Does species richness influence trophic diversity ? A food web study along the upstream downstream gradient of a temperate river

Nicolas Hette-Tronquart, Thierry Oberdorff, Evelyne Tales, Jérôme Belliard

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Rationale : structural vs. functional diversity – insights from stream food webs

Aim: relationship between species richness (structural) and trophic (functional) diversity

Food web ecology

Food web modifications

structural = different members

functional = different relationships

within the web

not necessarily related

Stream ecology

UDG (Upstream-downstream gradient) = key feature

⇓

resource availability, ecosystem size, and stability

species richness
assemblage composition

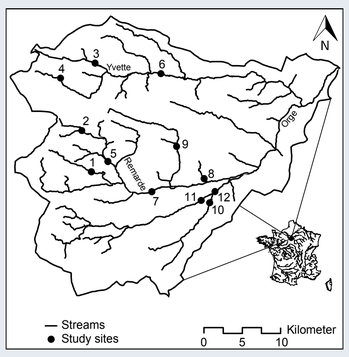
competition
dietary regimes
specialist vs. generalist

⇓

structural and functional

modifications of food webs along the UDG

Method 1/2: study sites



small catchment (937 km^2):

- rather homogeneous climatic conditions and geology
- same moderate anthropogenic pressures

site position along the UDG:

- upstream catchment area: 17 to 210 km^2
- distance from the sources: 2.7 to 26.6 km
- mean stream width: 1.4 to 7.0 m
- mean stream depth: 0.07 to 0.44 m

} PCA 1^{st} axis ≈ UDG

evaluation of structural diversity:

- focus on fish assemblages
- species richness, estimated with single pass electrofishing

Method 2/2: Trophic diversity and stable isotopes

Definition of trophic diversity

↪ in this study,

trophic diversity = { diversity of exploited resources ; diversity of trophic levels }

Principles of stable isotope analysis (SIA)

- "You are what you eat (plus a few per mil)" (DeNiro & Epstein, 1976)
- 2 elements C (sources of organic matter) & N (trophic levels)

↪ idea: variability of $\delta^{13}C$ and $\delta^{15}N$ ≈ trophic diversity

- **!** stable isotope signals are integrated over space and time **!**

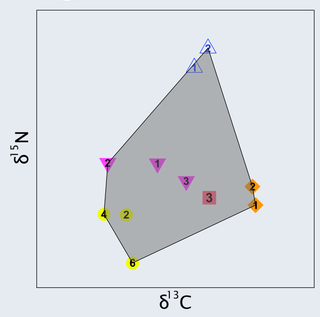
↪ the signal of an individual reflects the average signal of its diet items

analyses:

- performed on fin clips
- one per individual, several individuals per species
- in addition, SIA on basal resources to control for baseline variations

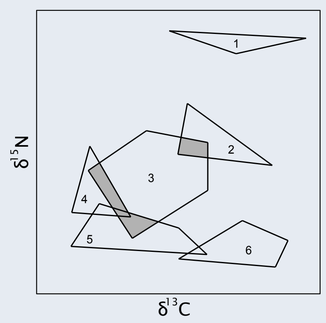
a double approach of trophic diversity using SIA

at assemblage level



isotopic space area (ISA) = area of the convex hull encompassing the signals of all individuals (above, in grey)
integrates both diversity of exploited resources ($\delta^{13}C$) and trophic levels ($\delta^{15}N$)

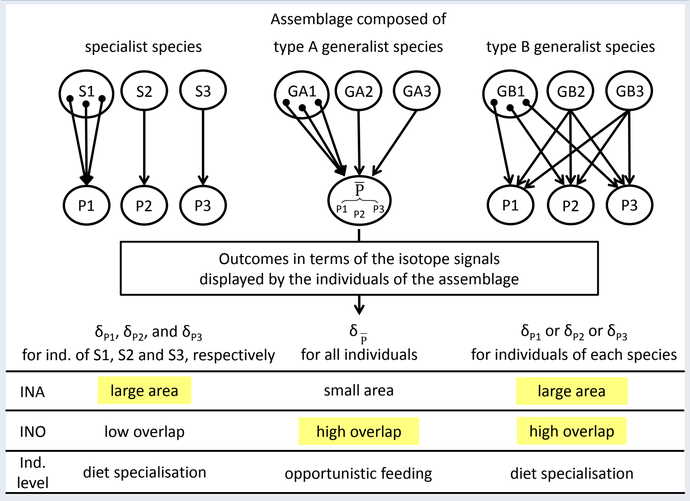
at species level



isotopic niche overlap (INO) = niche area of one species occupied by others (above, in grey for species 3), divided by the whole niche area
measures the trophic redundancy of one species in the assemblage

We calculated both metrics using a bootstrap method (adapated from Jackson et al. 2012) to avoid biases due to different sample sizes among sites. We tested the effects of UDG and species richness on both metrics using path analysis and linear models.

Feeding strategy and trophic diversity



	δ_{P1}, δ_{P2}, and δ_{P3} for ind. of S1, S2 and S3, respectively	$\delta_{\bar{P}}$ for all individuals	δ_{P1} or δ_{P2} or δ_{P3} for individuals of each species
INA	large area	small area	large area
INO	low overlap	high overlap	high overlap
Ind. level	diet specialisation	opportunistic feeding	diet specialisation

after Bearhop et al. 2004. Black dots represent individuals. The yellow boxes highlight the complementarity of ISA and INO.

Results

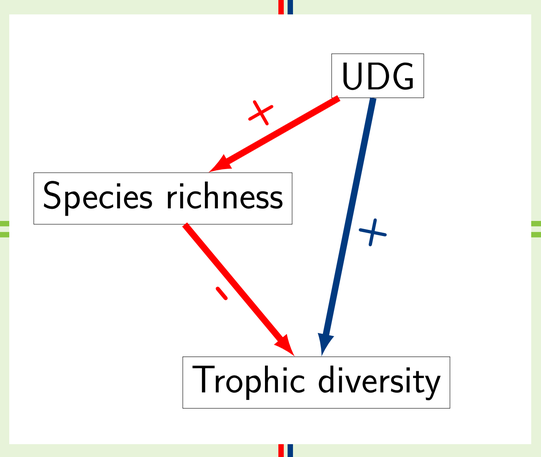
Indirect, structural effect via species richness

Assemblage level

- We found structural modifications along the UDG: species richness increased significantly, but assemblage composition did not change significantly (no predominant group of species in the assemblage along the whole UDG).
- Species richness significantly decreased the ISA at constant position in the UDG: more species ⇒ smaller area

Species level

- No effect of species identity on the INO:
- Species richness significantly increased the INO at constant position in the UDG: more species ⇒ larger overlap



Direct, functional effect

- The UDG significantly increased the ISA at constant species richness: more downstream site ⇒ larger area
- The UDG significantly decreased the INO at constant species richness: more downstream site ⇒ lower overlap

Both analyses

Using our conceptual framework linking feeding strategy and trophic diversity, we deduced

an assemblage with more species tends to have more type A-generalist species than an assemblage with less species and located at the same position along the UDG

Interpretation:
The trend towards type A-generalist species could be related to competition for resources. Species richness could increase faster than resource availability along the UDG leading each individual to take a similar range of all available resources to satisfy their energetic needs.

an assemblage located at a more downstream site tends to have more specialist species than an assemblage located upstream and with the same species richness

Interpretation:
The trend towards specialist species could be explained by two non-exclusive reasons: along the UDG higher stability (1) and/or habitat heterogeneity (2) could allow fish to focus on preferential food items corresponding to their optimal feeding requirement.

3 "take home" messages

Steam ecology:

- the UDG seems to increase trophic diversity in temperate rivers. This result is to be confirmed considering a larger gradient

Food web ecology:

- An increase in species richness (=structural modification) leads to a decrease in trophic diversity via a change in the feeding strategy of the fish (=functional modification)
- The double approach of trophic diversity at assemblage (isotopic space area, ISA) and species (isotopic niche overlap, INO) levels was useful to elucidate the feeding strategy of the assemblage that explains the observed trophic diversity

Bearhop S, Adams C, Waldron S, Fuller R, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012
DeNiro M, Epstein S (1976) You are what you eat (plus a few per mil): the carbon isotope cycle in food chains. Geol Soc Am 8:834–35 (Abstr.)
Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS ONE 7:e31757

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