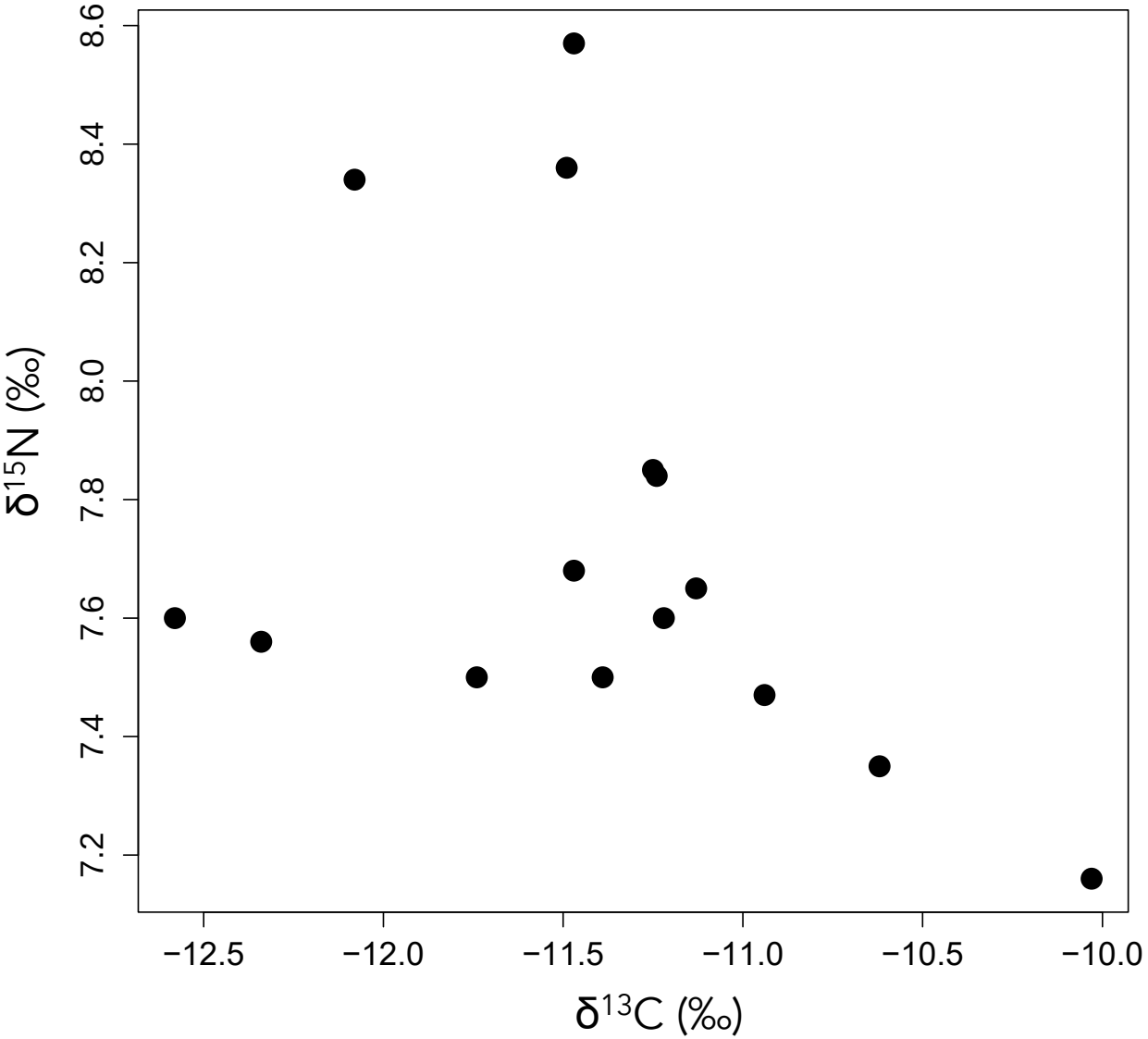
Stable isotope ratios of C and N

Typical food web representation using an isotopic biplot



Stable isotopes as niche proxies

Typical SI analysis output : points in "isospace"



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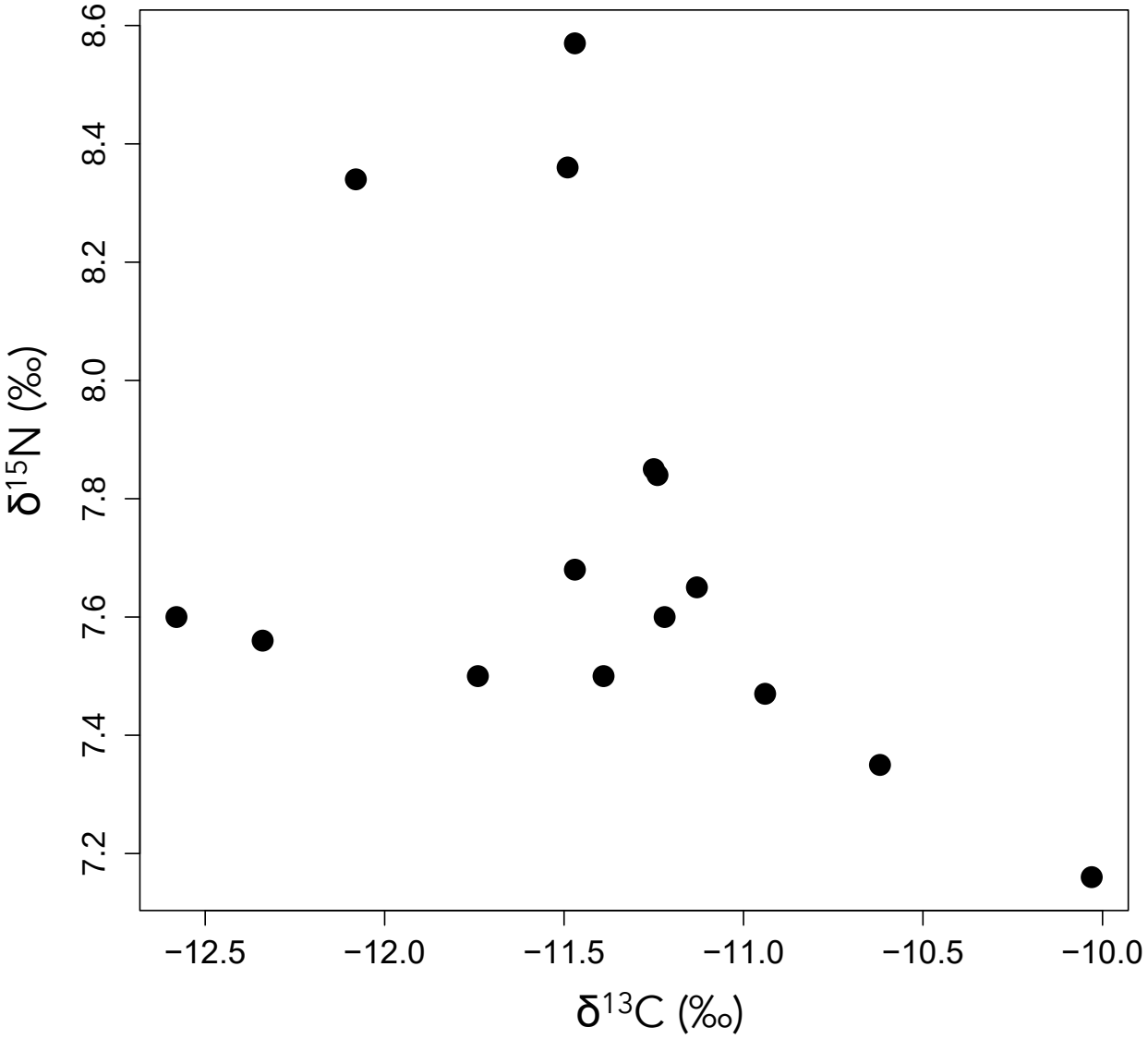

Position of consumers in the isospace is driven by

1) Differences in consumed resources (different preys can have different isotopic compositions)

Stable isotopes as niche proxies

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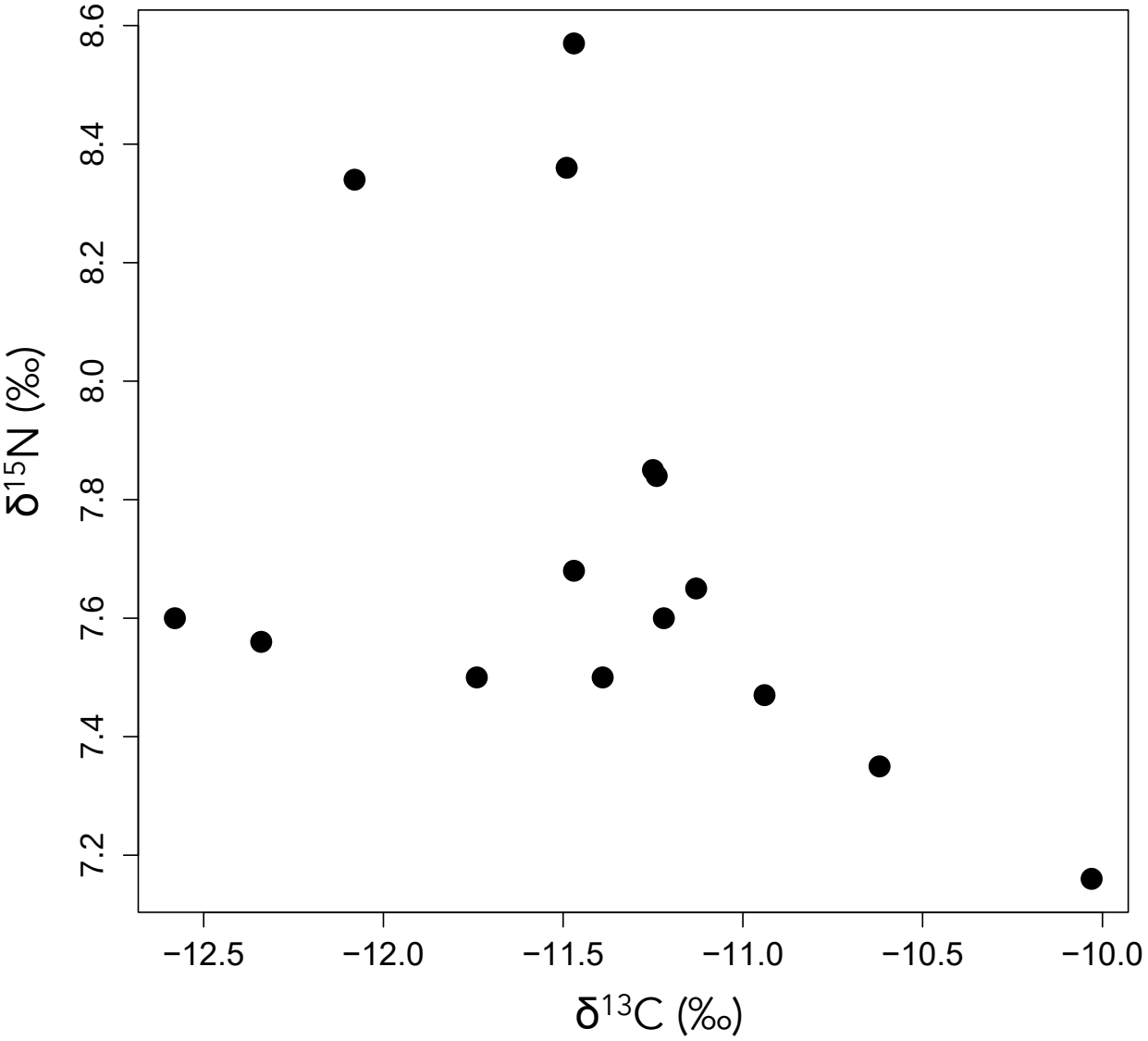


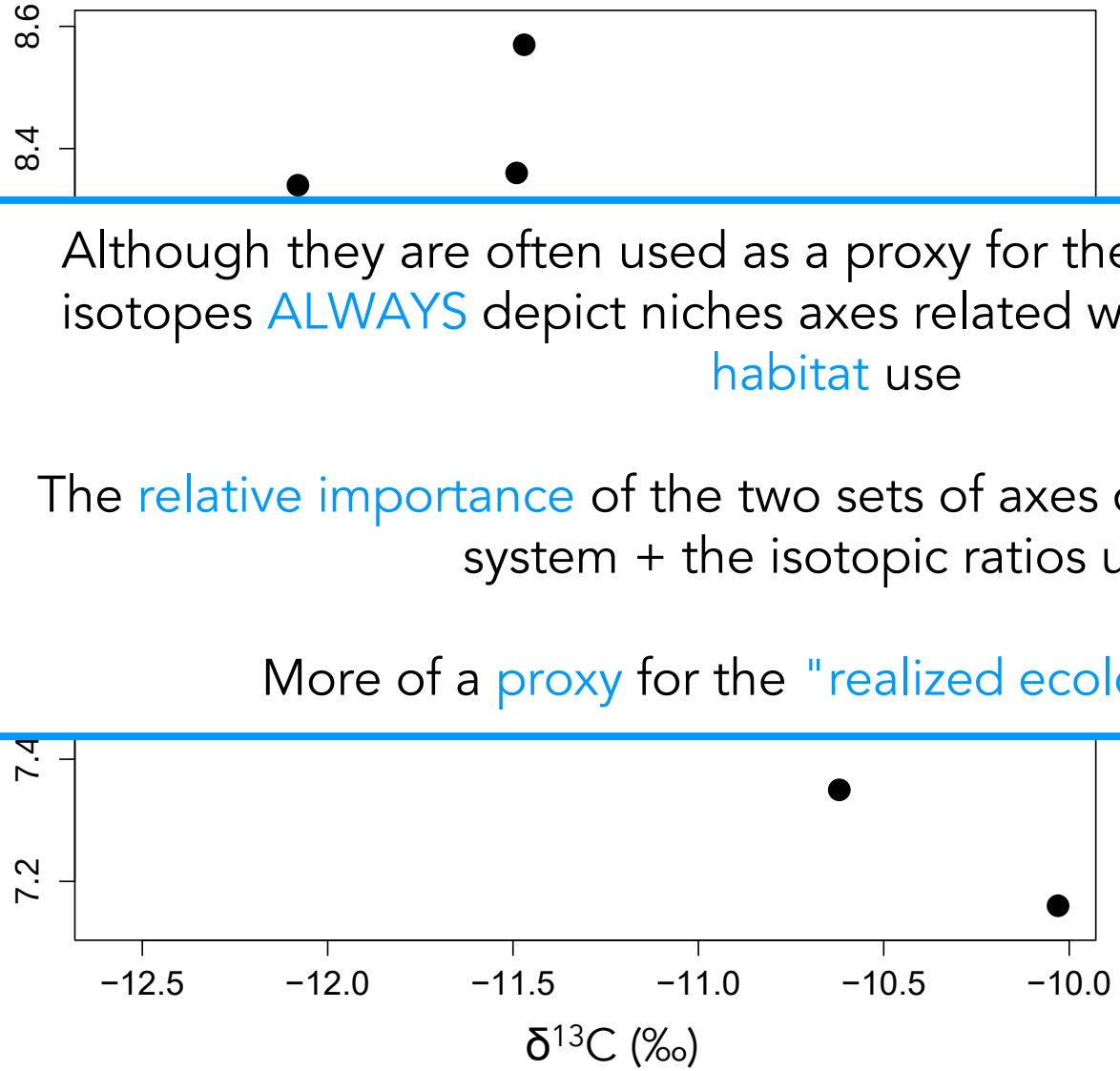
Position of consumers in the isospace is driven by

1) Differences in consumed resources (different preys can have different isotopic compositions)

2) Differences in foraging habitat
(the same prey can have different isotopic compositions in different habitats)

Stable isotopes as niche proxies

Typical SI analysis output : points in "isospace"



Position of consumers in the isospace is driven by

habitats)

Although they are often used as a proxy for the trophic niche, stable isotopes ALWAYS depict niches axes related with both resource and habitat use

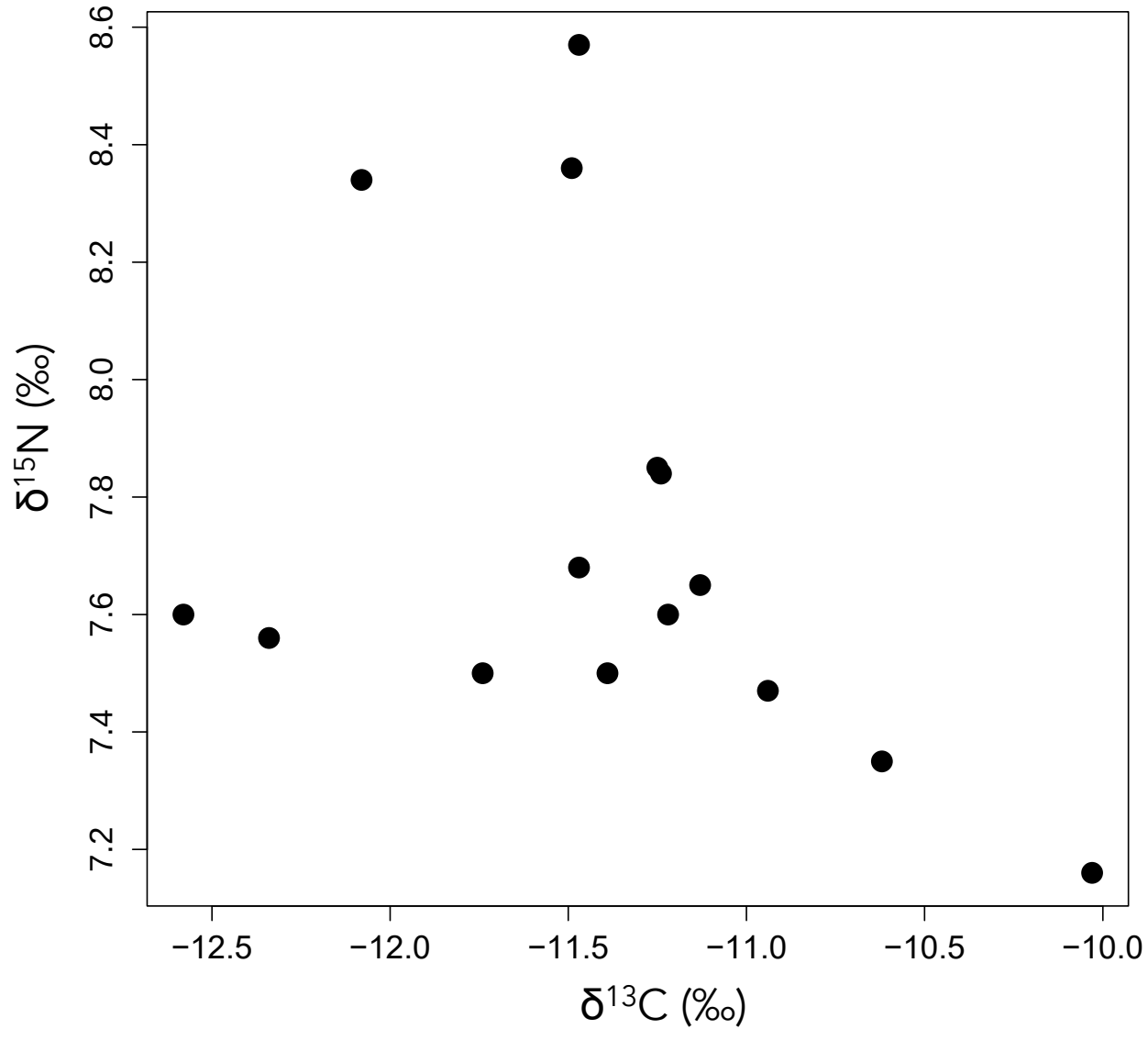
The relative importance of the two sets of axes depend on the studied system + the isotopic ratios used

More of a proxy for the "realized ecological niche"

CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?

Craig A. Layman,[1,5] D. Albrey Arrington,[2] Carmen G. Montaña,[3] and David M. Post[4]

Ecology, 88(1), 2007, pp. 42–48



Geometric approach
(Layman *et al.*, 07):

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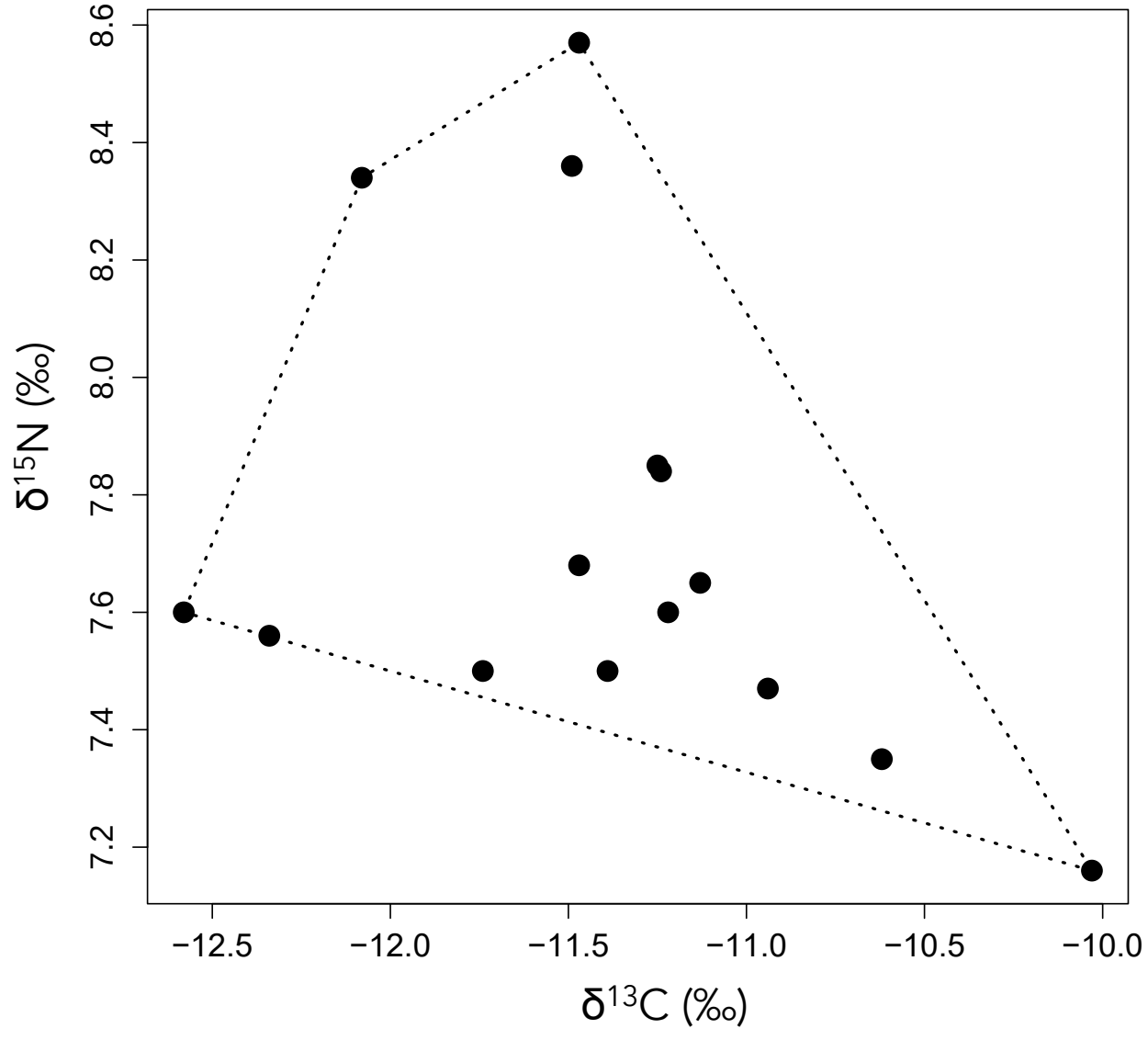


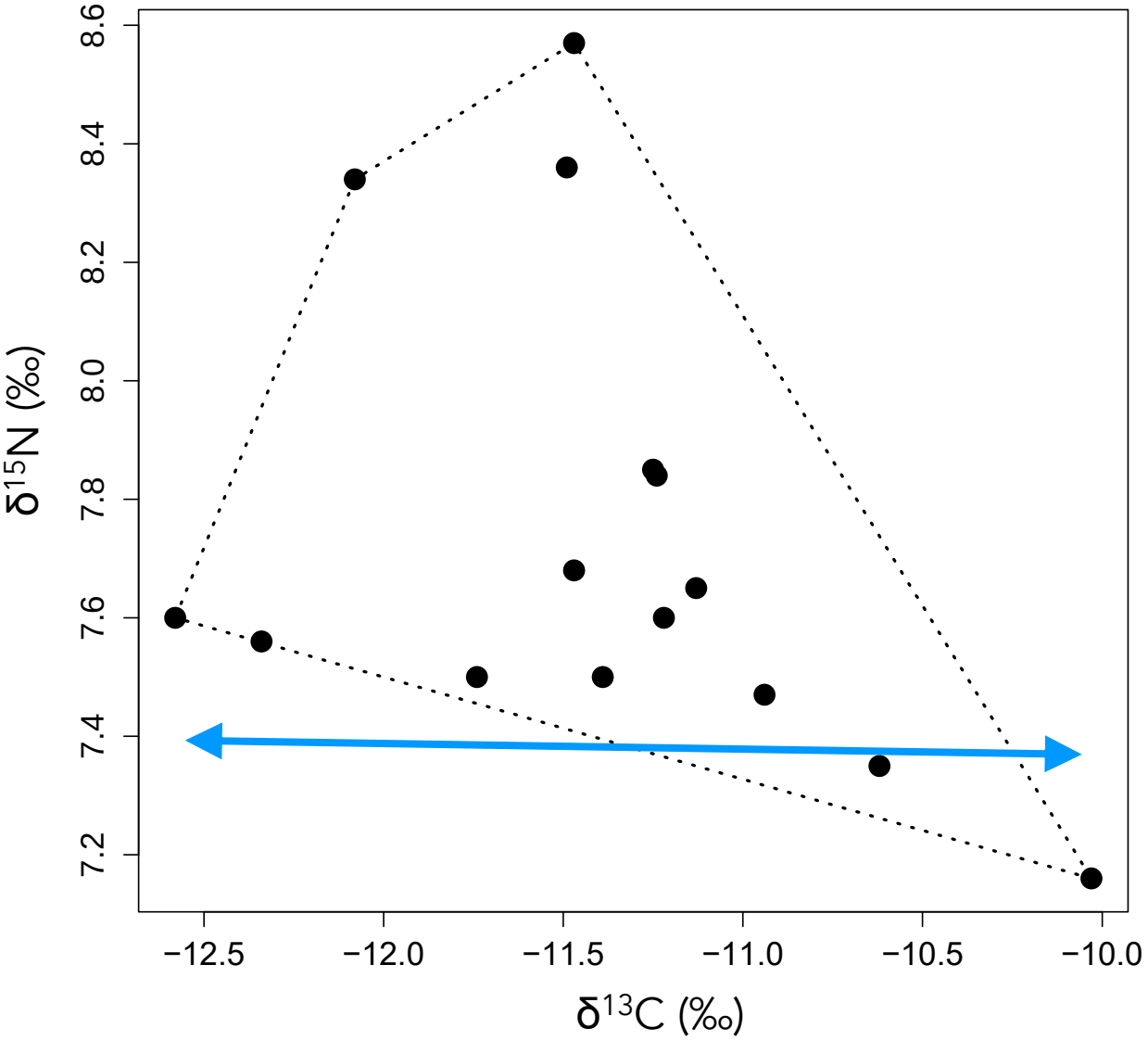
Geometric approach (Layman *et al.*, 07):

Fit a convex hull (*i.e.,* the smallest possible surface that encompasses all points) to the 2D data

This convex hull represents the isotopic niche of the group of consumers (proxy for their ecological niche)

Layman metrics

Set of descriptors based on convex hull



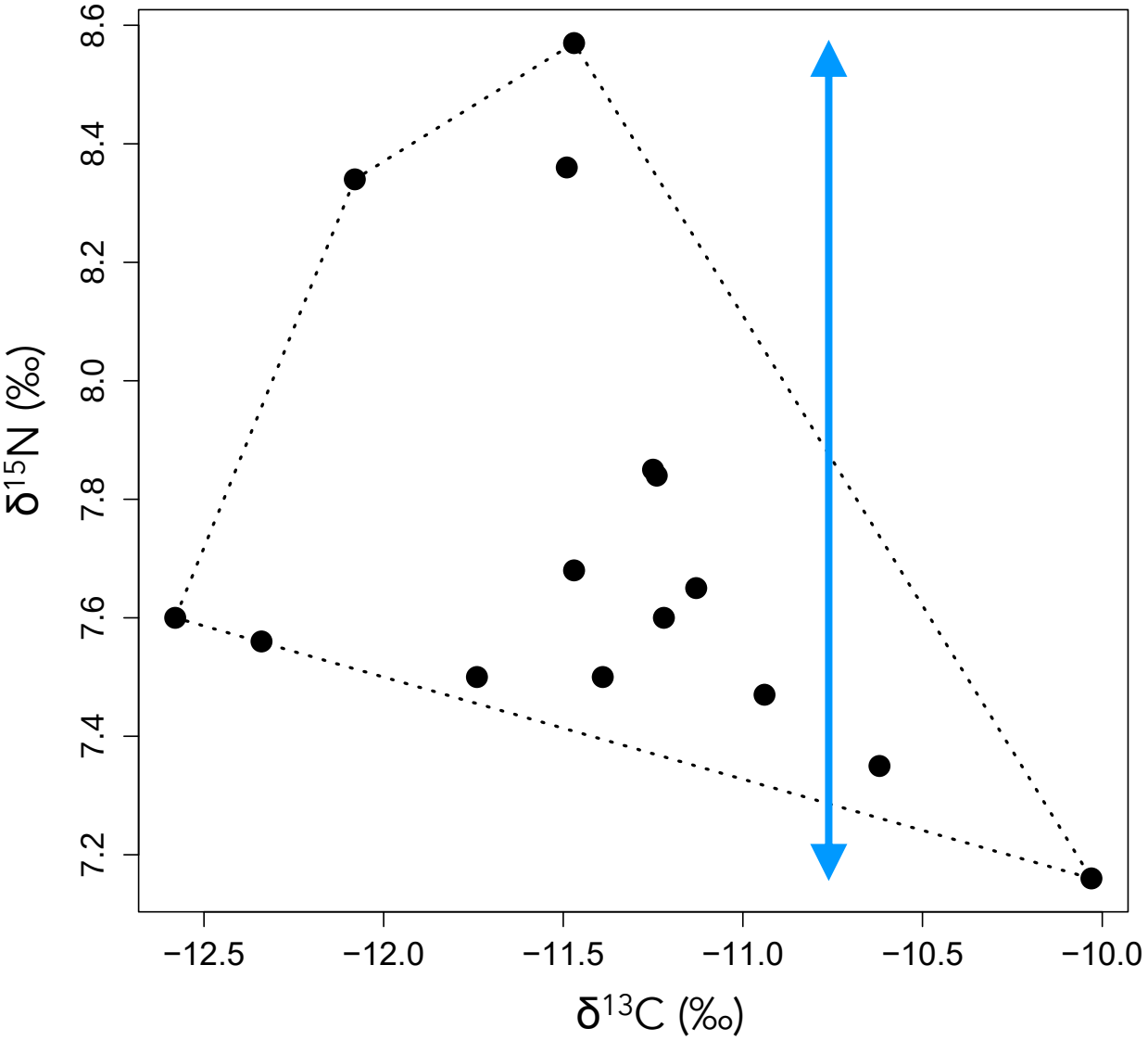
1) $\delta^{13}C$ range

Proxy of the diversity of resources supporting the consumers

Greater when more primary producers are important for the community

Layman metrics

Set of descriptors based on convex hull



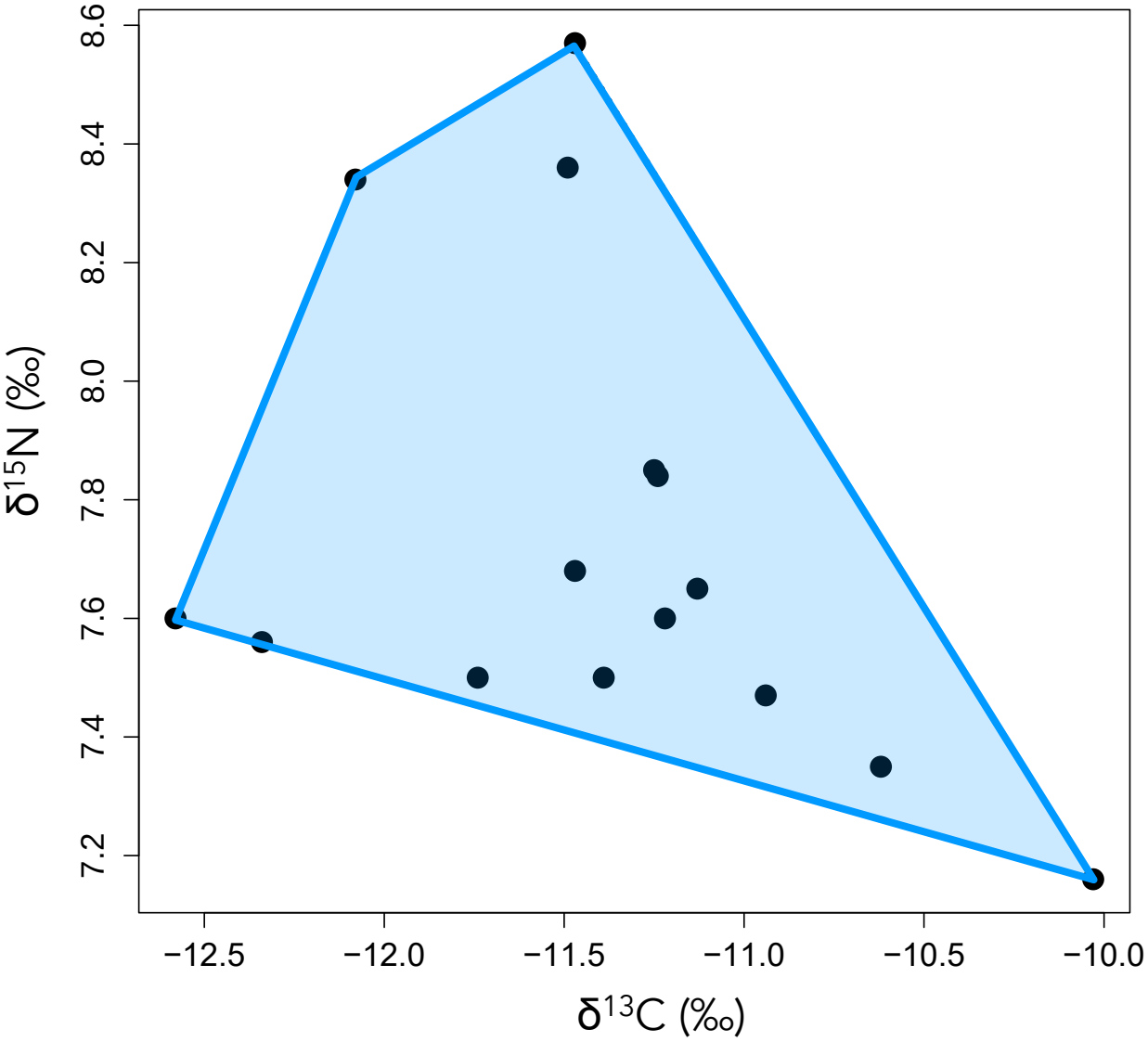
1) $\delta^{13}C$ range
2) $\delta^{15}N$ range

Proxy of the vertical trophic structure of the community

Greater when consumers belong to more "trophic levels"

Layman metrics

Set of descriptors based on convex hull

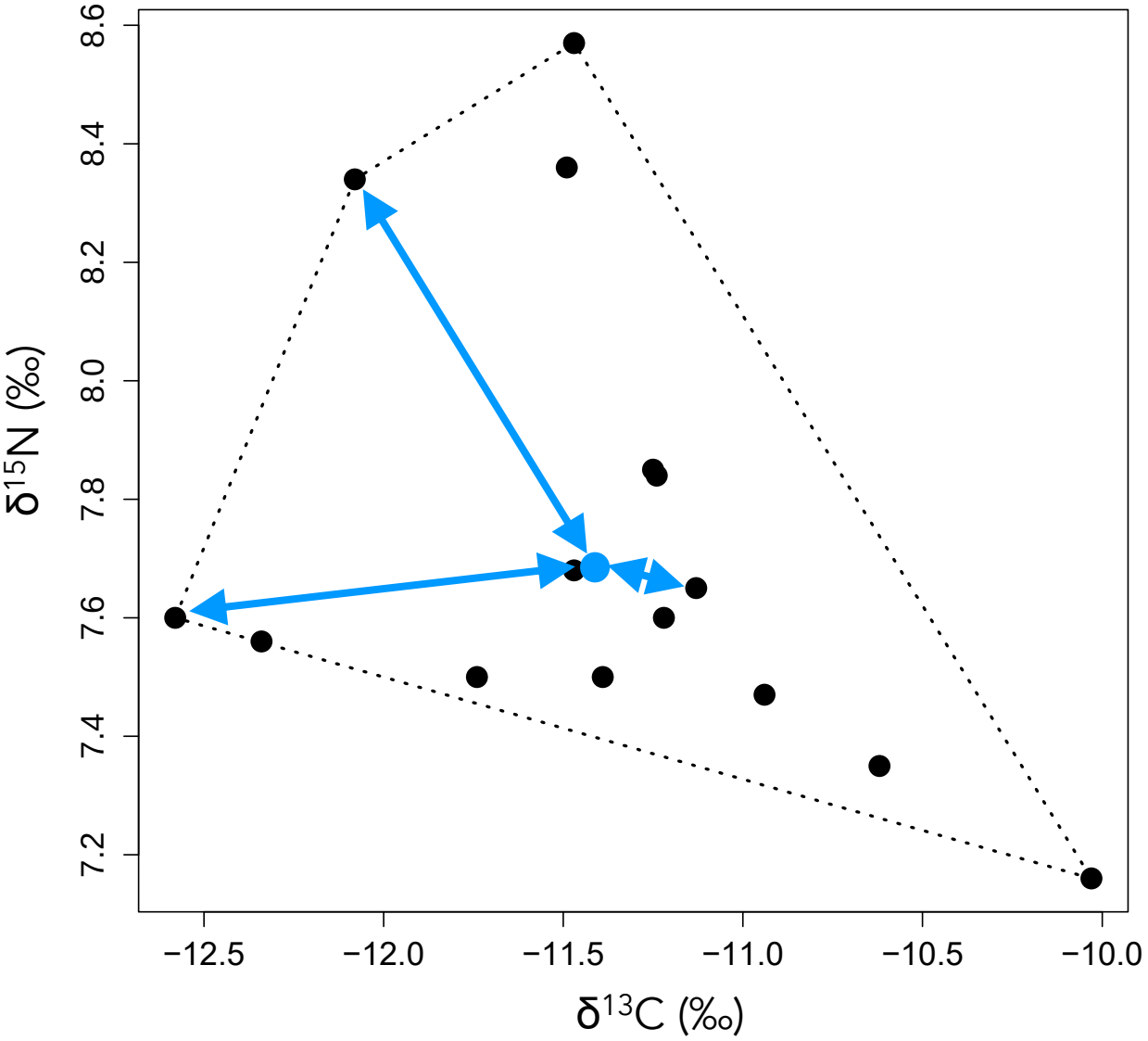


1) $\delta^{13}C$ range
2) $\delta^{15}N$ range
3) Total area of the convex hull

Proxy of the total diversity of resources used by the community

Layman metrics

Set of descriptors based on convex hull



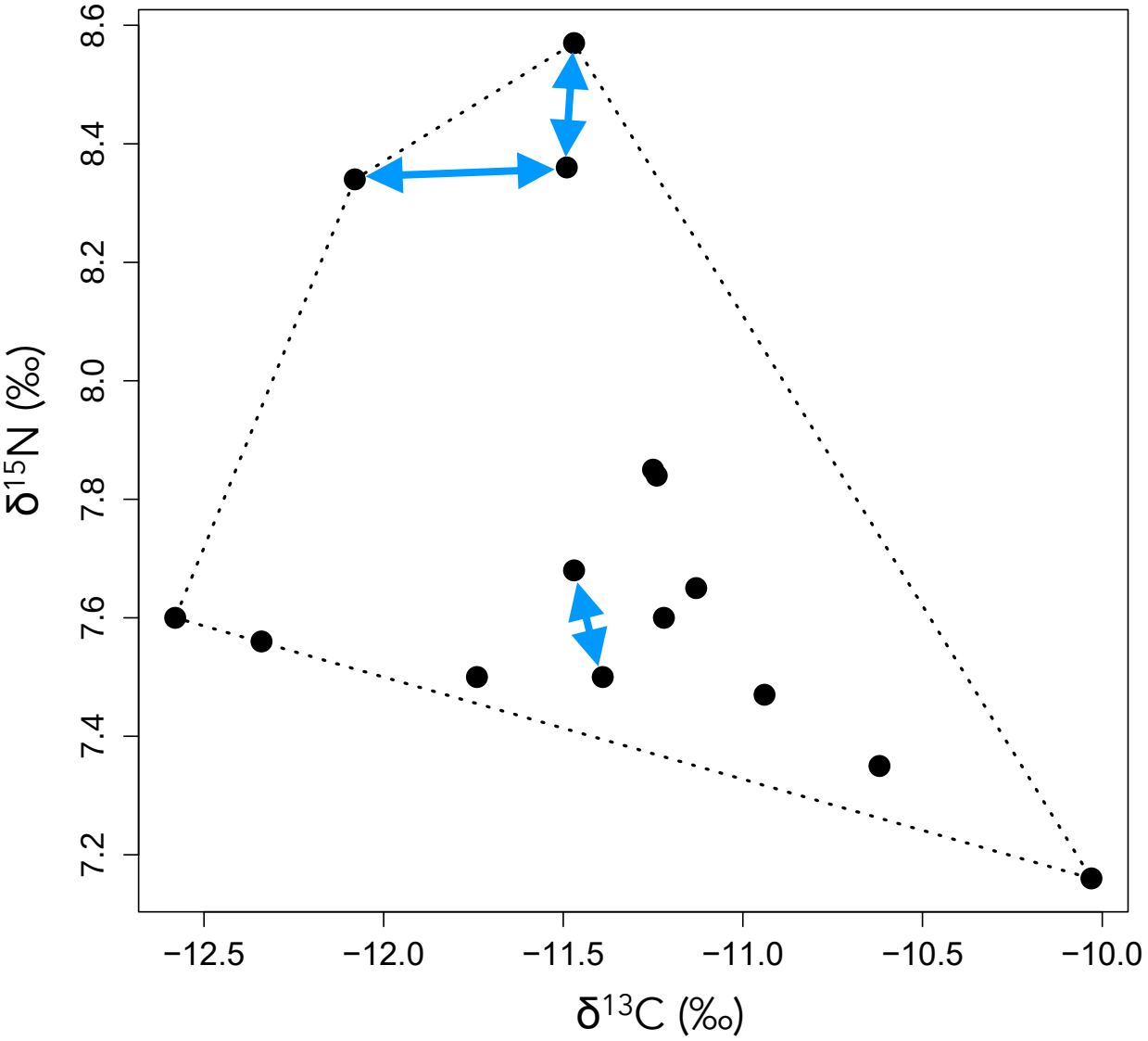
1) $\delta^{13}C$ range
2) $\delta^{15}N$ range
3) Total area of the convex hull
4) Mean distance to centroid

Averaged measure of ecological diversity among consumers

Greater when many consumers have "extreme" isotopic ratios, i.e. very specific ecological habits

Layman metrics

Set of descriptors based on convex hull



1) $\delta^{13}C$ range
2) $\delta^{15}N$ range
3) Total area of the convex hull
4) Mean distance to centroid
5) Mean nearest neighbor distance

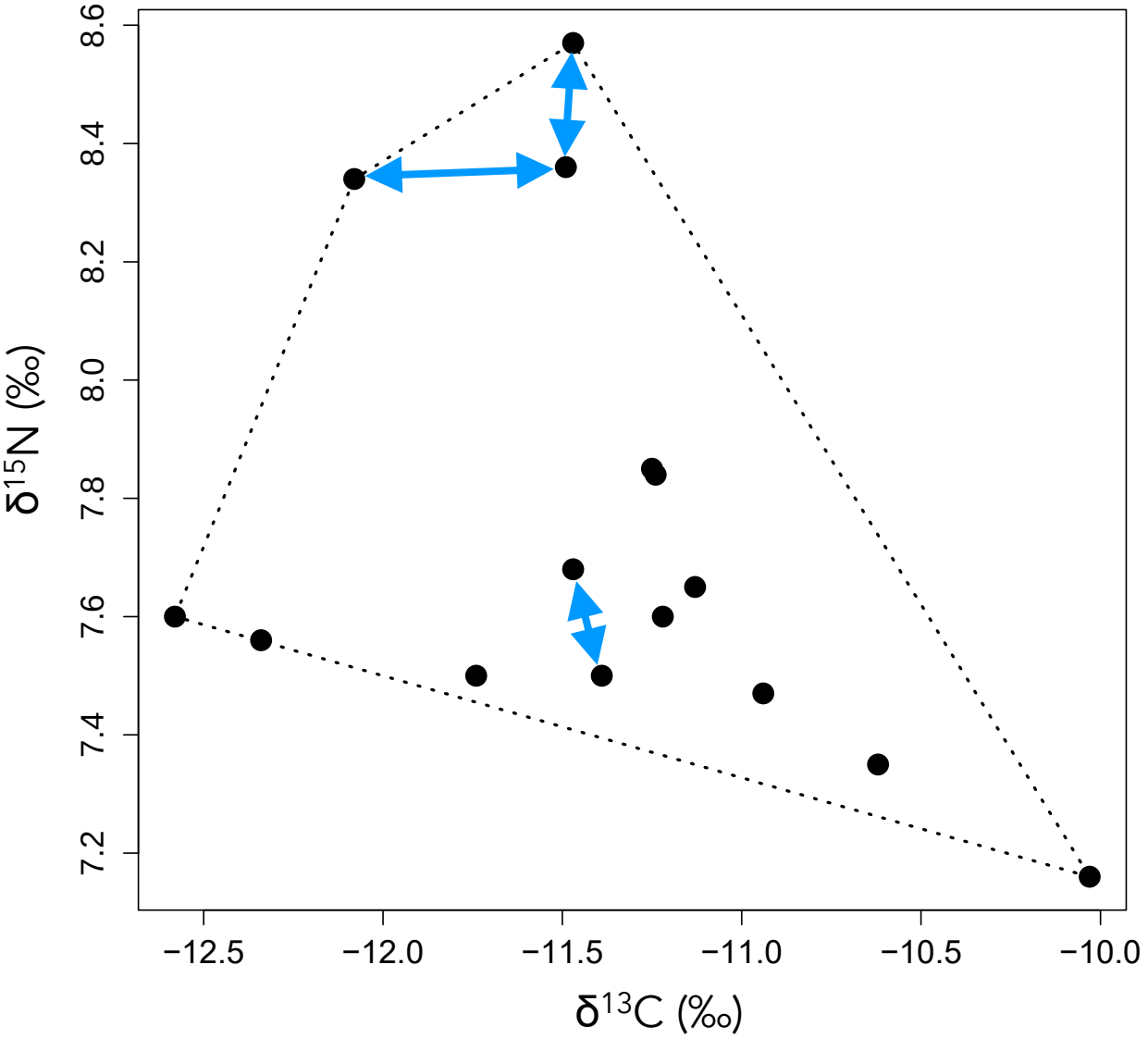
Overall density of point packing

High when consumers are more divergent in terms of ecological niche

Low when ecological habits of consumers are similar (ecological redundancy)

Layman metrics

Set of descriptors based on convex hull



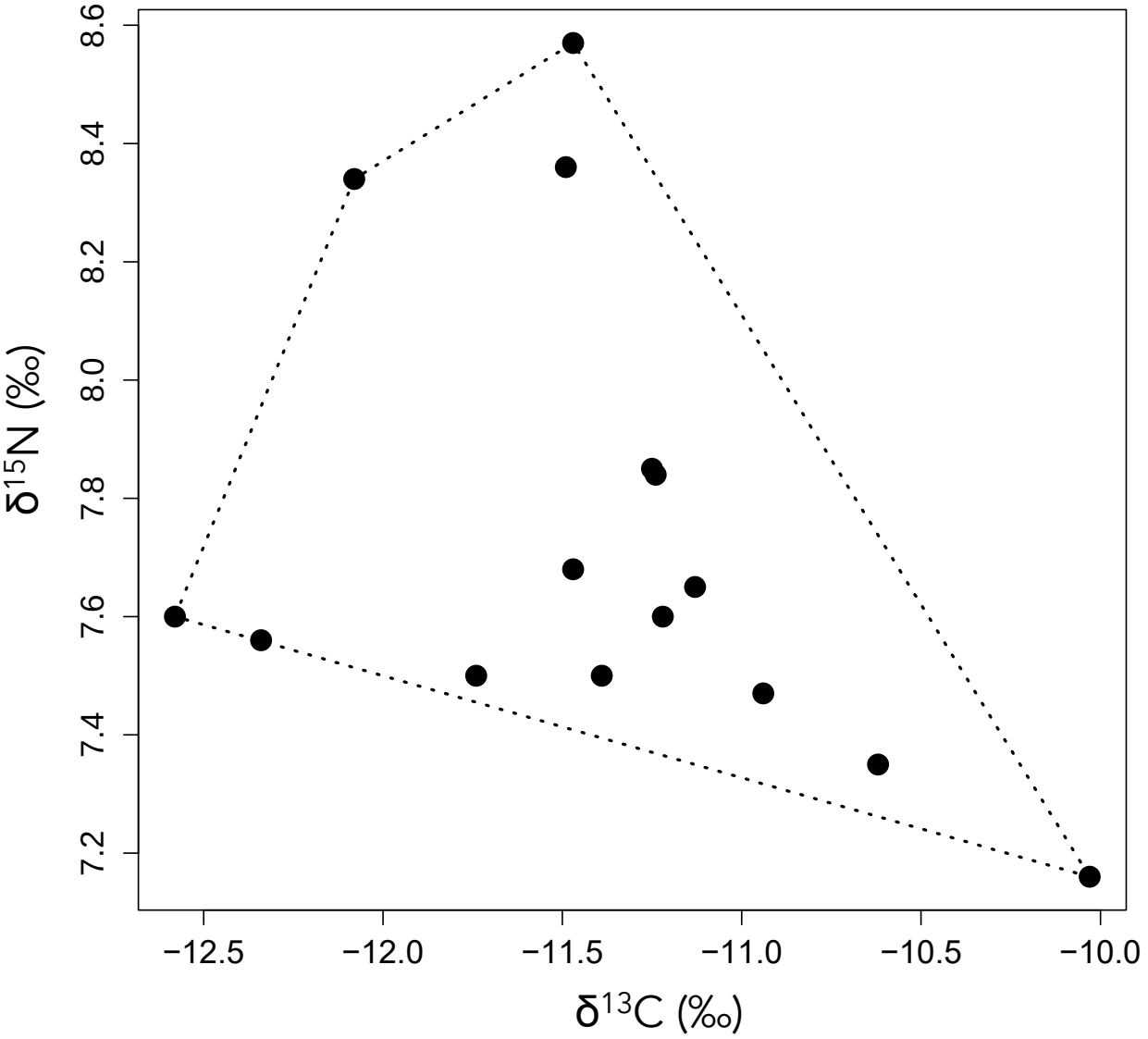
1) $\delta^{13}C$ range
2) $\delta^{15}N$ range
3) Total area of the convex hull
4) Mean distance to centroid
5) Mean nearest neighbor distance
6) Standard deviation of nearest neighbor distance

Measures how evenly ecological diversity is distributed among consumers

Low when space is evenly filled, high when "high density regions" are present

Layman metrics

Set of descriptors based on convex hull



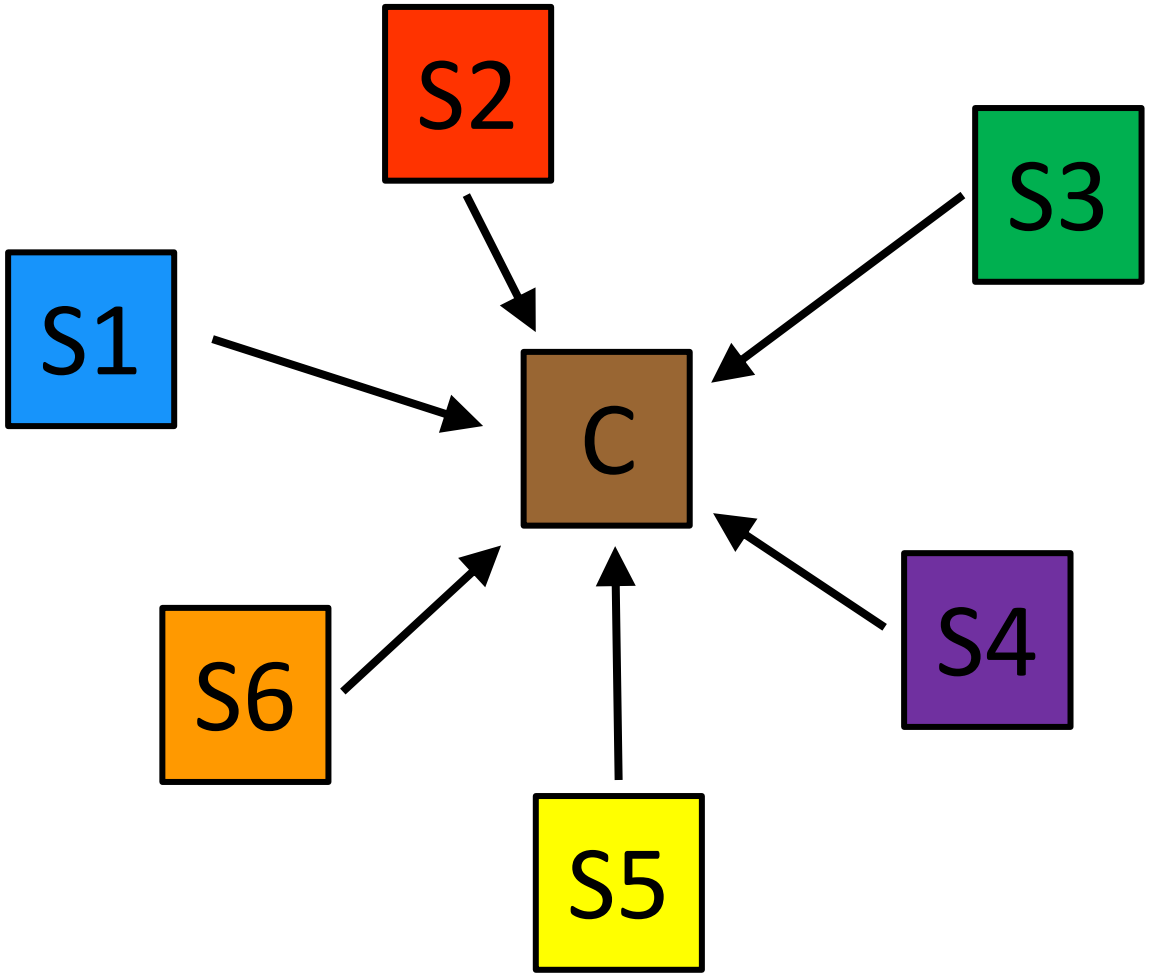
1) $\delta^{13}C$ range
2) $\delta^{15}N$ range
3) Total area of the convex hull
4) Mean distance to centroid
5) Mean nearest neighbor distance
6) Standard deviation of nearest neighbor distance

Comprehensive set of complementary (and partly redundant) tools that provide global information about the ecological niche

Designed for study of whole communities, but can also be used for populations

Geometric approach: limitations

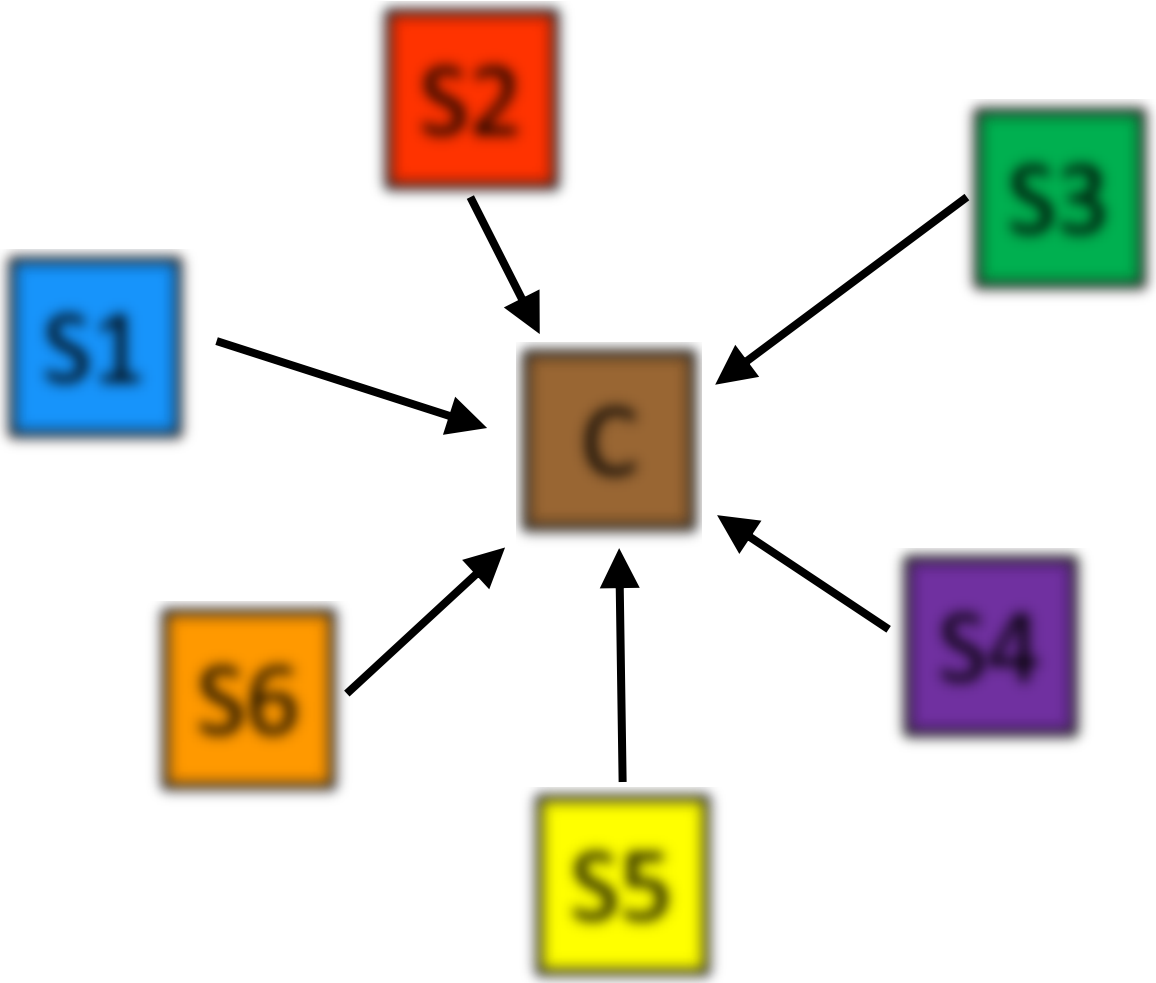
Isotopic compositions of consumers and food items are uncertain



Geometric approach: limitations

Isotopic compositions of consumers and food items are uncertain

2 main sources of uncertainty: natural variability (holds ecological info - we want to keep it!) and analytical error (we aim to minimise it, but we have to deal with it anyway)



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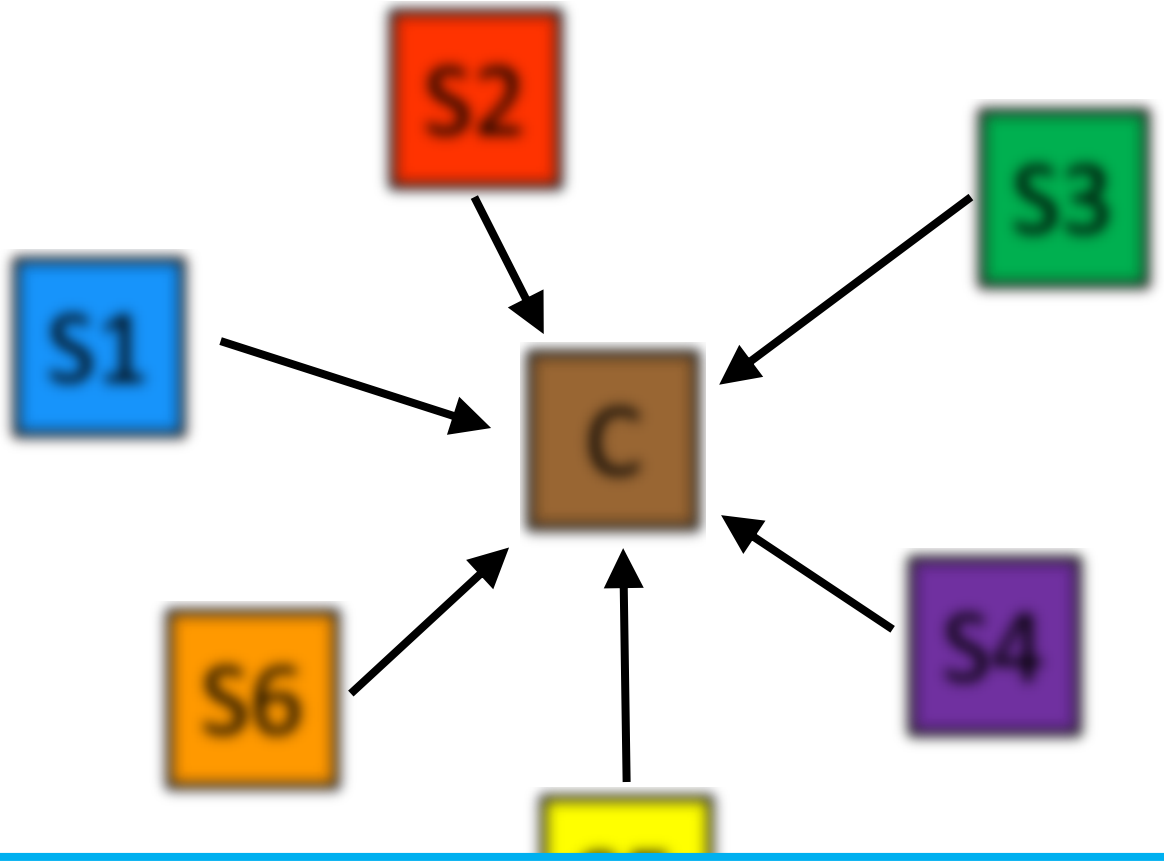

To build more realistic niche models, we need to take uncertainty into account!

Bayesian isotopic niches

Instead of calculating niche metrics using geometry: estimation using Bayesian inference

More robust + takes uncertainty into account

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011

doi: 10.1111/j.1365-2656.2011.01806.x

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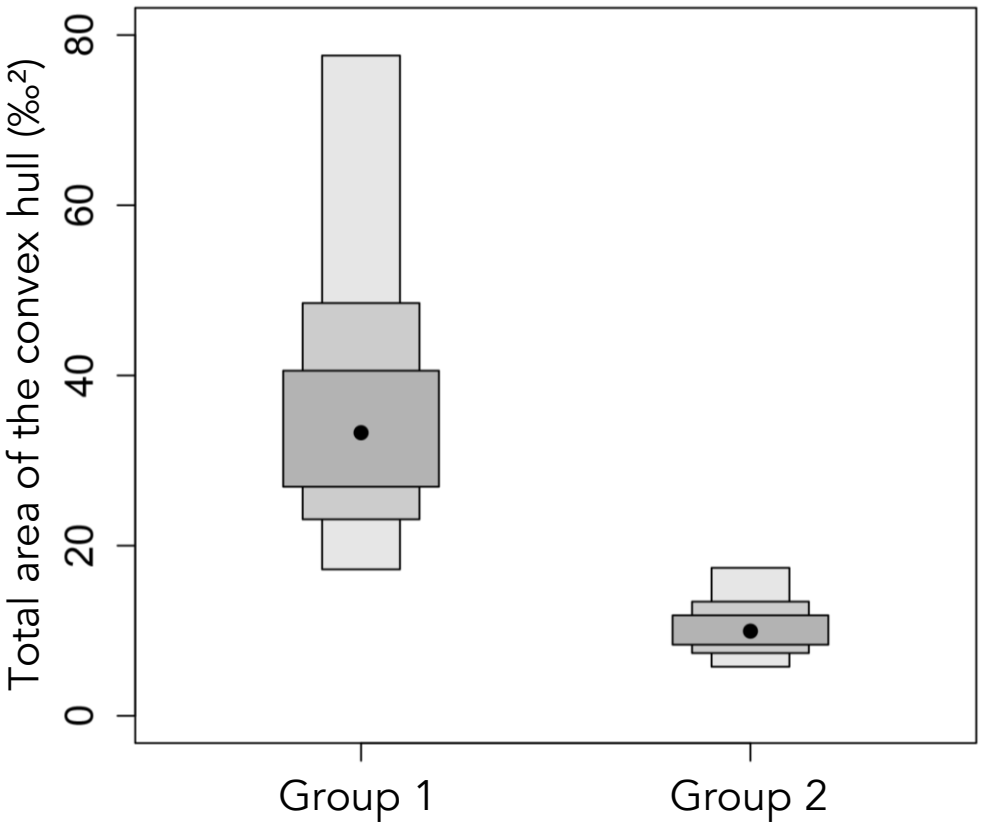

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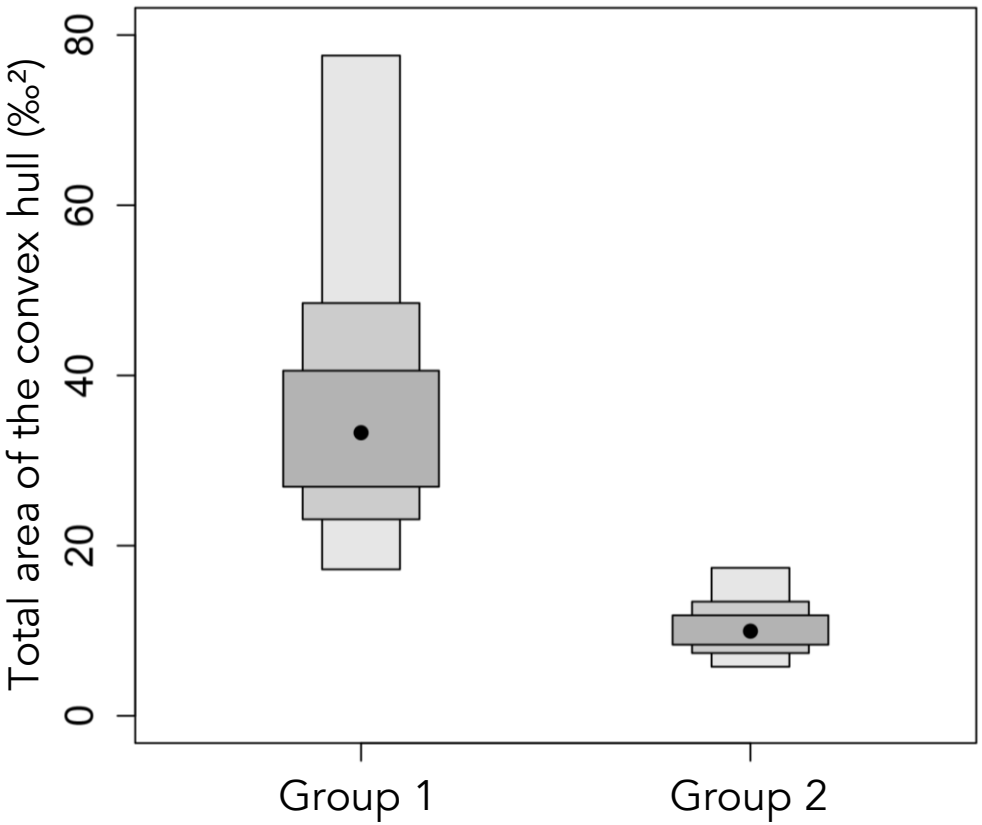

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Statistical comparisons of metrics across groups

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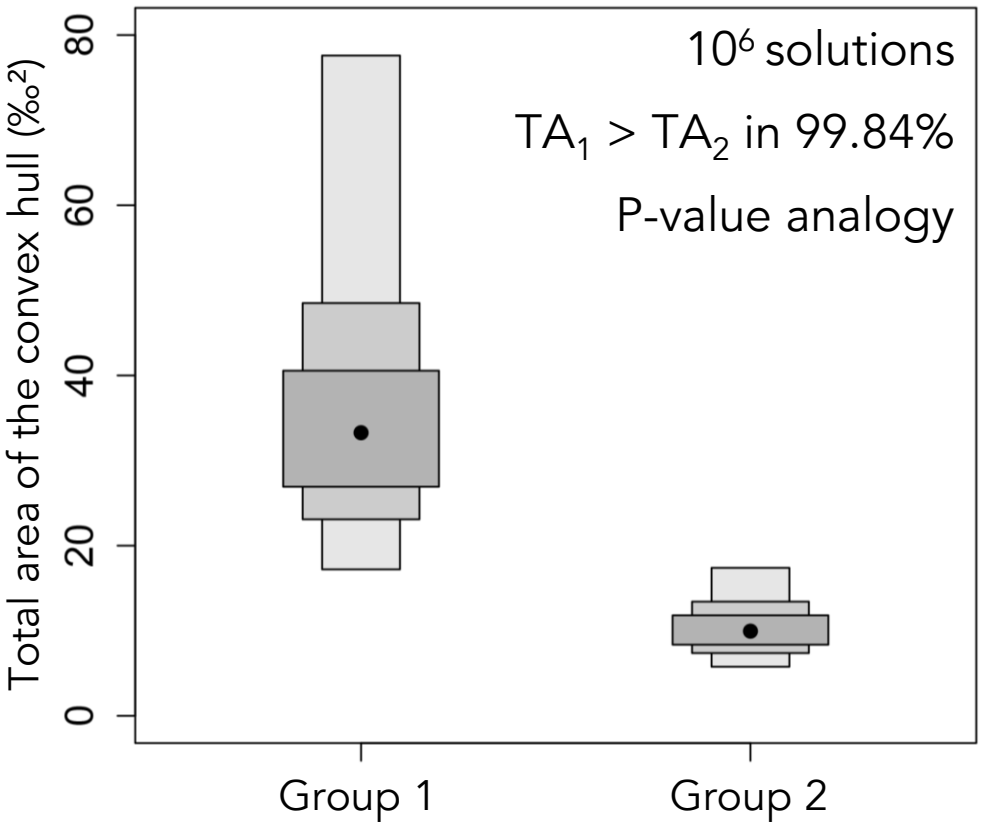

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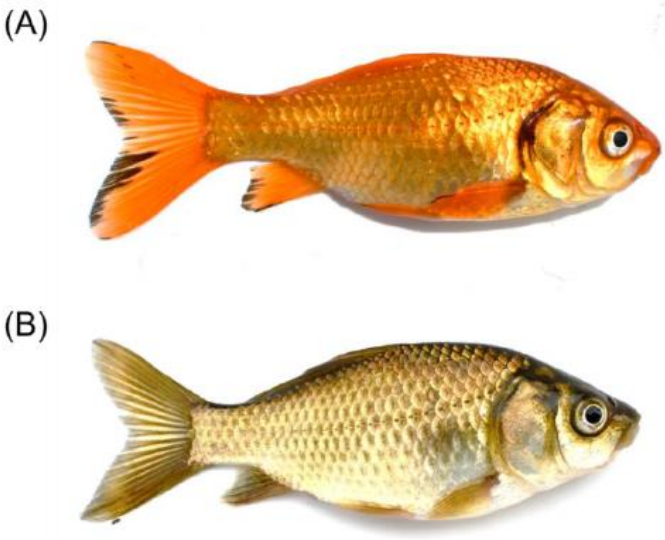
Layman metrics: an example

Benjamin LEJEUNE
PhD at ULiège
Now postdoc at the National Museum
for Natural History, Paris

Layman metrics: an example

▲ *Lissotriton helveticus* (female / male)

Carassius auratus (ornamental / wild morphotypes) ▼



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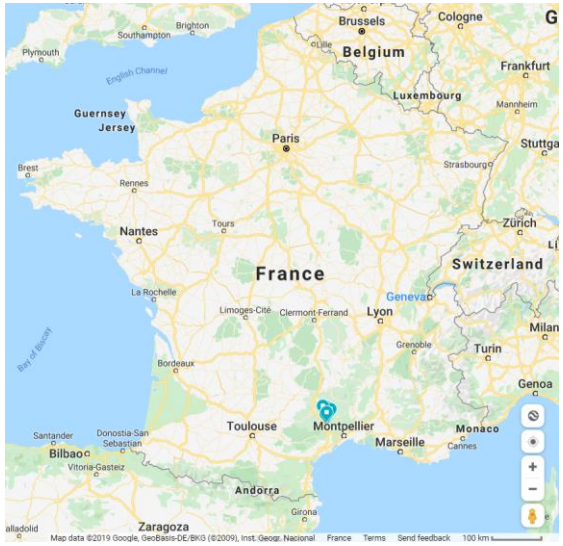
Ponds of the Larzac Plateau: traditionally dominated by palmate newts, but increasing presence of goldfish (invasive species)



Lejeune 2019 – http://hdl.handle.net/2268/234127
Lejeune *et al.*, In Prep.

Layman metrics: an example

Human-mediated goldfish introduction cause newt exclusion

Mechanism not well understood… Behavioural interference? Predation on eggs/larvae? Competition for food? Ecosystem changes? (macrophyte depletion, phytoplankton blooms facilitation, turbidity increase)

How does goldfish introduction influence food web structure and ecological interactions?

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Lejeune *et al.*, In Prep.

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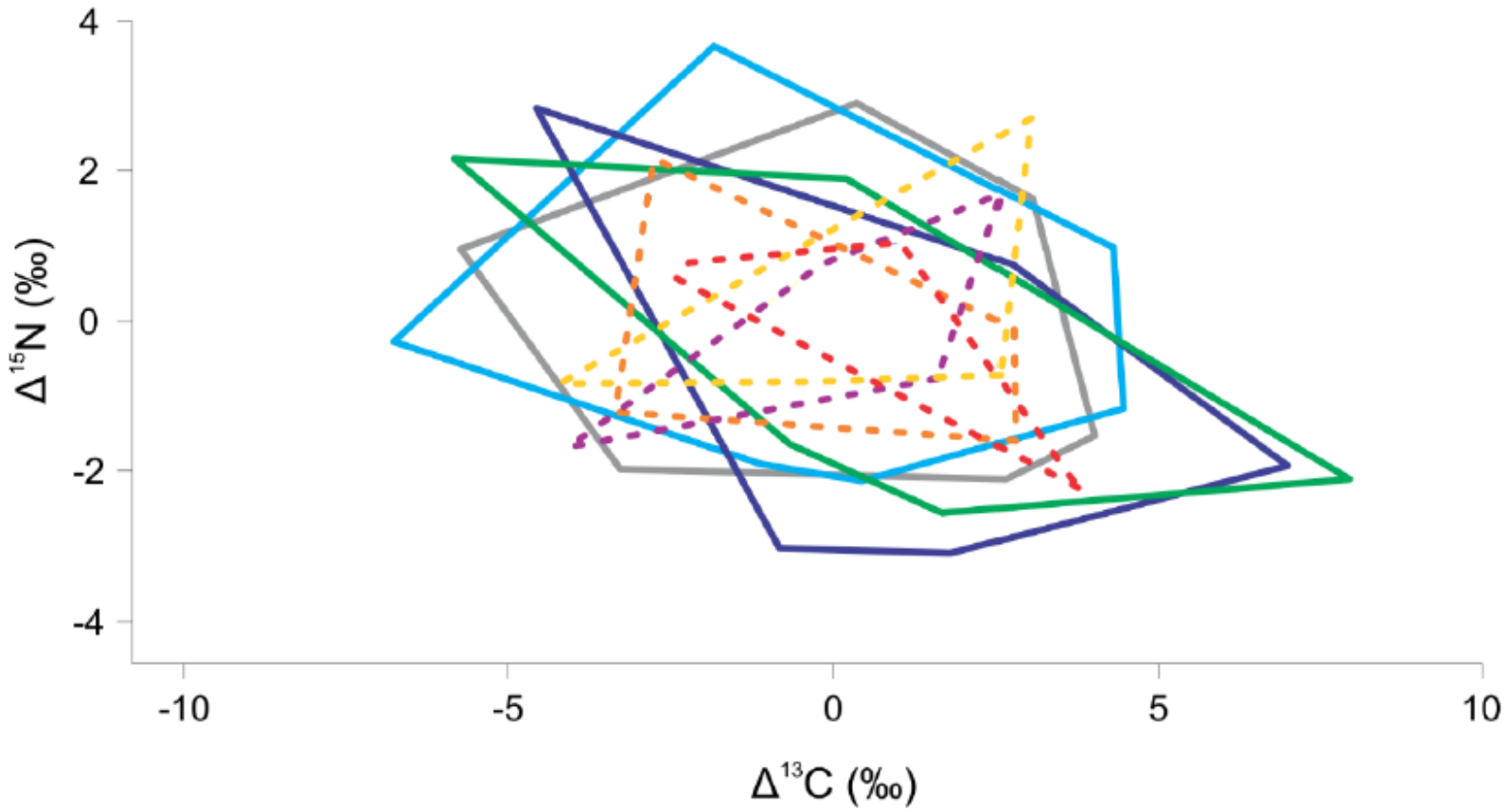

Standardised convex hulls associated with each pond's consumers (built using species means, not taking into account newts or goldfish).
Solid lines: newt-dominated ponds.
Dashed lines: goldfish-dominated ponds

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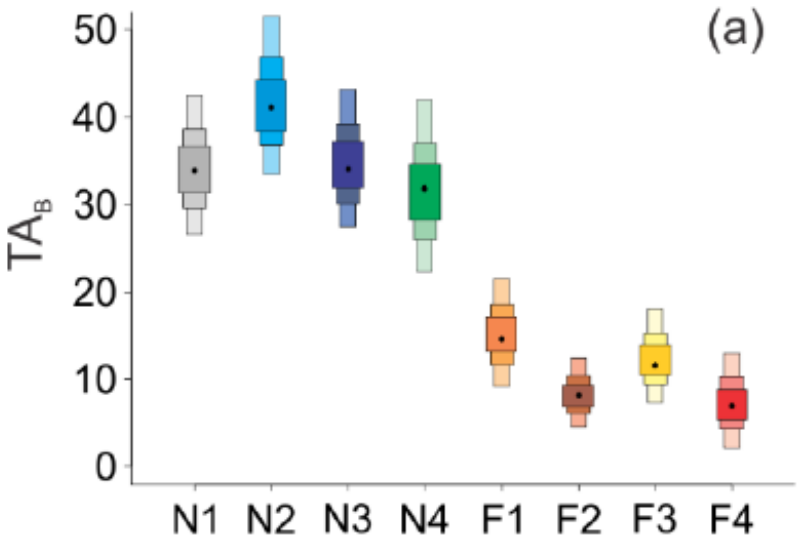
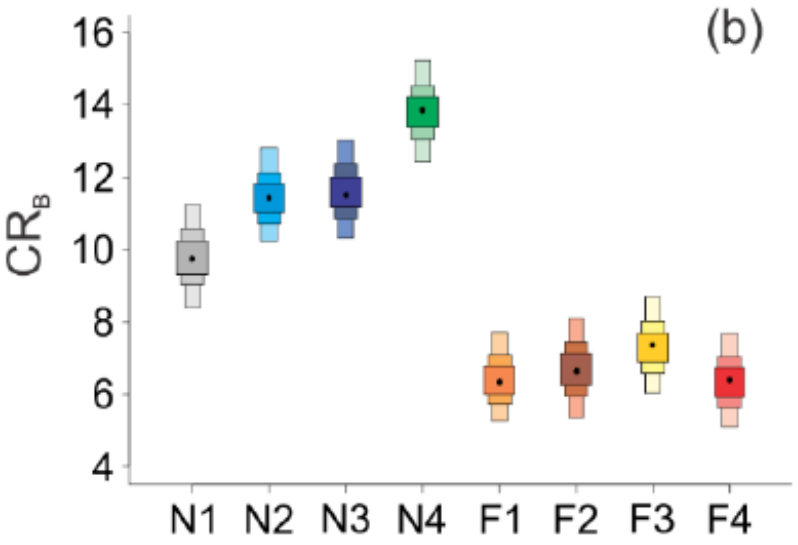


Lower total area of the convex hull in invaded ponds: lower overall diversity in resources used by the community

Lejeune 2019 – http://hdl.handle.net/2268/234127, Lejeune *et al.*, In Prep.

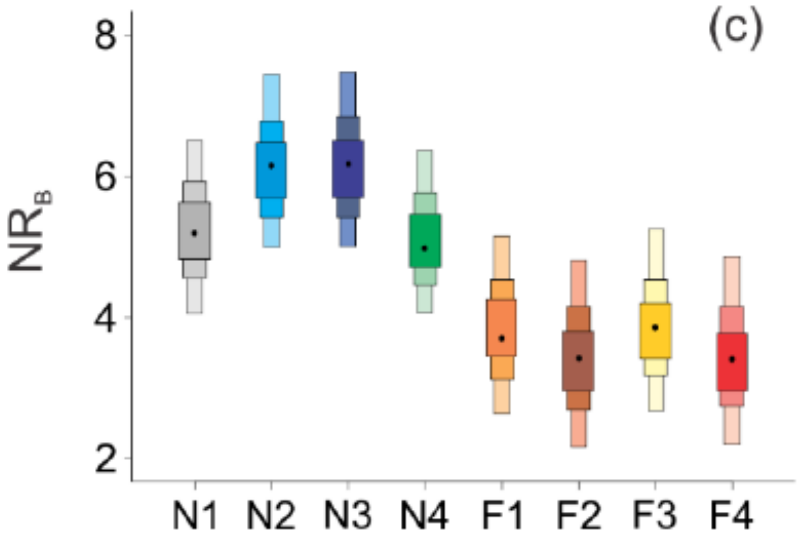
Layman metrics: an example



Lower $\delta^{13}C$ range in invaded ponds: consumers depend on less basal resources (primary producers, organic matter pools) and/or exploit less feeding habitats

Lejeune 2019 – http://hdl.handle.net/2268/234127, Lejeune *et al.*, In Prep.

Layman metrics: an example



Lower $\delta^{15}N$ range in invaded ponds: consumers belong to less different trophic levels, food chain length is lower

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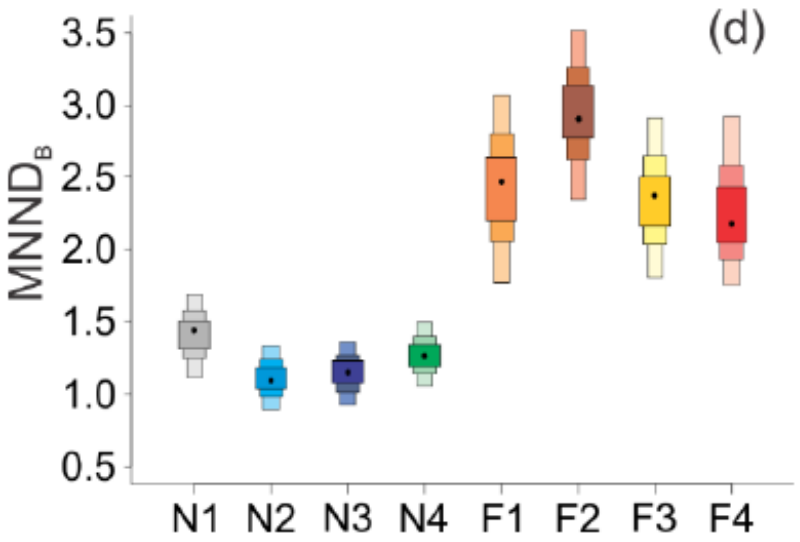

Higher mean distance to nearest neighbour in invaded ponds: consumers are more divergent in their ecological habits, lower trophic / ecological redundancy

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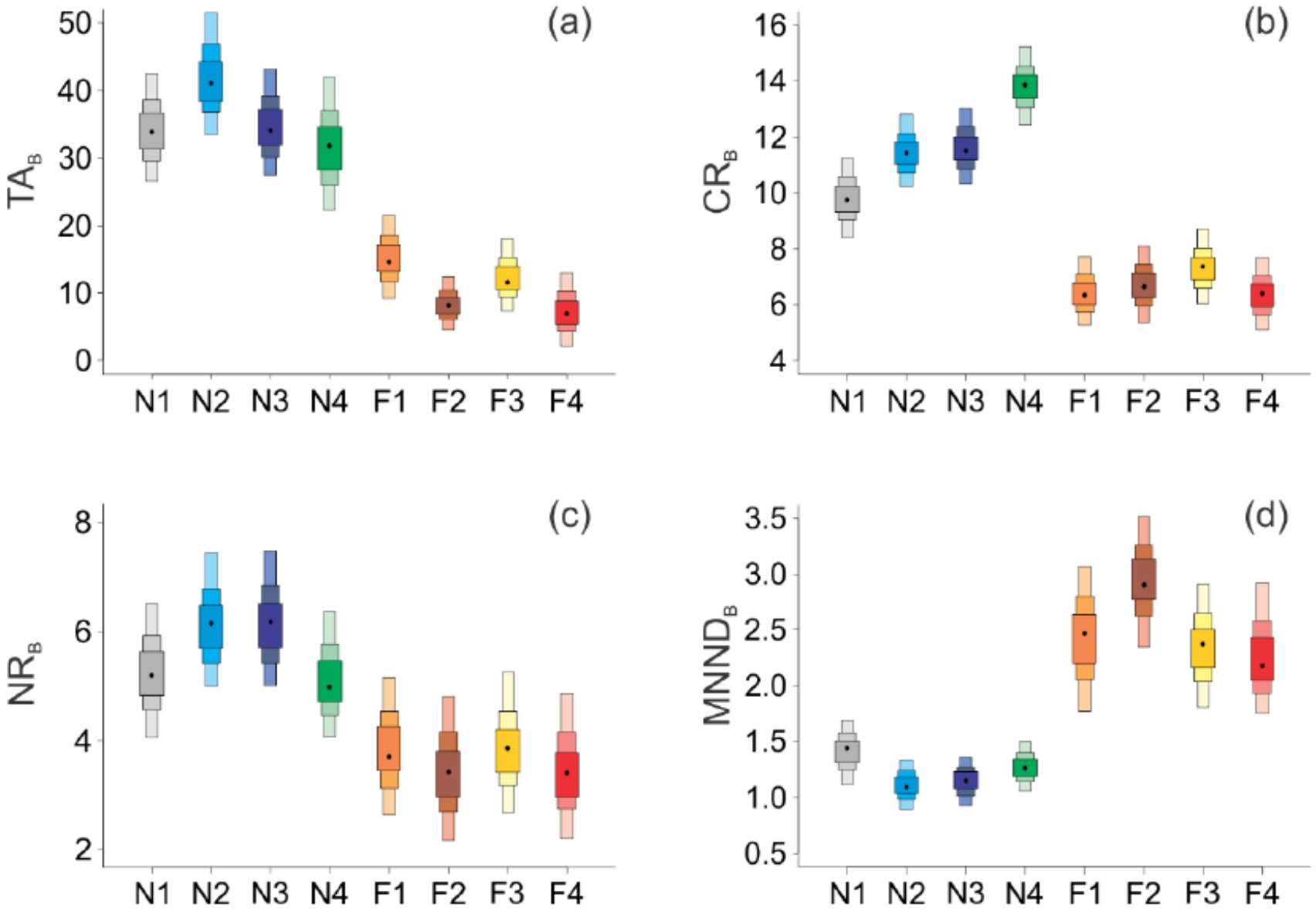

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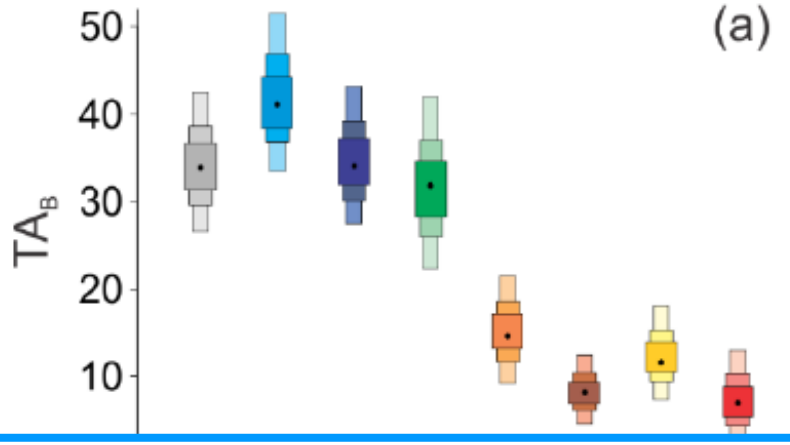
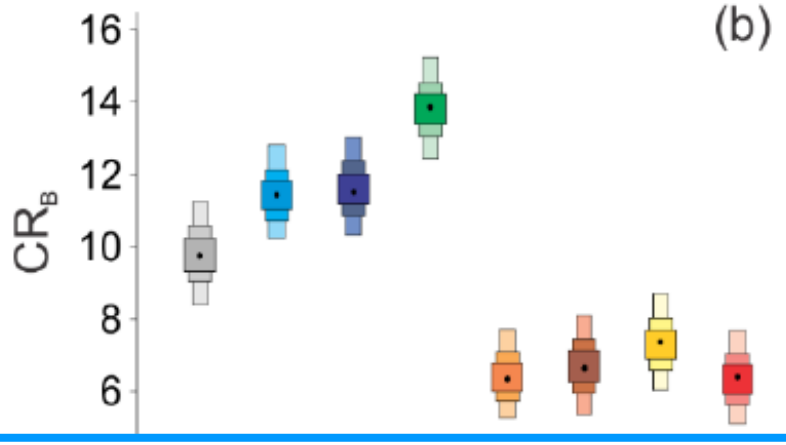
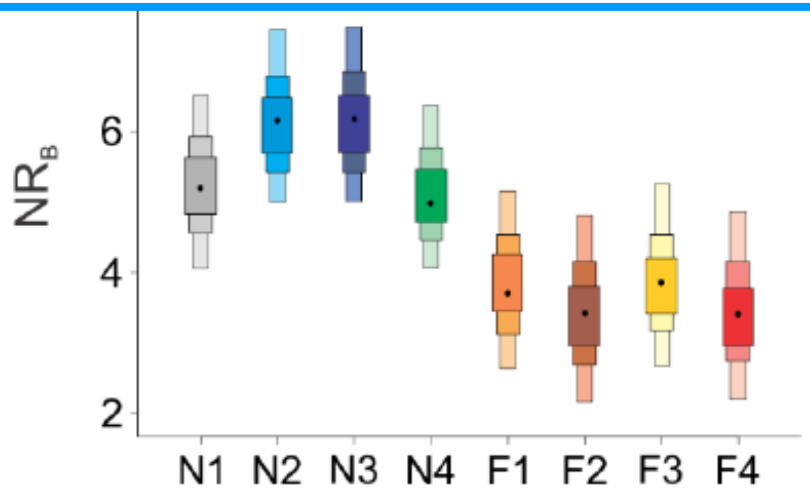
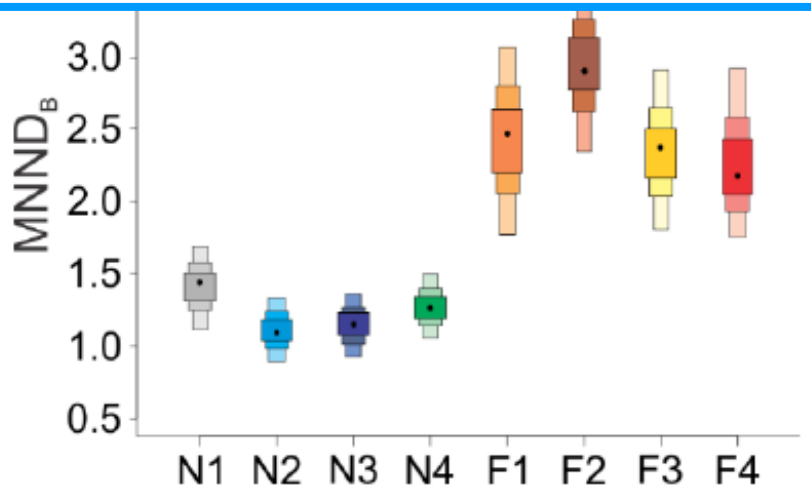




Goldfish introduction: shift from a diverse consumer community to a system dominated by detritivores and plankton feeders
Community niche contraction, "trophic downgrading"
Ultimately: perturbation of ecosystem functioning





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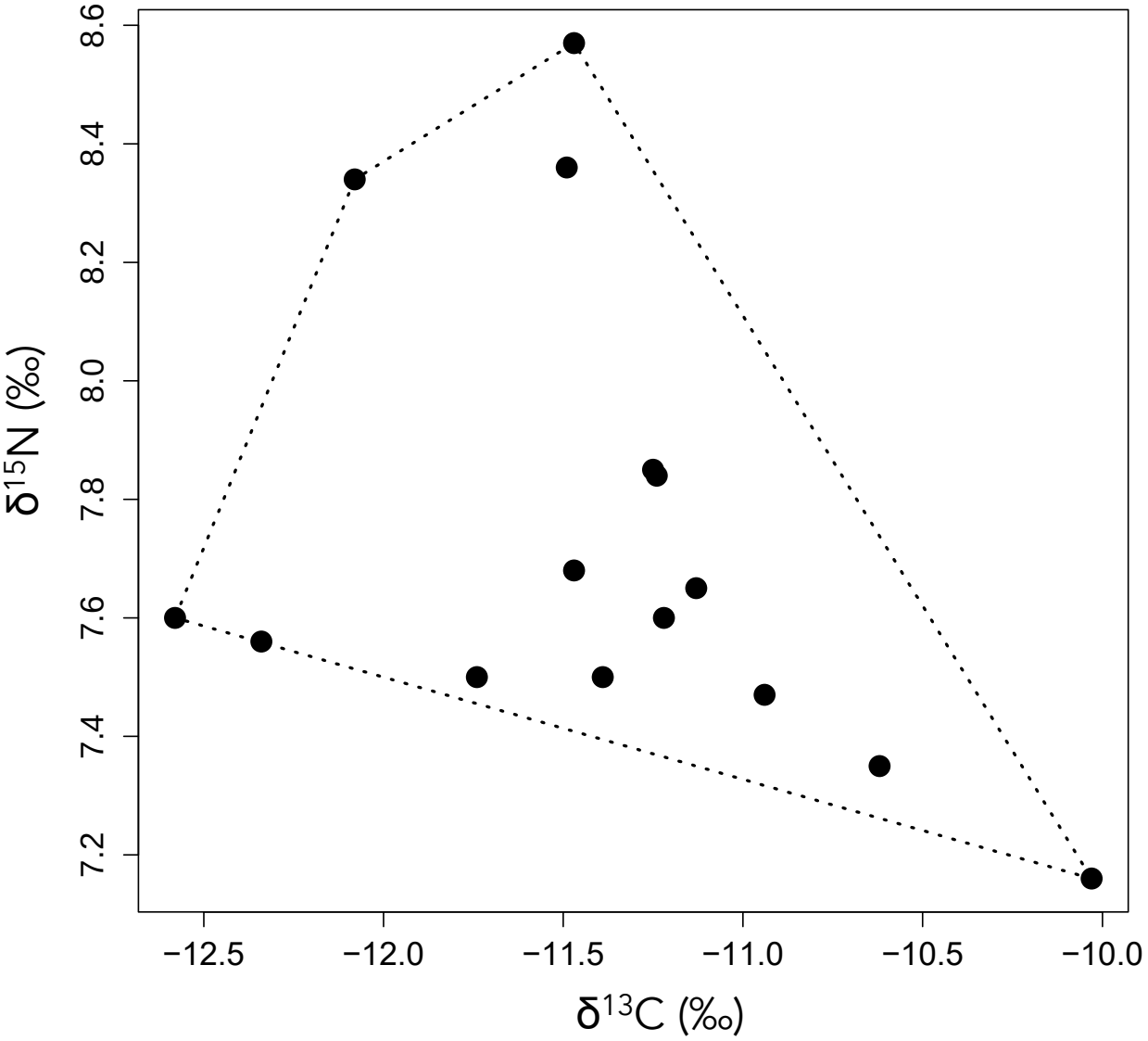
Stable isotopes as niche proxies

Some hull-based metrics are highly sensitive to small sample size and to the presence of extreme points

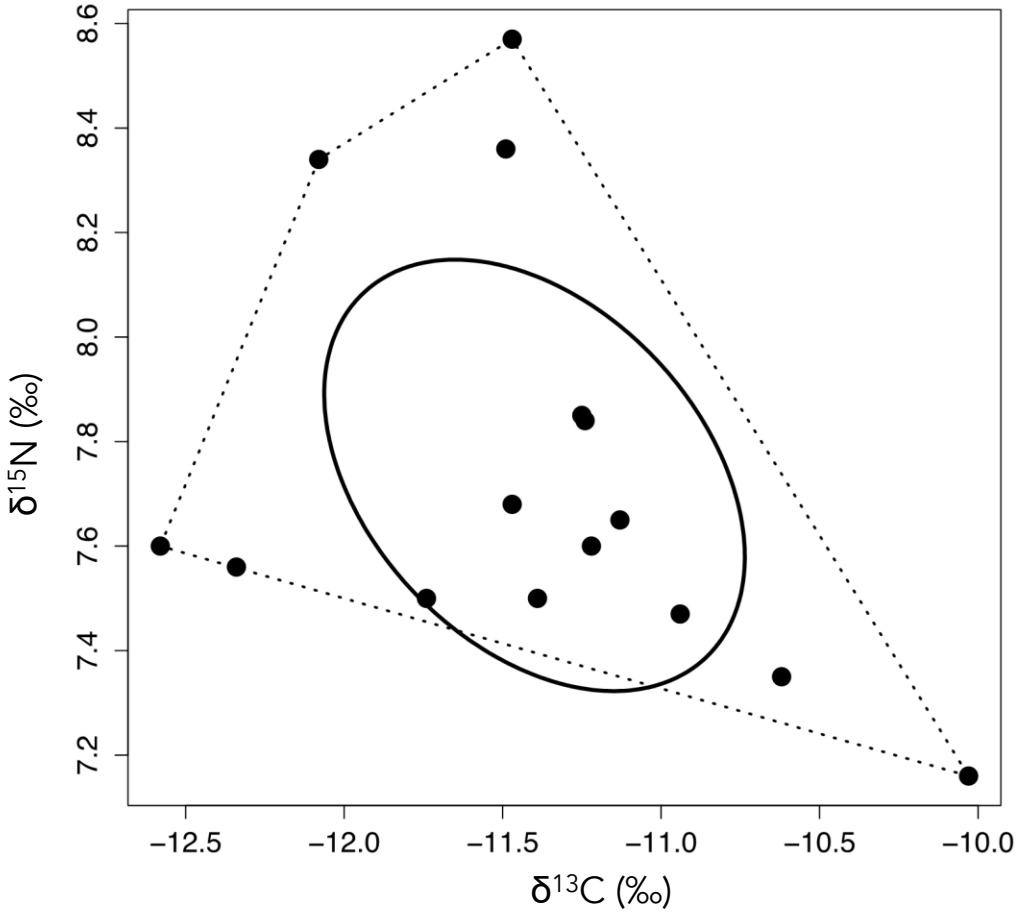


According to your research question, it can be a good or a bad thing…

Stable isotopes as niche proxies

Standard ellipse vs. convex hull (SD vs. full range)

Represents "core isotopic niche" of the group of consumers



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Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R

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Stable isotopes as niche proxies

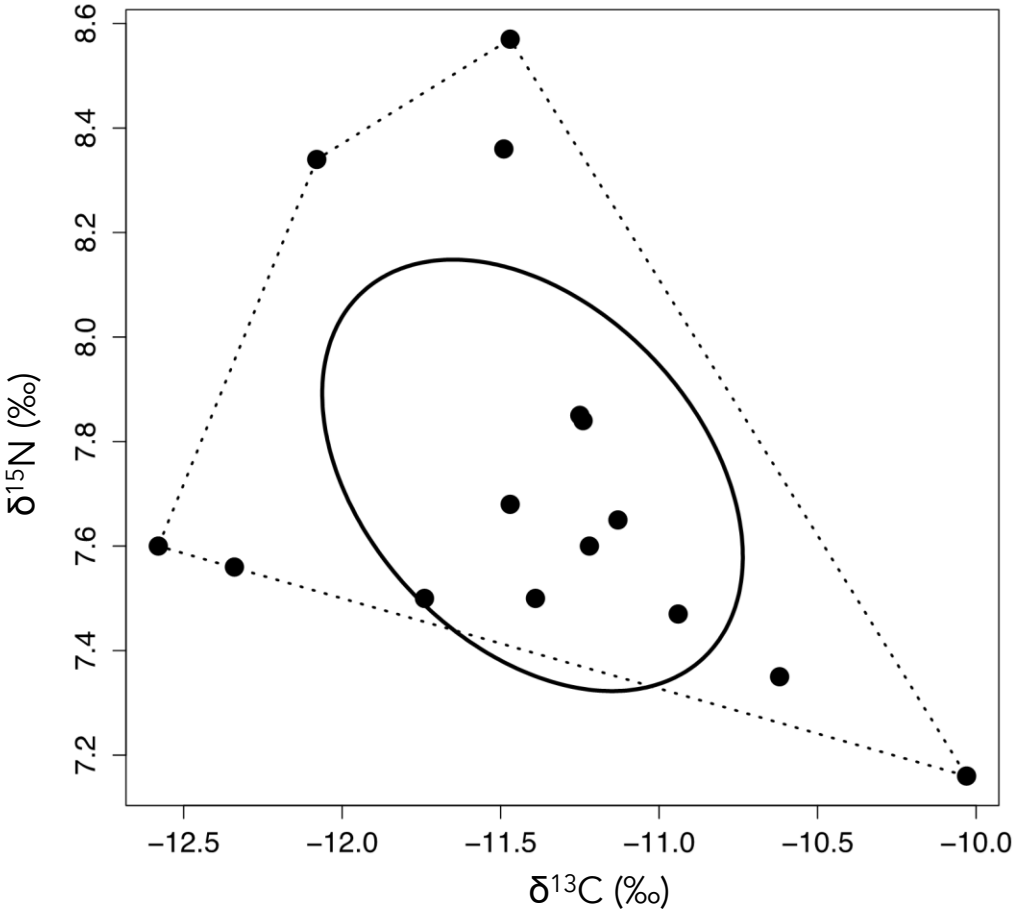
Standard ellipse vs. convex hull (SD vs. full range)

Represents "core isotopic niche" of the group of consumers

Main metric: standard ellipse area (SEA), proxy for the diversity of most commonly used ecological resources

More robust and less sensitive to extreme values and small sample size

Ellipses and hulls can be complementary



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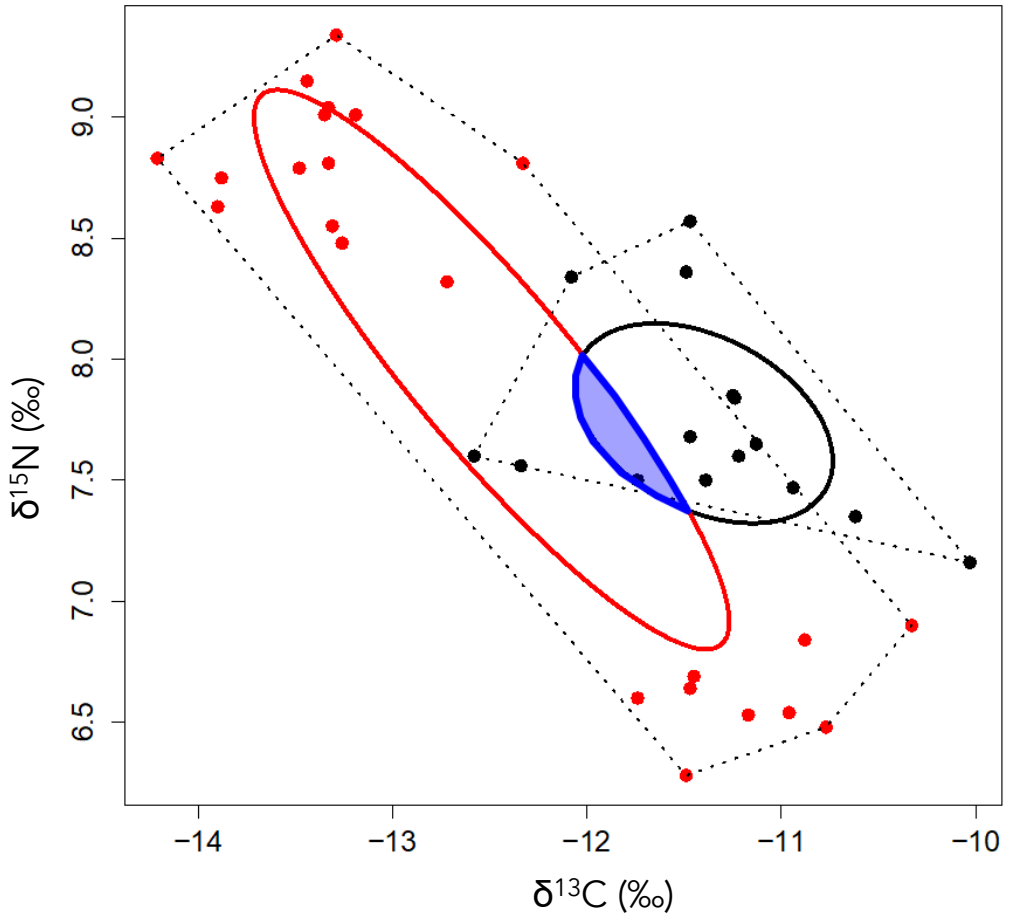
Quantification of isotopic niche overlap



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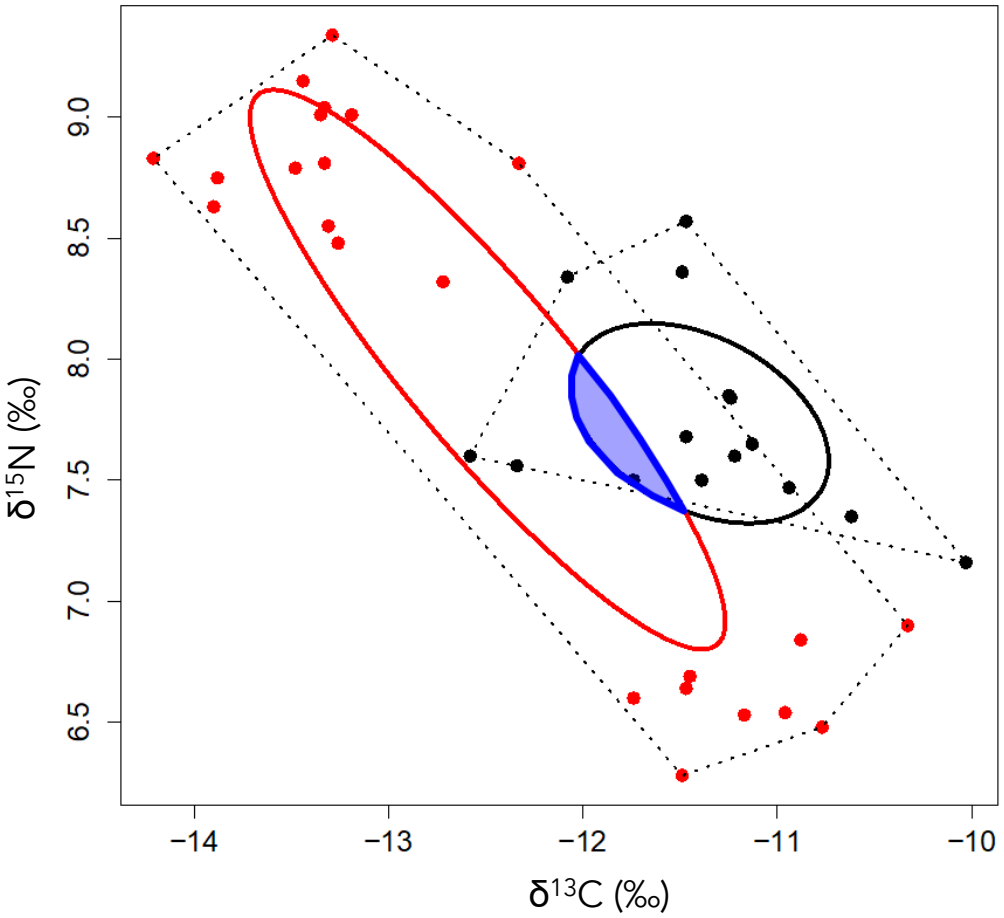
Stable isotopes as niche proxies

Quantification of isotopic niche overlap

All niche parameters can be calculated (geometric approach) or estimated through Bayesian inference

Take uncertainty into account & facilitate explicit comparisons



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Example: Iphimediidae amphipods

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PhD at UCLouvain / RBINS
Now postdoc at ULiège

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Iphimediidae in the Southern Ocean: widely distributed and common family with high ecological diversity

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How do environmental parameters influence their ecological features? How will they react to current and future environmental changes?

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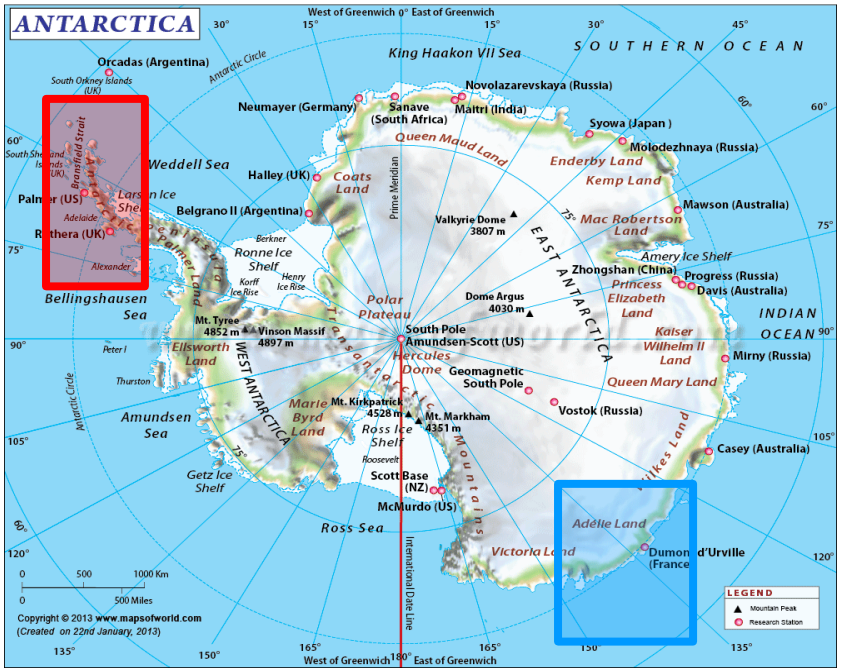
In the framework of vERSO and RECTO BELSPO projects: comparison between West Antarctic Peninsula (rapid warming + sea ice loss) and Adélie Land (moderate changes in water temperature and sea ice cover)



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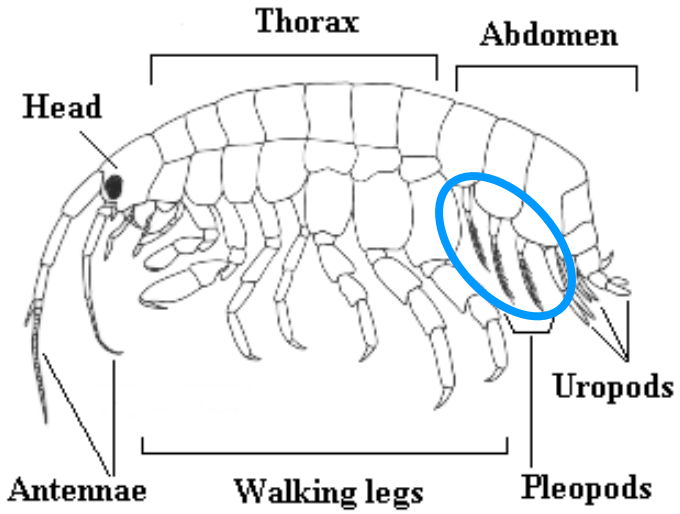
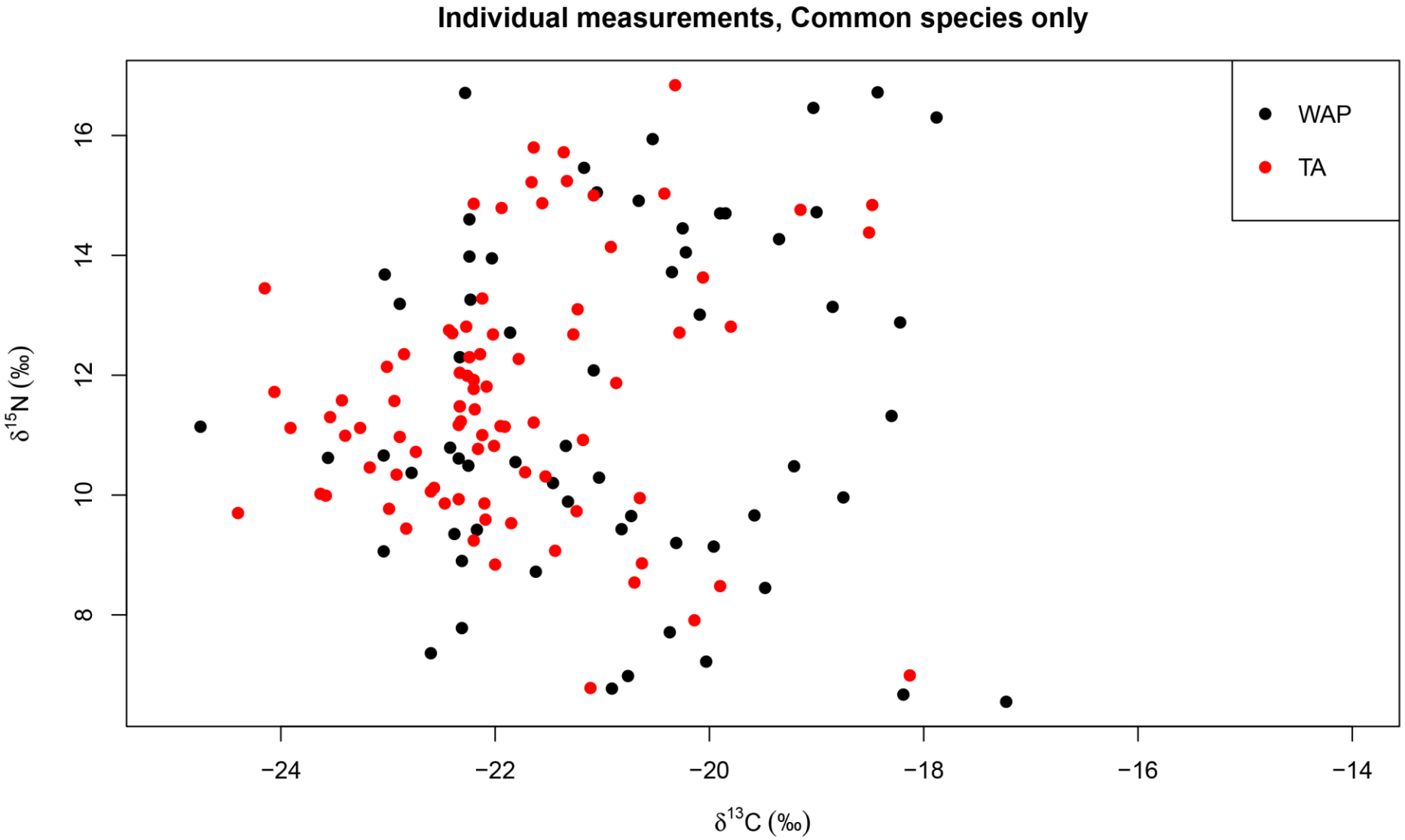
Use of museum specimens: isotopic measurements made on pleopods to limit destruction of samples



Example: Iphimediidae amphipods

Common species only ($N_{species}$ = 11, $N_{individuals}$ = 145)



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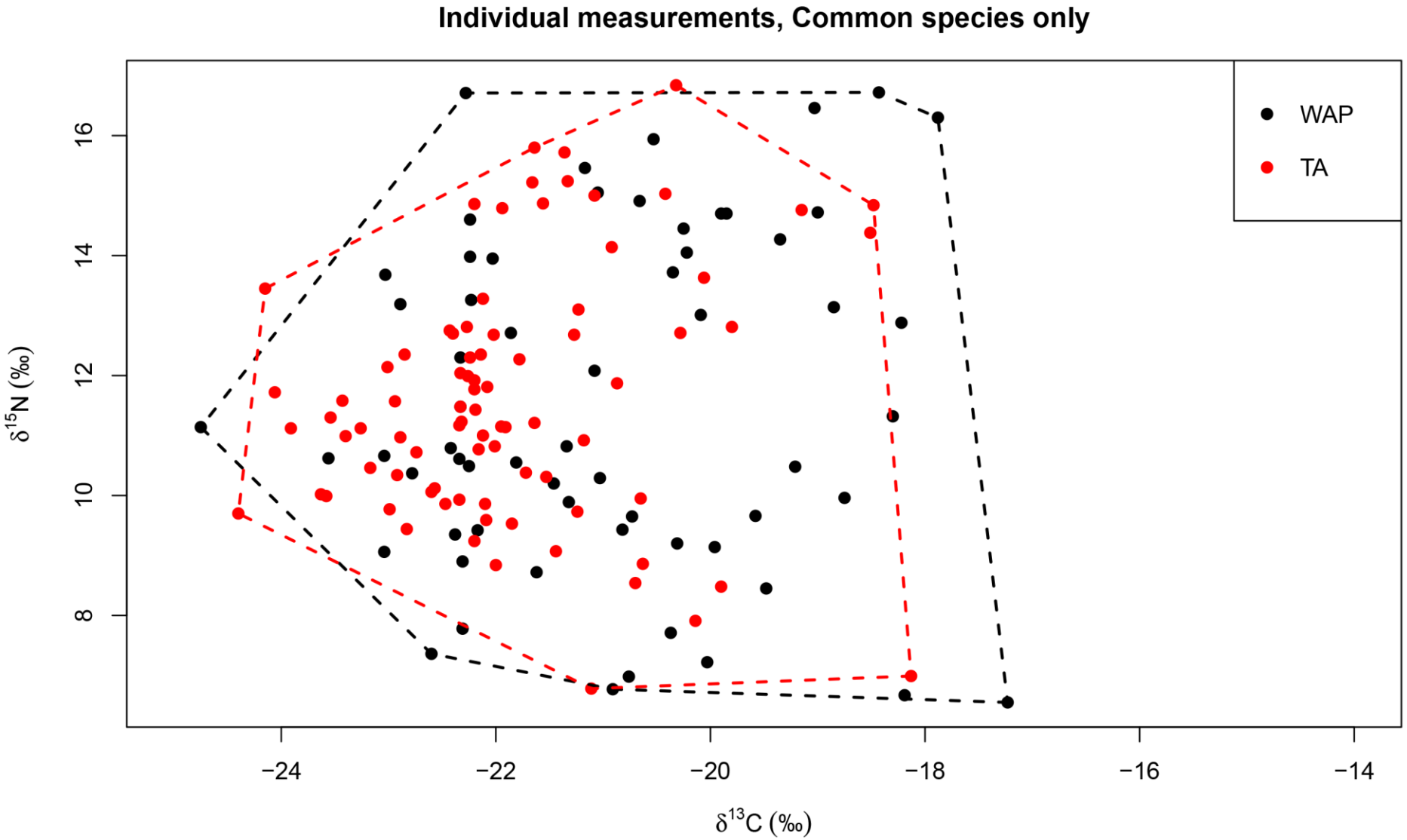

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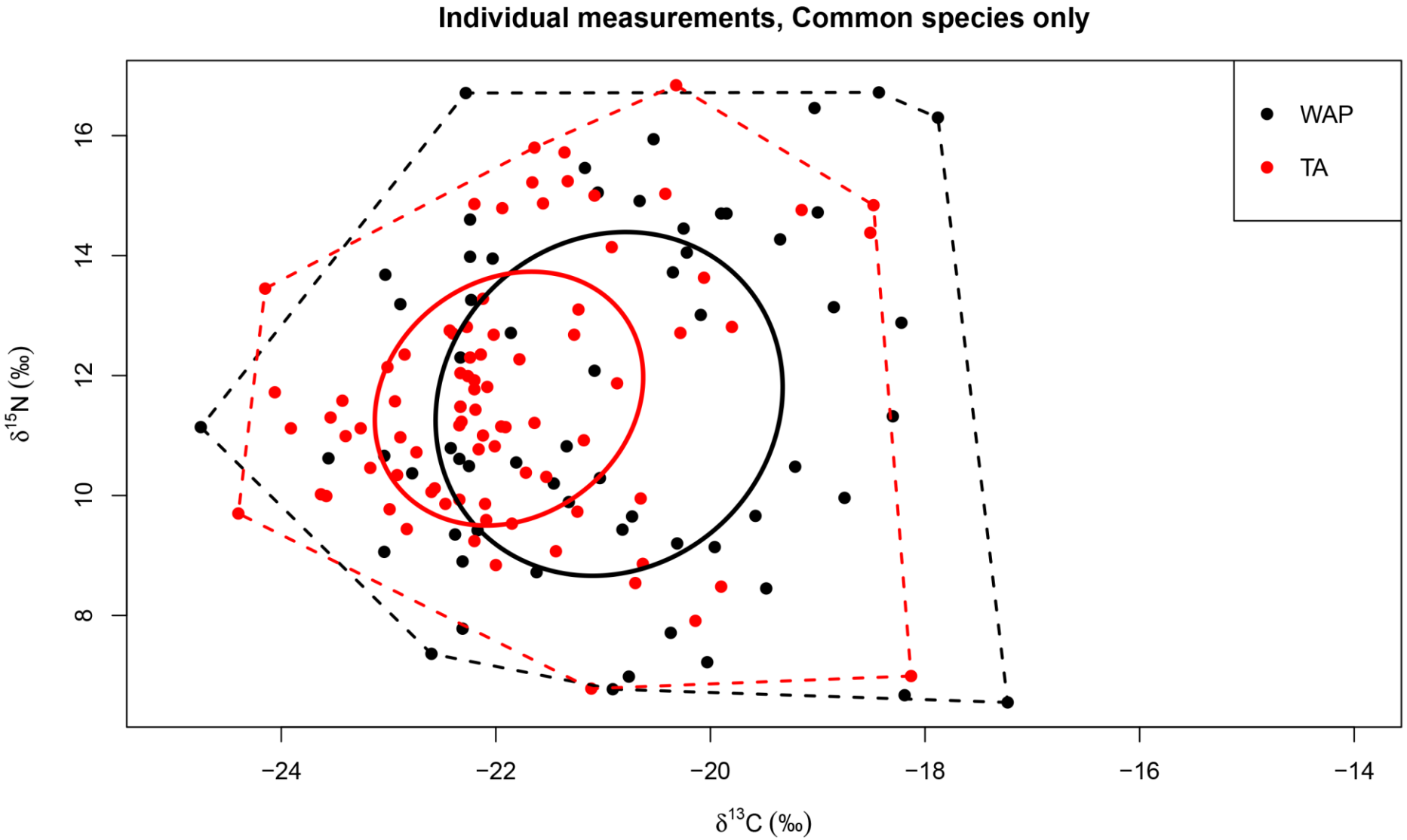

Example: Iphimediidae amphipods

Is assemblage niche larger in Western Antarctic Peninsula than in Adélie Land?

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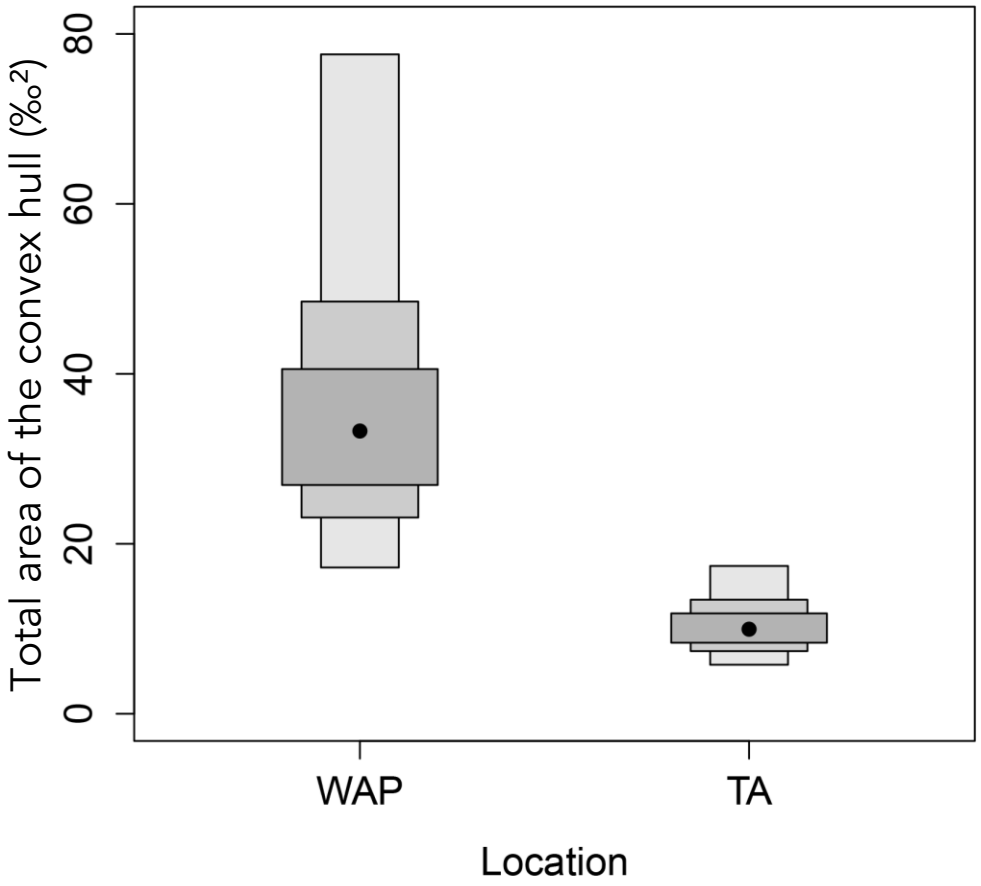
Is assemblage niche larger in Western Antarctic Peninsula than in Adélie Land?

Total niche: Yes
(99.84% of model runs)



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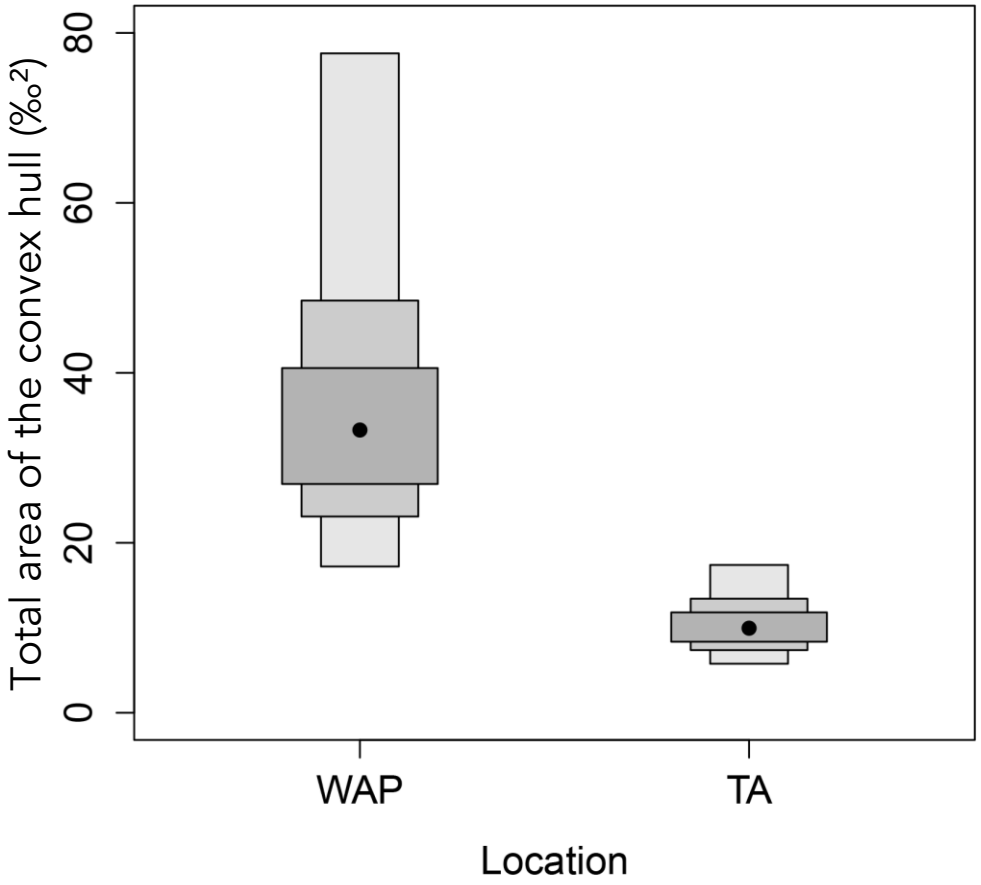

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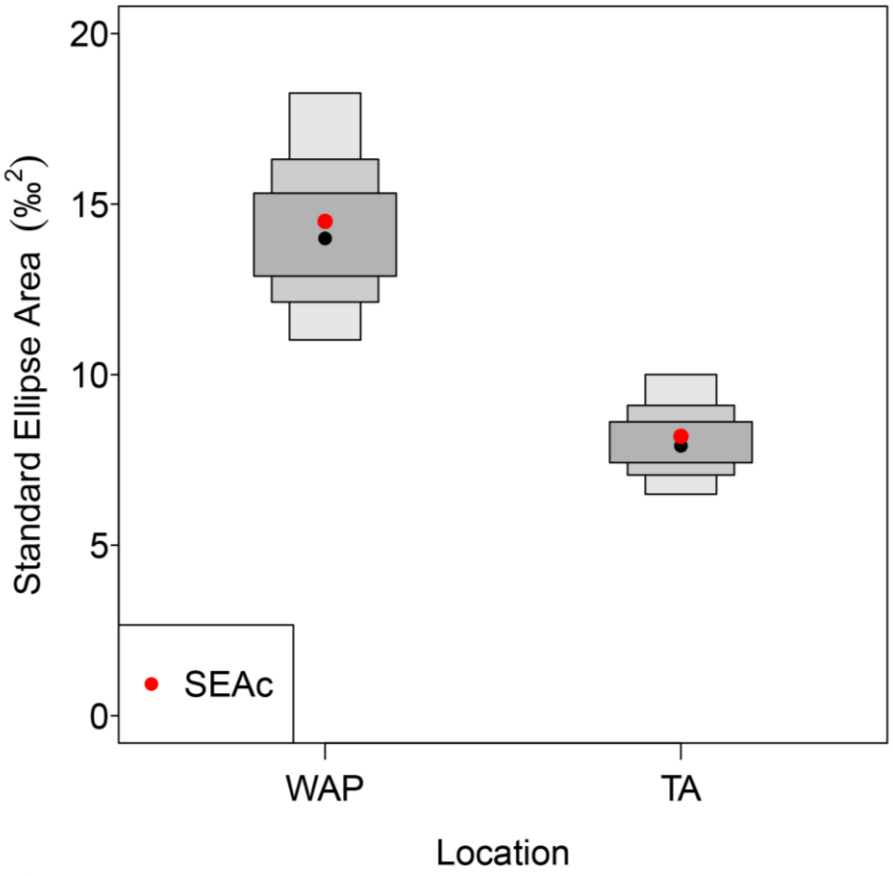

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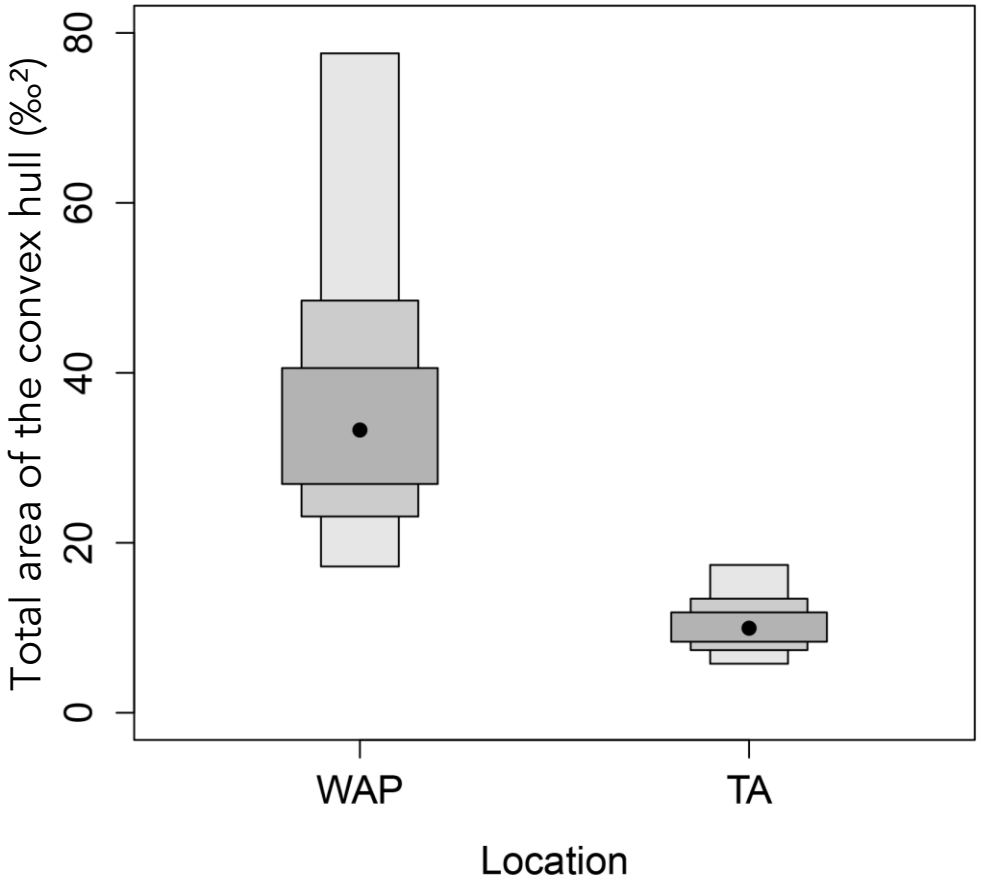

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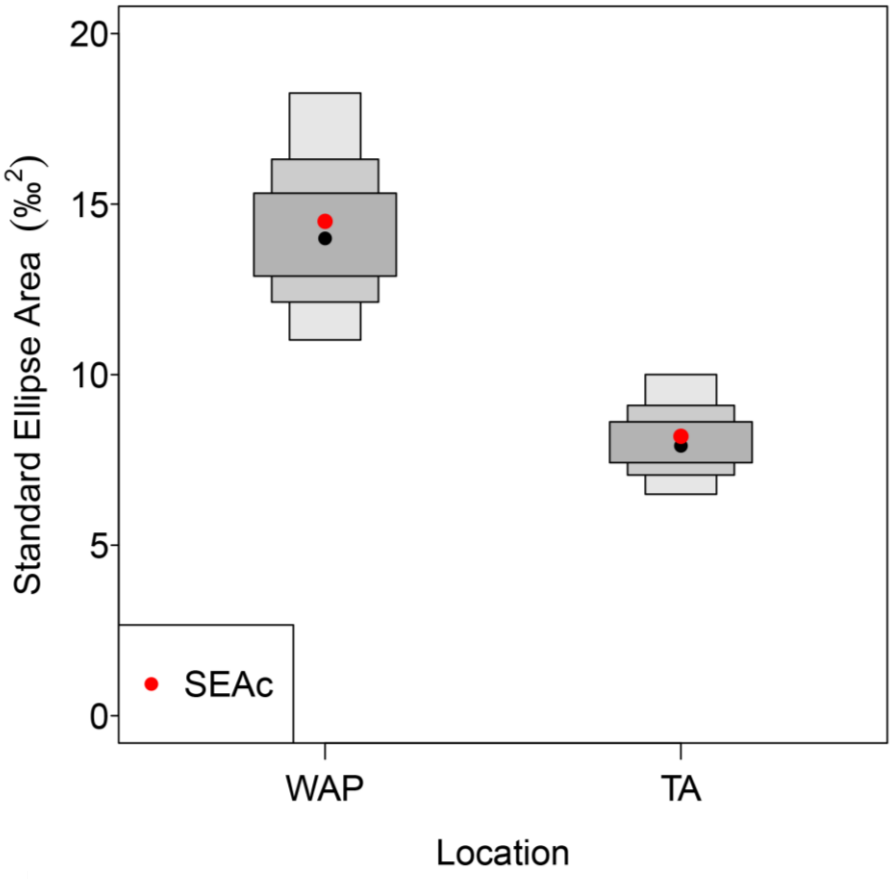


➔ Iphimediidae amphipods exploit more resources in WAP than in AL

Example: Iphimediidae amphipods

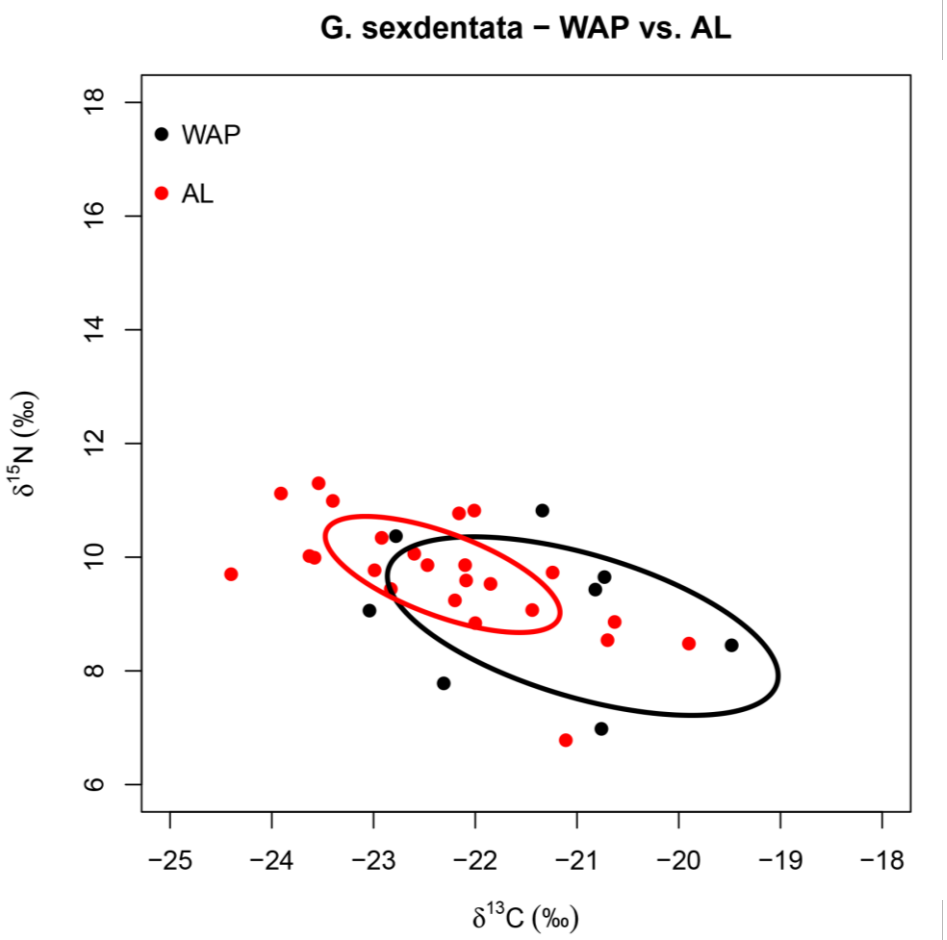
Is this trend of wider isotopic niche found at the species level?

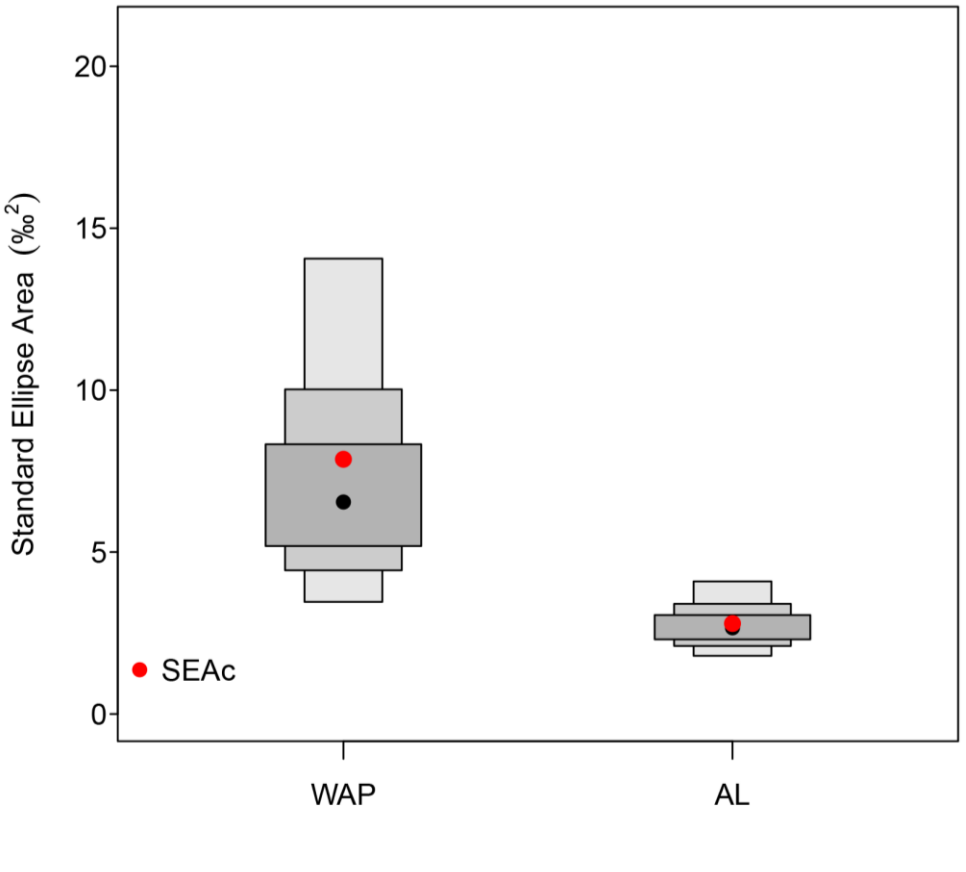
Example: Iphimediidae amphipods

Is this trend of wider isotopic niche found at the species level?

Gnathiphimedia sexdentata: Yes
Trend present in 99.56% of model solutions

Image source: d'Udekem d'Acoz & Verheye 2013





Example: Iphimediidae amphipods

Is this trend of wider isotopic niche found at the species level?

Echiniphimedia echinata: No
Trend present in only 80.64% of model solutions

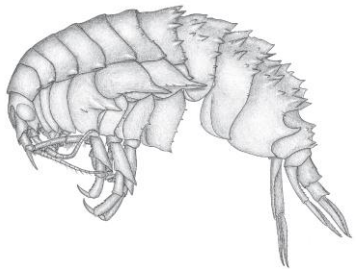
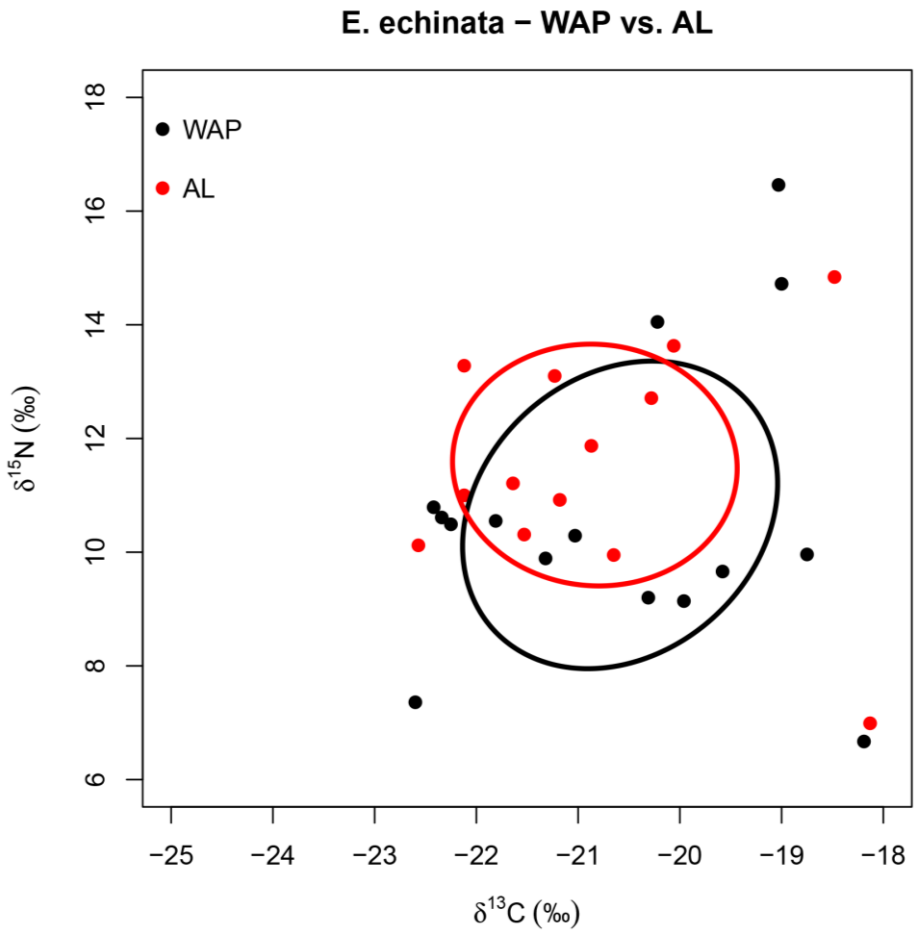
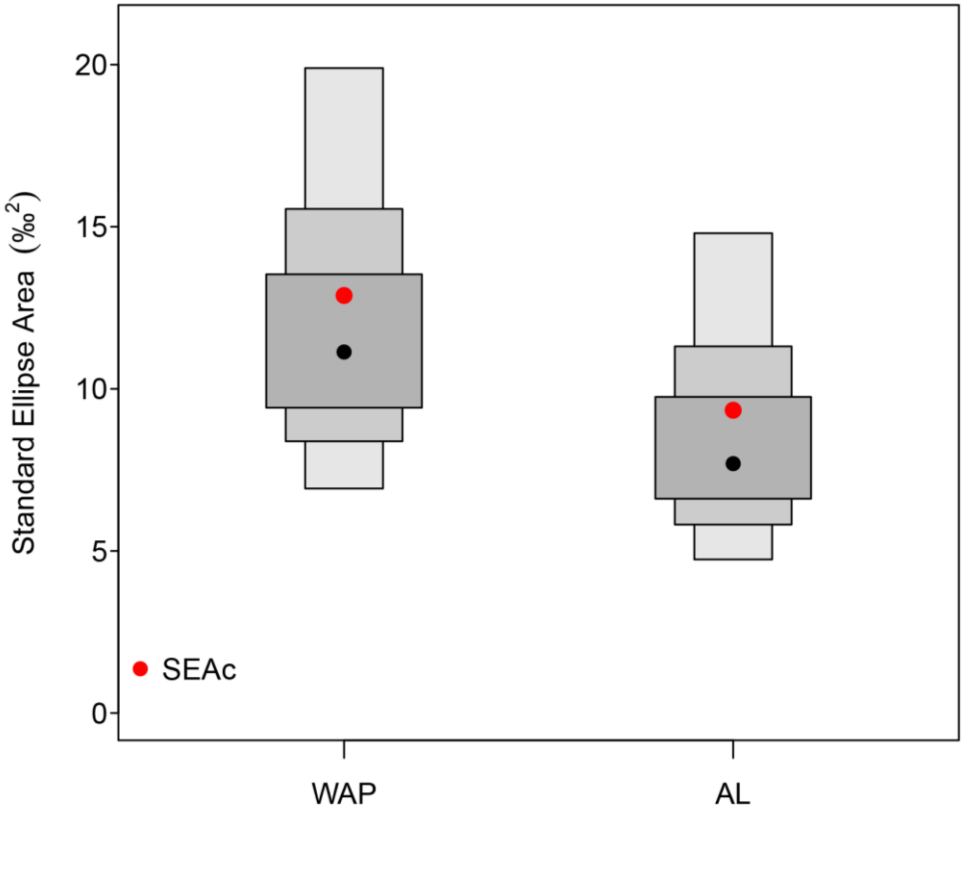


Image source: Coleman 2007



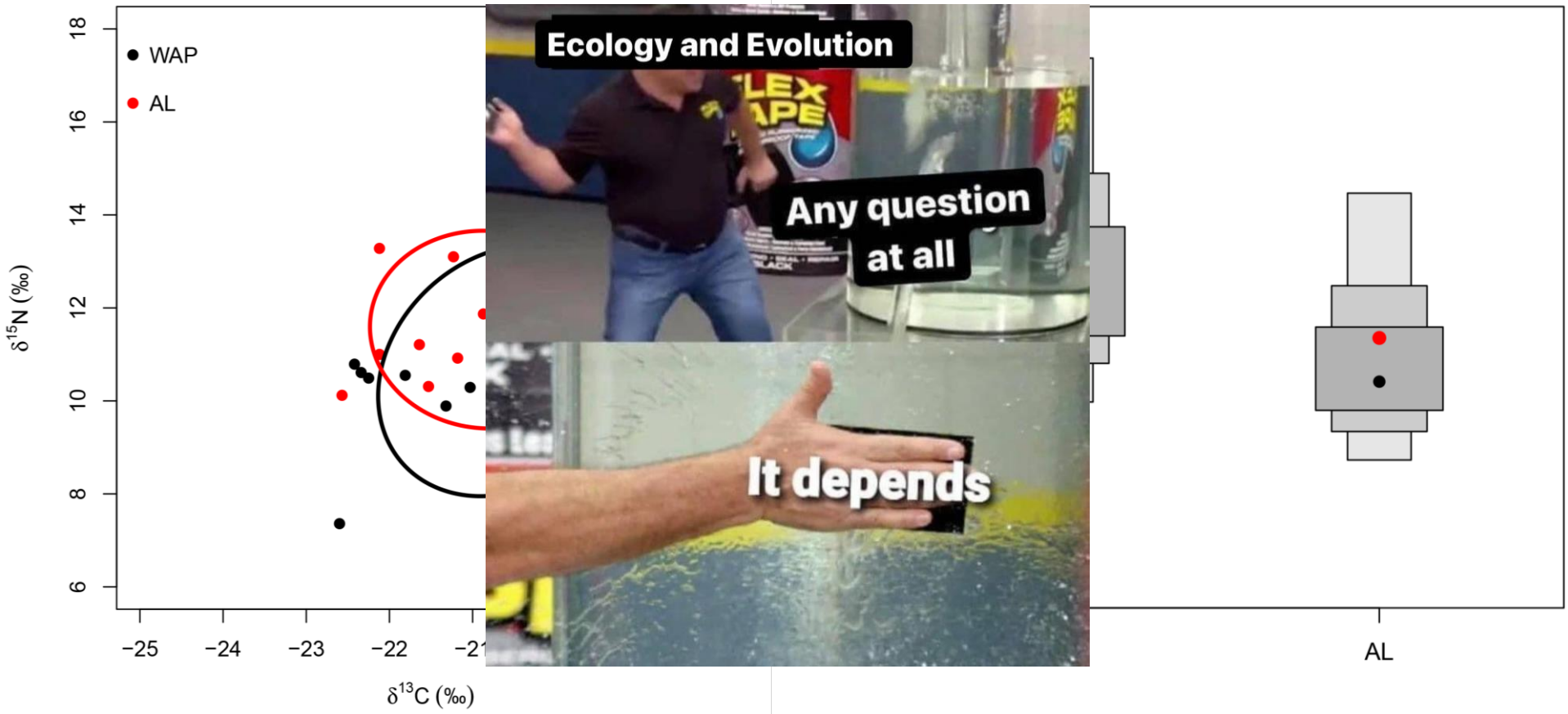


Example: Iphimediidae amphipods

Is this trend of wider isotopic niche found at the species level?

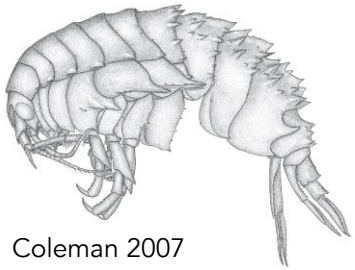
It depends…

➔ Species-specific patterns of ecological plasticity among amphipod assemblage



Example: Iphimediidae amphipods

Is niche overlap between close species the same in both regions?



Coleman 2007

← *Echiniphimedia echinata*

and

Echiniphimedia hodgsoni →

d'Udekem d'Acoz & Verheye 2013

Example: Iphimediidae amphipods

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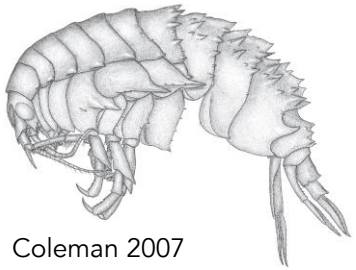

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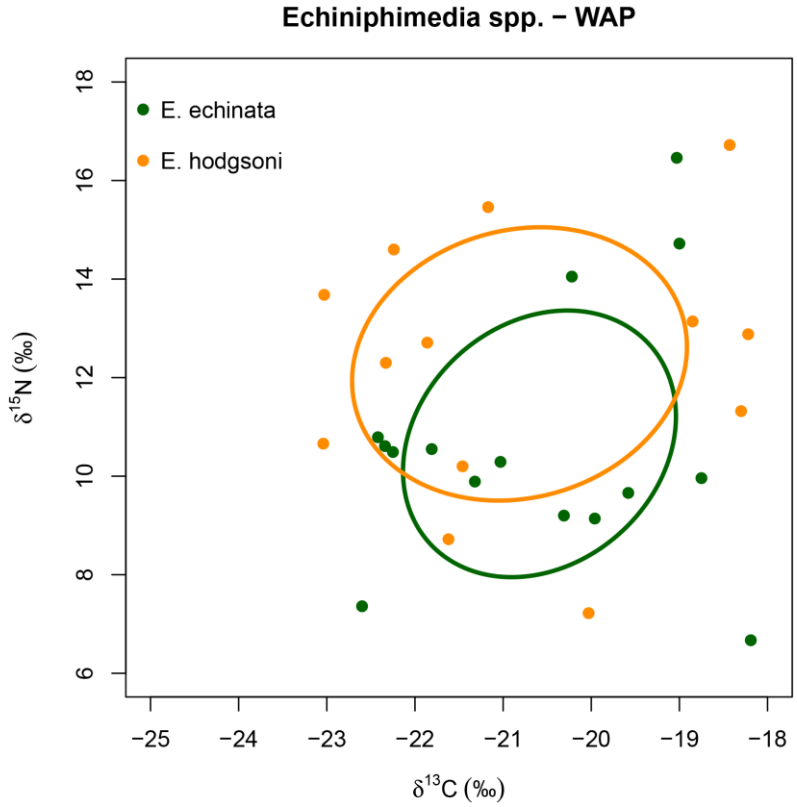

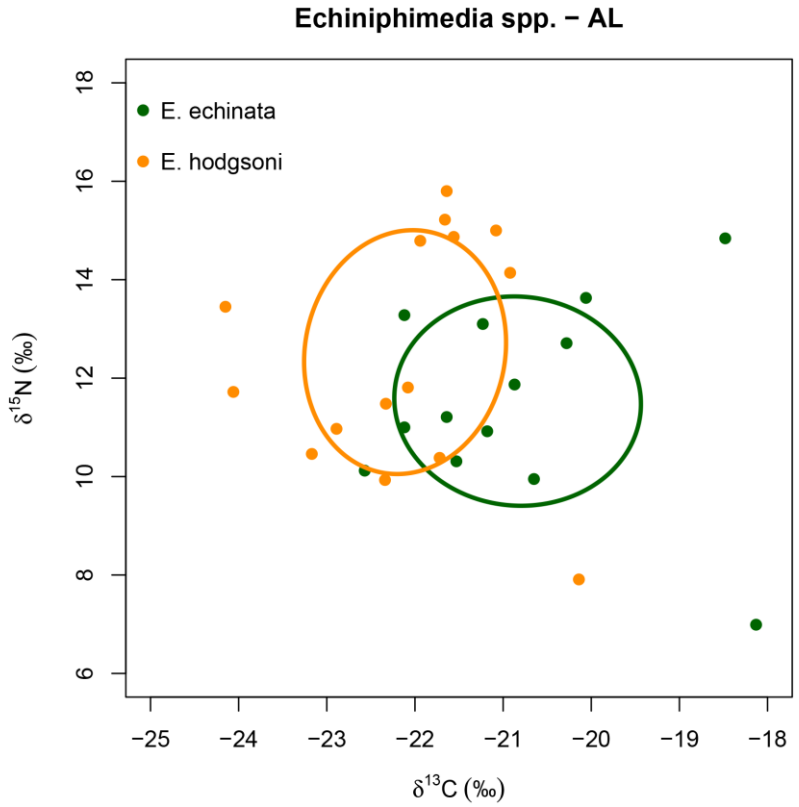

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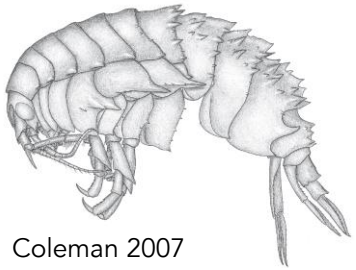

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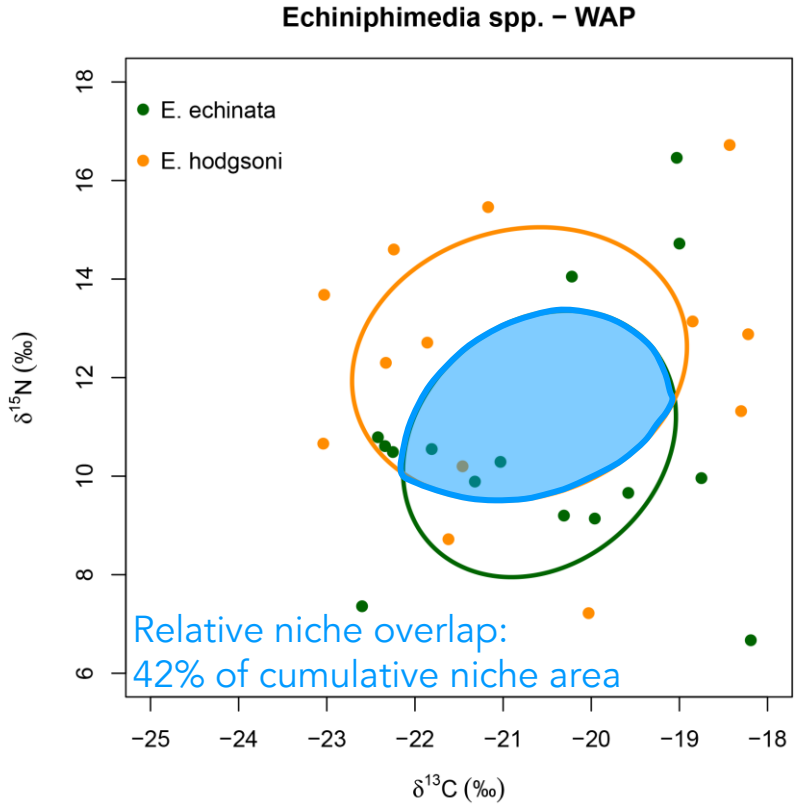

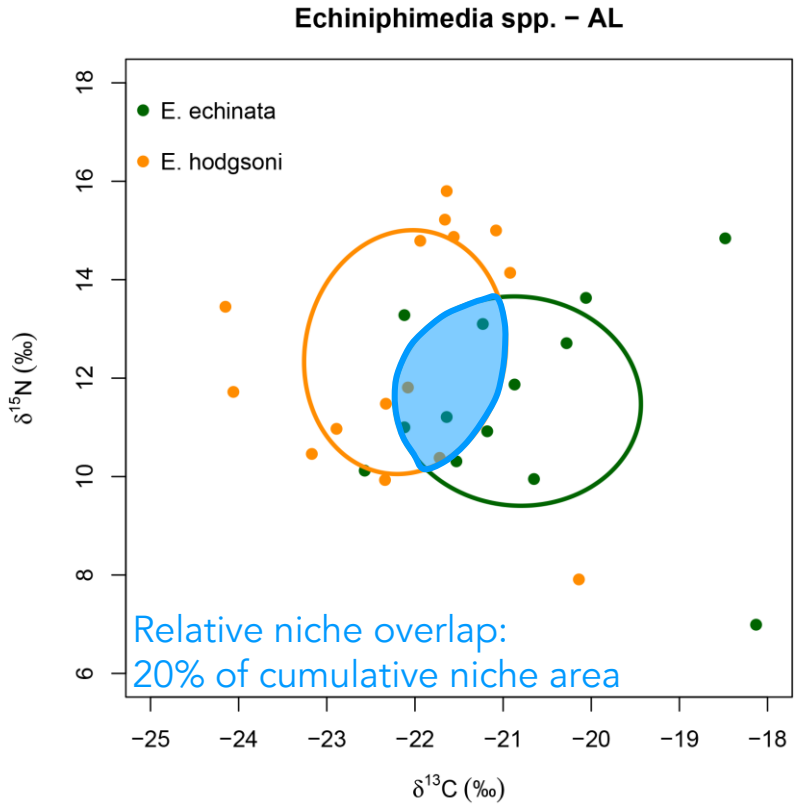

Example: Iphimediidae amphipods

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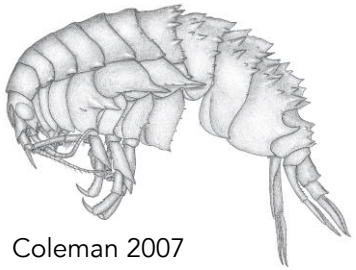

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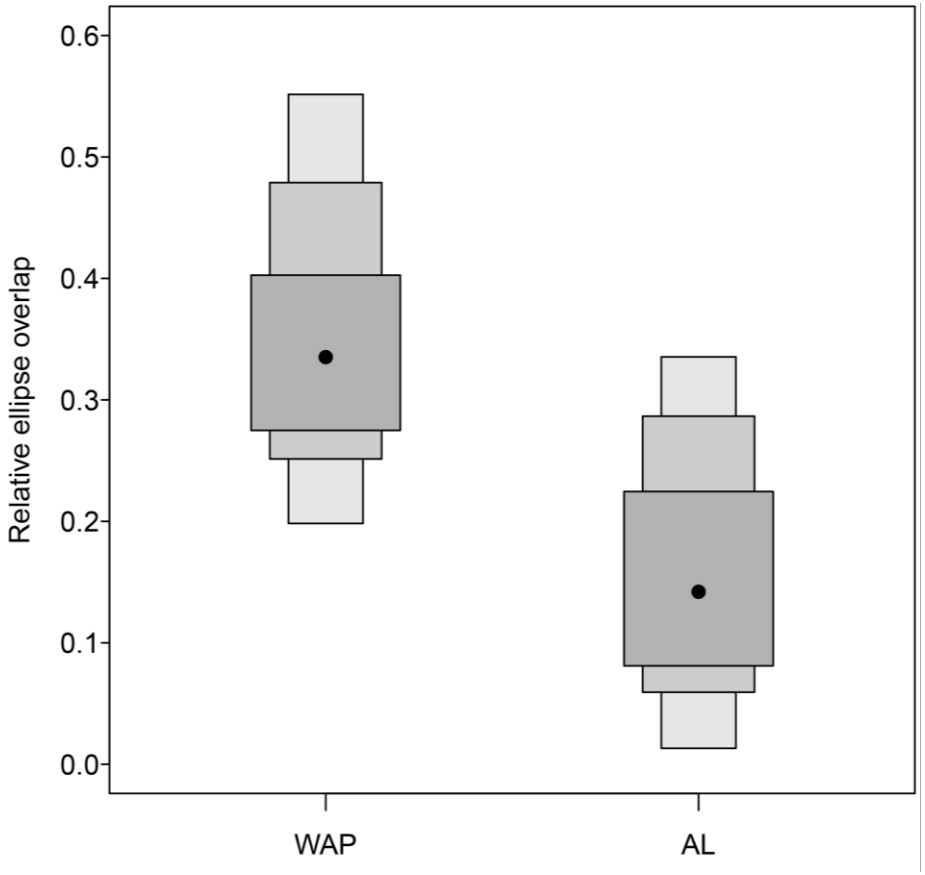
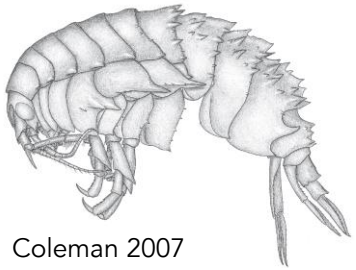


$Overlap_{WAP} > Overlap_{AL}$

Probability = 99.00%

Example: Iphimediidae amphipods

Is niche overlap between close species the same in both regions?



Coleman 2007

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Echiniphimedia hodgsoni →

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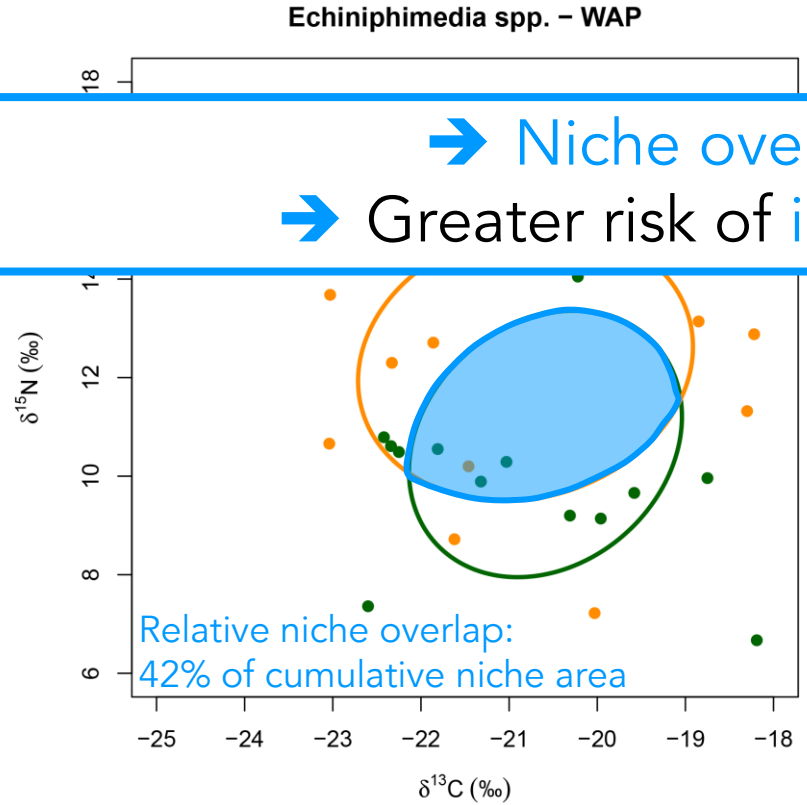
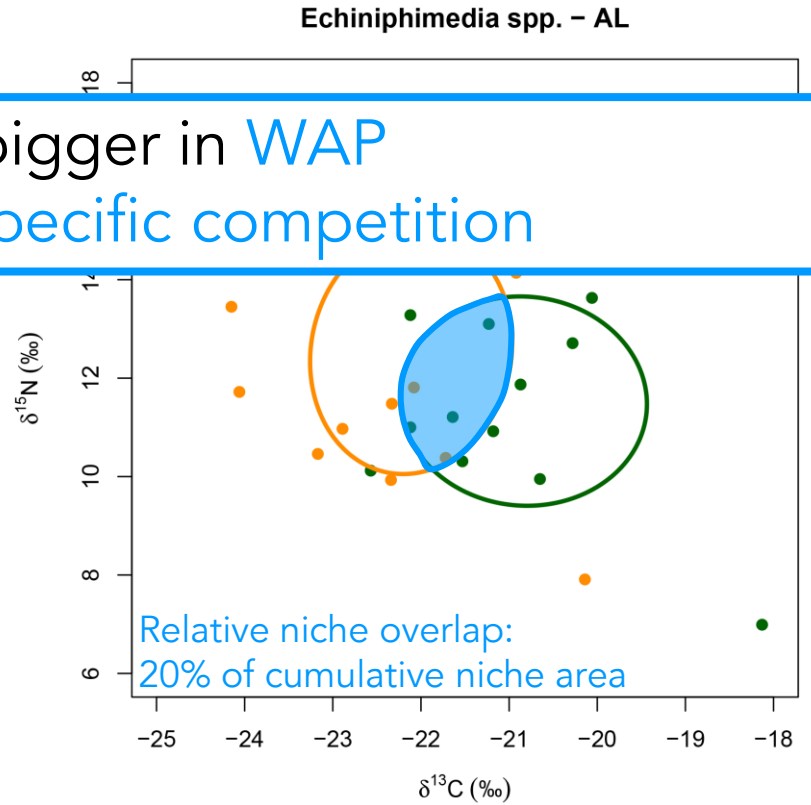


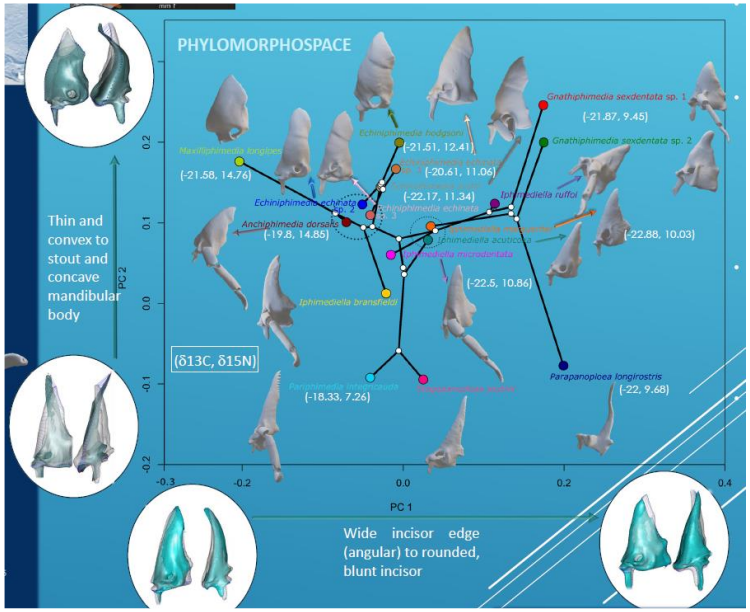


➔ Niche overlap bigger in WAP

➔ Greater risk of interspecific competition

Example: Iphimediidae amphipods

Marie VERHEYE
PhD at UCLouvain / RBINS
Now postdoc at ULiège



Links between morphology, ecology and phylogeny among Antarctic Iphimediids

Velella velella niche shifts

By-the-wind sailor, *Velella velella*

Cosmopolitan neustonic organism

Colonial hydrozoan (not a jellyfish)

Gilles LEPOINT
(F.R.S.-FNRS senior research associate, FOCUS, ULiège)

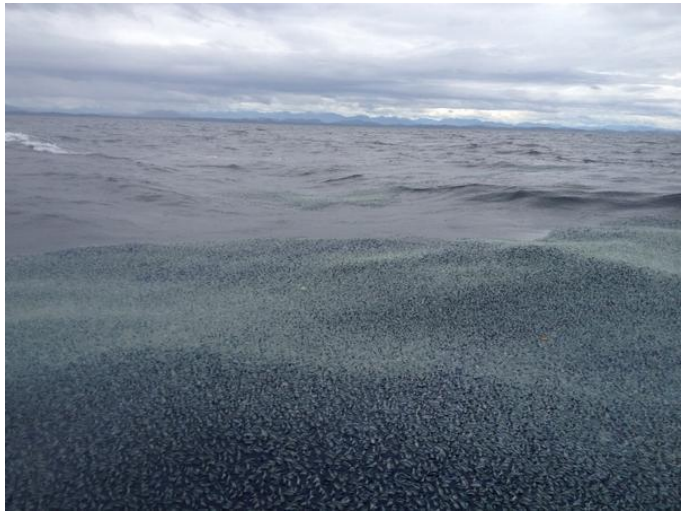
Velella velella niche shifts

By-the-wind sailor, *Velella velella*

Cosmopolitan neustonic organism

Colonial hydrozoan (not a jellyfish)

Able to form huge swarms



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Velella velella niche shifts

By-the-wind sailor, *Velella velella*

Cosmopolitan neustonic organism

Colonial hydrozoan (not a jellyfish)

Able to form huge swarms

➔ Which resources sustain such large populations?

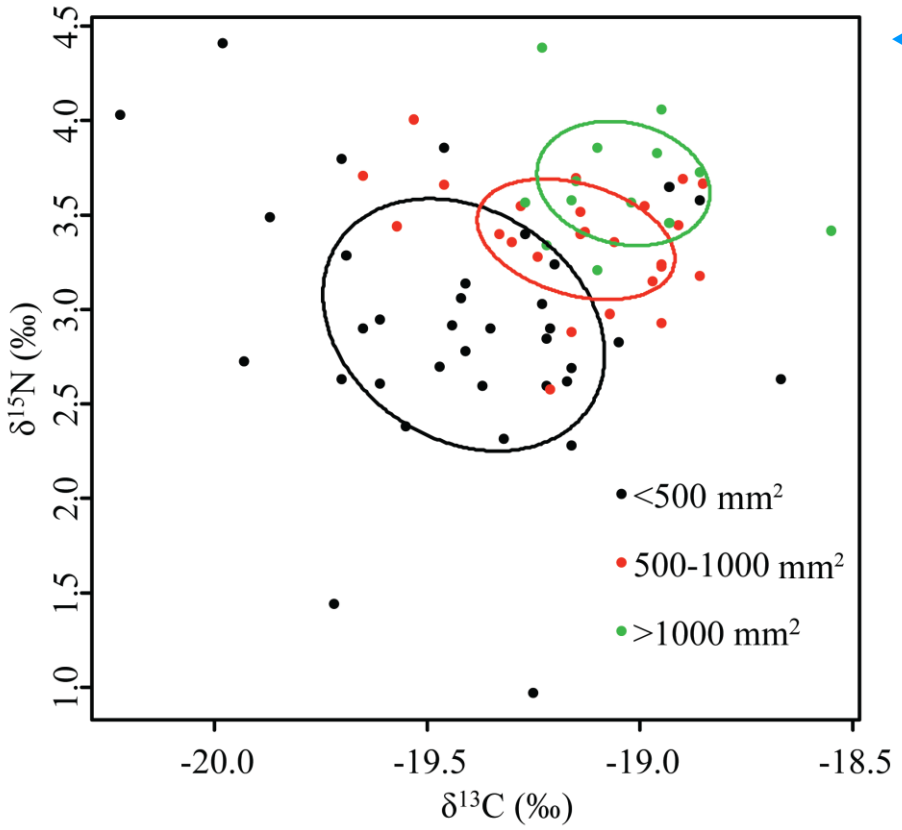
➔ Are there any intraspecific (e.g. size-related) resource segregation mechanisms?

Belg. J. Zool., 146 (2) : 123–133 July 2016

Trophic interactions between two neustonic organisms: insights from Bayesian stable isotope data analysis tools

Gilles Lepoint[1,*], Laurent Bernard[1], Sylvie Gobert[1] & Loïc N. Michel[1]

Velella velella niche shifts



- Little to no overlap between niches of small colonies and other size classes: size-related shift in resource use

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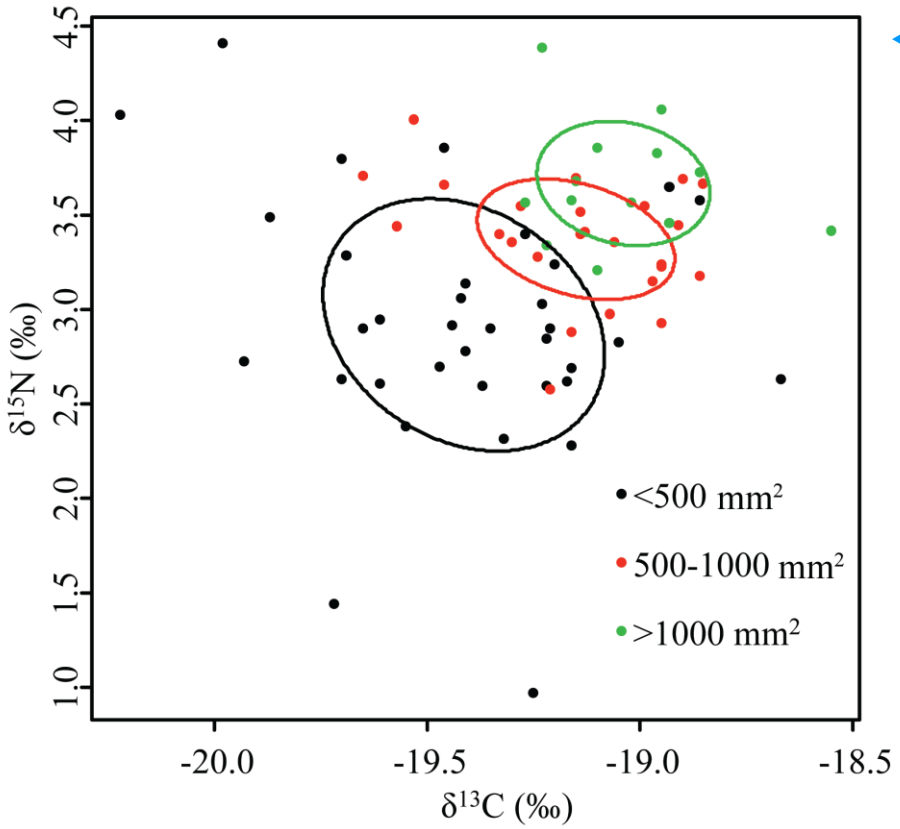
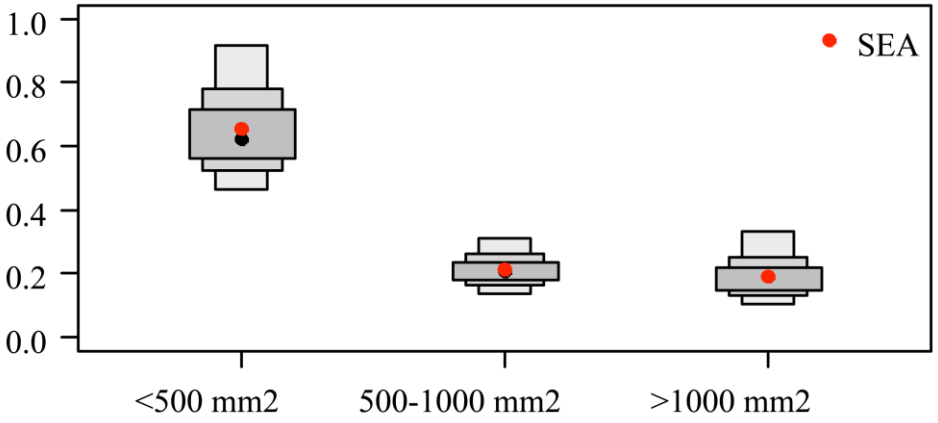


◀ Little to no overlap between niches of small colonies and other size classes: size-related shift in resource use

Larger ellipse area (*i.e.* higher ecological diversity) in small colonies ▼



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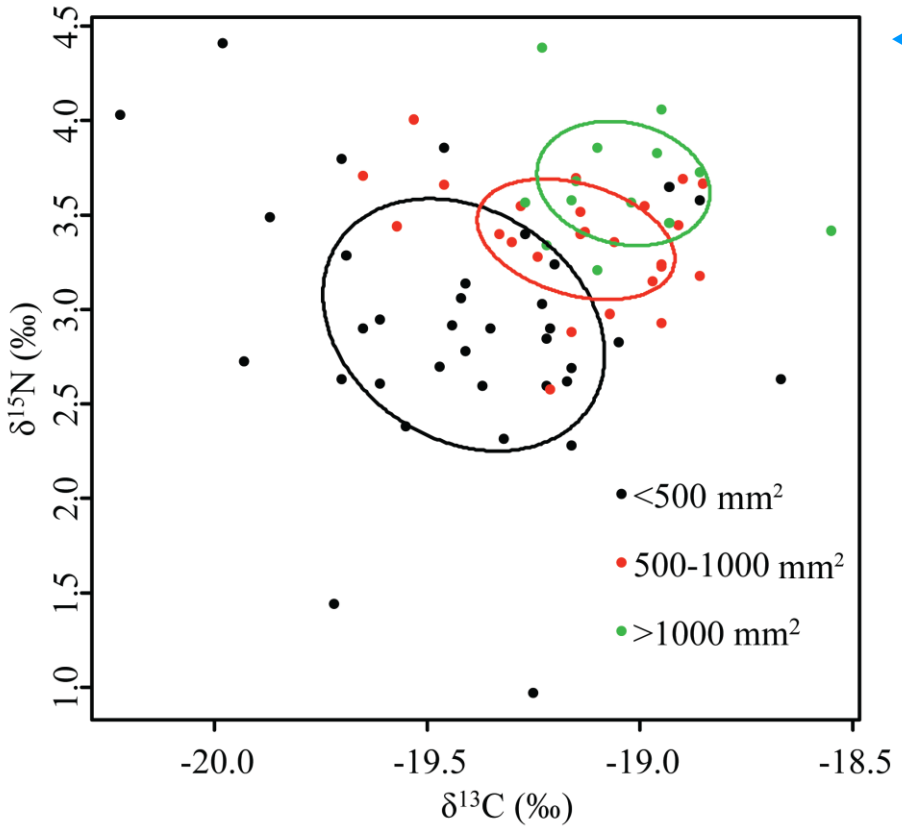

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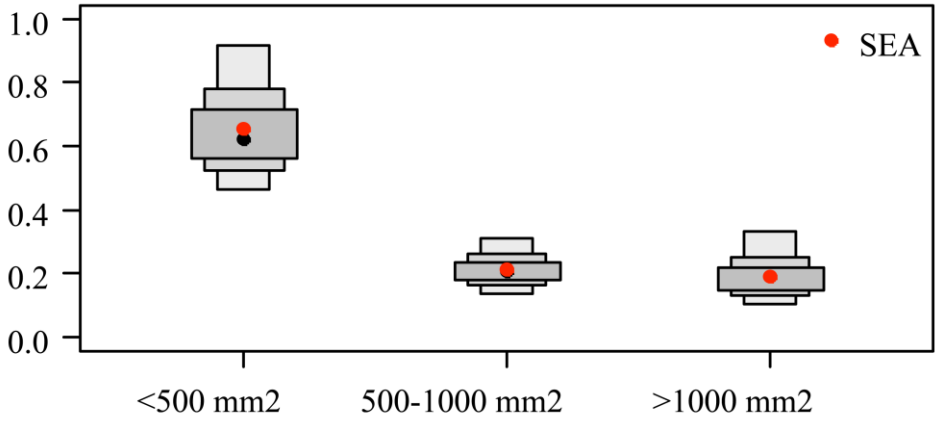

➔ Smaller colonies rely on different and more diverse resources

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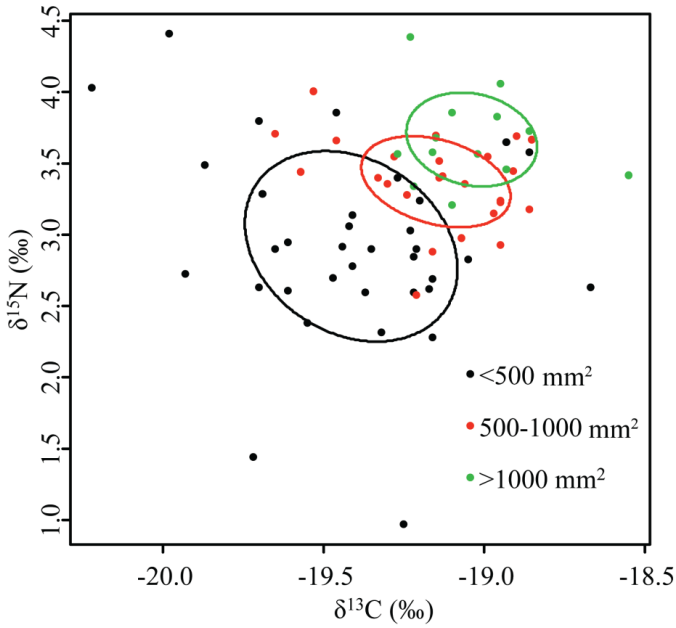
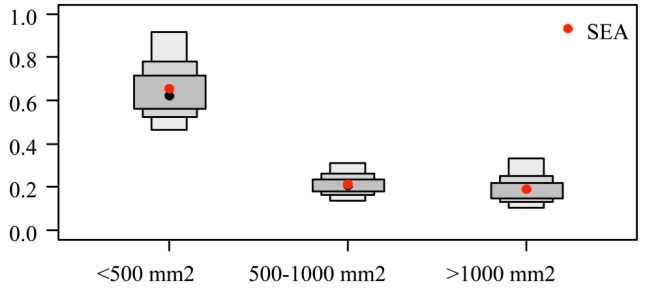
Gilles Lepoint[1,*], Laurent Bernard[1], Sylvie Gobert[1] & Loïc N. Michel[1]

Velella velella niche shifts

Several non-exclusive hypotheses:

1) *V. velella* is a generalist species with size-related prey selection: large colonies favour high trophic level prey (e.g. copepods, fish larvae, fish eggs) while smaller feed on more diverse items at a lower trophic level.





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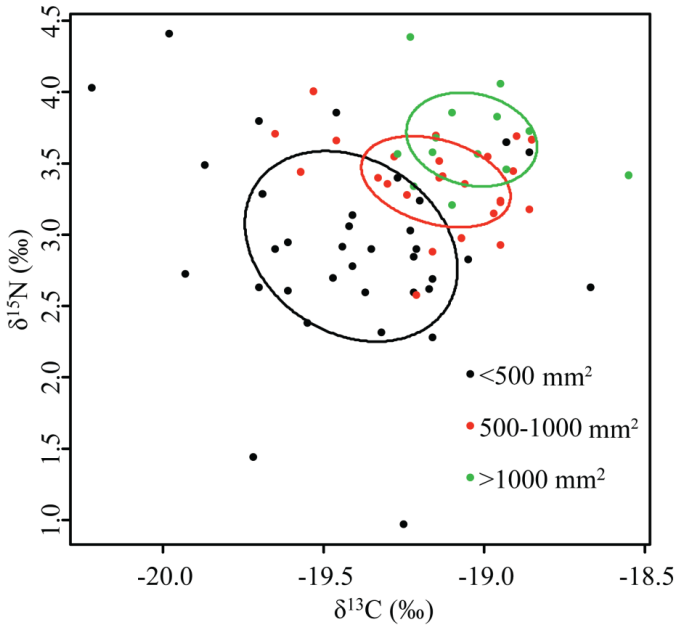
Gilles Lepoint[1,*], Laurent Bernard[1], Sylvie Gobert[1] & Loïc N. Michel[1]

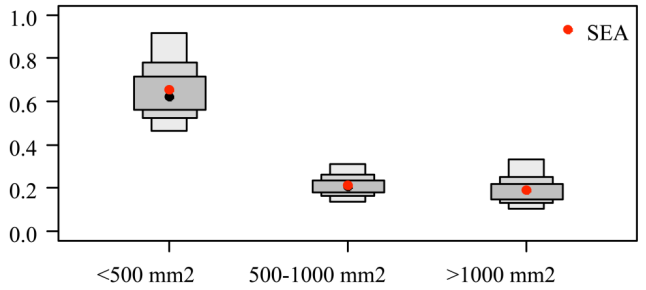
Velella velella niche shifts

Several non-exclusive hypotheses:

1) *V. velella* is a generalist species with size-related prey selection.

2) Smaller colonies rely more on alternative energy acquisition pathways (e.g. symbiotic zooxanthellae), resulting in lower apparent trophic position.





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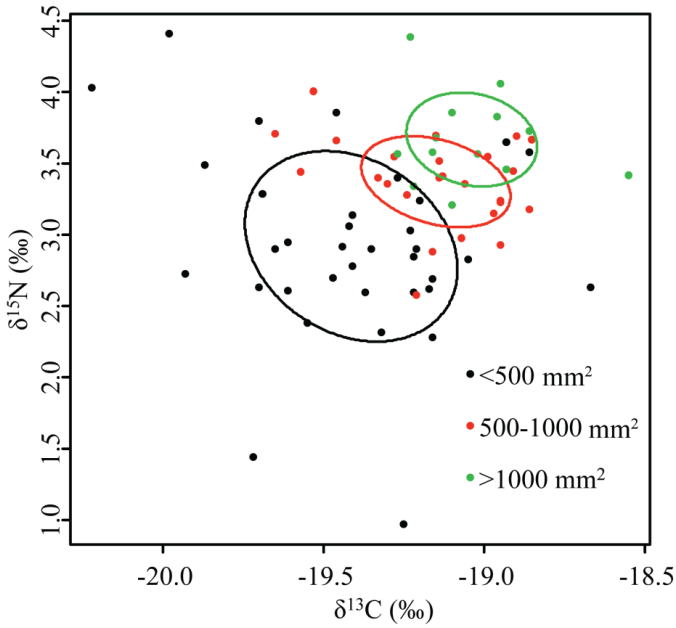
Velella velella niche shifts

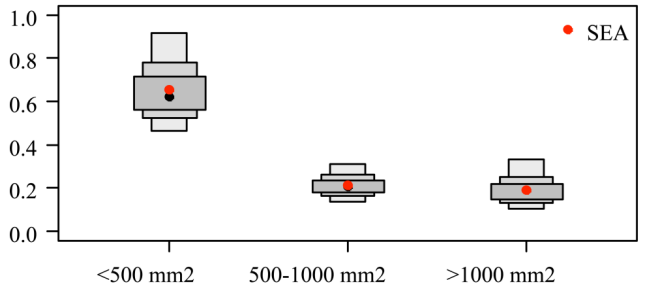
Several non-exclusive hypotheses:

1) *V. velella* is a generalist species with size-related prey selection.

2) Smaller colonies rely more on alternative energy acquisition pathways.

3) Smaller colonies still bear the "signature" of deep water layers (800-1000 m) where colony founders are produced through sexual reproduction. Since swarms are formed through passive accumulation, colonies from multiple areas could be present together (hence the higher isotopic variability).





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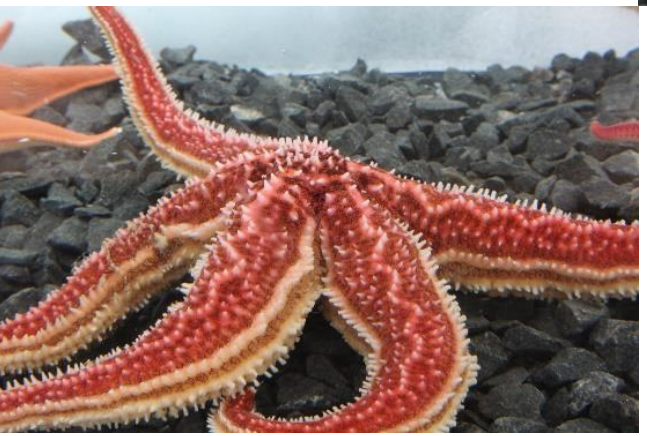
Gilles Lepoint[1,*], Laurent Bernard[1], Sylvie Gobert[1] & Loïc N. Michel[1]

Moving on from 2D niches

Baptiste LE BOURG
PhD at ULiège
Now postdoc at the Mediterranean Institute of Oceanography, Marseilles



Trophic ecology of Southern Ocean sea stars

Moving on from 2D niches

Vol. 674: 189–202, 2021
https://doi.org/10.3354/meps13821

MARINE ECOLOGY PROGRESS SERIES
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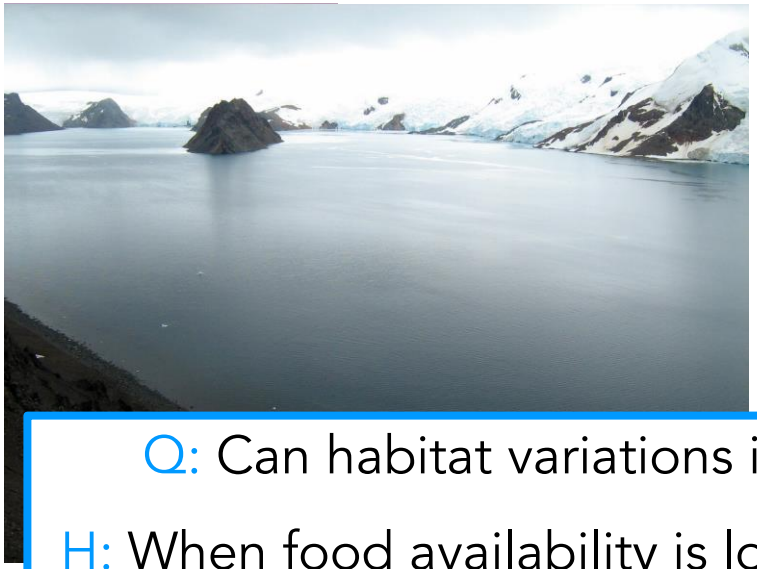
Published September 16

Interactive effects of body size and environmental gradient on the trophic ecology of sea stars in an Antarctic fjord

Baptiste Le Bourg[1,3,*], Piotr Kuklinski[2], Piotr Balazy[2], Gilles Lepoint[1], Loïc N. Michel[1,4]

Ezcurra Inlet (King George Island, WAP): strong environmental gradients. High glacier disturbance: ↗ turbidity, ↘ salinity in inner stations.

Moving on from 2D niches



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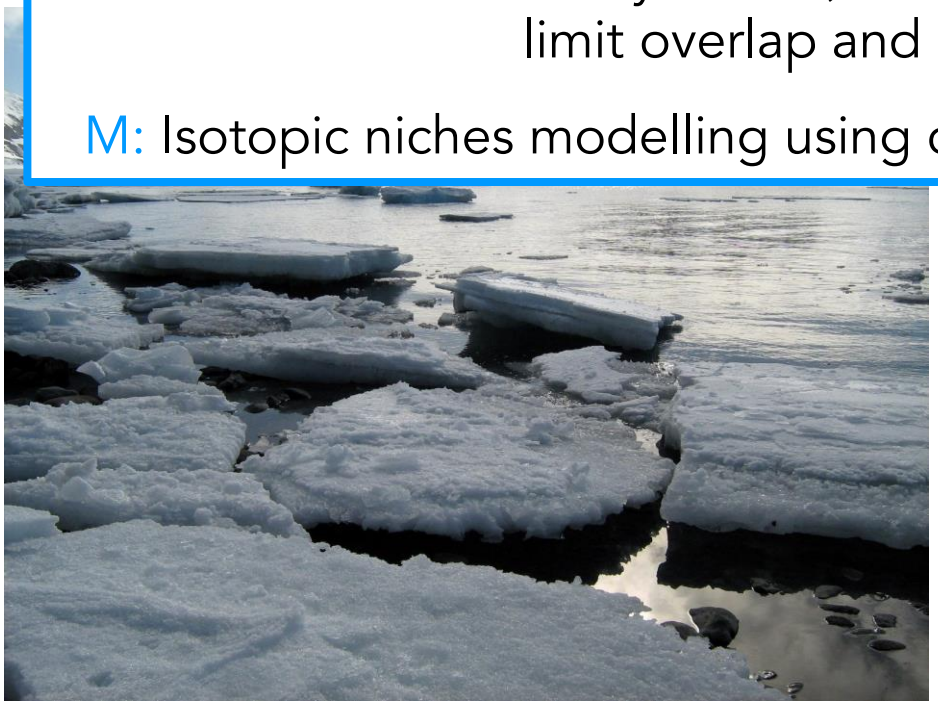
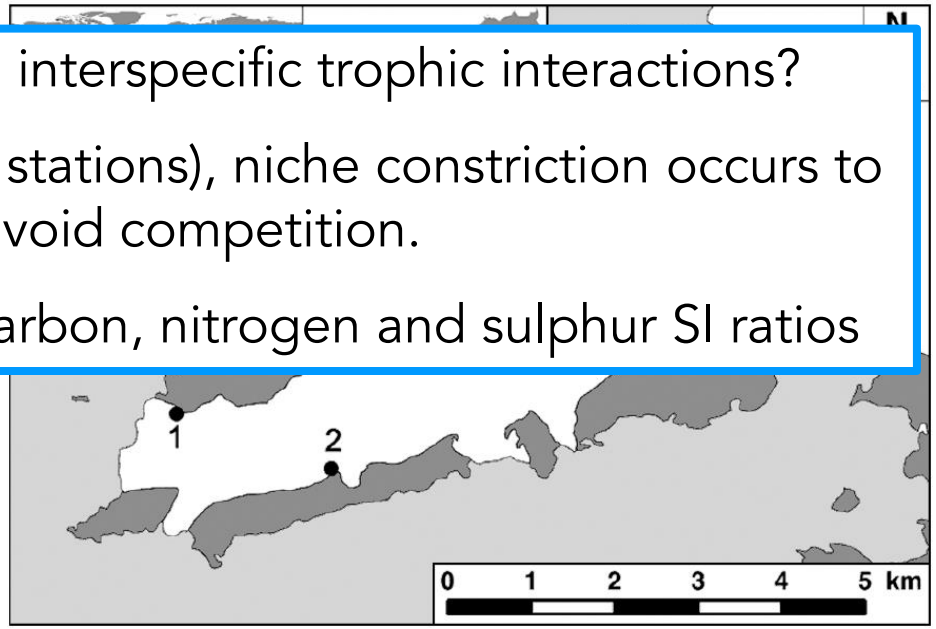
Baptiste Le Bourg[1,3,*], Piotr Kuklinski[2], Piotr Balazy[2], Gilles Lepoint[1], Loïc N. Michel[1,4]

Q: Can habitat variations influence interspecific trophic interactions?

H: When food availability is low (inner stations), niche constriction occurs to limit overlap and avoid competition.

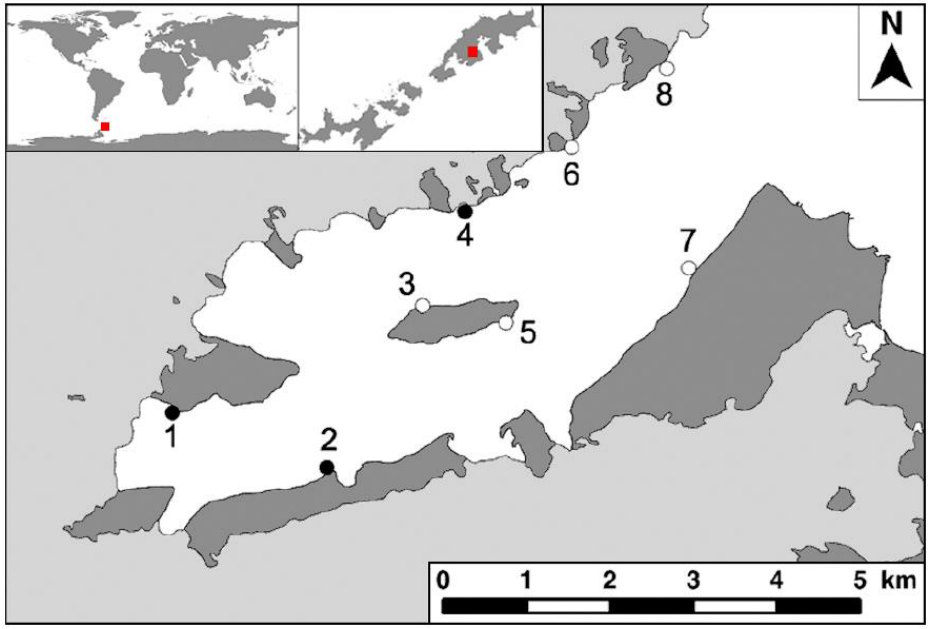
M: Isotopic niches modelling using carbon, nitrogen and sulphur SI ratios

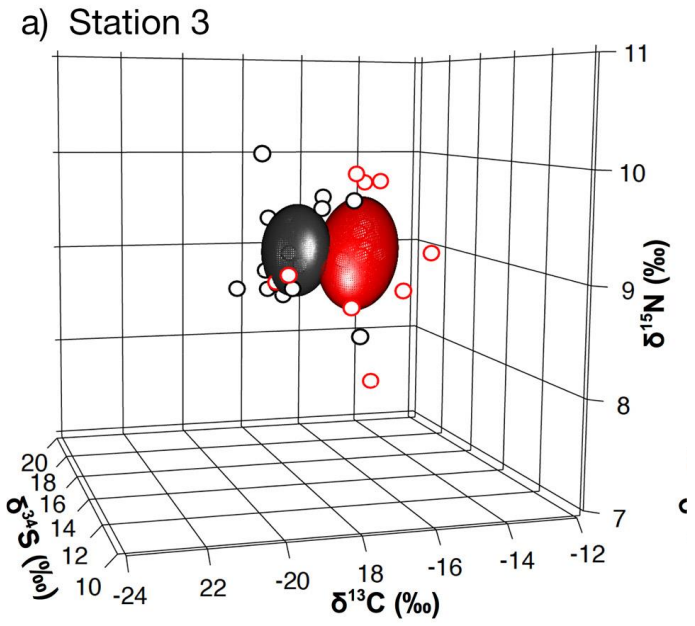


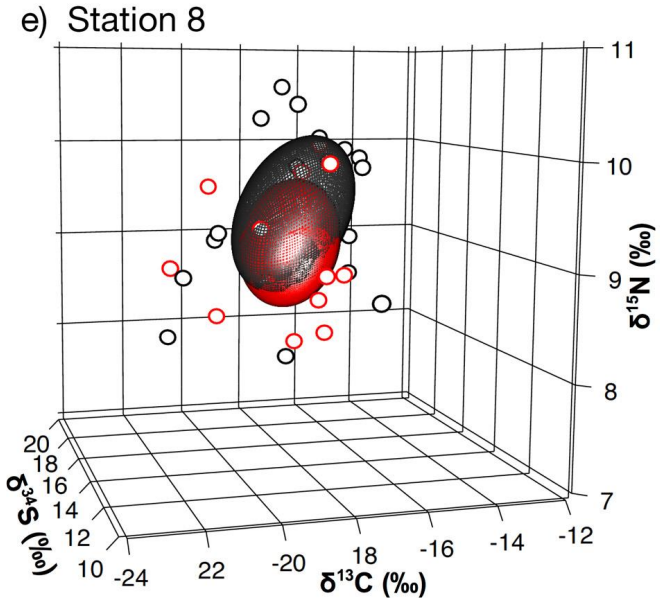


Ezcurra Inlet (King George Island, WAP): strong environmental gradients. High glacier disturbance: ↗ turbidity, ↘ salinity in inner stations.

Moving on from 2D niches







Interspecific niche overlap almost inexistent in inner stations (top) but very strong in outer stations (bottom)

Better seen at https://www.int-res.com/articles/suppl/m674p189_supp/m674p189_supp2.html

Multidimensional niche analysis

Ecology and Evolution

Open Access

Beyond carbon and nitrogen: guidelines for estimating three-dimensional isotopic niche space

Sam Rossman[1,2,3], Peggy H. Ostrom[1,2], Forrest Gordon[4] & Elise F. Zipkin[1,2]

Ecology and Evolution 2016; 6(8): 2405–2413

doi: 10.1002/ece3.2013

A new probabilistic method for quantifying *n*-dimensional ecological niches and niche overlap

Heidi K. Swanson,[1,4] Martin Lysy,[2] Michael Power,[1] Ashley D. Stasko,[1] Jim D. Johnson,[3] and James D. Reist[3]

Ecology, 96(2), 2015, pp. 318–324

Methods able to compute metrics for niche spaces built using 3 or more dimensions (i.e. tracers) exist

Alternative: dimensional reduction through multivariate ordination (e.g. PCA)

SCIENTIFIC REPORTS

OPEN

Multidimensional metrics of niche space for use with diverse analytical techniques

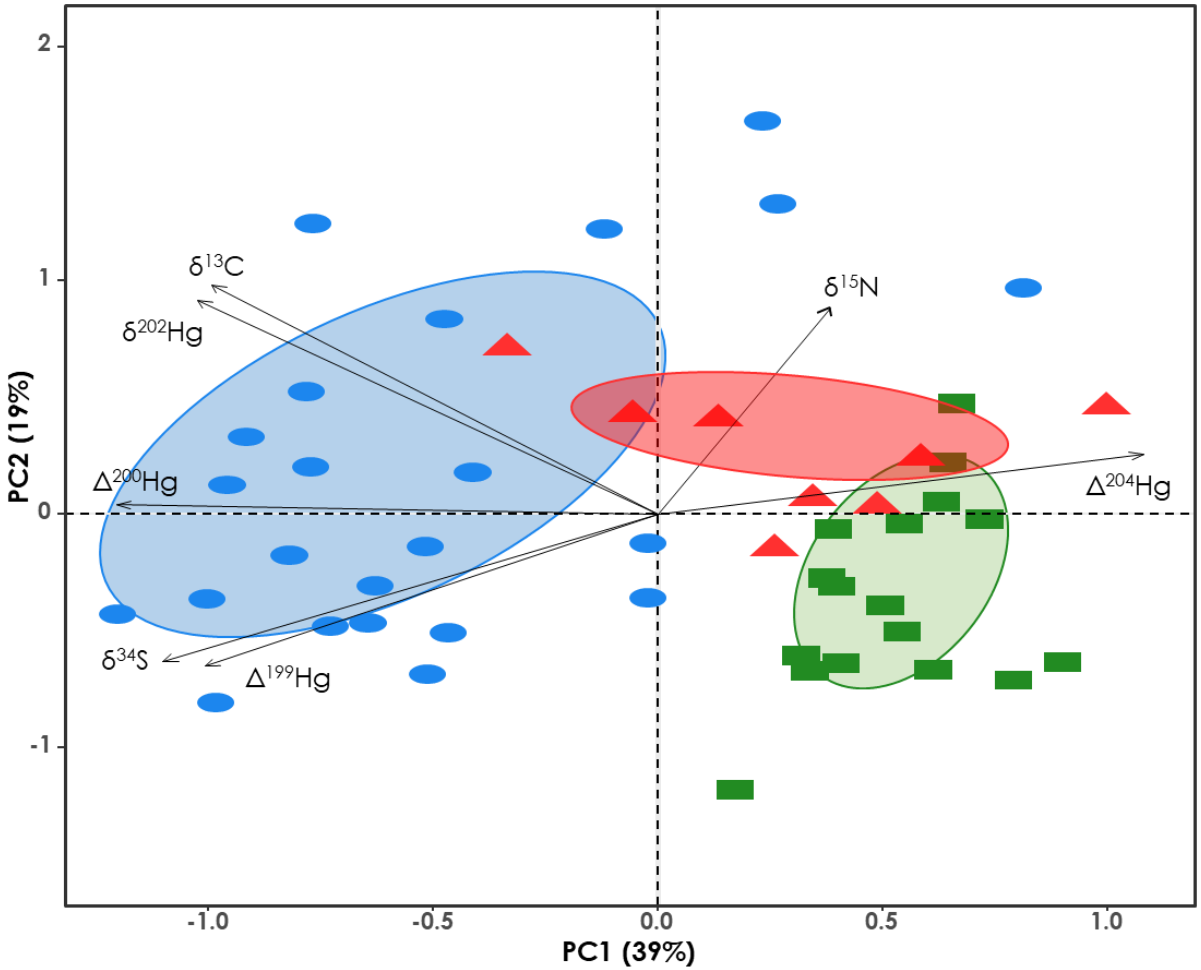
Rachel E. Bowes[1], James H. Thorp[1] & Daniel C. Reuman[1,2]

SCIENTIFIC REPORTS | 7:41599 | DOI: 10.1038/srep41599

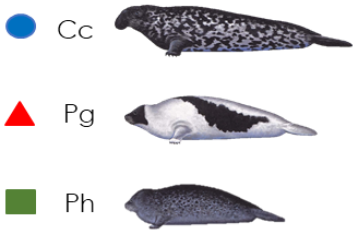
Multidimensional niche analysis

Marianna PINZONE
PhD at ULiège
Now looking for a postdoc
Hire her – she's great!

Niches of arctic seals built using SI ratios of C, N, S and Hg (7 tracers)



Colors = Species



Shapes = Habitat

- Offshore / Bentho-pelagic
- Offshore / Pelagic
- Inshore / Sympagic

Multidimensional niche analysis

Progress in Oceanography 146 (2016) 75–88

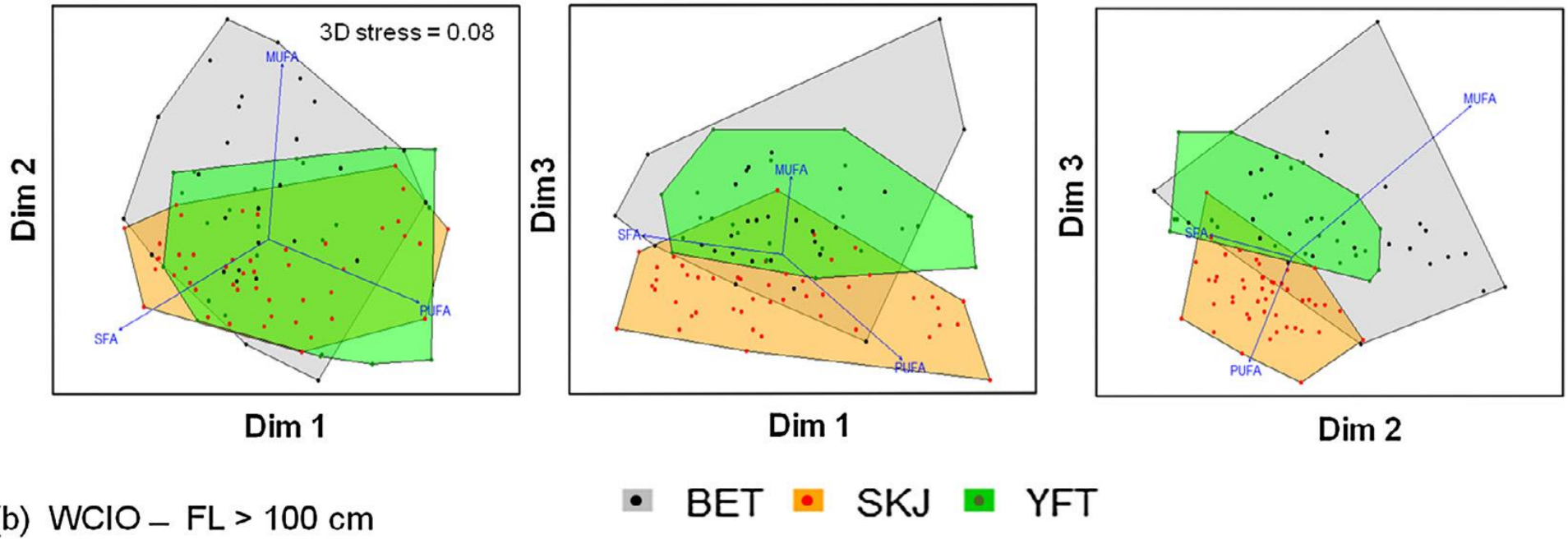
Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Trophic niches of sympatric tropical tuna in the Western Indian Ocean inferred by stable isotopes and neutral fatty acids

Fany Sardenne [a,*], Nathalie Bodin [a], Emmanuel Chassot [a], Aurélien Amiel [a,b], Edwin Fouché [a,b], Maxime Degroote [a], Stéphanie Hollanda [c], Heidi Pethybridge [d], Benoit Lebreton [e], Gaël Guillou [e], Frédéric Ménard [f]



(b) WCIO – FL > 100 cm

Niches of tunas built using 27 fatty acid concentrations

Multidimensional niche analysis

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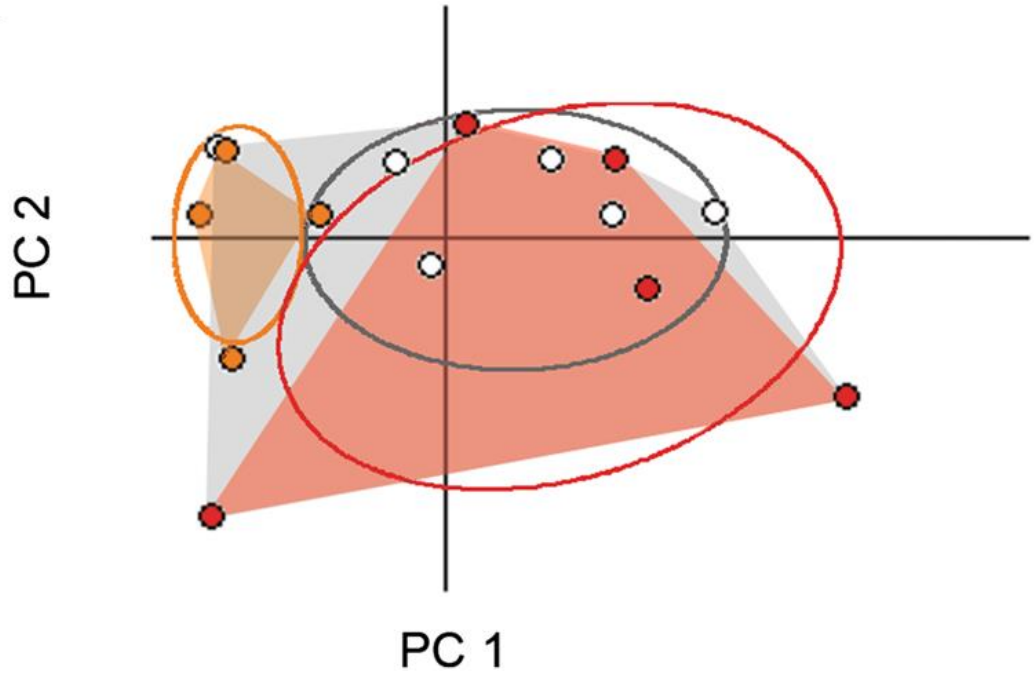
ORIGINAL ARTICLE

ORGANISMS DIVERSITY & EVOLUTION

Evolution and diversity of ram-suction feeding in damselfishes (Pomacentridae)

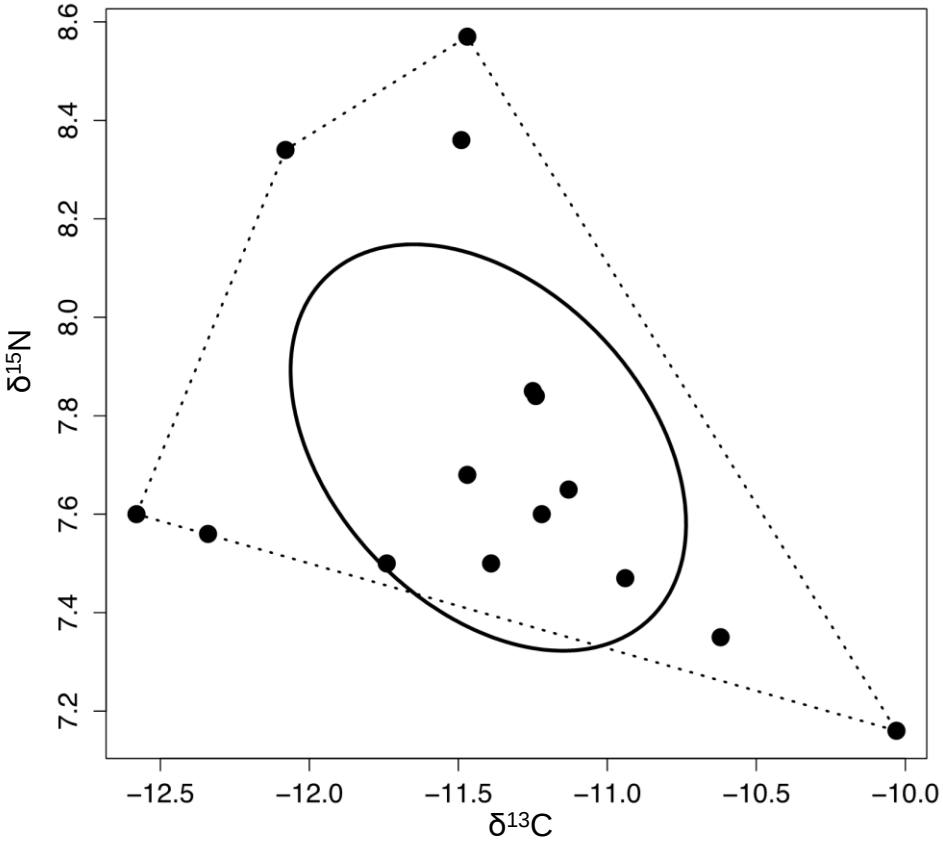
Damien Olivier[1] · Laura Gajdzik[1] · Eric Parmentier[1] · Bruno Frédérich[1]



Niches of damselfishes built using 5 kinematic traits linked with feeding behaviour

Isotopic niches – a word of caution

The isotopic niche is a proxy! It is influenced by both resource and habitat use. Relative importance of those two drivers is case-dependent. Know your system.



Isotopic niches – a word of caution

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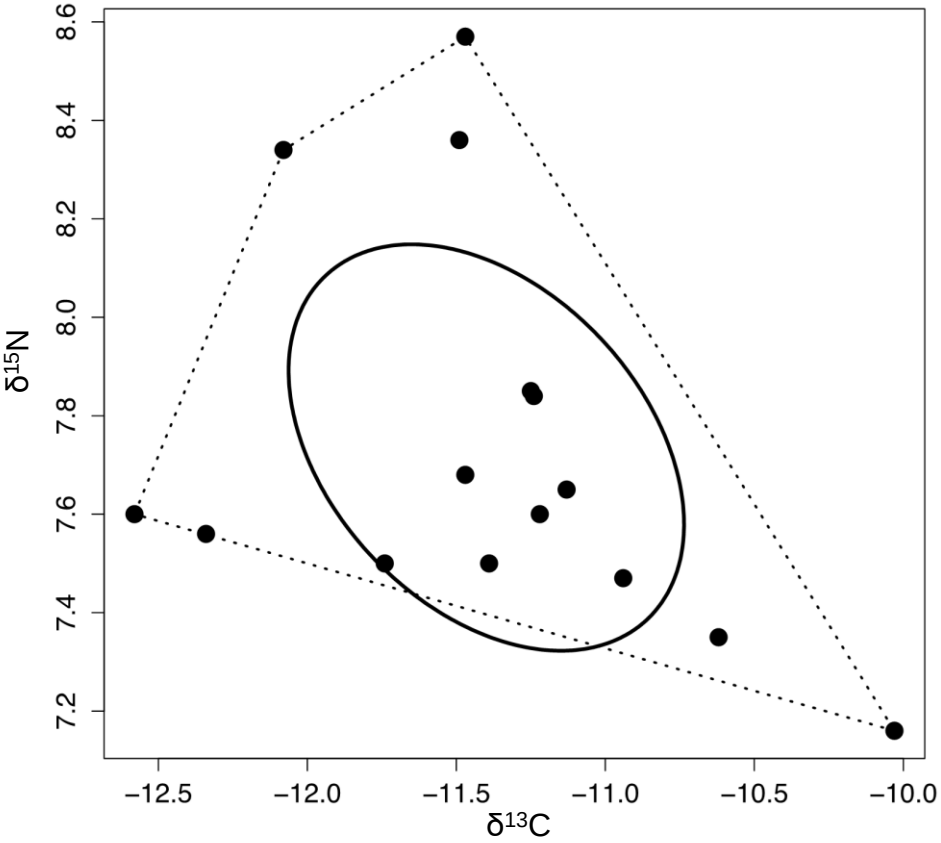
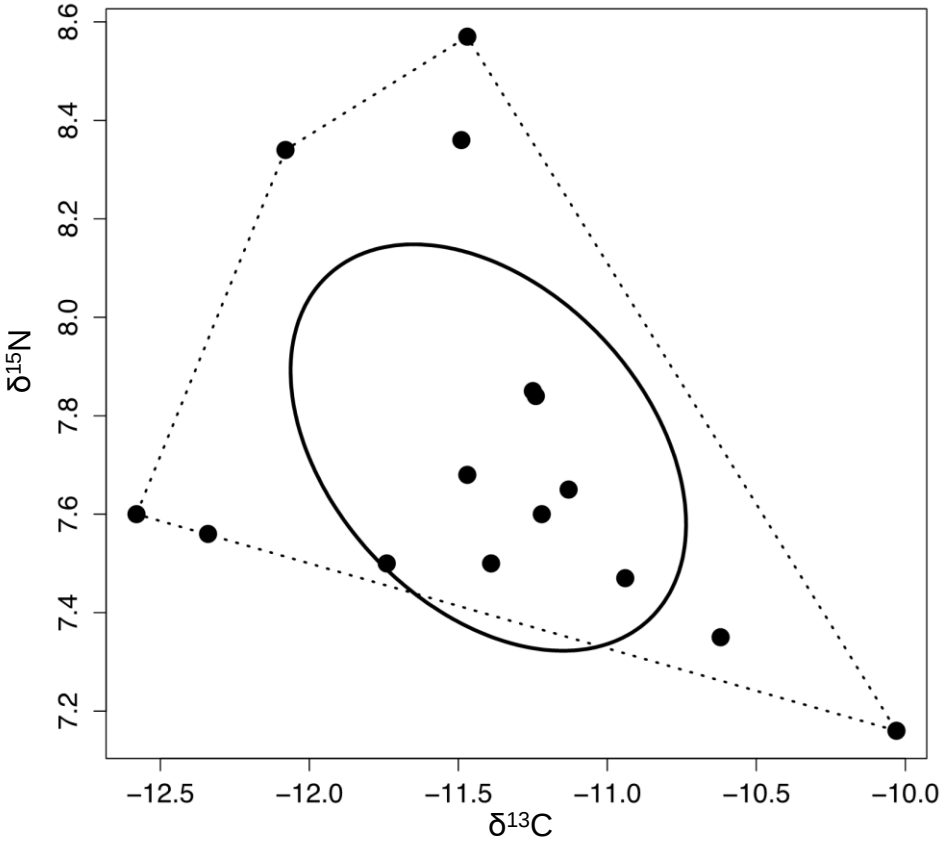
The isotopic niche is a proxy! Its resolution is limited. It only pictures adequately ecological phenomena that significantly influence stable isotope ratios. It will be insensitive to many others (*e.g.* diet shift between two prey that have similar isotopic compositions).



Isotopic niches – a word of caution

"Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful."

George E.P. Box
1919-2013



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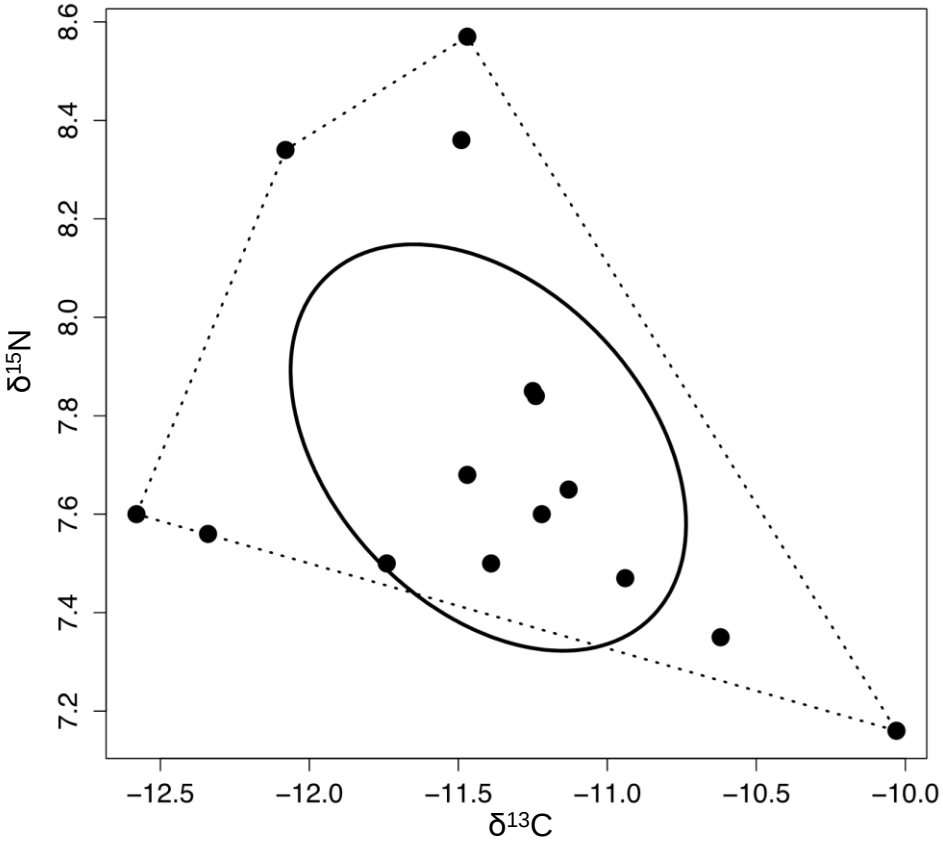

Isotopic niche study is a rapidly evolving field supported by many different approaches and concepts

When used sensibly, it is a robust and widely applicable method that can help solving many fundamental or applied ecological questions.

Images: Kevin Ebi - http://livingwilderness.blogspot.com. Full sequence: https://vimeo.com/272024913