Using stable isotopes to assess trophic niche differentiation in facultatively paedomorphic newts and the impact of fish introductions in their native habitats in Europe

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INTRODUCTION – Main questions

PART I. Testing the 'trophic advantage' hypothesis of facultative paedomorphosis

A) Does facultative paedomorphosis promote niche differentiation between paedomorphs and metamorphs in lakes ?
B) What about less heterogeneous, species-rich environments (i.e. ponds) ?

PART II. Try to elucidate trophic interactions with introduced fish and their impact on ecosystem, leading to newt extirpation

INTRODUCTION – Facultative paedomorphosis in newts

Example: Alpine newt (*Ichthyosaura alpestris*)
Salamandridae

Larvae

Metamorphic Adult

Strictly Aquatic Larvae

1. Metamorphosis
2. Terrestrial phase
3. Sexual maturity

Semi terrestrial Adults (aquatic breeding)

INTRODUCTION – Facultative paedomorphosis in newts

Larvae

1. ~~Metamorphosis~~
2. ~~Terrestrial phase~~
3. Sexual maturity

Metamorphic Adult

Paedomorphic Adult

INTRODUCTION – Species and habitats

2 ≠ habitats:

Semi-permanent ponds in mid-elevated lands

Deep oligotrophic high altitudinal **lakes**

Denoël 2007
Denoël et al. 2001

INTRODUCTION – Selective advantages ?

Metamorphic Adult

Paedomorphic Adult

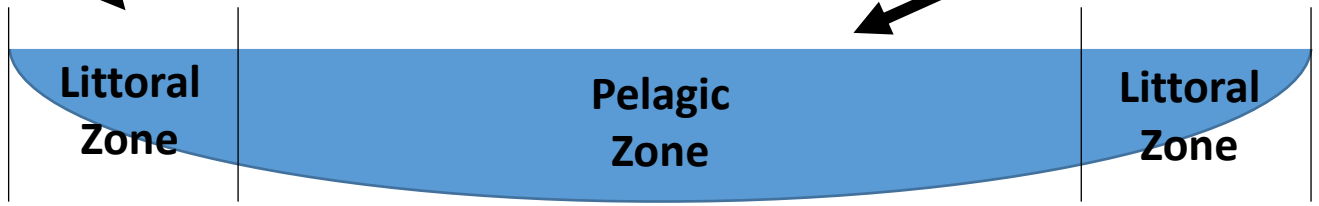
INTRODUCTION – The **'Trophic advantage'** hypothesis

Metamorphic Adult

No gills, large mouth
Feeding by snapping

Paedomorphic Adult

Gills, smaller mouth
Feeding by suction (unidirectional flow)



Denoël and Joly, 2001

INTRODUCTION – The **'Trophic advantage'** hypothesis

Metamorphic Adult

Feeding by snapping
Insectivorous, Littoral zone

RESOURCE PARTITIONING

Paedomorphic Adult

Feeding by suction (unidirectional flow)
Zooplanktivorous, Pelagic zone

<u>Hypothesis:</u> In a heterogenous environment, devoid of competitors, facultative paedomorphosis may promote trophic differentiation among morphs

Denoël and Joly, 2001

Part I – A) Trophic niche differentiation in lakes

Let's go investigate !

Part I – A) Methods

Stomach flushing + Caudal skin sample

Both techniques are non lethal !

‘La Cabane’ Lake

Last population *I. alpestris alpestris*

SAMPLING:

3 months after the start of reproduction:
amphibian skin turnover 2~3 months (Cloyed et al 2015)

- 2 phenotypes – 2 sexes

- Food sources

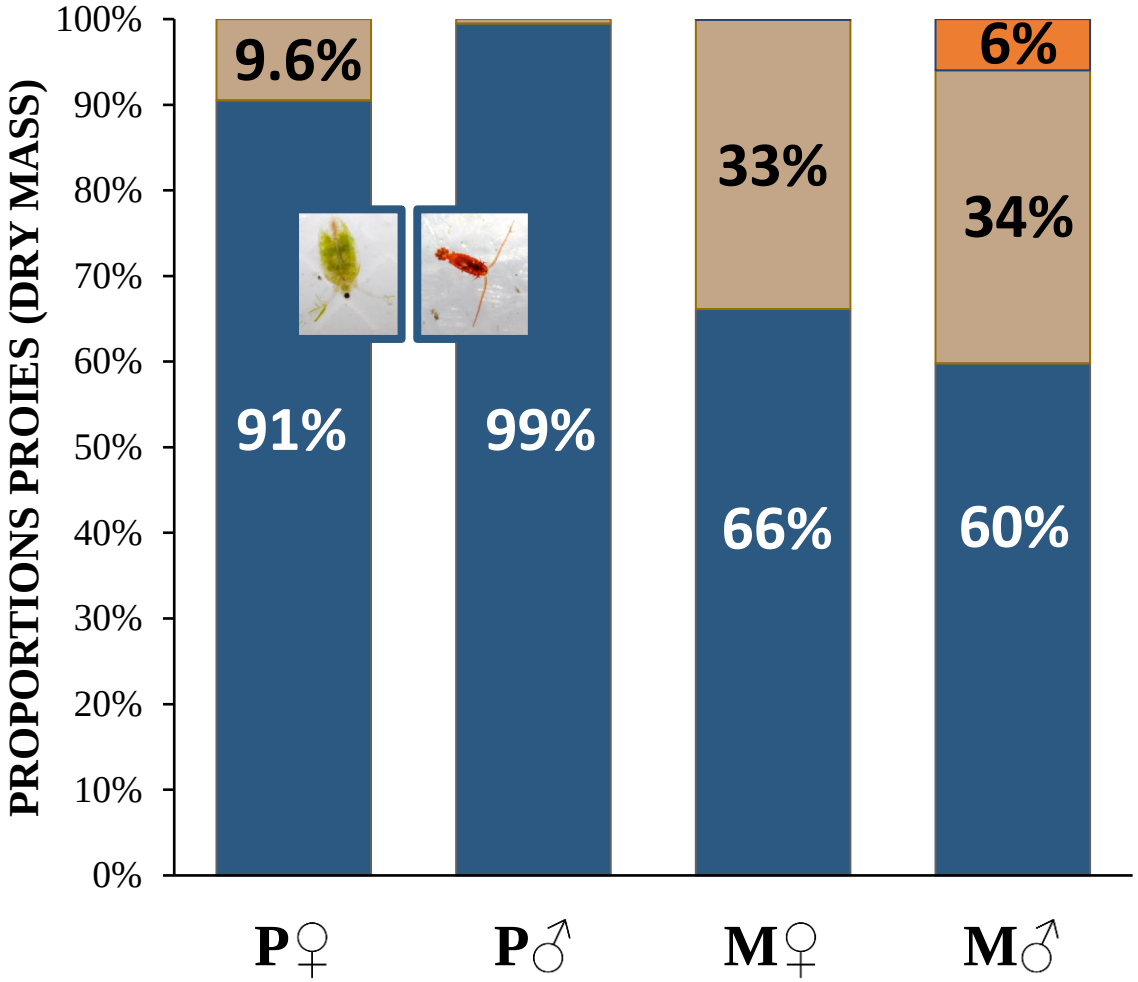
ANALYSIS:

➔ **Stomach content analysis**

➔ EA-IRMS : Bulk $\delta^{13}C$, $\delta^{15}N$: **Isotopic Niches, Mixing Models**

Part I – Stomach content analysis

Lejeune et al. 2018 Oikos



Terrestrial prey

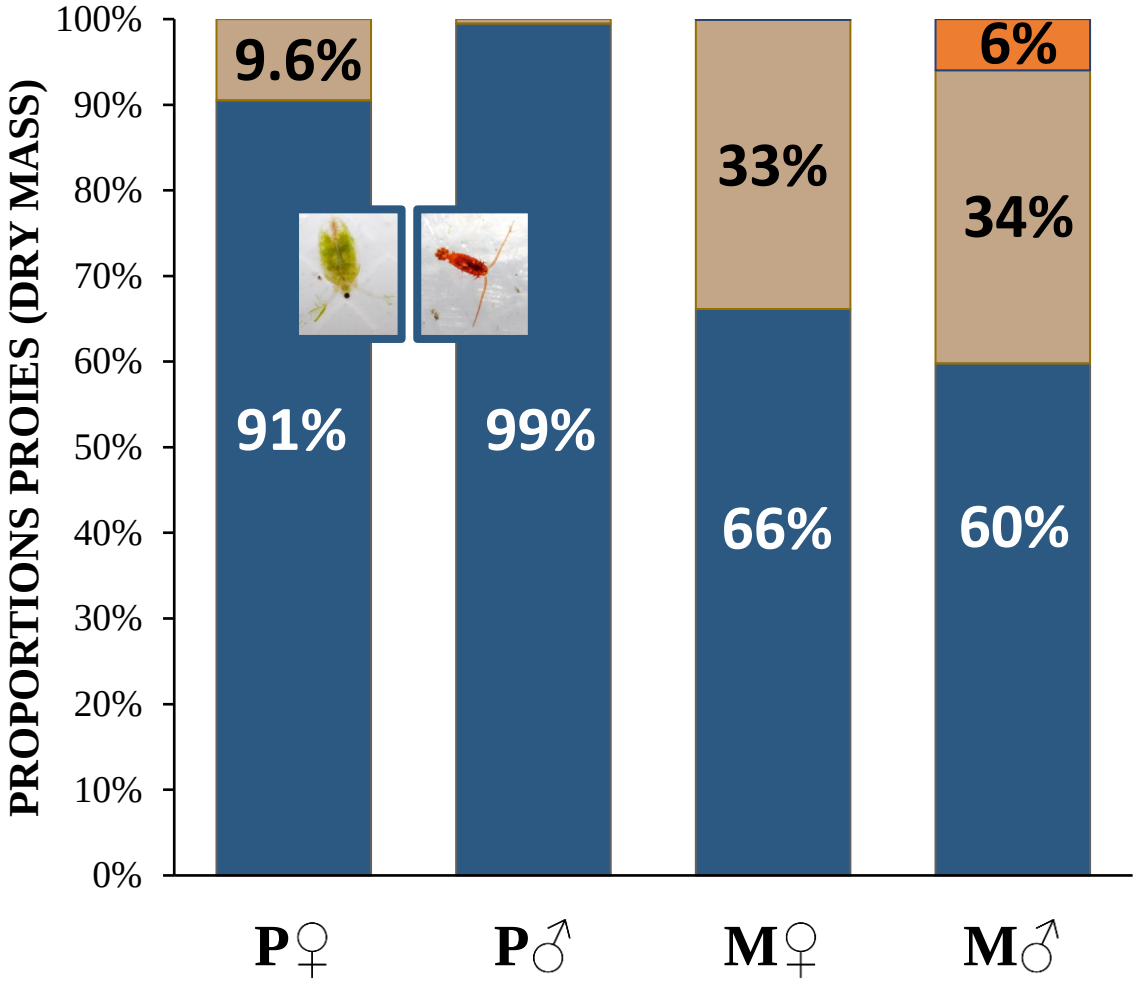
Littoral-benthic prey

Pelagic prey

Part I – Stomach content analysis

Lejeune et al. 2018 Oikos

H'	*H'*	*H'*	*H'*
0.47 ± 0.08	0.54 ± 0.11	0.89 ± 0.07	0.79 ± 0.08



Diet breadth (*H'*)

Paedomorphs < Metamorphs (**p<0.001**)

Diet differences

→ PERMANOVA :

Phenotype p<0.01

→ SIMPER :

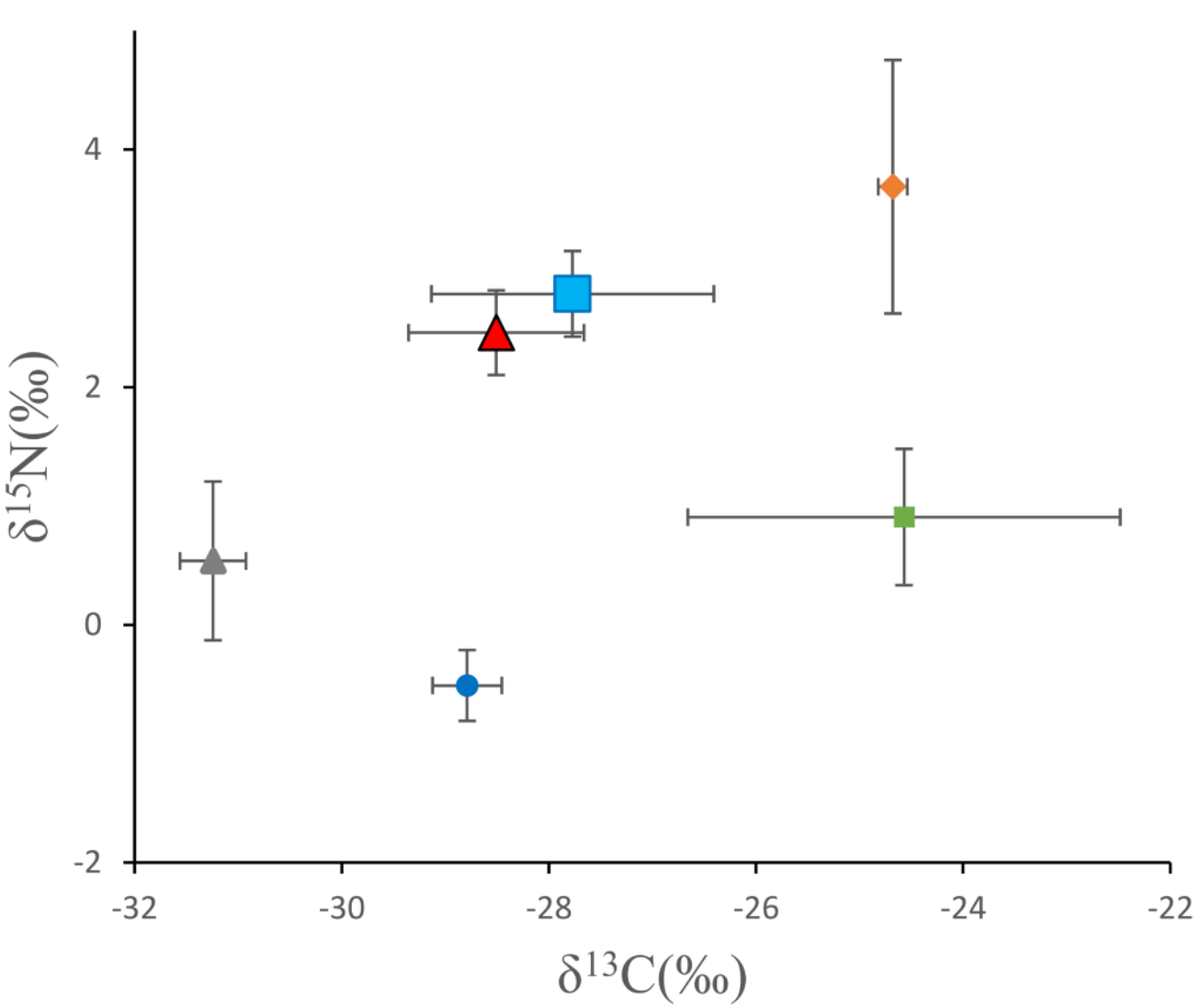
Zooplankton ~ 30%

2 ≠ strategies, similar efficiency

No effect of phenotype, sex or interaction on **Body condition** and **total ingested dry mass**

Part I – A) Stable isotope analysis

Lejeune et al. 2018 Oikos



Isotopic niche modelling (SIBER)

➔ Niche differentiation

Bayesian mixing models (SIAR)

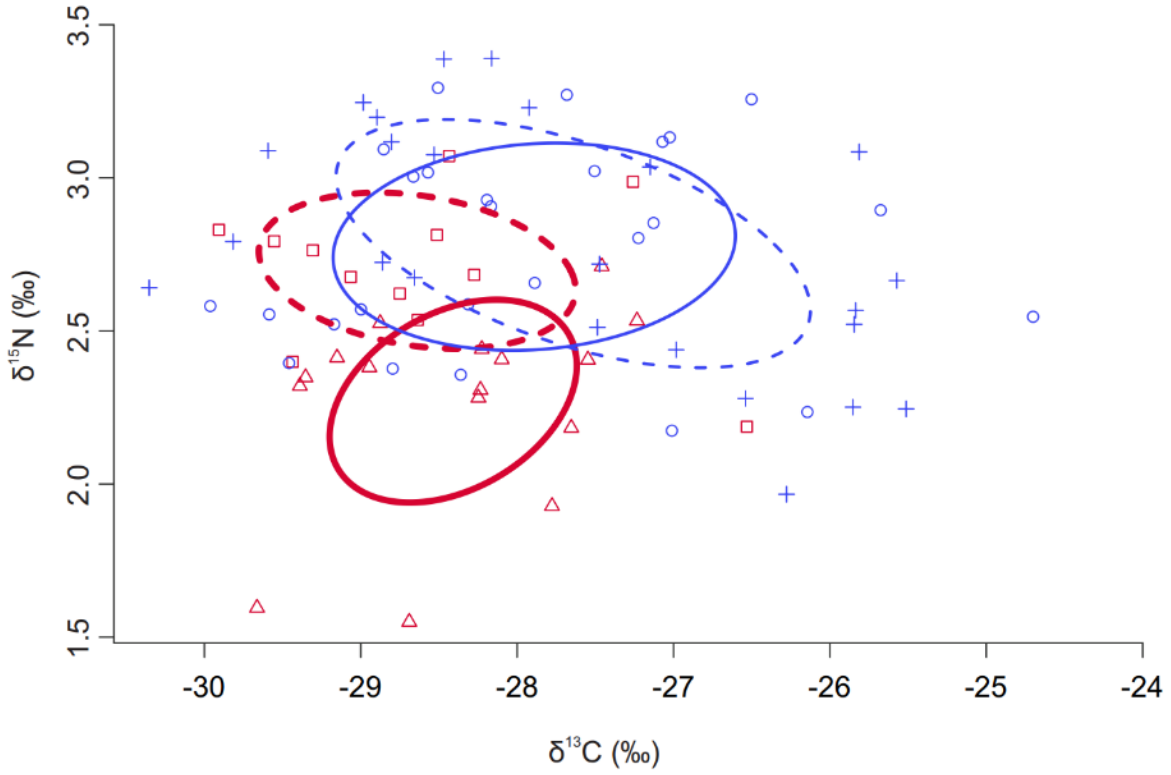
➔ Food source contribution to stable isotope composition of newts

SIBER: Jackson et al. 2011, SIAR: Parnell et al. 2010

Part I – A) Stable isotope analysis

Lejeune et al. 2018 Oikos

Isotopic niche analysis



Legend:

Paedomorphs, **metamorphs**

Full lines = **Females**

Dashed lines = **Males**

Isotopic niche width vs diet breadth:

	SEA_B (95% CI)	H' (± SD)
P♀	0.70 (0.40–1.16)	0.47 ± 0.08
P♂	0.66 (0.38–1.25)	0.54 ± 0.11
M♀	1.25 (0.86–1.89)	0.89 ± 0.07
M♂	1.50 (1.02–2.36)	0.79 ± 0.08

Niche overlaps:

P♂ overlap more with M♀/♂ than with P♀

Centroïd differences:

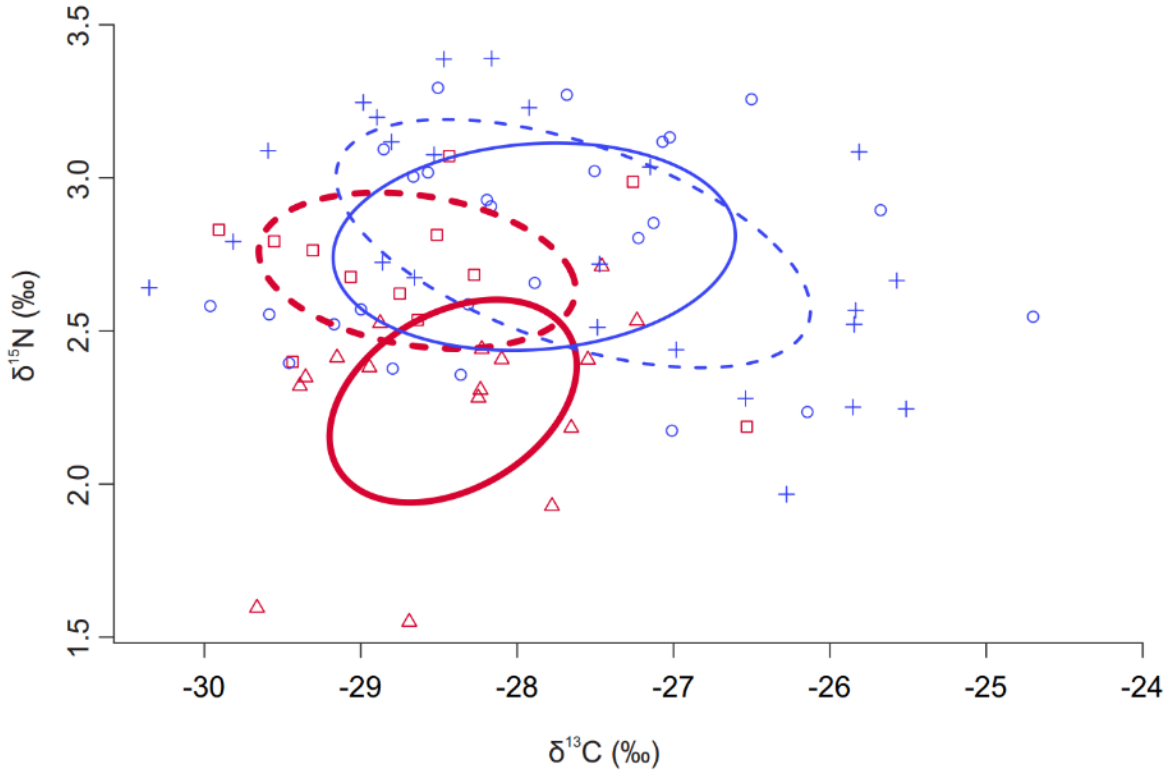
Phenotype: p < 0.001

Phenotype x Sex: p < 0.01

Part I – A) Stable isotope analysis

Lejeune et al. 2018 Oikos

Isotopic niche analysis



Dude, why do you behave like a metamorph ?

Sex mate, it's all about sex !

Legend:

Paedomorphs, **metamorphs**

Full lines = **Females**

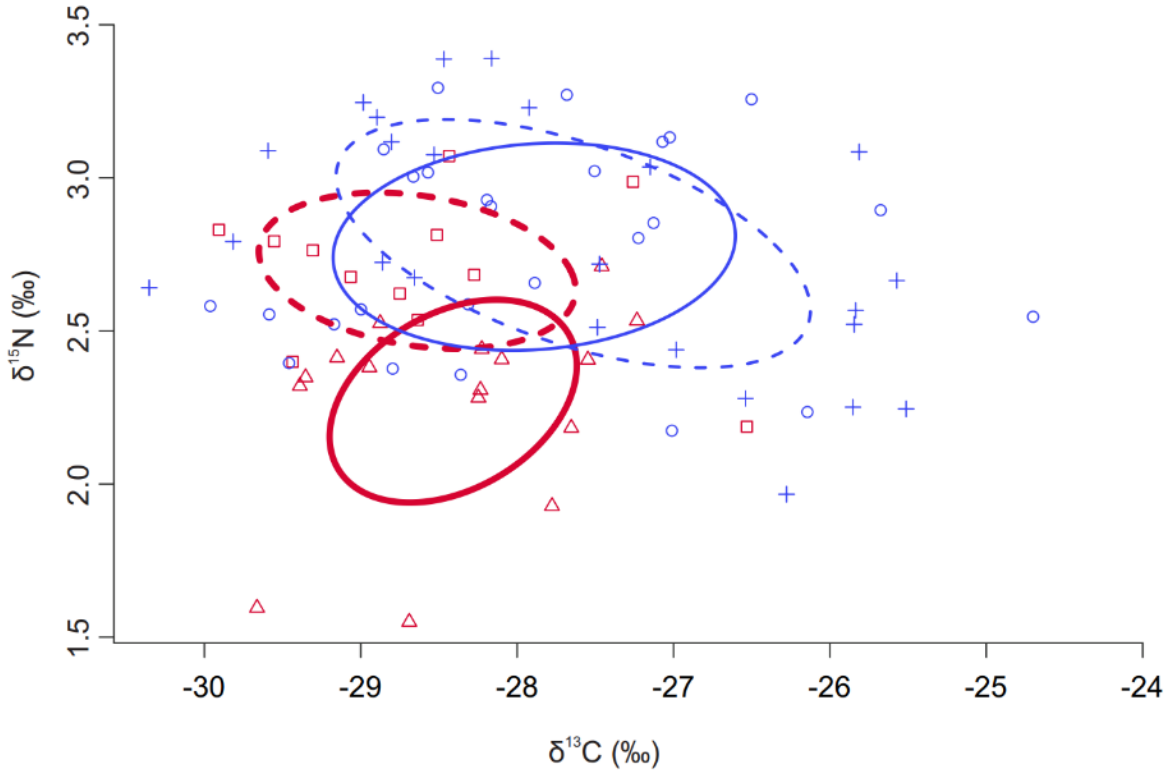
Dashed lines = **Males**

Courtship behaviour = LITTORAL ZONE

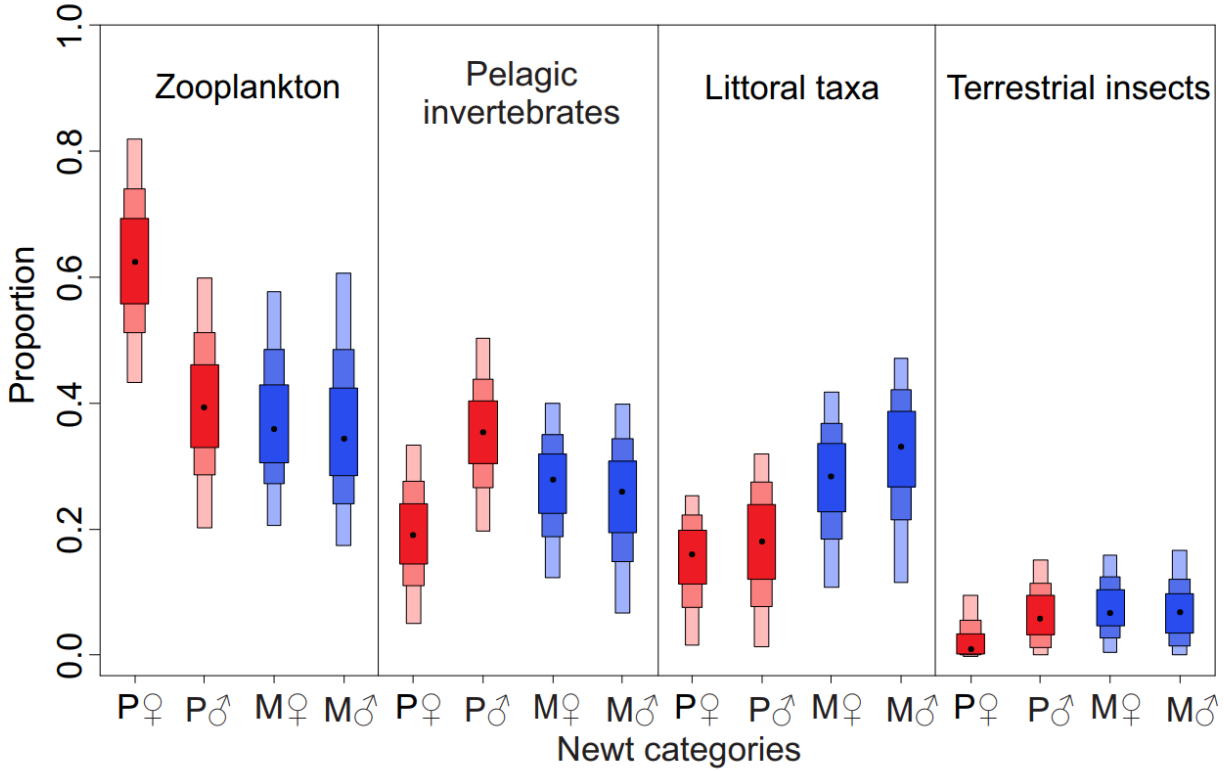
Part I – A) Stable isotope analysis

Lejeune et al. 2018 Oikos

Isotopic niche analysis



Diet analysis using mixing models



Legend:

Paedomorphs, **metamorphs**

Full lines = **Females**

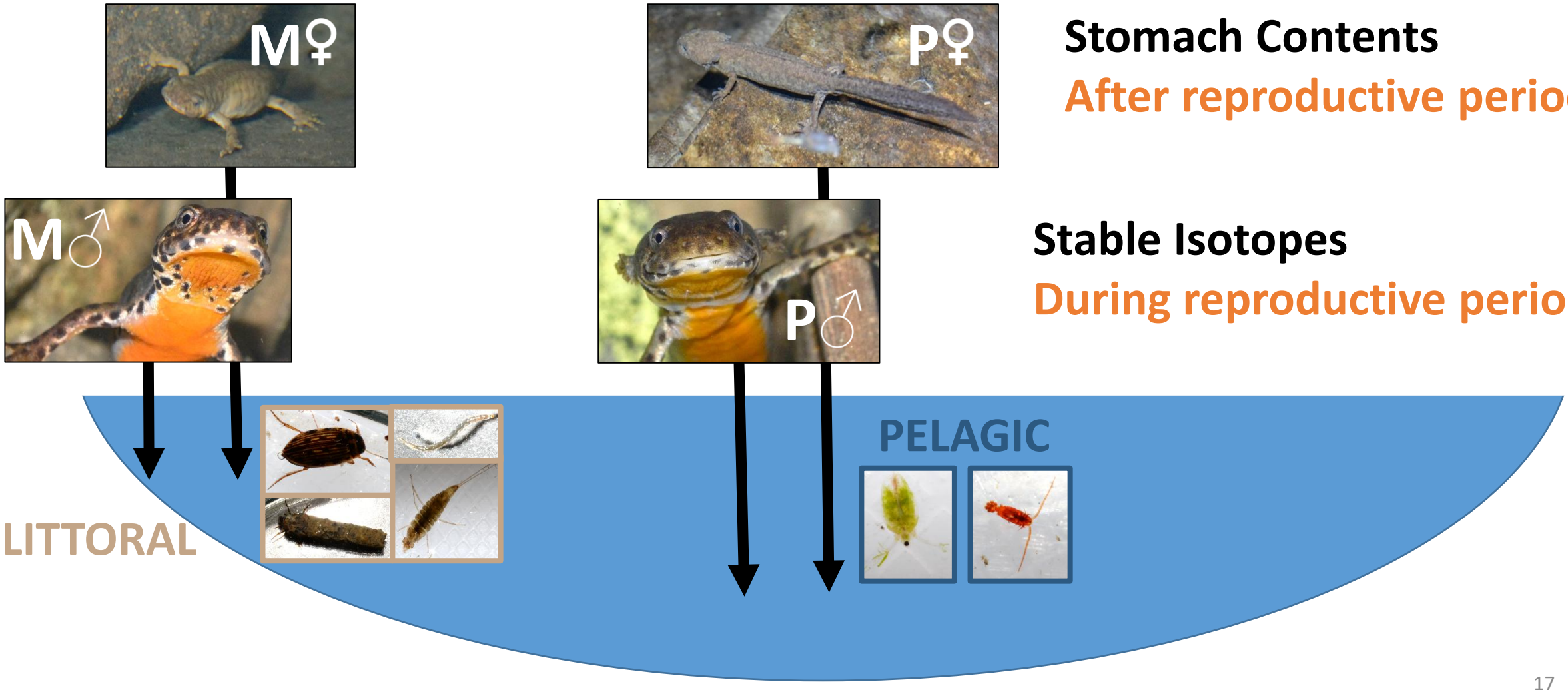
Dashed lines = **Males**

Niche expansion by paedomorphs = **30%**

Lejeune et al. 2018 Oikos

METAMORPHS

PAEDOMORPHS



Stomach Contents

After reproductive period

Stable Isotopes

During reproductive period

Part I – A) Conclusion

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Trophic niche differentiation (littoral-pelagic axis)
Niche expansion to underused resources (‘vacant niche’)
Importance of sex difference in the maintenance of polyphenisms

But what about species-rich, less heterogeneous environments … ?

Part I – B) Palmate newt and the pond ecosystem

Larzac region (France)

Hotspot for facultative paedomorphosis

(Denoël, 2007)

'Lavogne' : Typical man-made pond

→ Very diverse aquatic ecosystems in 'arid' terrestrial environment

Can facultative paedomorphosis also promote niche differentiation in such habitats?

Part I – B) Methods

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4 permanent ponds

A → D (↑ dimensions, ↓ newt density)

Palmate newt (*Lissotriton vulgaris*)

SAMPLING:

3 months after the start of reproduction:
amphibian skin turnover 2~3 months (Cloyed et al 2015)

- 2 phenotypes –grouped sexes

- Food sources

ANALYSIS:

➔ **Stomach content analysis**

➔ EA-IRMS : Bulk $\delta^{13}C$, $\delta^{15}N$: **Isotopic Niches, Mixing Models with SC data as priors** (Mixsiar)

Mixsiar: Stock & Semmens 2016

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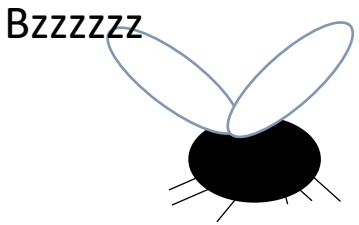
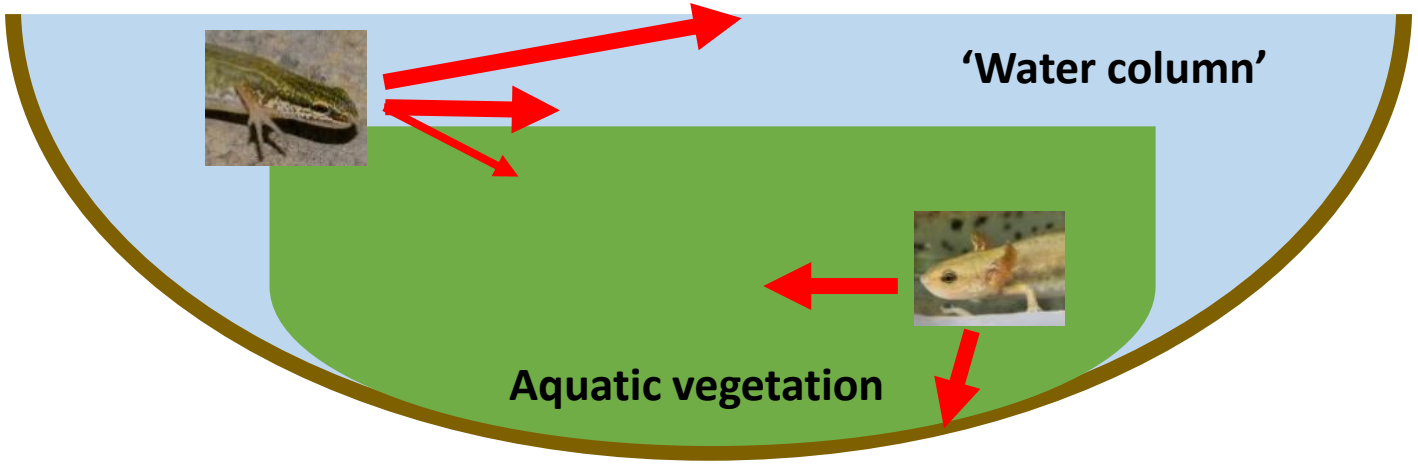
Stomach contents and stable isotope mixing model results

Stomach Content data

Stable isotope mixing models





Part I – B) Isotopic niche differentiation across sites

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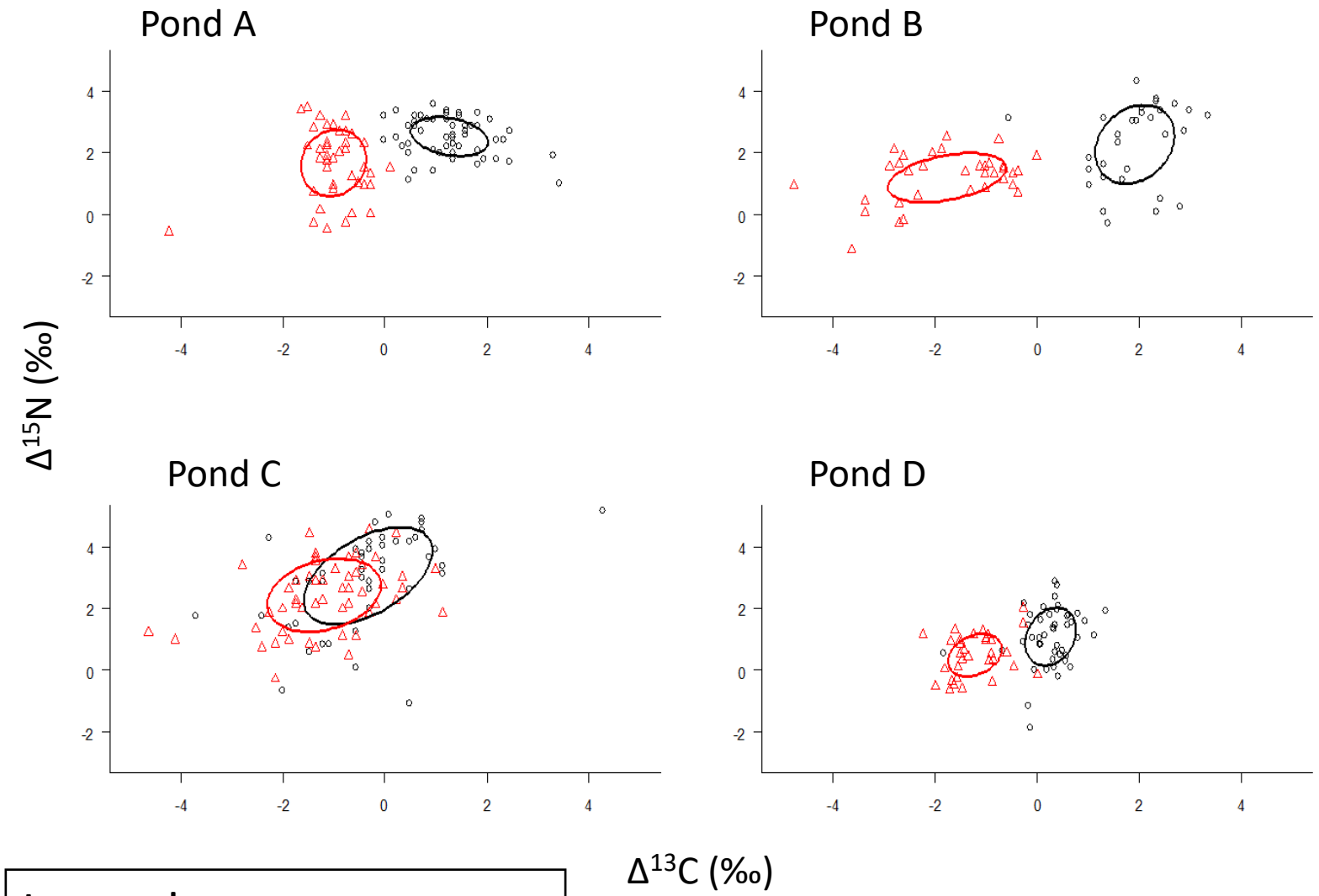


Legend:
Metamorphs, **paedomorphs**

➔ **Standardisation of isotope data according to isotopic variability of resources across sites**

Patterns of niche location

➔ Segregation in all ponds

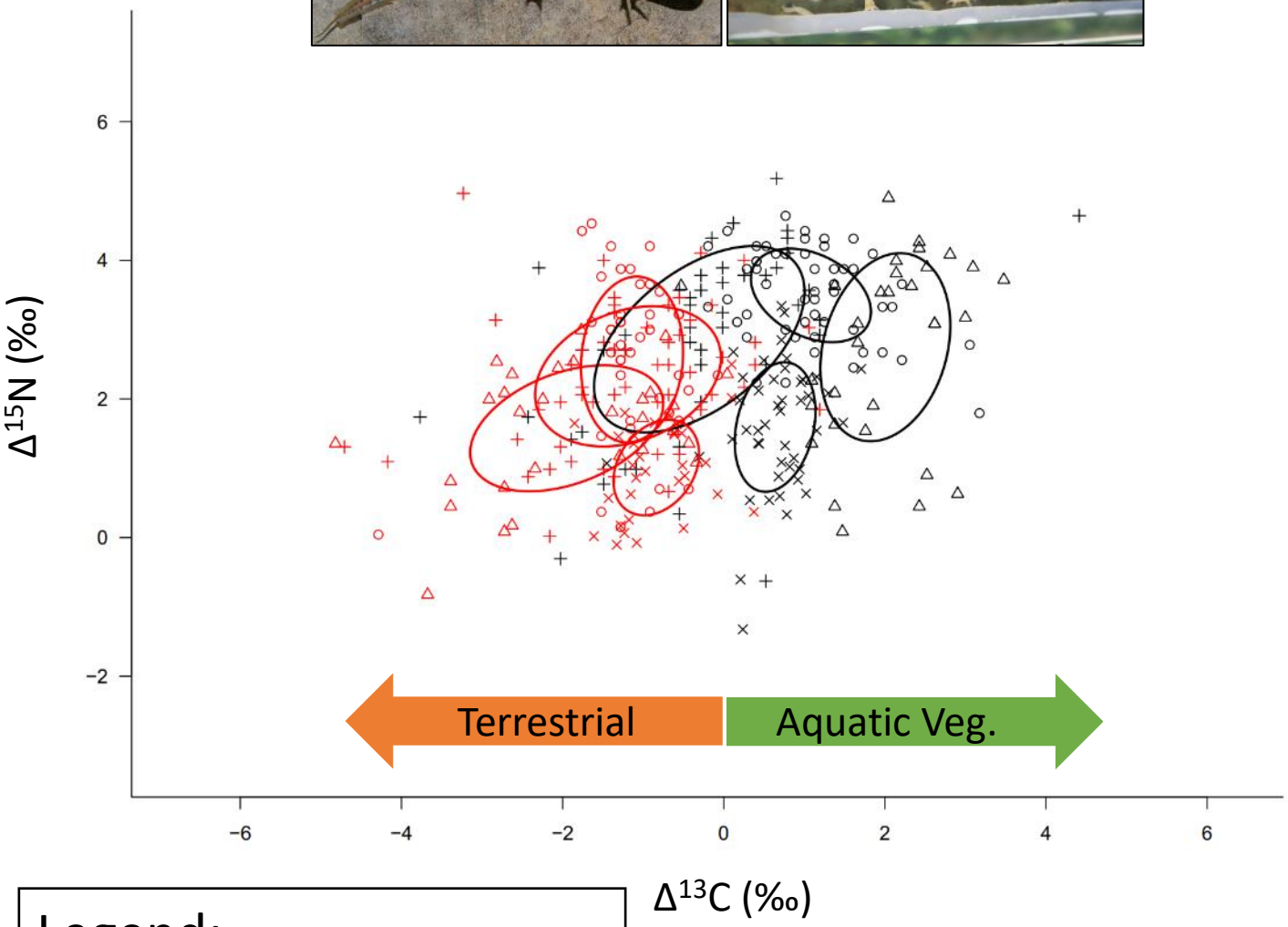
Smallest – Largest (lowest density)

➔ Similar pattern across ponds: $\Delta^{13}C$ Metamorphs < Paedomorphs

➔ Partial overlap in Pond C (linked to the overabundance of one type of prey)

Part I – B) Isotopic niche differentiation across sites

Lejeune et al. *in prep*



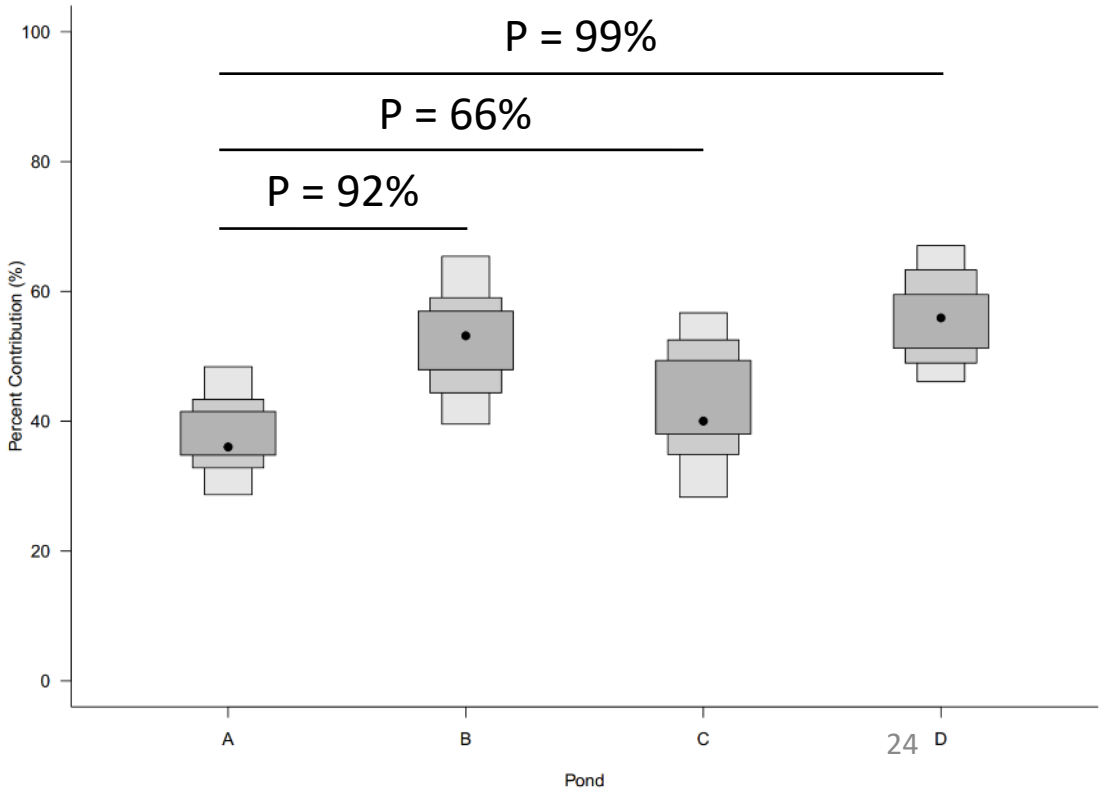
Legend:

Metamorphs, **paedomorphs**

➔ Metamorphic niche appears stationary

➔ Paedomorphic niche is shifting

% Contribution of paedomorphosis:



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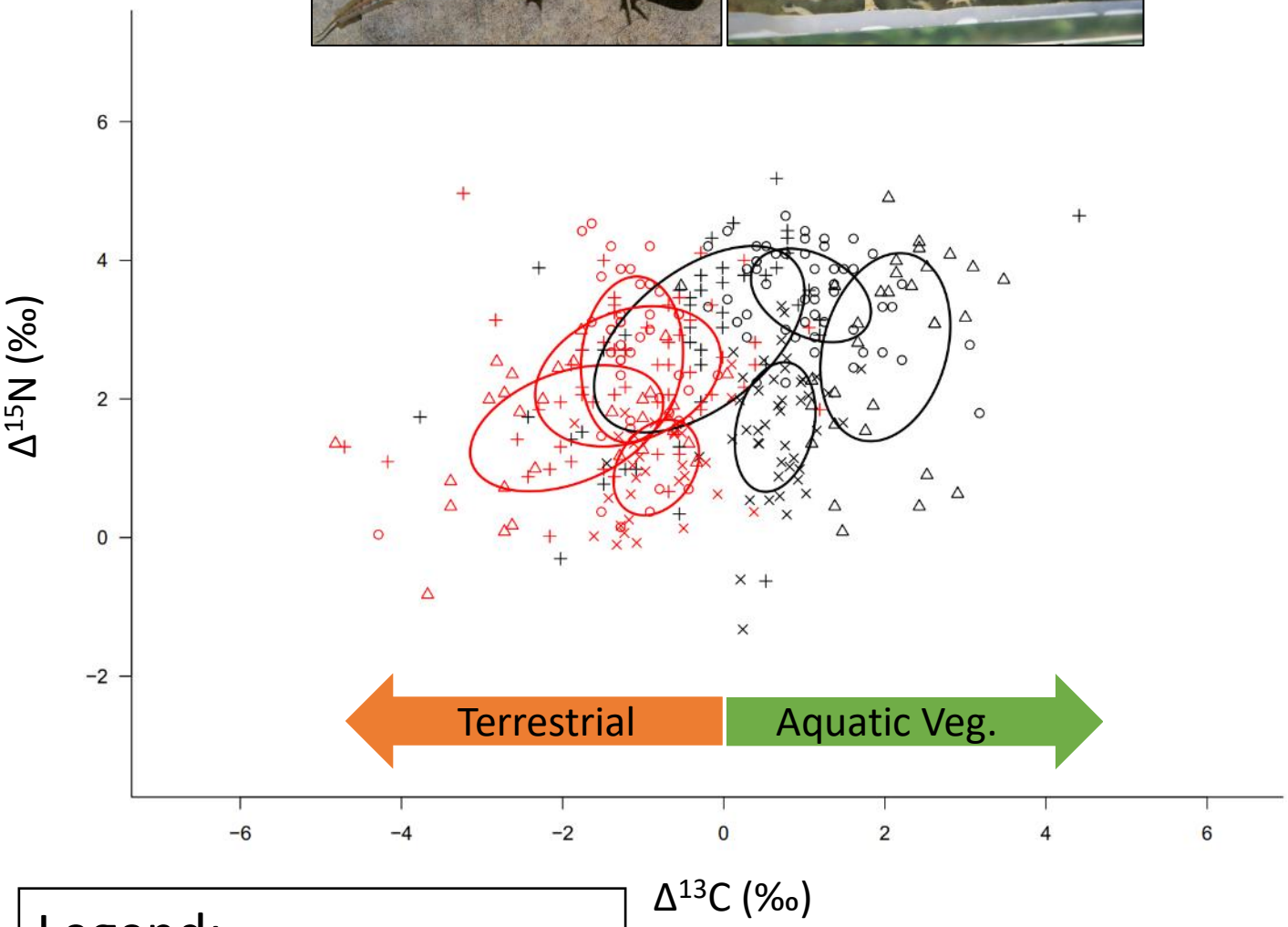
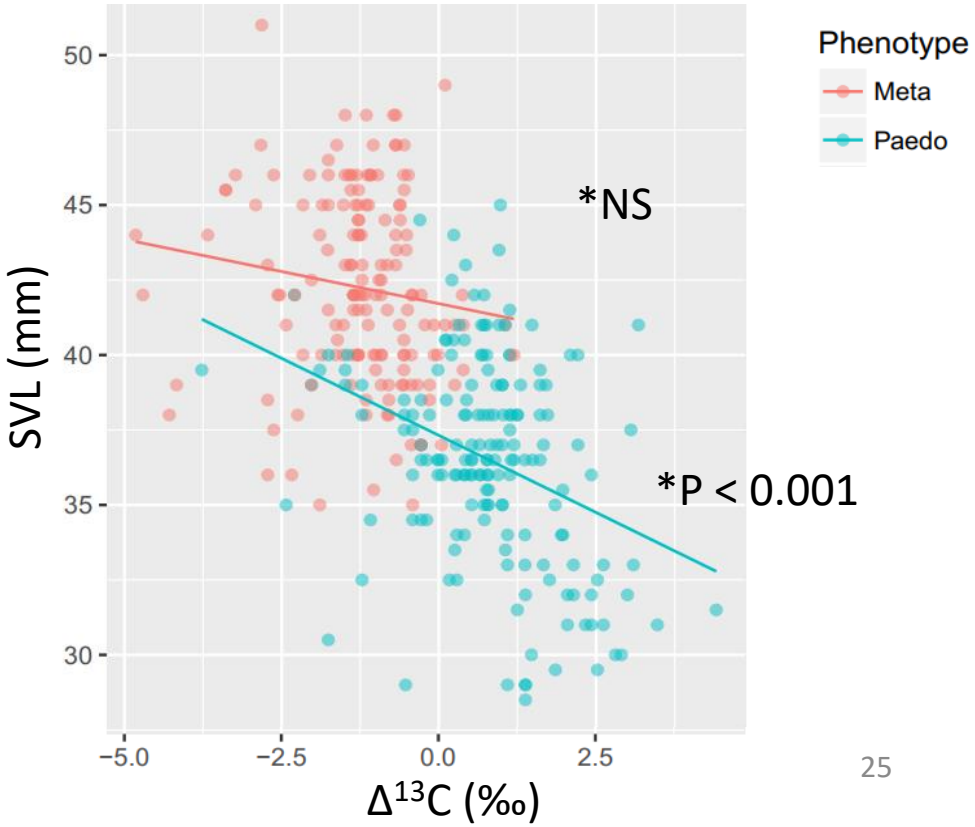


➔ Metamorphic niche appears stationary

➔ Paedomorphic niche is shifting

Body length ~ Δ^{13}C * Phenotype



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Metamorphs, **paedomorphs**

Part I – B) Conclusion

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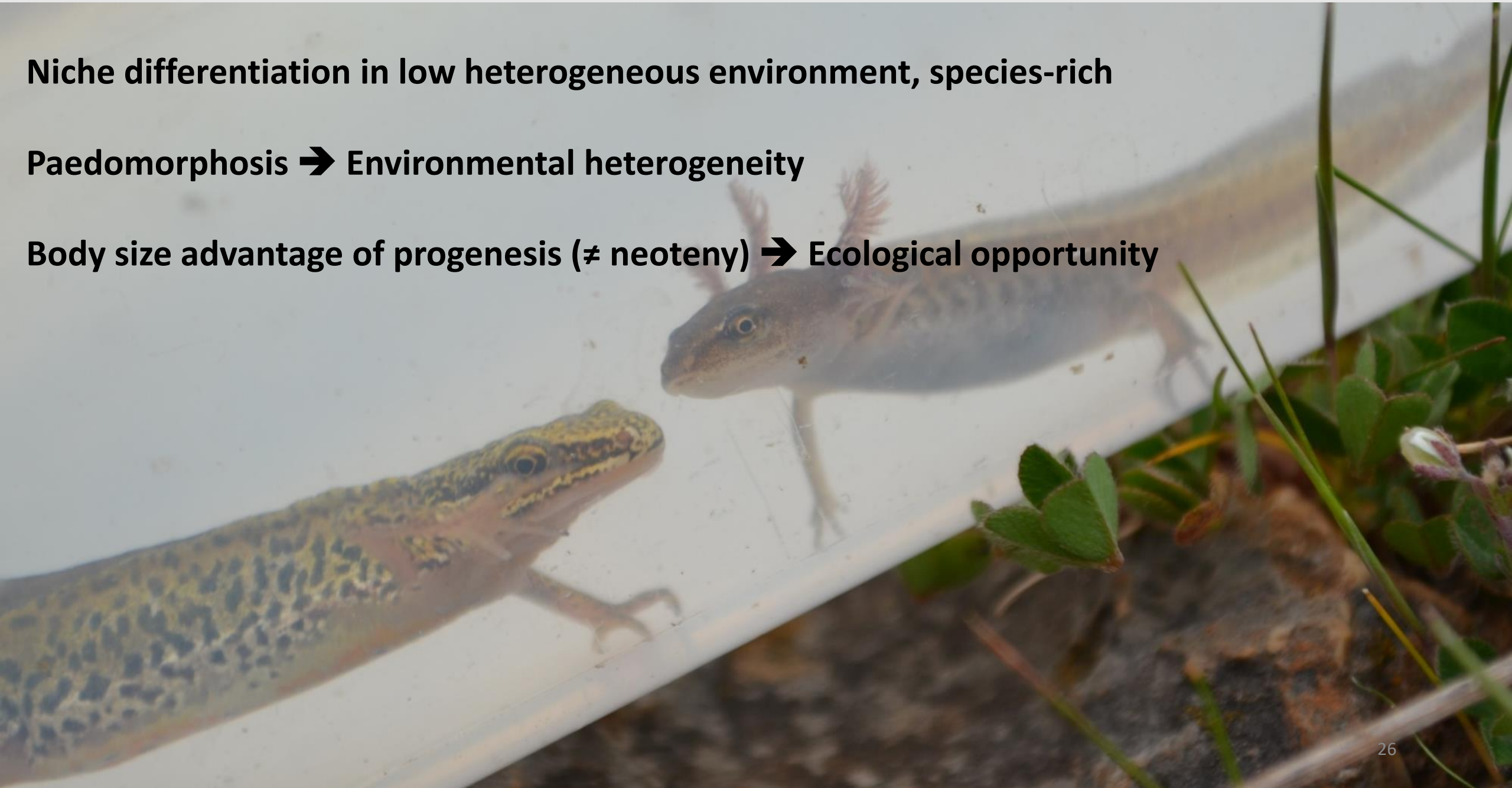


Niche differentiation in low heterogeneous environment, species-rich

Paedomorphosis ➔ Environmental heterogeneity

Body size advantage of progenesis (≠ neoteny) ➔ Ecological opportunity

Part II – The impact of fish introductions

Part II – Invasive fish species and amphibians decline

Invasive species = global threat to amphibians (Stuart et al. 2004)

Fish introductions = global threat to aquatic ecosystems (Lodge et al. 1998)

Cases of '**non predatory**' species introductions are sometimes disregarded…

→ Impact of **omnivorous** species is often very complex

→ May be highly detrimental to the whole community

Part II – Palmate newt population decline in Larzac (France)

Larzac region (France)

Fish introductions→ Decline of palmate newts

(Denoël & Lehman, 2006; Denoël & Winandy, 2015)

Main invasive: *Carassius auratus*

'Lavogne' : Typical man-made pond

→ Shelter for many amphibian species, rare aquatic insects…

Part II – Effect of Goldfish on palmate newt ?

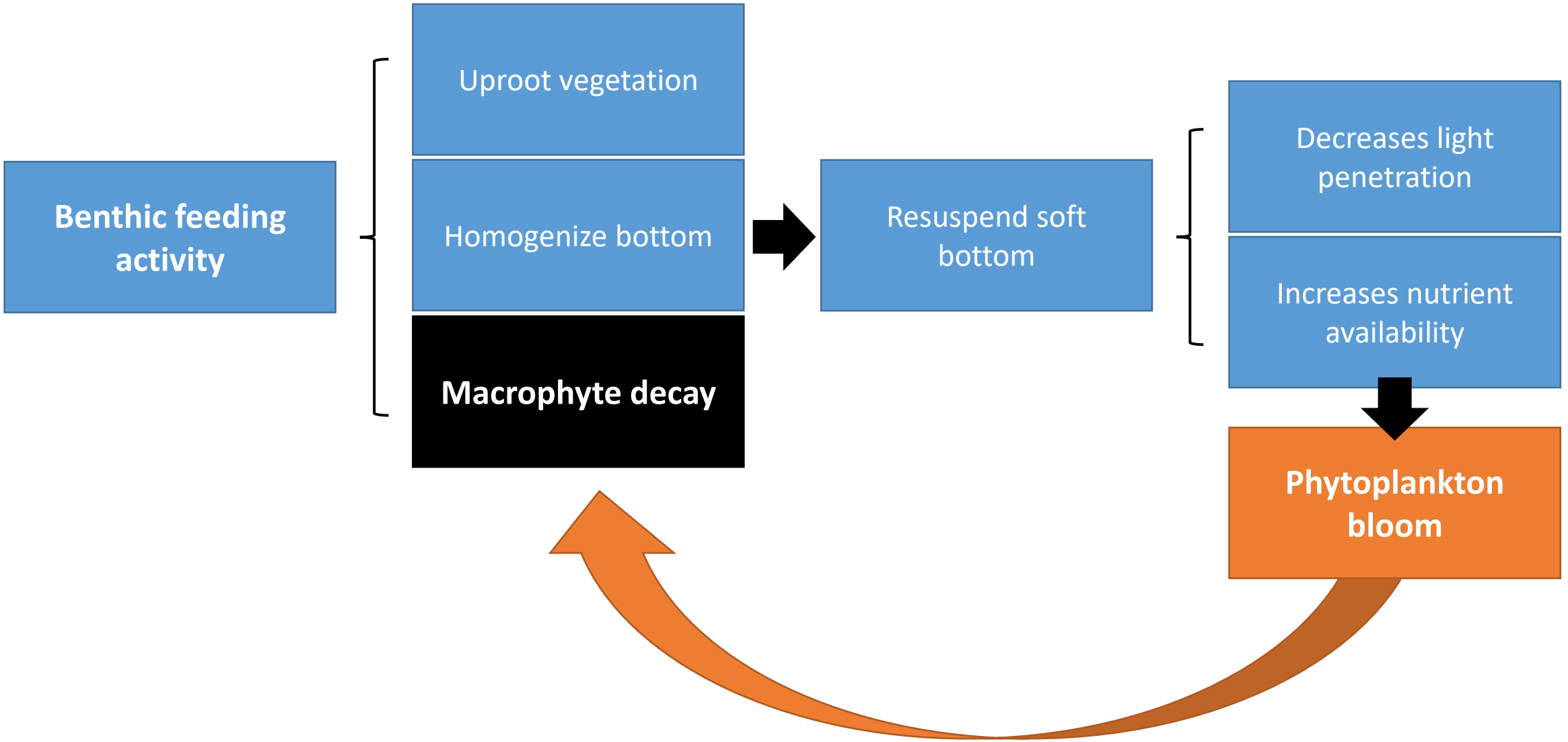
Mechanisms of exclusion of palmate newt ?

Part II – Impact of Goldfish on permanent pond foodweb

Lejeune et al. *in prep*

You cannot miss it, yet how do you explain it ?

Part II – A fish that modifies the habitat when introduced



➔ **What impact on the consumer foodweb?**

Richardson et al. 1995

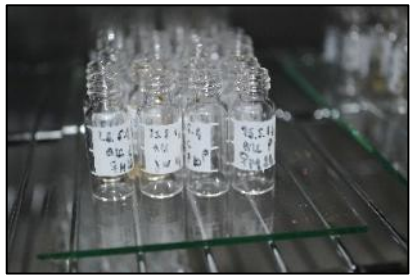
Part II – Effect of Goldfish on palmate newt ?

Quantifying the long-term impact of goldfish on the foodweb of permanent ponds using stable isotopes

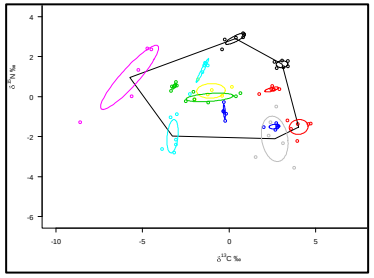
➔ **Exclusion of palmate newts ?**

➔ **Consumer compartment** – isotopic niche approach to describe changes

Part II – Summary of the methods





Sites:

8 ponds in Larzac region (France)

- 4 with **introduced goldfish**
- 4 **without fish**

Samples:

Aquatic consumers (n=6 per taxa)

Oven-dried for 72h, 60°C

EA-IRMS : **Bulk $\delta^{13}C$, $\delta^{15}N$**

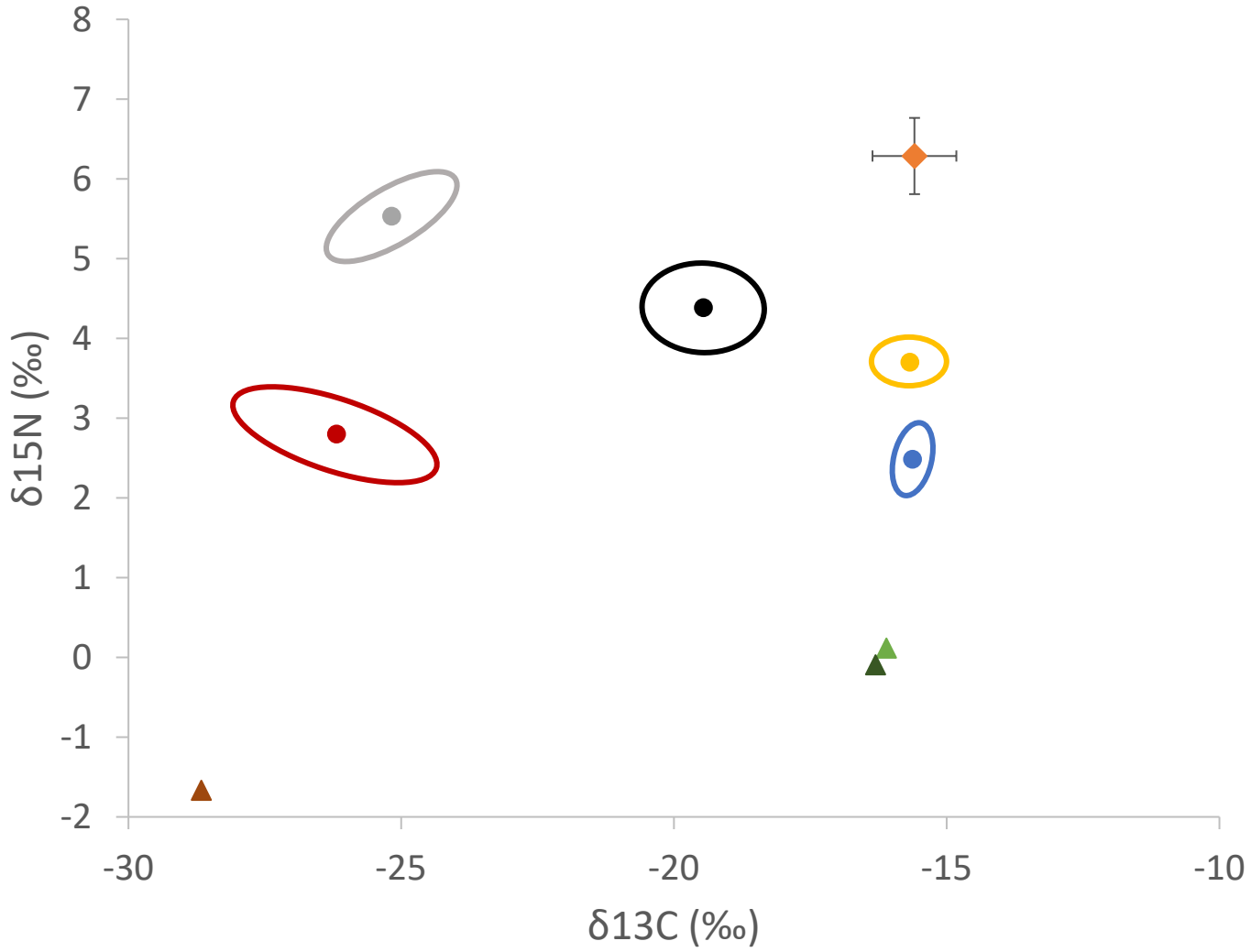
Tools:

Stable isotope niche modelling (Jackson et al. 2011) and Layman metrics (Layman et al. 2007) in a Bayesian framework

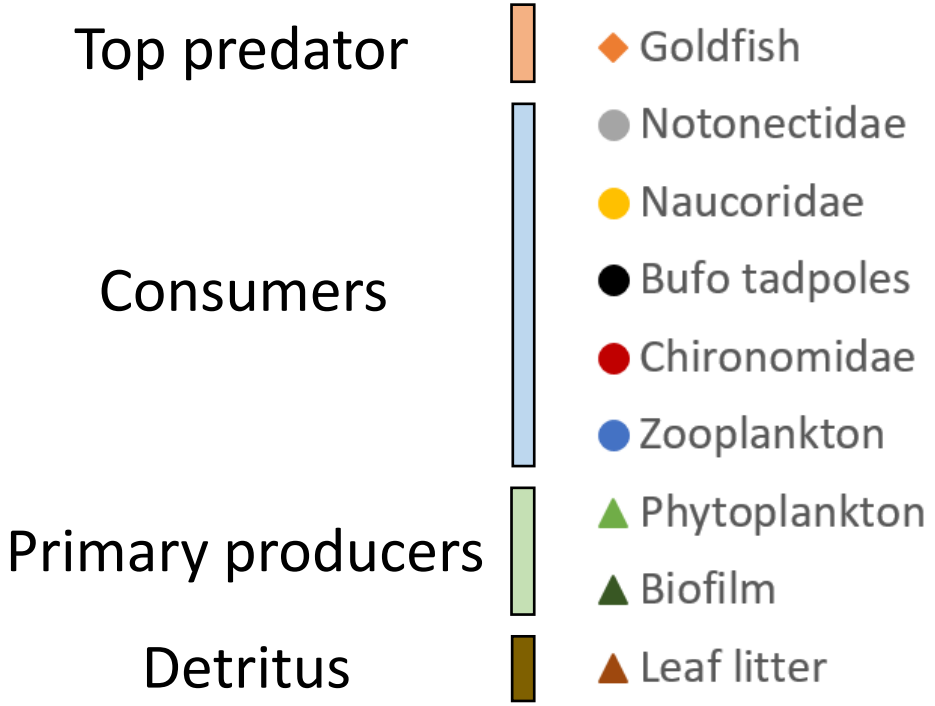
Density measurements

Part II – Community isotopic niche approach

Example of a community in the 'isospace'



Source: http://www.bbc.com/earth



Part II – Community isotopic niche approach

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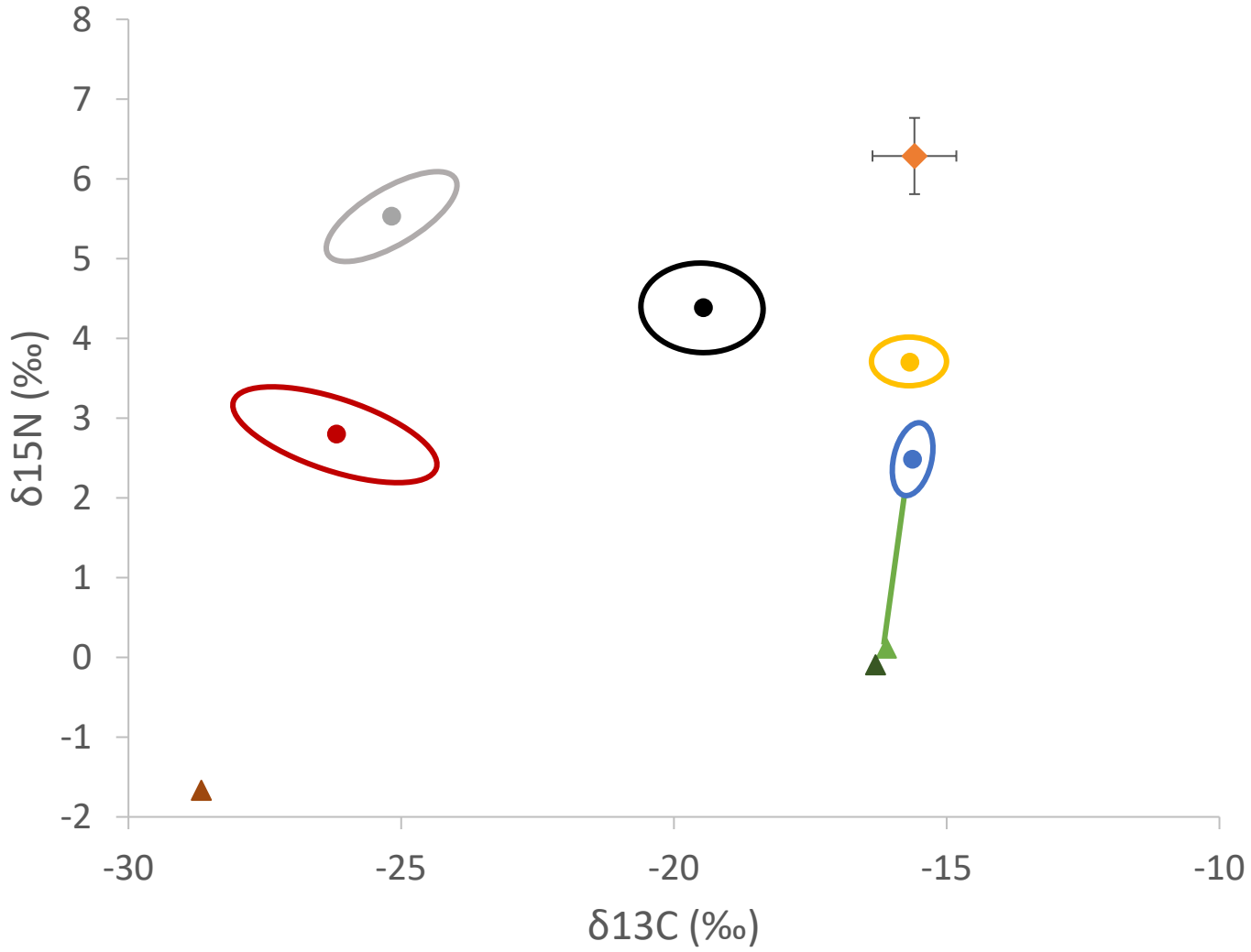
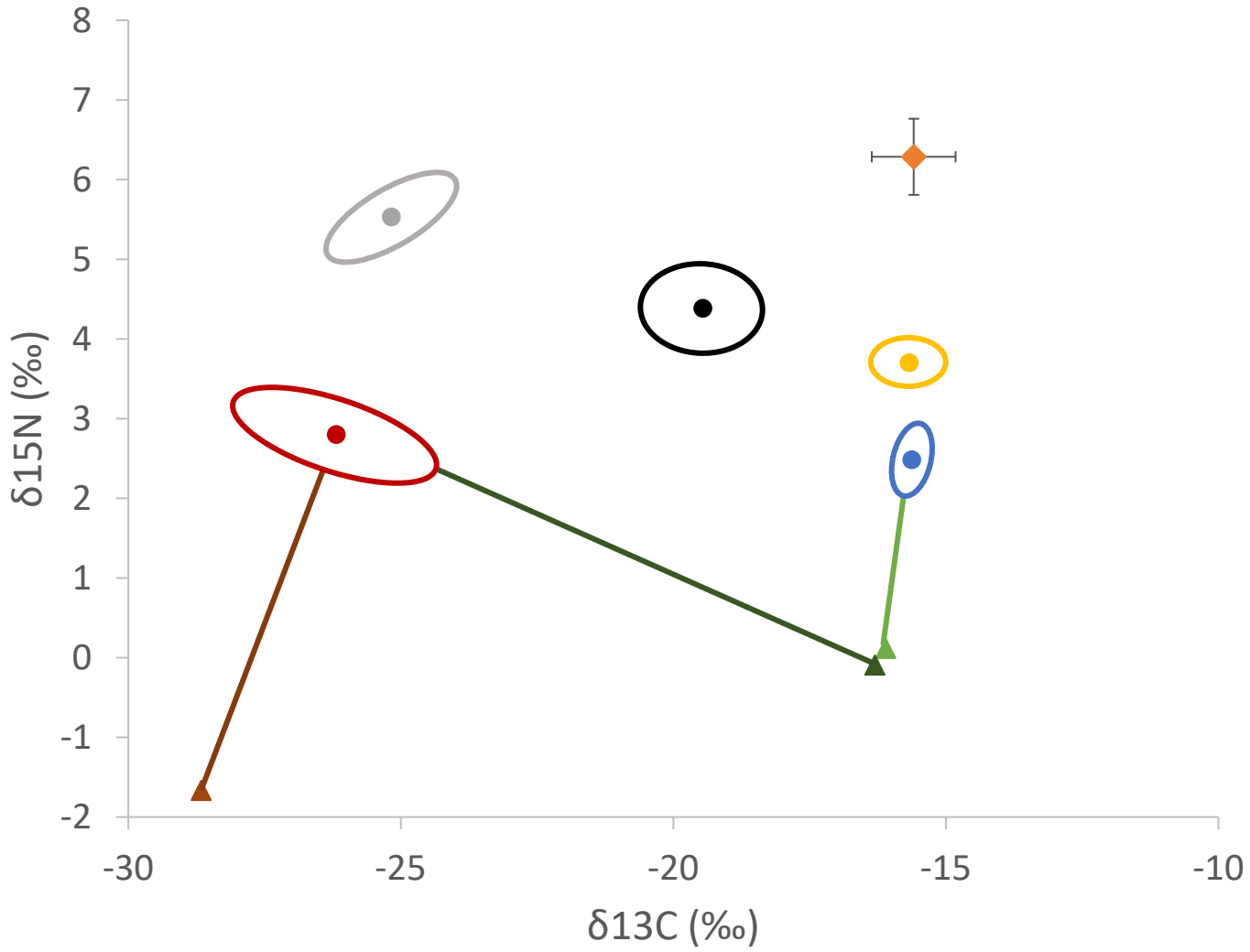


δ15N increases with trophic level

- Goldfish
- Notonectidae
- Naucoridae
- Bufo tadpoles
- Chironomidae
- Zooplankton
- Phytoplankton
- Biofilm
- Leaf litter

Part II – Community isotopic niche approach

δ13C indicates basal sources reliance



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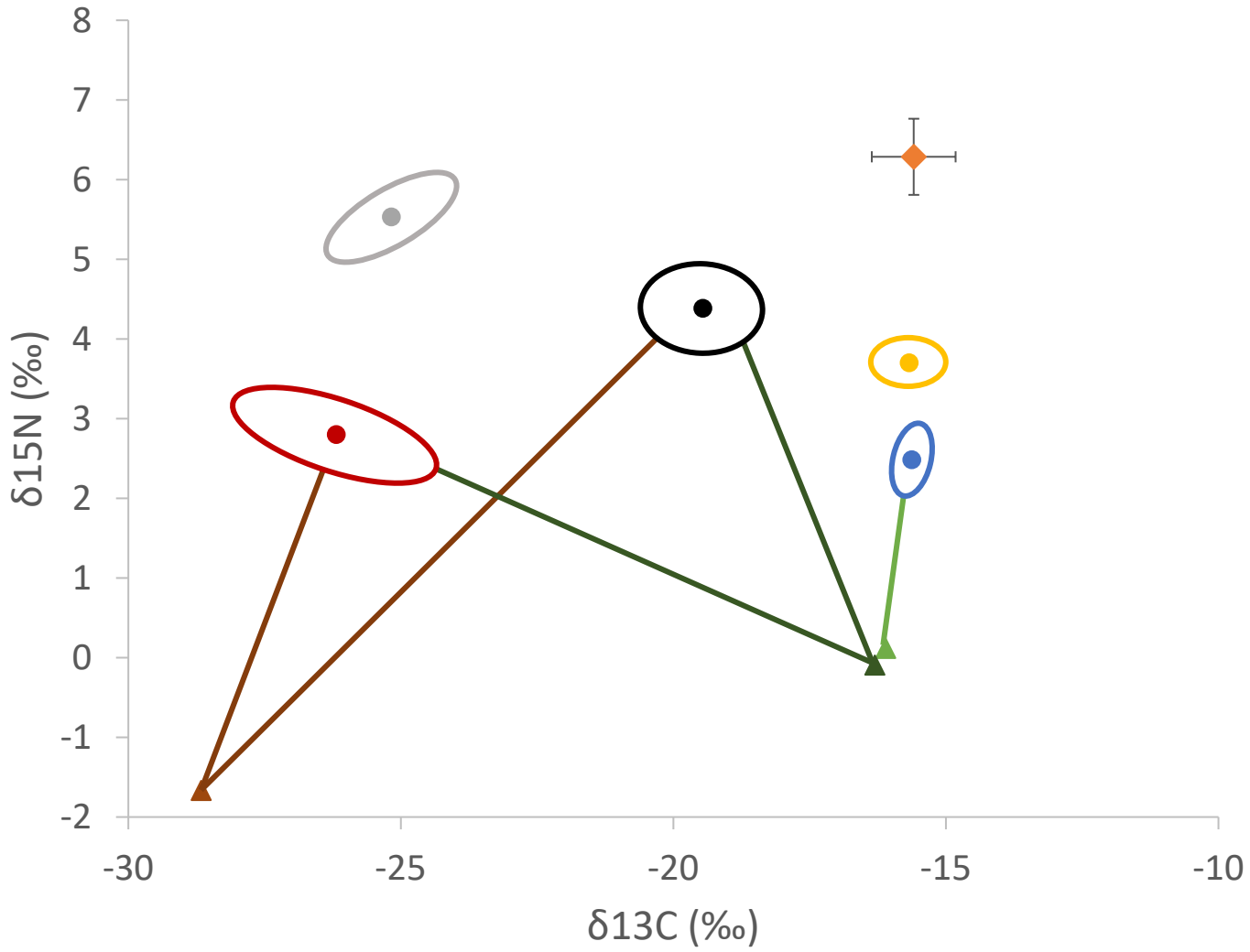

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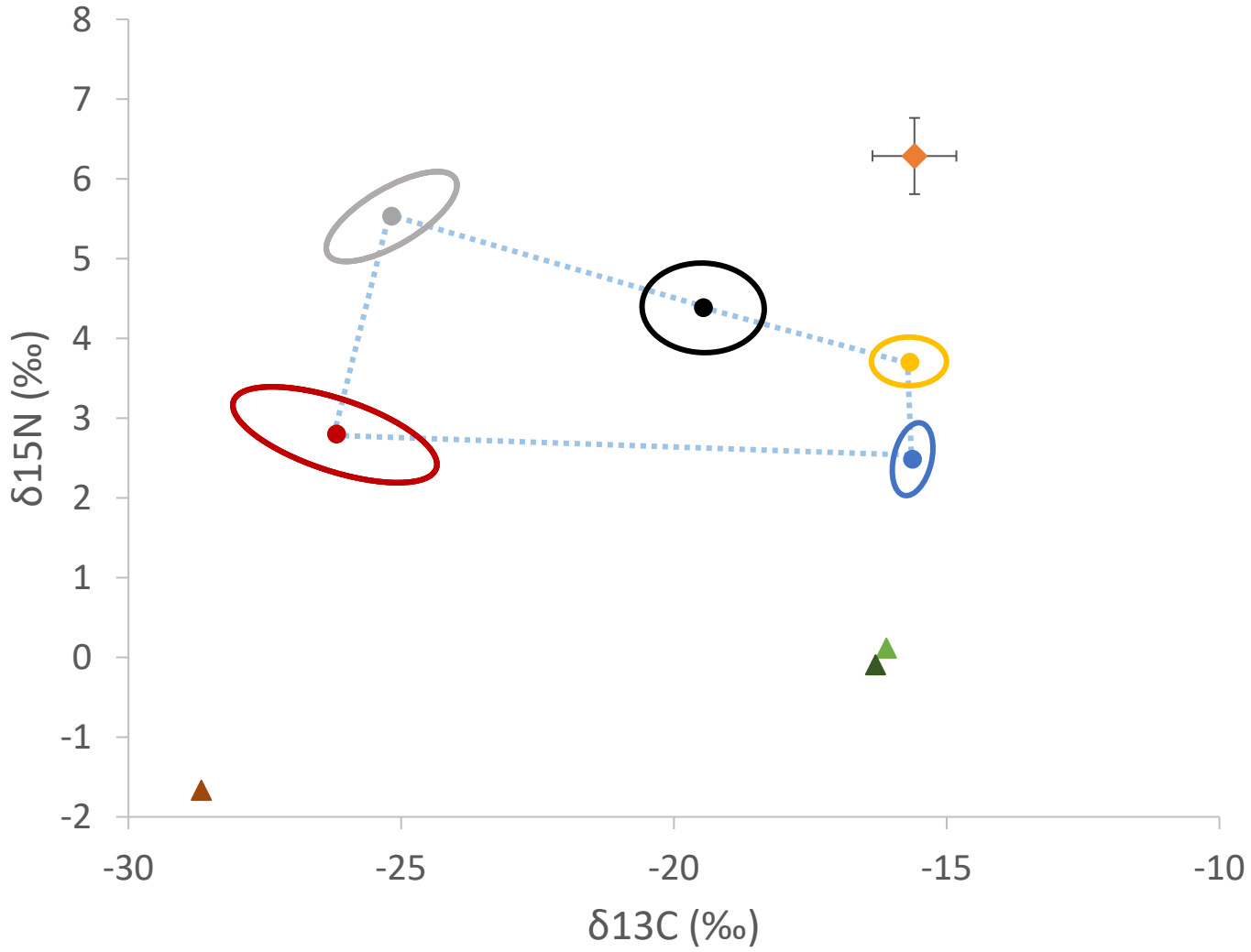
Part II – Community isotopic niche approach

Geometric approach to 'Community niches'

Source: http://www.bbc.com/earth

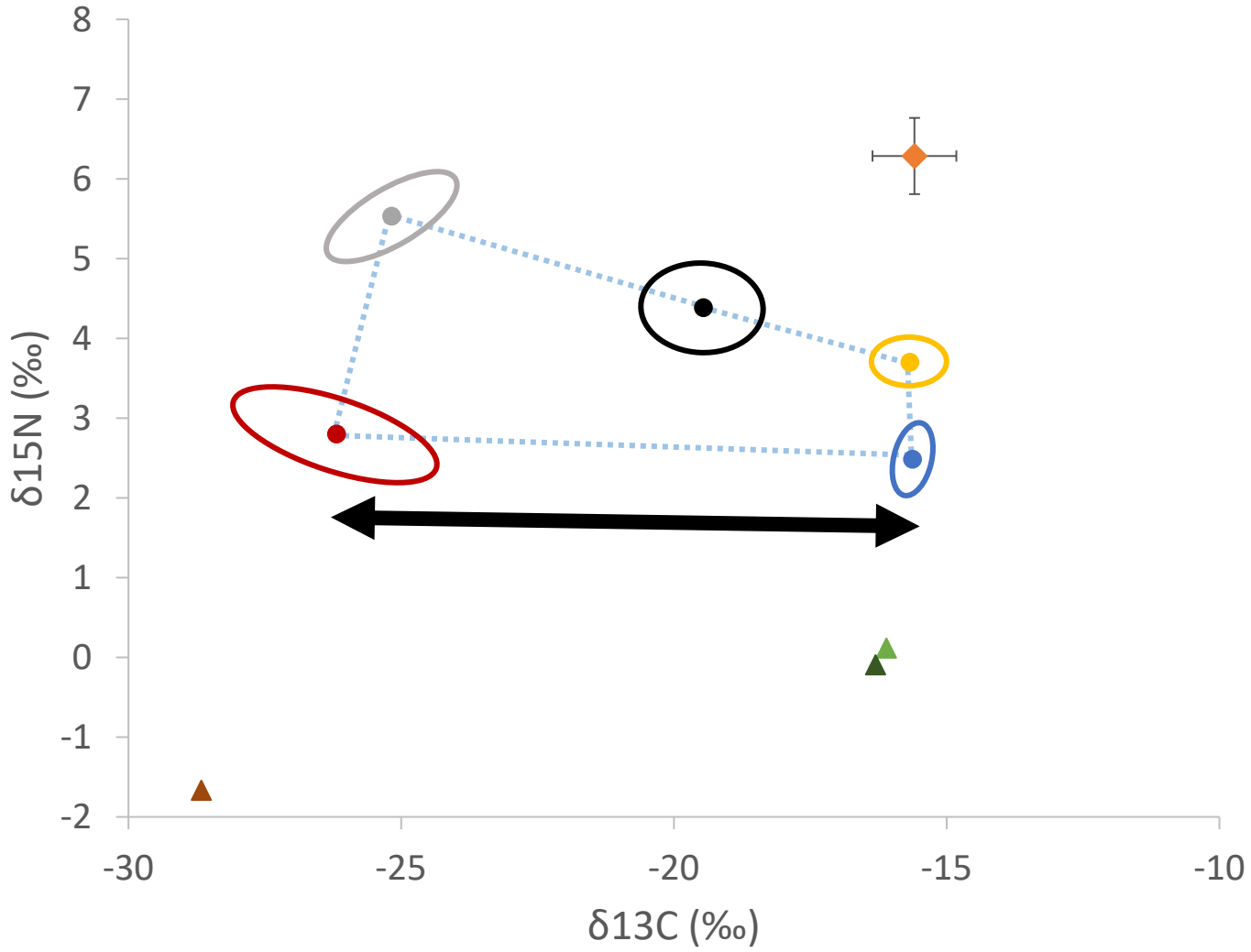


Consumers community niche

- Goldfish
- Notonectidae
- Naucoridae
- Bufo tadpoles
- Chironomidae
- Zooplankton
- Phytoplankton
- Biofilm
- Leaf litter

Part II – Community isotopic niche approach

Geometric approach: Community metrics

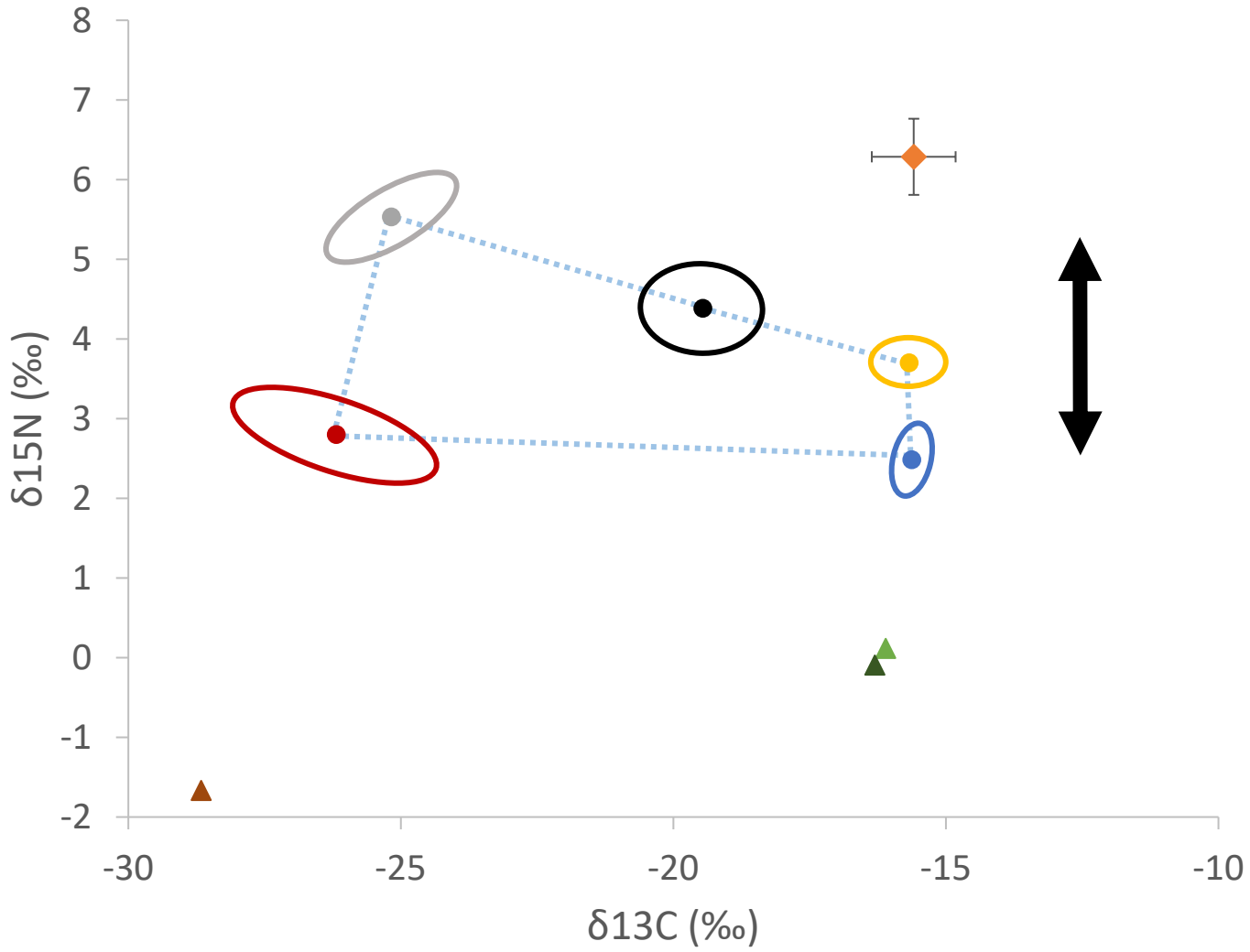


Source: http://www.bbc.com/earth

- δ13C range
  ~ basal resources diversity

Part II – Community isotopic niche approach

Geometric approach: Community metrics



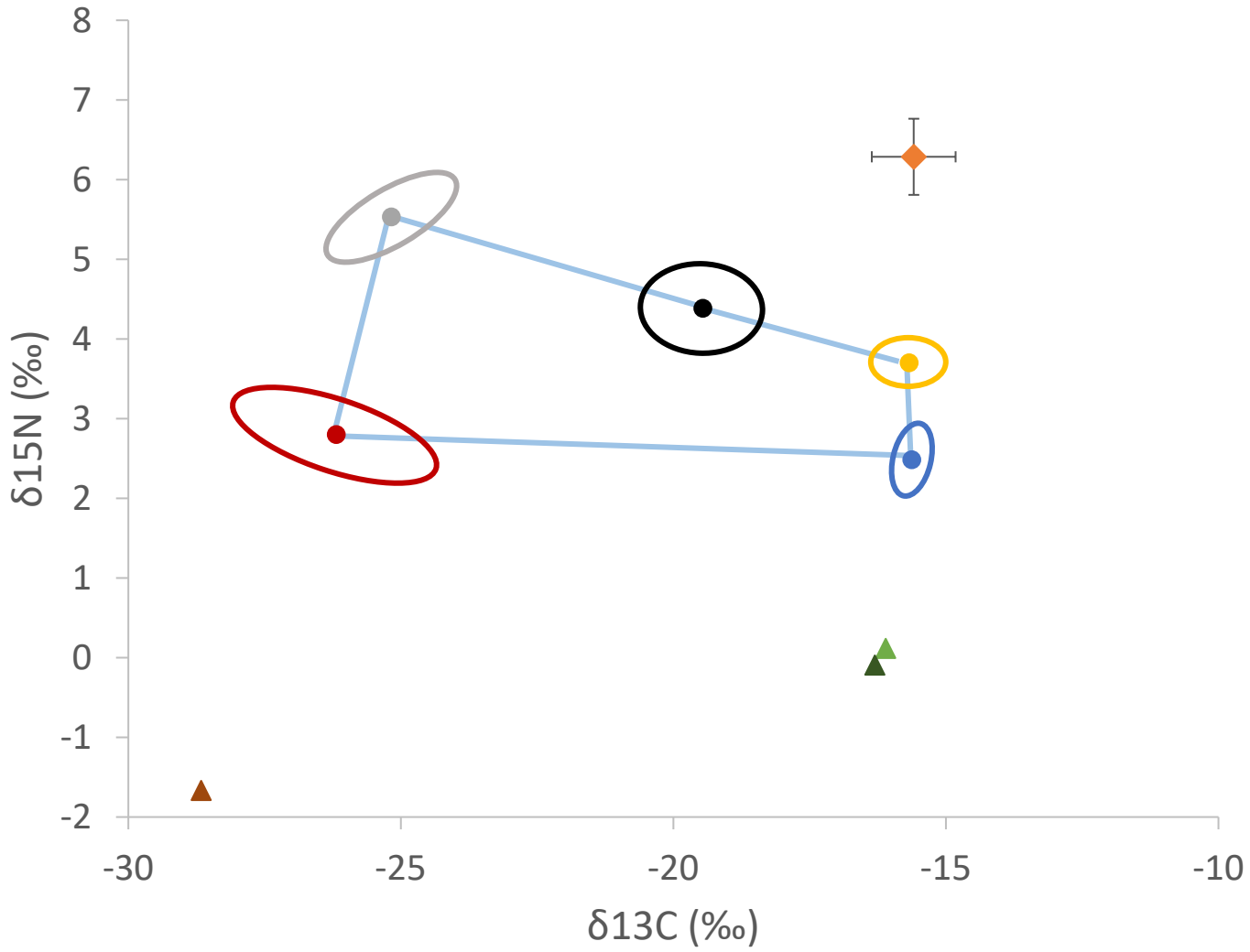
Source: http://www.bbc.com/earth

- δ13C range
  ~ basal resources diversity

- δ15N range
  ~ trophic chain length

Part II – Community isotopic niche approach

Geometric approach: Community metrics

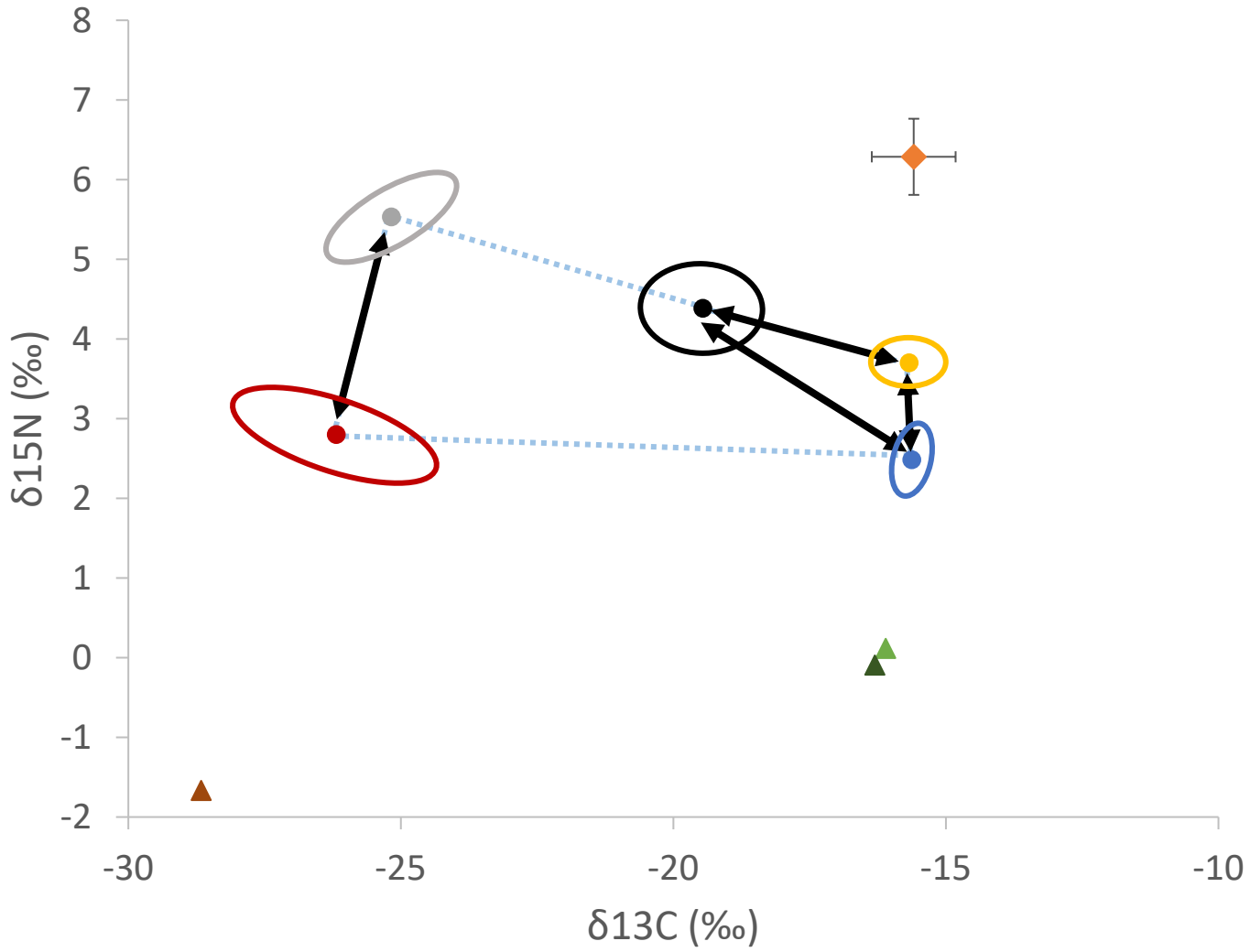


Source: http://www.bbc.com/earth

- δ13C range
  ~ basal resources diversity
- δ15N range
  ~ trophic chain length
- Total area of the Convex hull
  ~ trophic diversity

Part II – Community isotopic niche approach

Geometric approach: Community metrics



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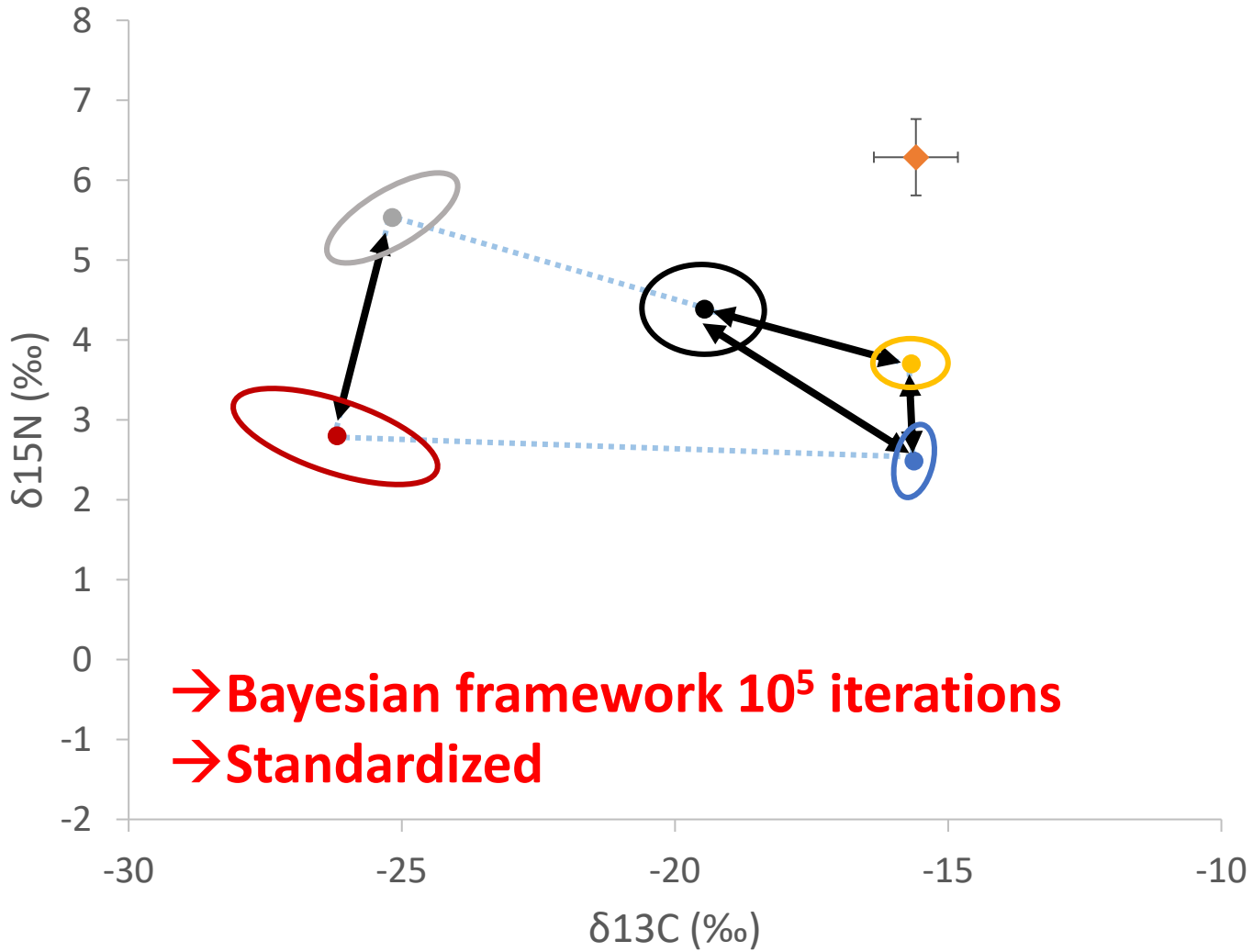
- δ13C range
  ~ basal resources diversity
- δ15N range
  ~ trophic chain length
- Total area of the Convex hull
  ~ trophic diversity
- Mean nearest neighbour distance
  ~ meshing of the web

Part II – Community isotopic niche approach

Geometric approach: Community metrics



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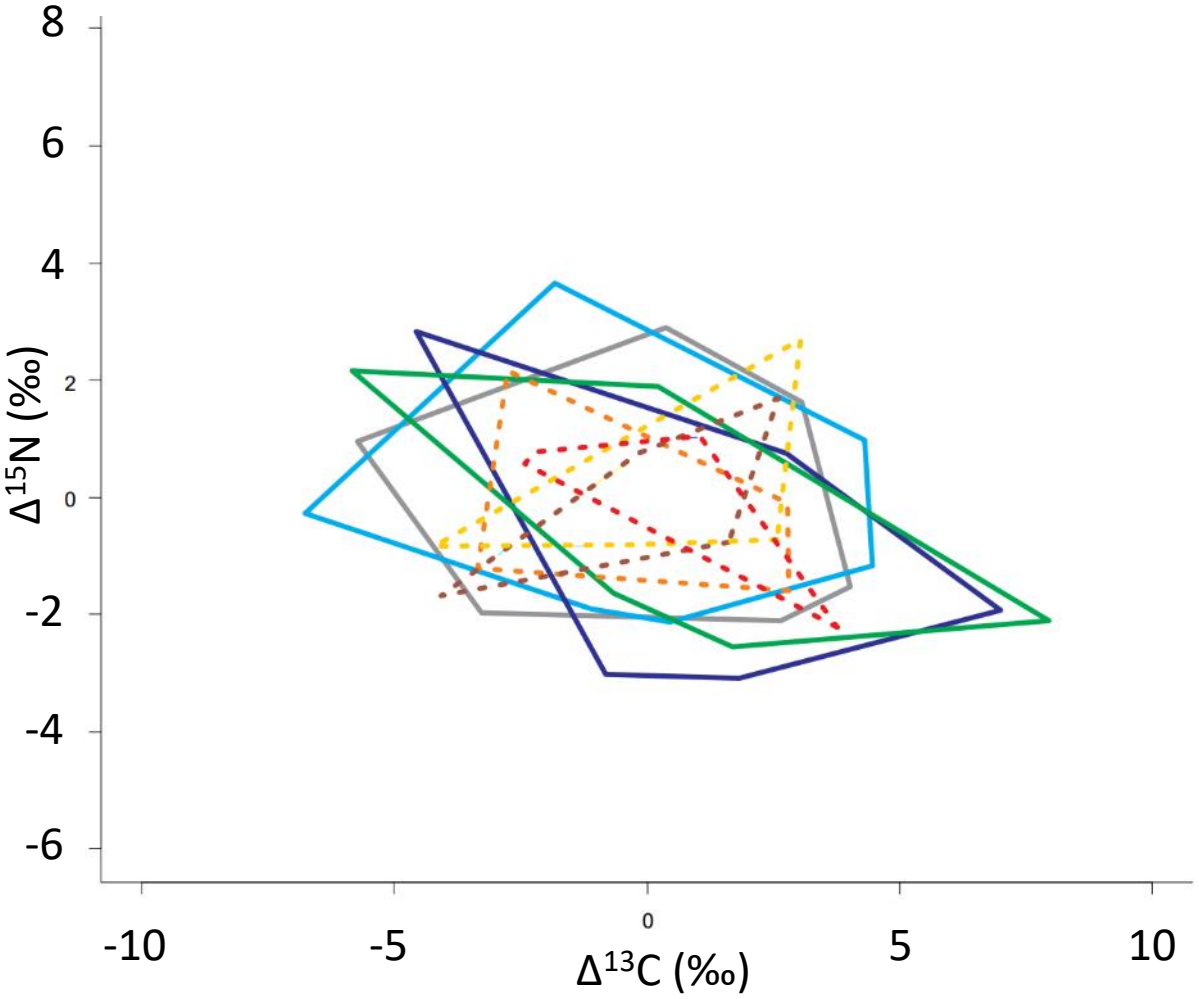
Part II – Comparing community niches

Lejeune et al. *in prep*



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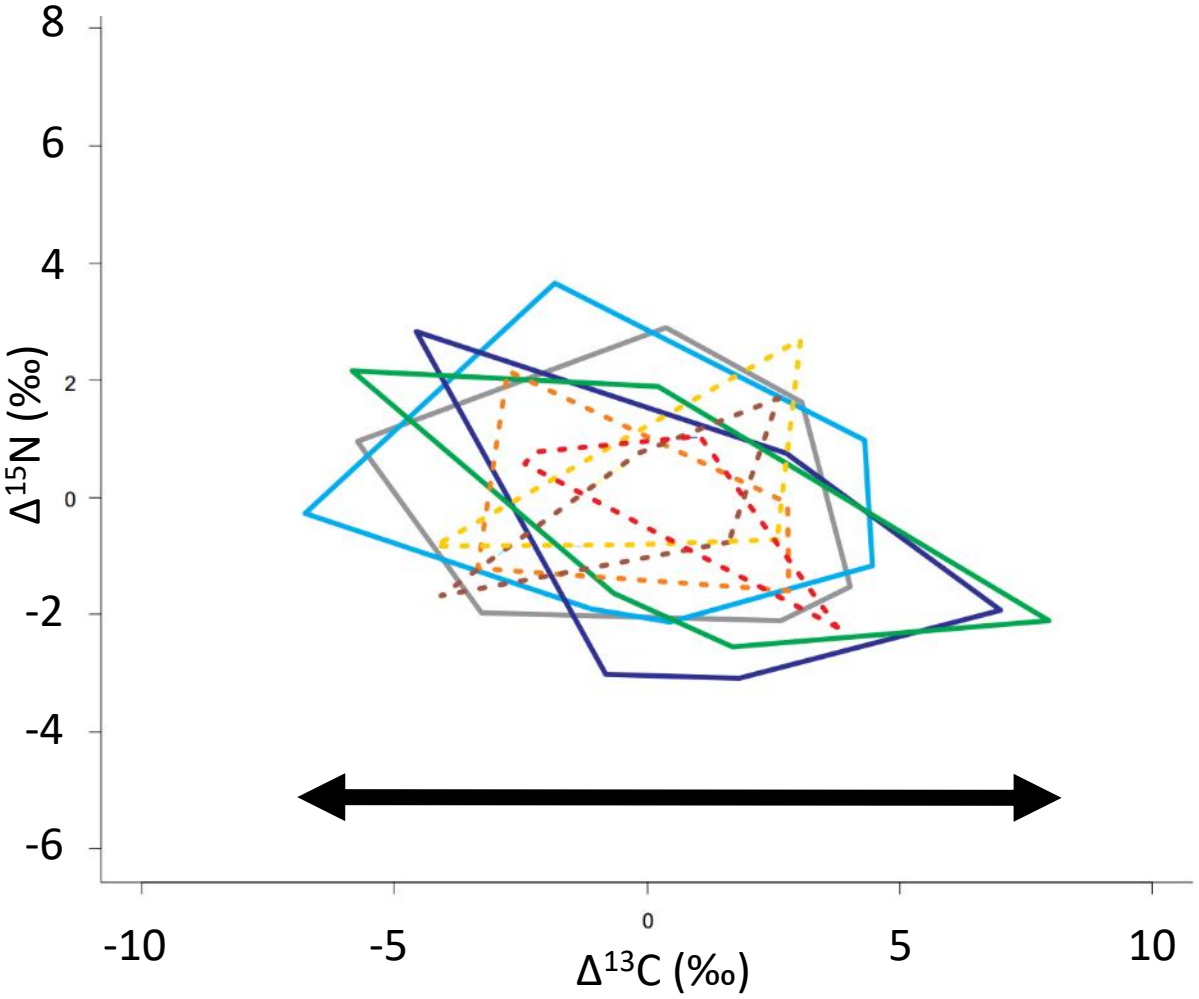
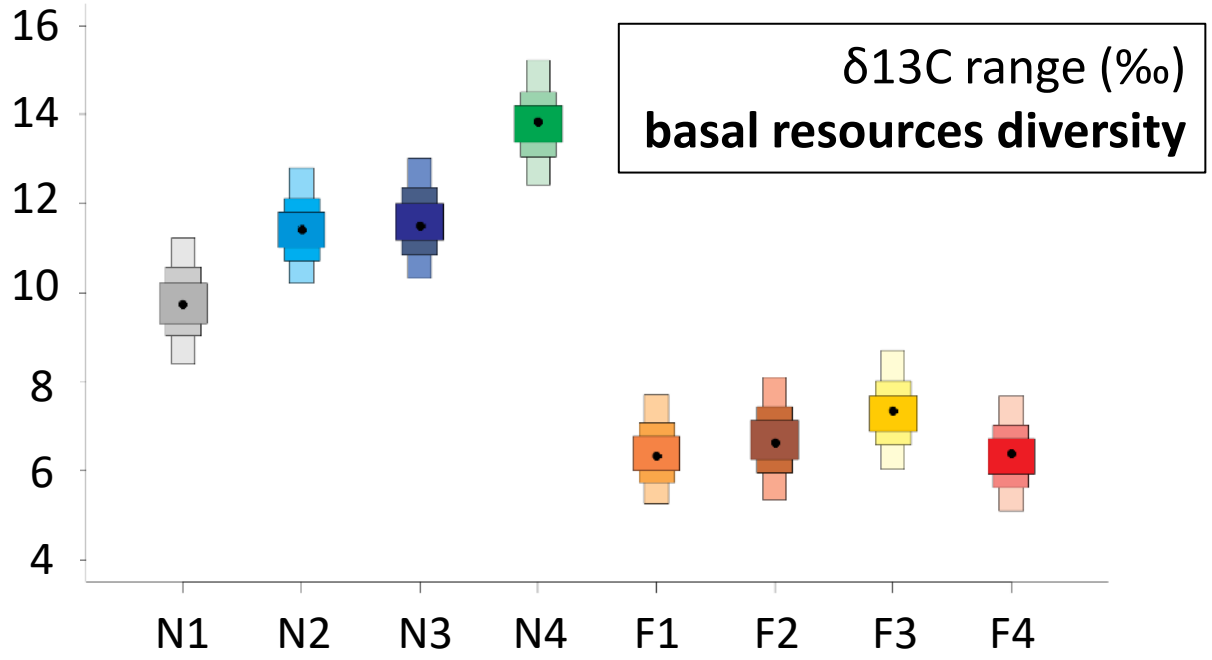
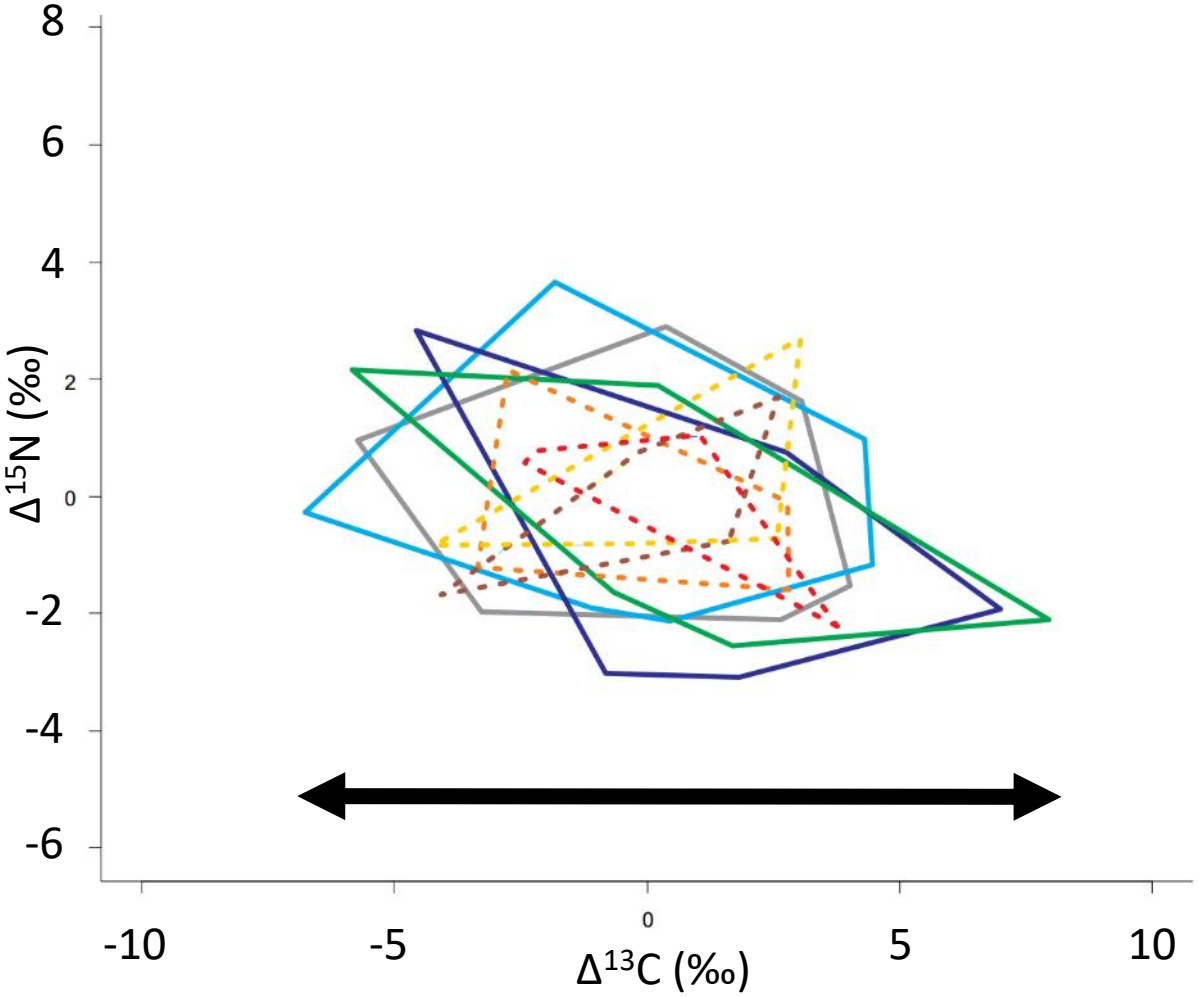
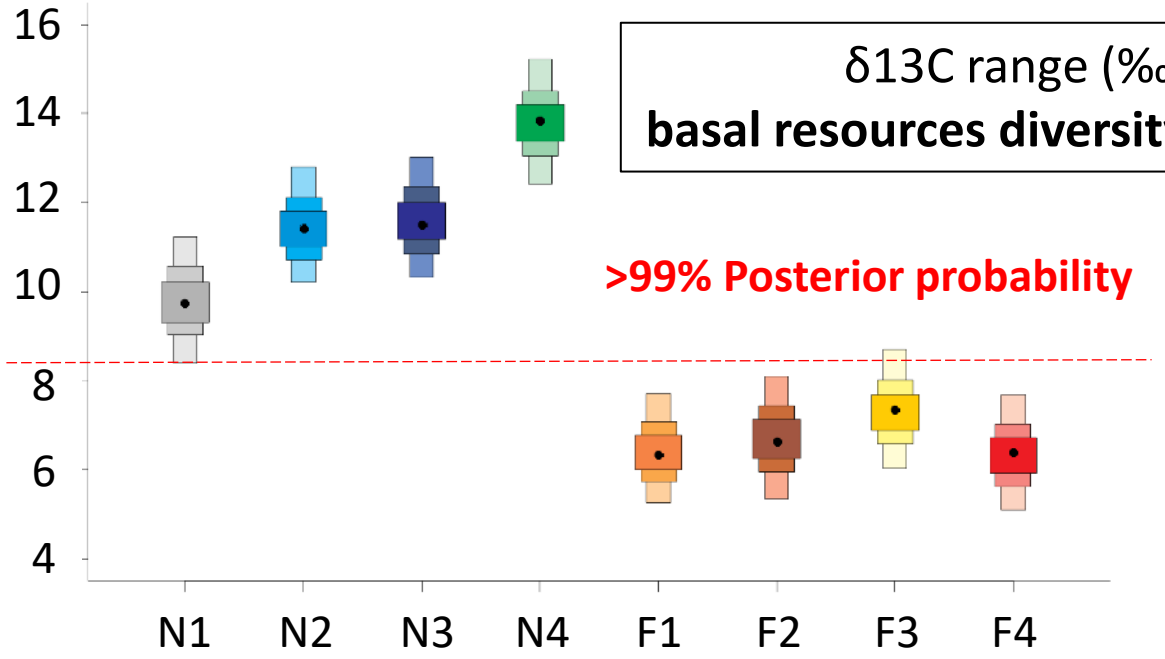


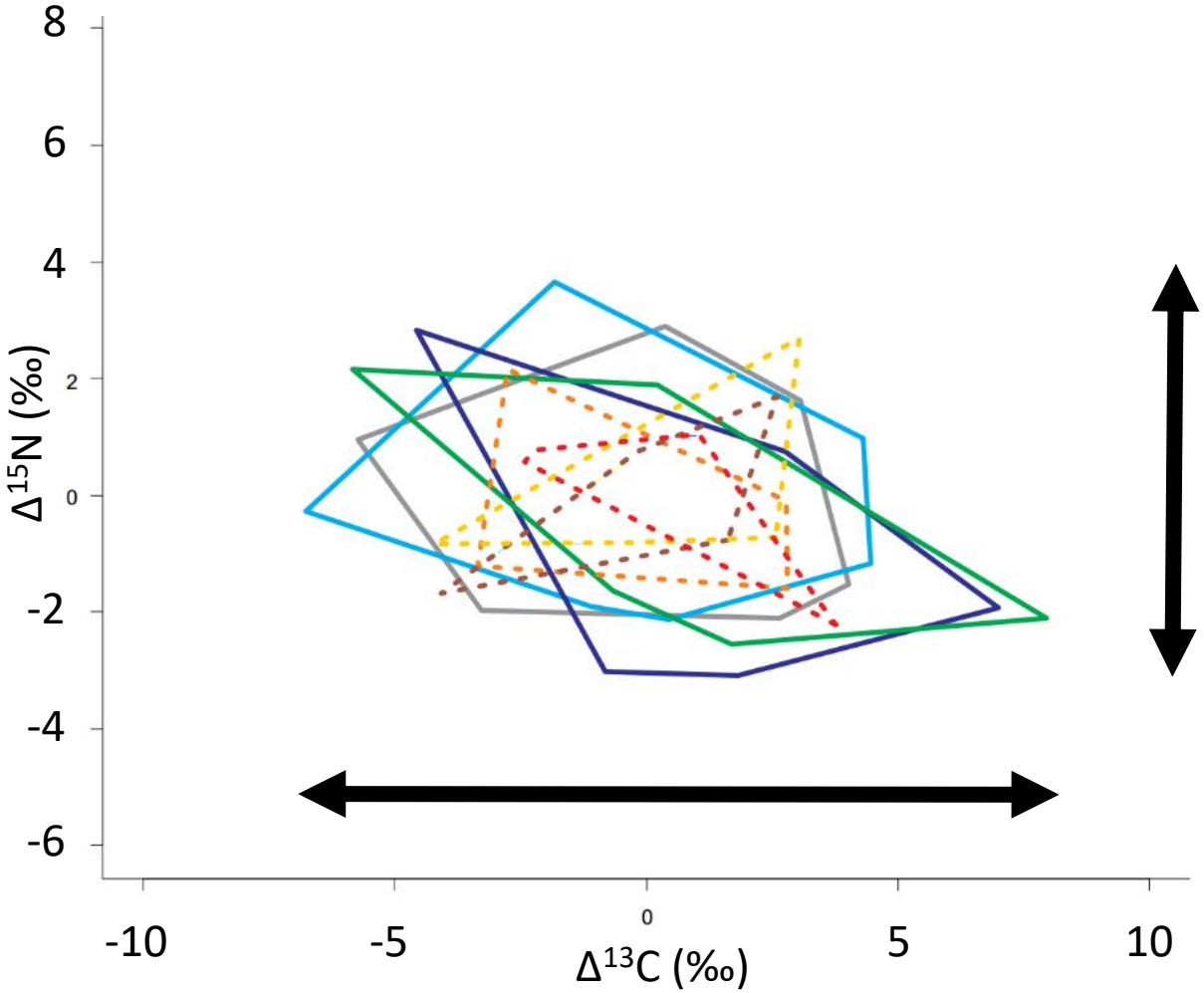


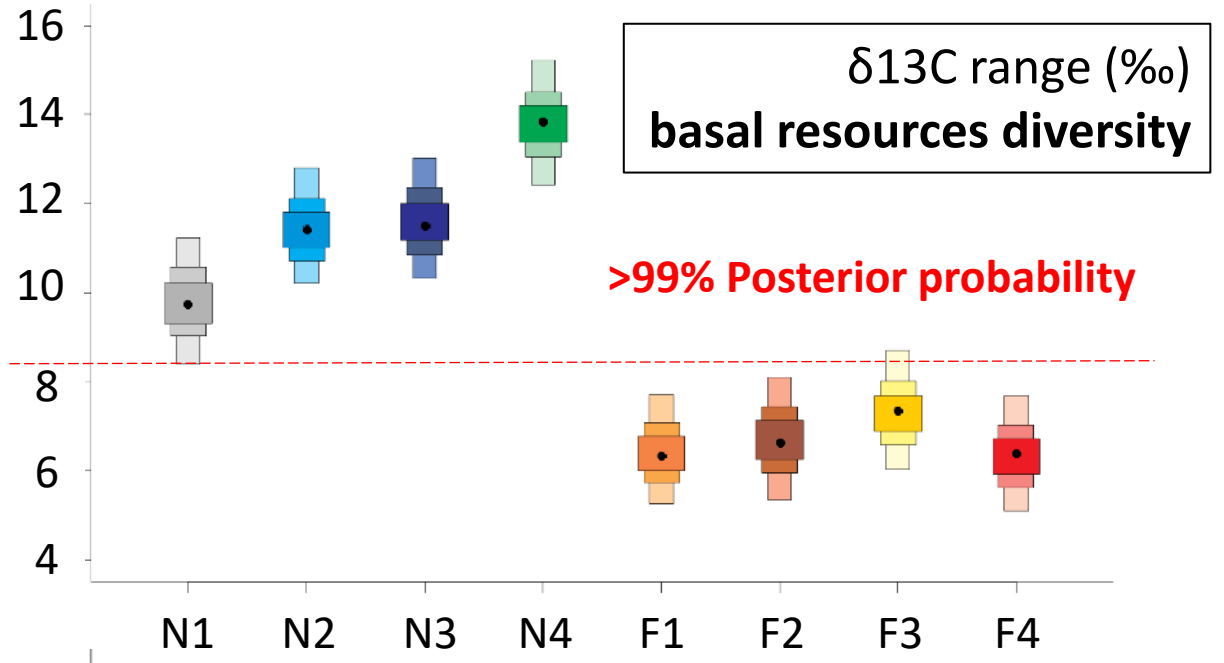
Part II – Comparing community niches

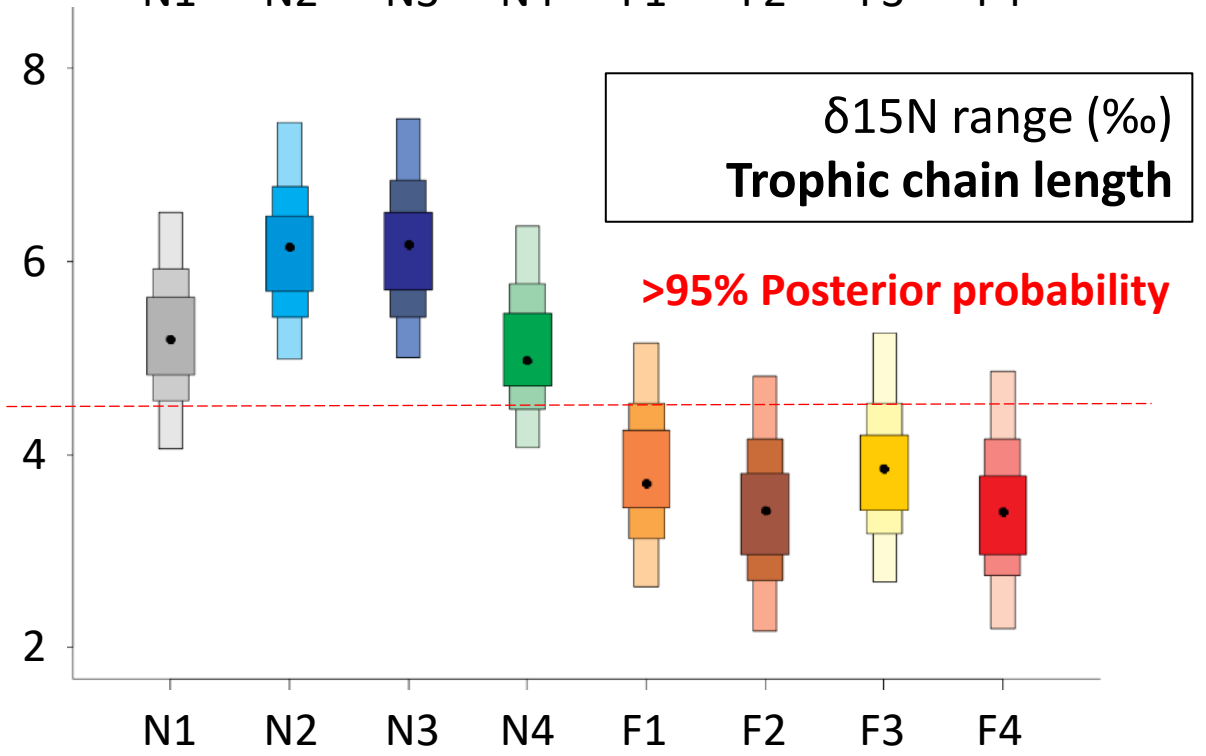




Part II – Comparing community niches

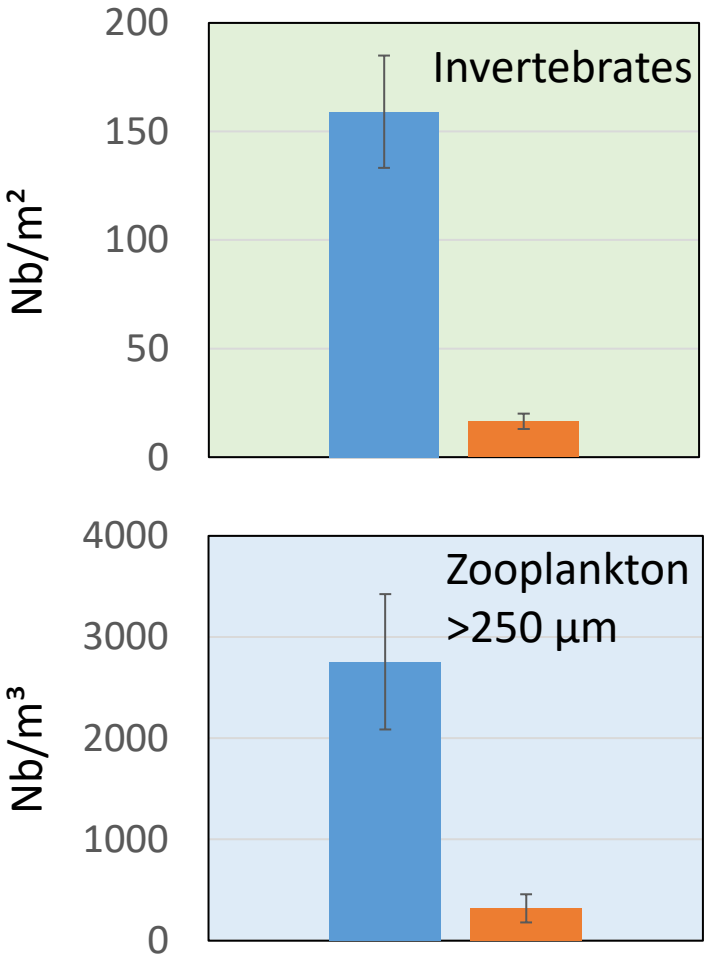




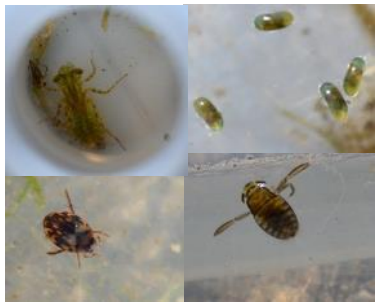


Part II – Comparing community niches

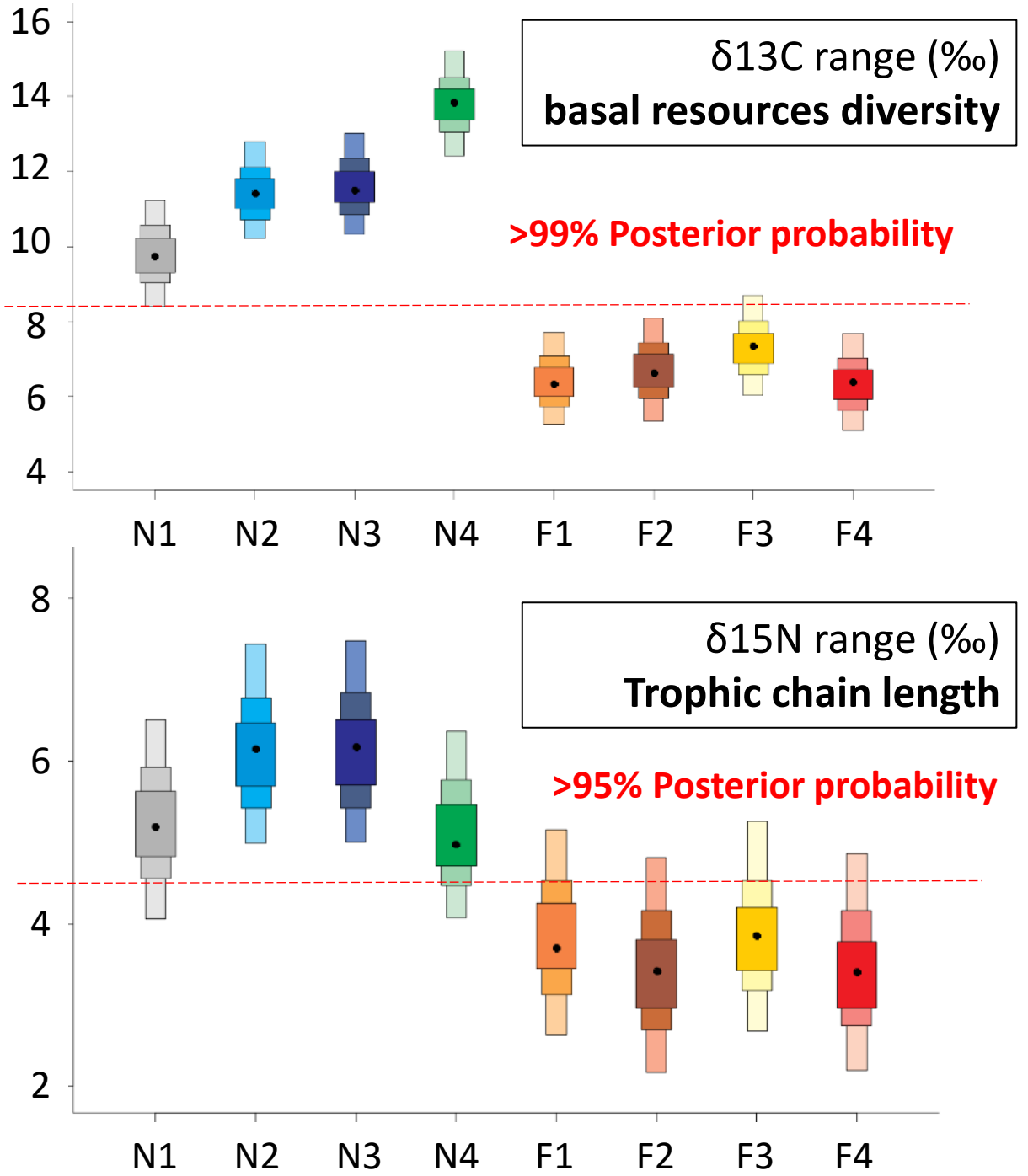

Abundance in the ponds



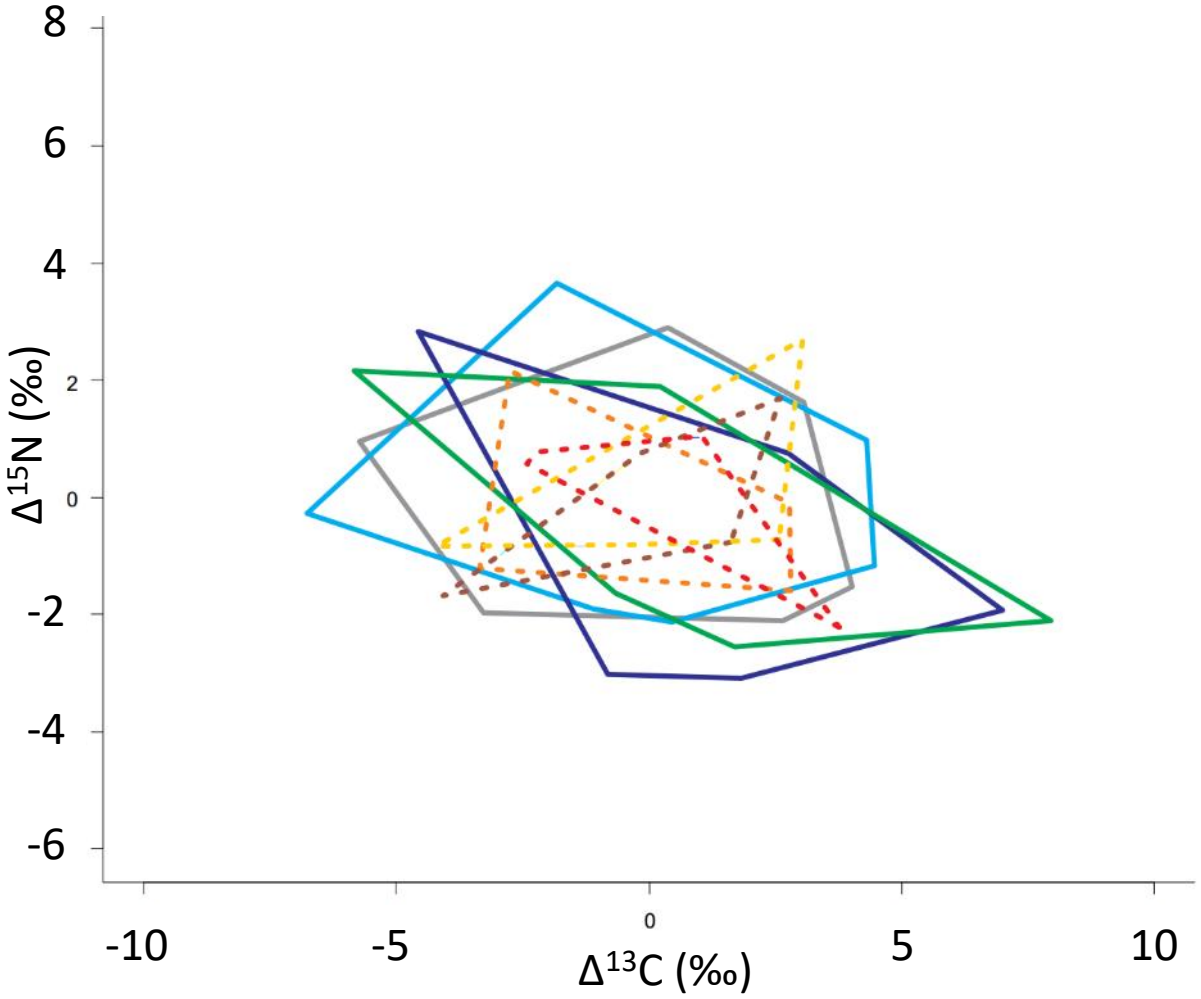
↓ **δ13C range**:
↓ trophic diversity

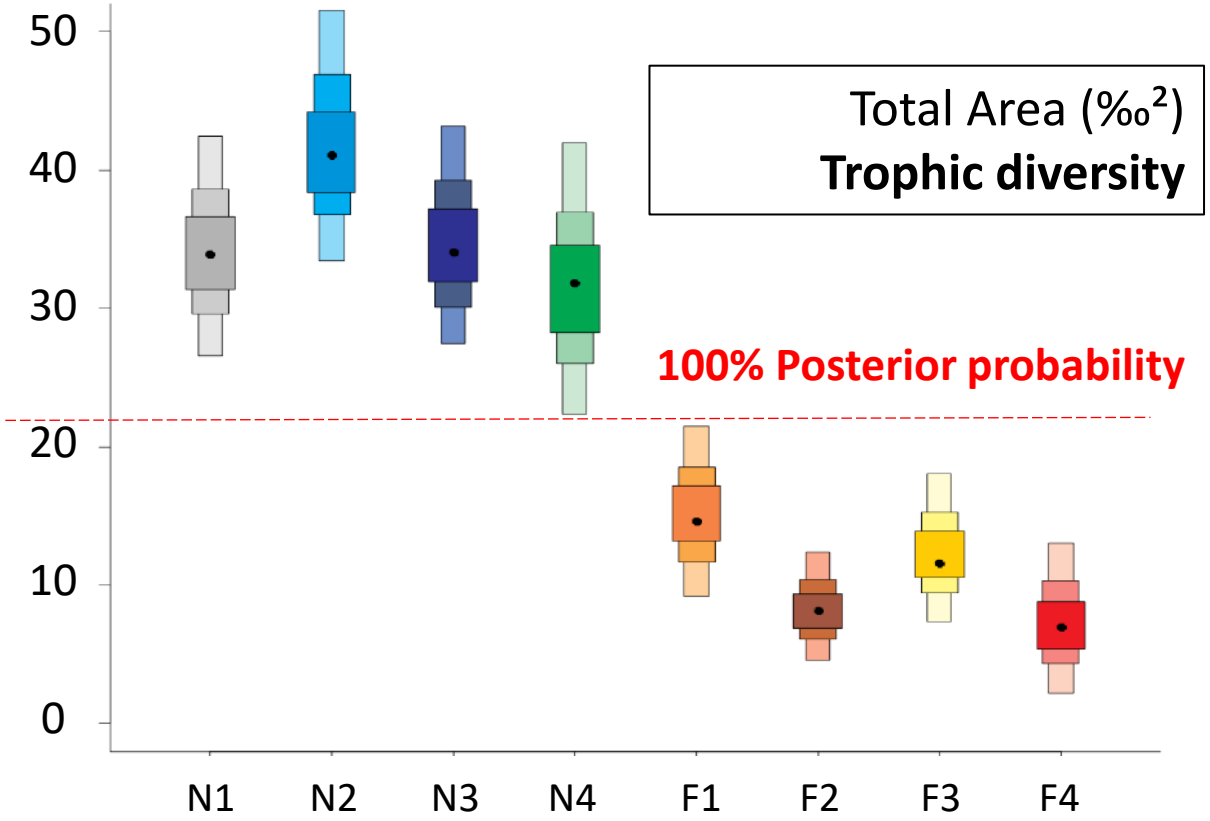


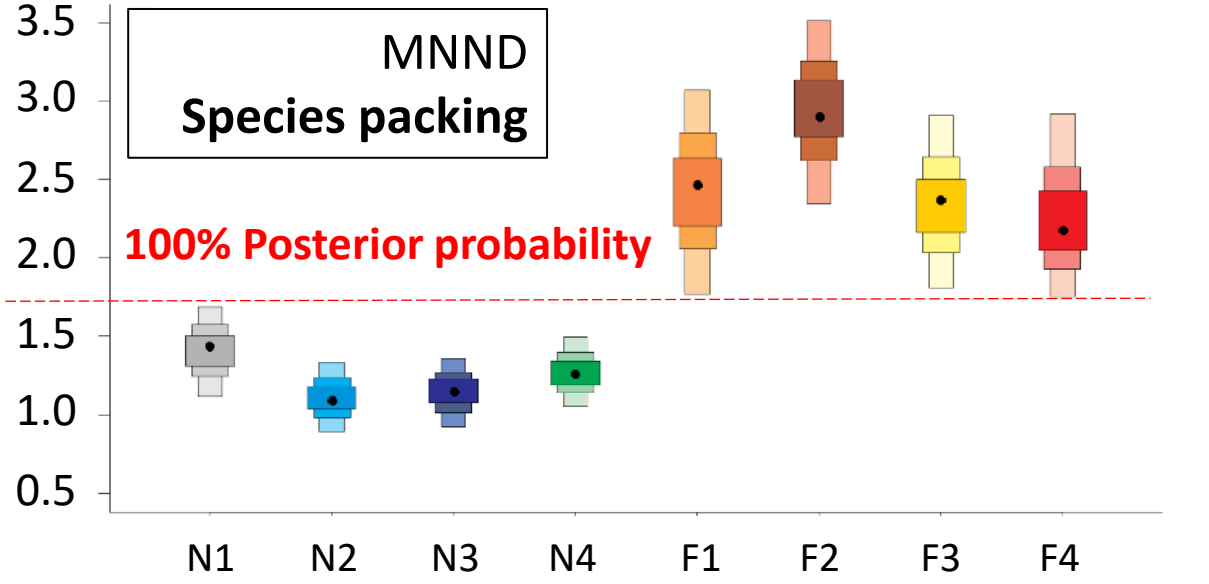
↓ **δ15N range**:
Trophic downgrading



Part II – Comparing community niches





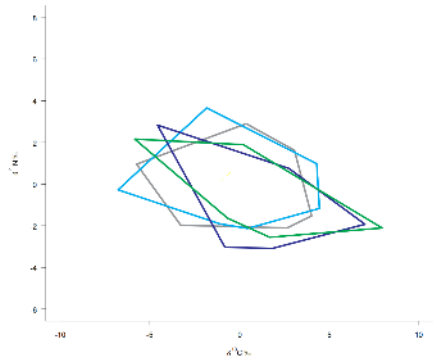


Part II – Conclusion

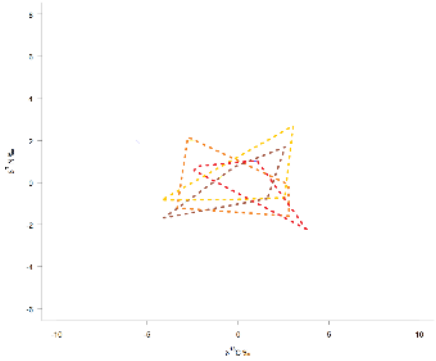
Bye bye aquatic vegetation…
and all that goes with it !

Regarding newts:

1. Destruction of the aquatic vegetation → ~~Food~~, ~~shelter~~
2. Elimination of upper trophic levels from the pelagic chain = ~~Food~~



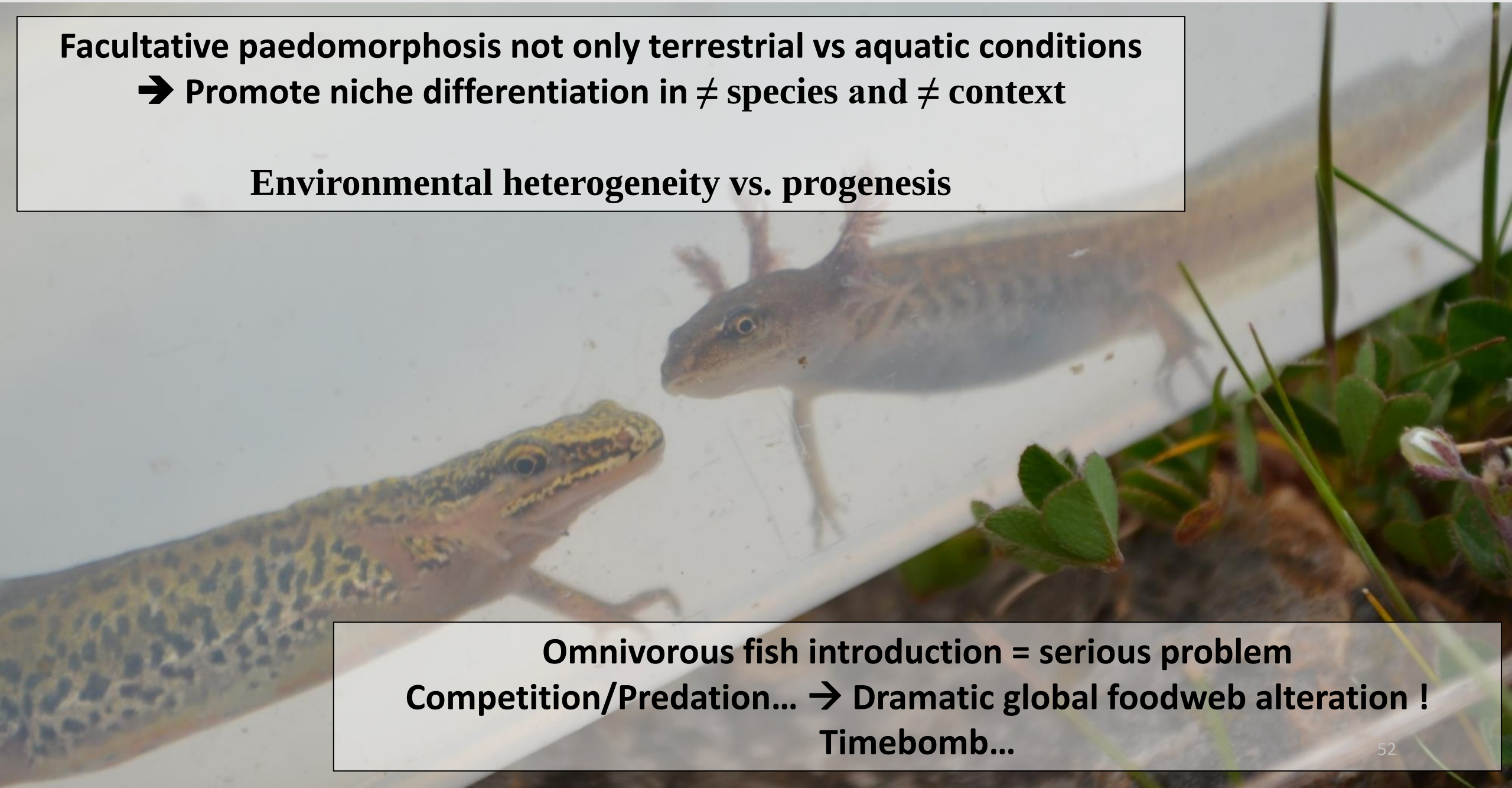




Globally:

↓ Trophic diversity (incl. amphibians), ↓ Trophic redundancy → **Ecosystem resilience** ?

Synthesis



Facultative paedomorphosis not only terrestrial vs aquatic conditions
➔ Promote niche differentiation in ≠ species and ≠ context

Environmental heterogeneity vs. progenesis

Omnivorous fish introduction = serious problem
Competition/Predation… → Dramatic global foodweb alteration !
Timebomb…

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Thank you !

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