How does hydrological stability affect food chain length in Mediterranean streams?

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Food Chain Length (FCL)

- Number of trophic transfers occurring between basal resources and top predators

- Fundamental property of food webs
  - Community structure > Distribution of trophic interactions and energy flow
    (Hairston Jr & Hairston Sr 1993; Persson 1999; Oksanen & Oksanen 2000)
  - Ecosystem processes > Key functions such as nutrient cycling and carbon exchange between freshwater ecosystems and the atmosphere
    (Schindler et al. 1997; McIntyre et al. 2007)
  - Bioaccumulation of contaminants in top predators
    (Kidd et al. 1995; Kidd et al. 1998)

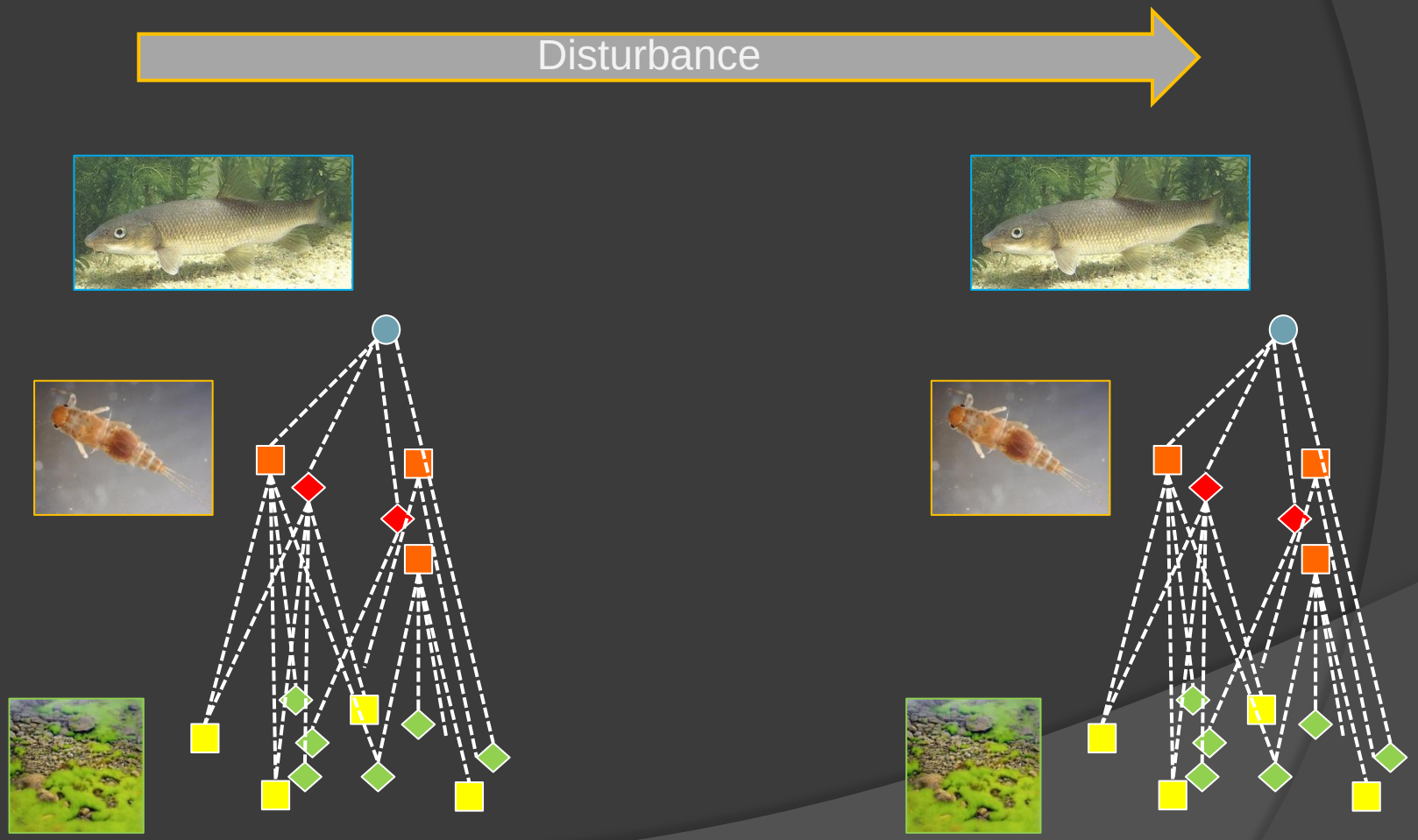
- FCL ≈ 2 - 5, but varies for poorly understood reasons

Food Chain Length: environmental controls

1. DYNAMICAL STABILITY hypothesis

Higher levels are more sensitive

(Pimm & Lawton 1977; Pimm 1982)

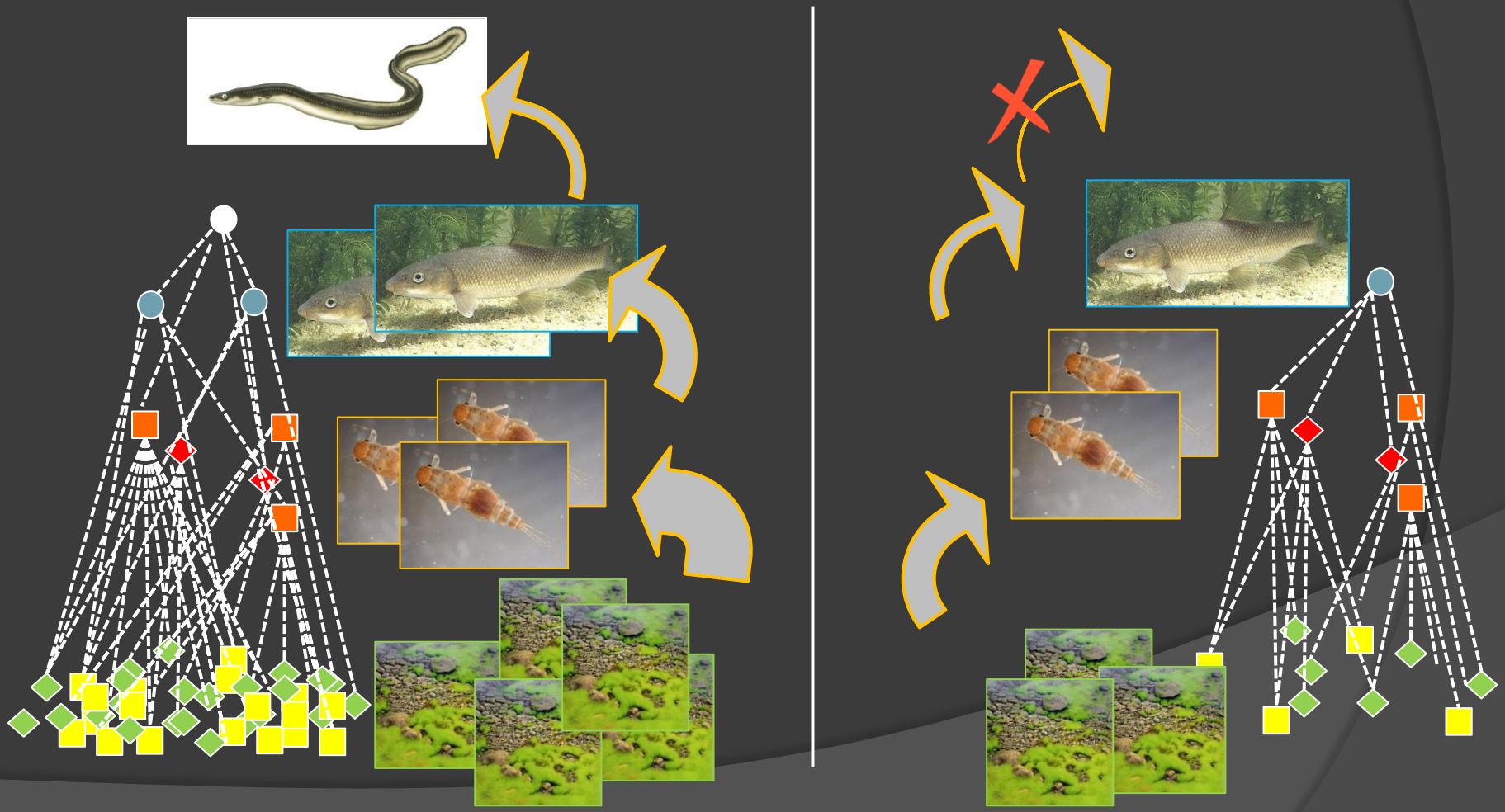


Food Chain Length: environmental controls

2. RESOURCE AVAILABILITY hypothesis

Energy losses occur with each trophic transfer

(Pimm 1982; Schoener 1989)

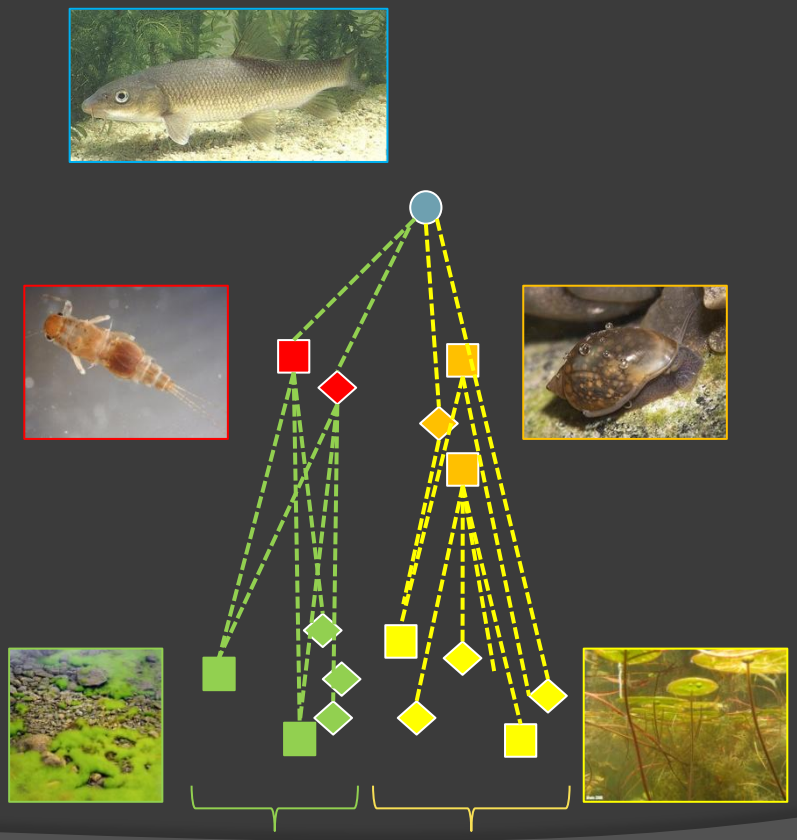


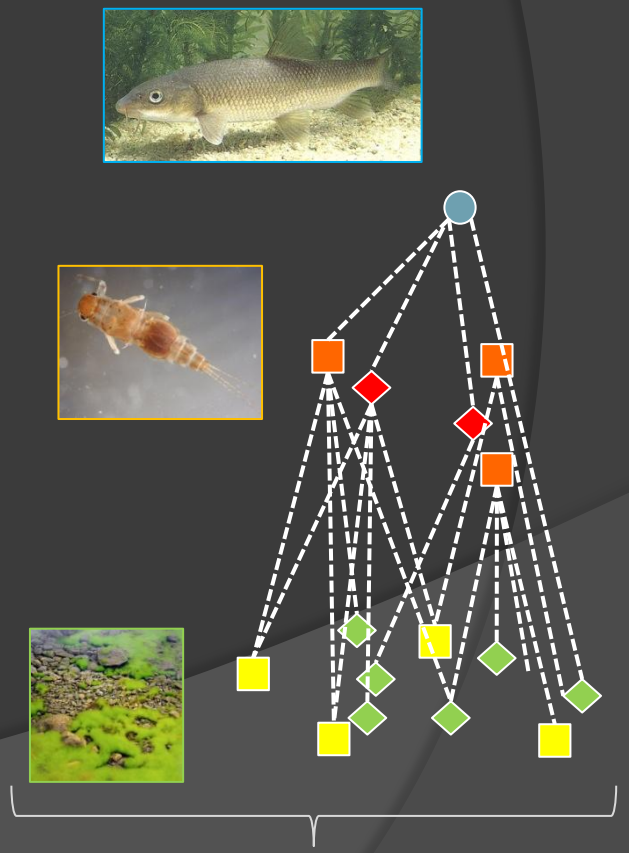
Food Chain Length: environmental controls

3. ECOSYSTEM SIZE hypothesis

Larger ecosystems > compartmentalized food webs

(Post et al. 2000; Krause et al. 2003)





Food Chain Length (FCL)

- To date, some hypotheses on FCL <u>environmental controls</u> have received empirical support in lotic ecosystems…
  - Dynamical stability and ecosystem size *(16 New Zealand streams, Mc Hugh et al. 2010)*
  - Dynamical stability mediated by drainage area *(36 North American rivers, Sabo et al. 2010)*

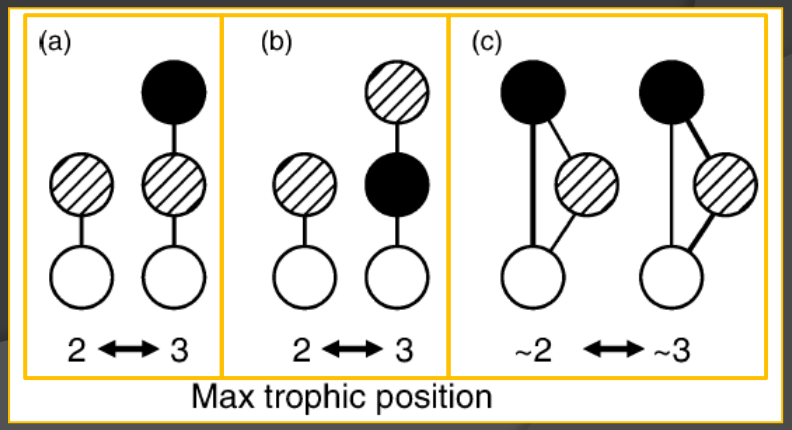
<u>Aim 1:</u>
What controls FCL in Mediterranean streams?

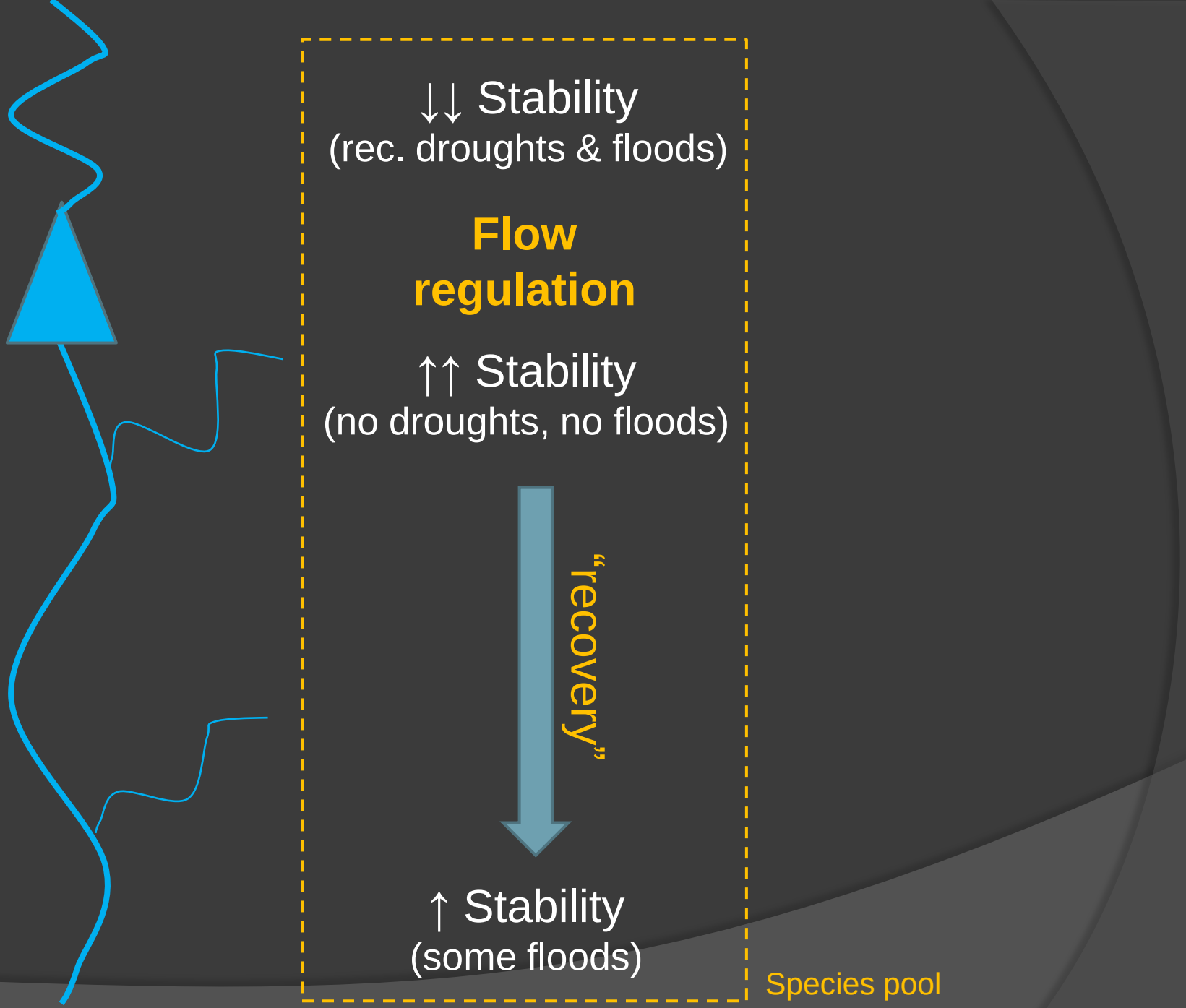
- ...but much less progress has been made in isolating the <u>proximate mechanisms</u> that determine FCL:

<u>Aim 2:</u>
Which is/are the proximate mechanism/s?

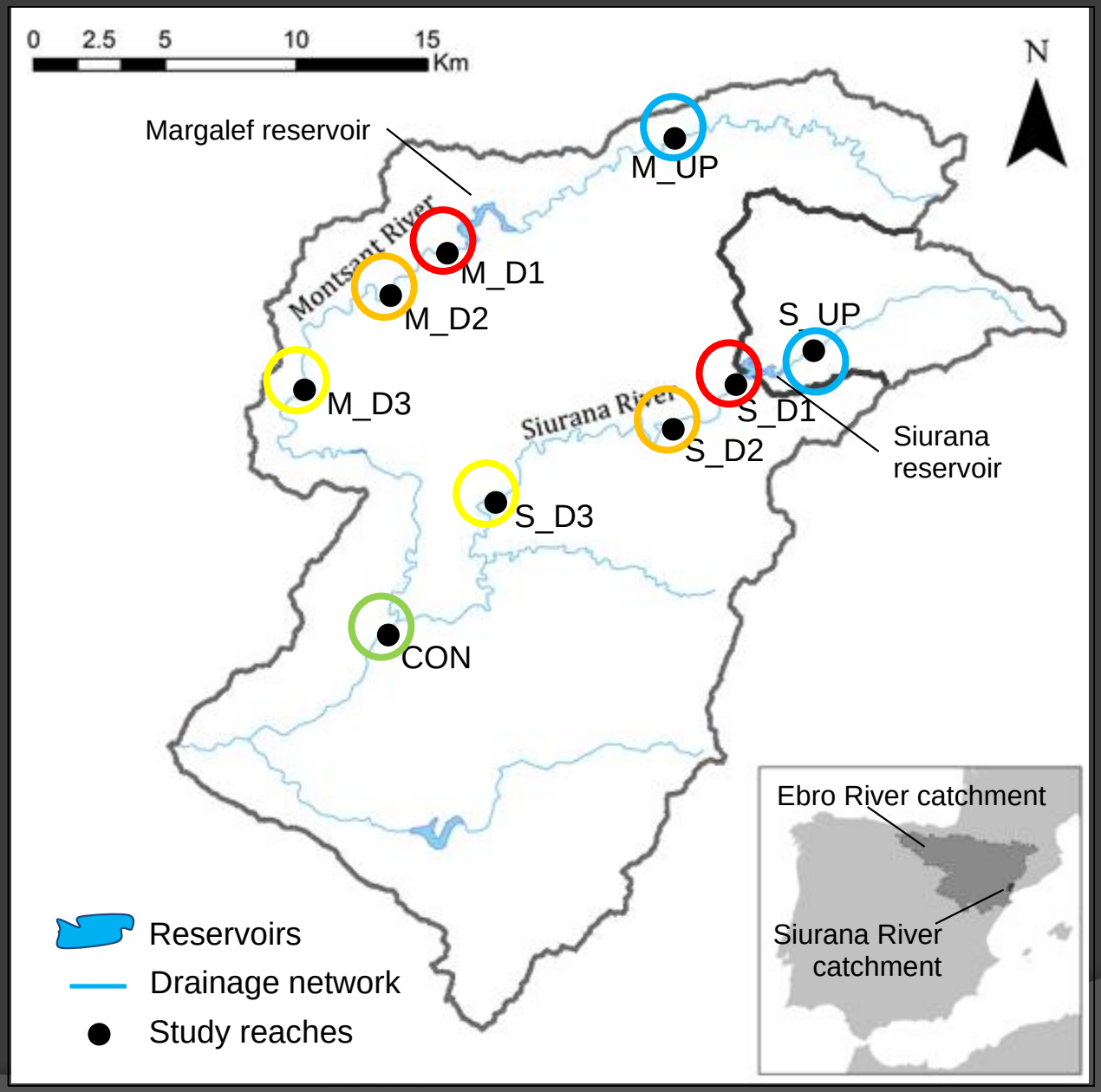
a) Additions
b) Insertions
c) Omnivory

Post & Takimoto 2007
Oikos 116: 775-782




↓↓ Stability
(rec. droughts & floods)
Flow regulation
↑↑ Stability
(no droughts, no floods)
"recovery"
↑ Stability
(some floods)
Species pool

Study site



- Siurana and Montsant rivers (Ebro catchment)
- 100-m reaches upstream and downstream of two major dams
- 5 extra reaches located throughout ca. 25 km downstream from the dam (until the confluence)

Reach	Catchment (km^2)	Regulated catchment (%)
M_UP	40.7	0 %
M_D1	97.6	95 %
M_D2	113.1	82 %
M_D3	141.4	66 %
S_UP	35.6	0 %
S_D1	61.0	100 %
S_D2	88.5	69 %
S_D3	140.2	63 %
CON	421.6	59 %

Sampling & sample processing outline

- Each reach (100 m long) was centred in a pool, comprised at least 2 riffles (up- and downstream of the pool), received 3 visits (Apr-Jun ’12):
  - 1st survey: nutrients, habitat mapping, biomasses, biofilms and invertebrate sampling
  - 2nd survey: electrofishing (fish & herps sampling)
  - 3rd survey: measures of grain-size distribution & river channel topography

- Habitat mapping:
  - 10 transects per reach (% of hab. types in contiguous 0.09 m^2)

- Samples for measures of biomass and for Stable Isotope Analyses (SIA):
  - SPOM, FBOM, CBOM
  - Algae, biofilm, macrophytes
  - Invertebrates (Surber + dip-net; quant + qual samples; 8/reach)
  - Fish (blocking nets; 3-pass depletion method)

- ID
  - Diatoms: count categories (10 fields/sample)
  - Invertebrates: counts and measures (minimum 1/8 subsamples or N = 25 per sample)
  - Fish and herps: counts (depletion estimation models) and measures

Environmental controls of FCL

1) Stability (*STAB*)

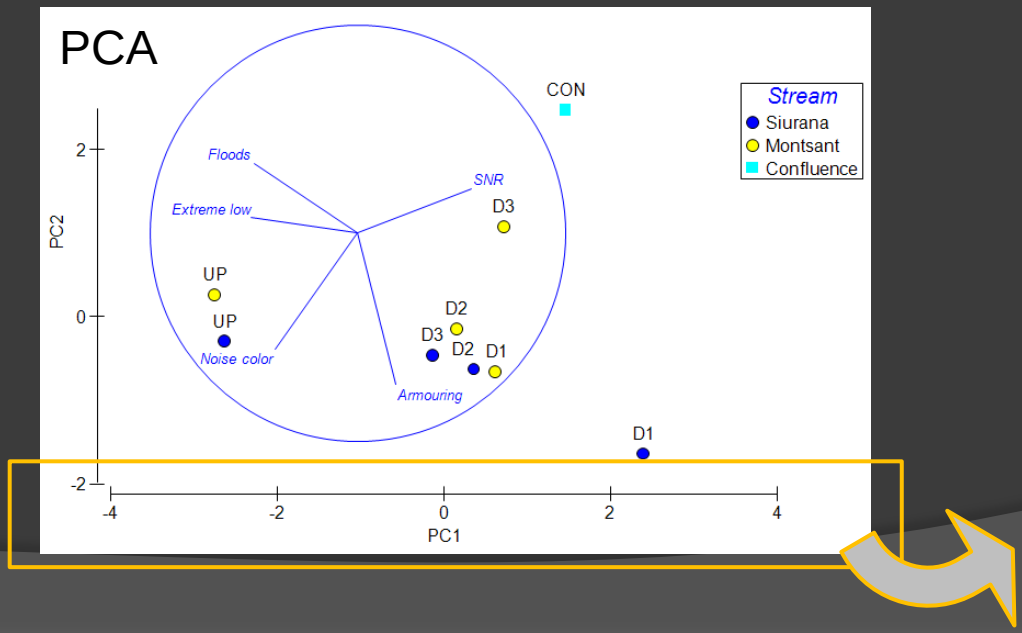
- SEDIMENTS: Sediment armouring (D50sup/D50sub)
- HYDROLOGY: Distributed hydrological model (TETIS)

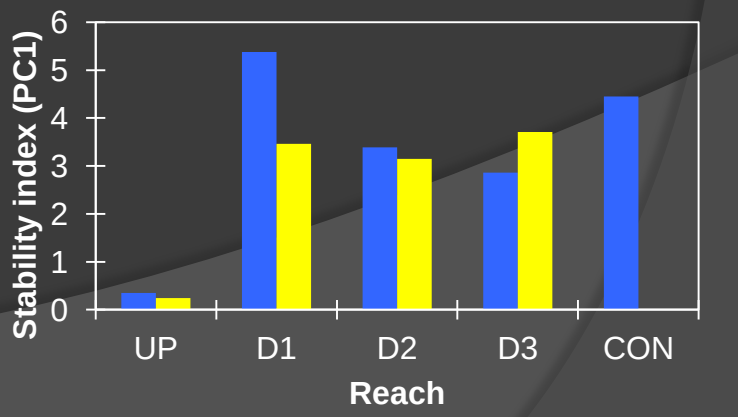
➔ series of av. daily flow 1998-2012 (15 y)

➔ spectral analyses > periodic, stochastic, and catastrophic variation *(Sabo & Post 2008)*

➔ several flow metrics:

- Floods (days)
- Low flows (days)
- Noise color (≈ flashiness)
- Signal-to-noise ratio (≈ relative importance of stochastic vs. periodic events)





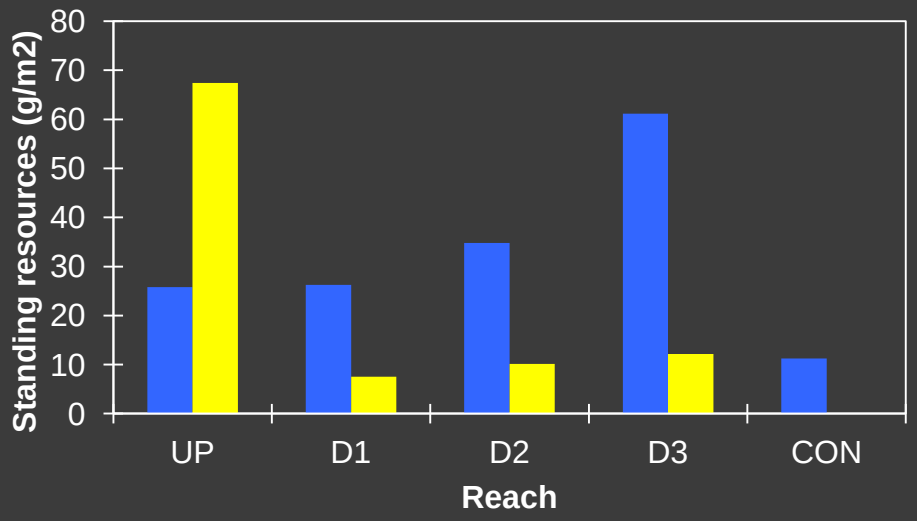
Environmental controls of FCL

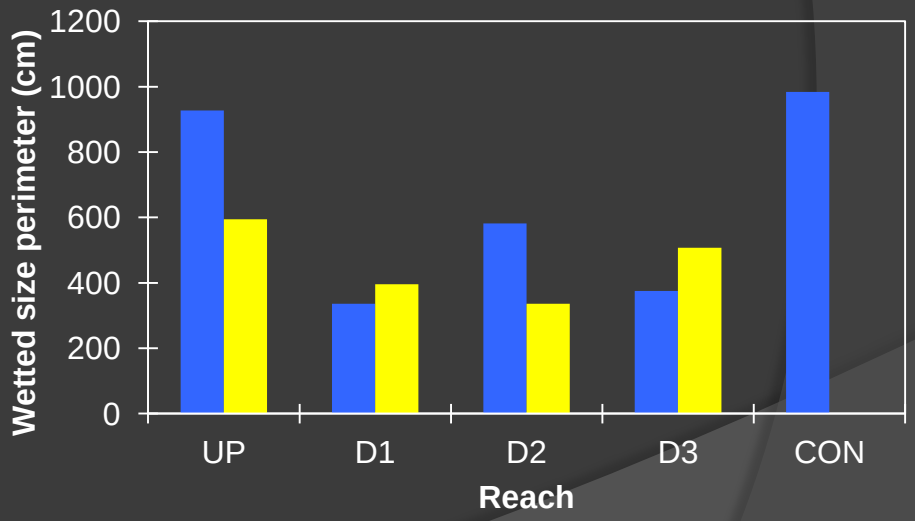
2) Resource availability (*RES*)

- Standing biomass of basal resources
  (from habitat mapping and biomass estimation)

3) Ecosystem size (*SIZE*)

- Wetted cross-sectional perimeter
  (Average of 10 measures/reach)





Are the 3 hypotheses correlated?

RES <> SIZE: Rho = -0.03

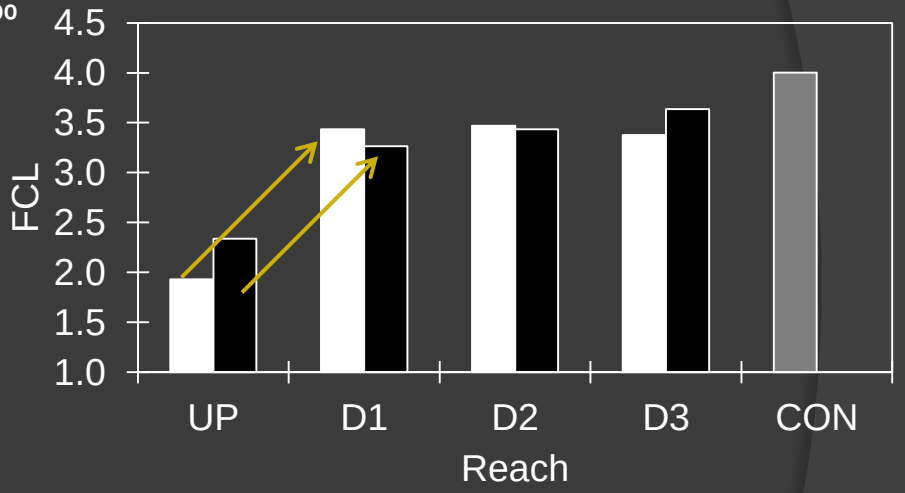
STAB <> SIZE: Rho = -0.38

STAB <> RES: Rho = -0.46

Environmental controls of FCL

FCL:
Maximum trophic position of a predator taxa with regards to the average d15N of basal resources (SPOM, CPOM, CBOM, biofilm, macrophytes)

Assuming uniform mean fractionation rate 3.4 ‰
(after *Post 2002*)



Maximum trophic positions:

Top predator	M_UP	M_D1	M_D2	M_D3	S_UP	S_D1	S_D2	S_D3	CON
Natrix maura	1.93			3.14		3.26		3.57	3.48
Anguilla anguilla		3.43	3.47						4.00
Barbus sp		3.31	3.35	3.38	2.34	3.23	3.43	3.49	3.64
Gobius lozanoi		3.17	3.05	3.15					
Salmo trutta		3.36							
Squalius laietanus					2.15			3.64	3.37

Environmental controls of FCL

FCL ~ Environmental controls

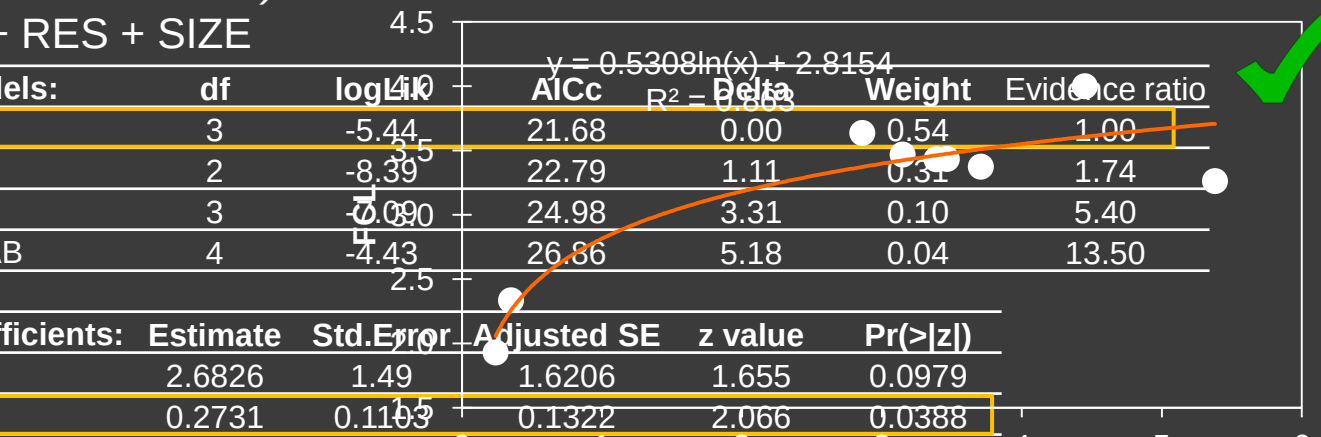
Information-theoretic model-selection approach
(Burnham & Anderson 2002)

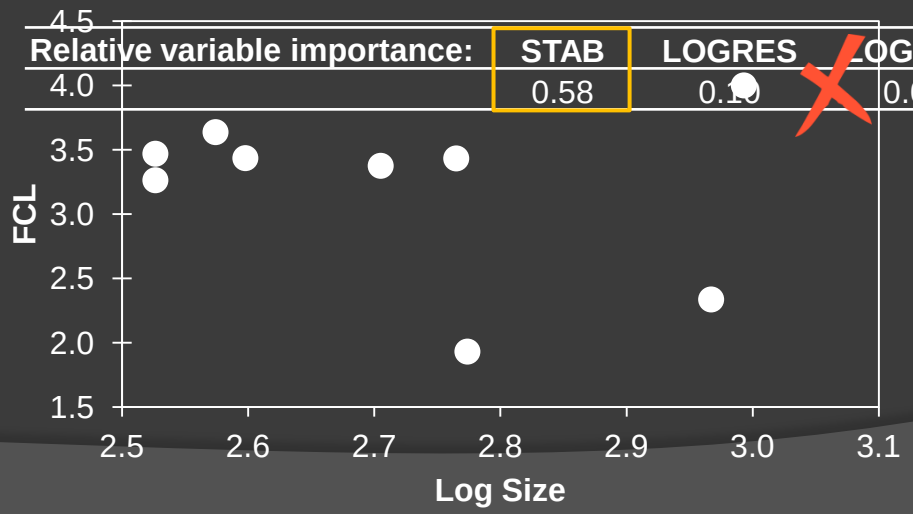
FCL ~ STAB + RES + SIZE

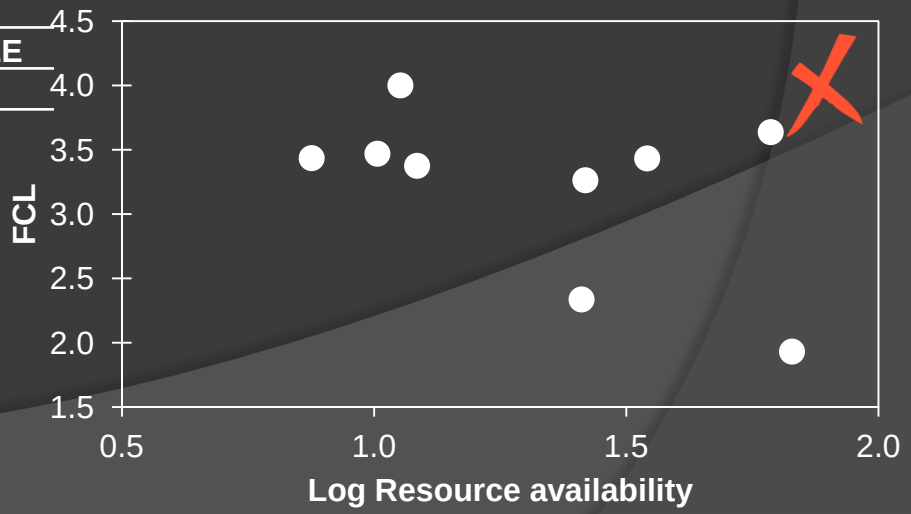
Component models:	df	logLik	AICc	Delta	Weight	Evidence ratio
STAB	3	-5.44	21.68	0.00	0.54	1.00
(Null)	2	-8.39	22.79	1.11	0.31	1.74
LOGRES	3	-6.09	24.98	3.31	0.10	5.40
LOGSIZE, STAB	4	-4.43	26.86	5.18	0.04	13.50

Model-averaged coefficients:	Estimate	Std.Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	2.6826	1.49	1.6206	1.655	0.0979
STAB	0.2731	0.1103	0.1322	2.066	0.0388
LOGRES	-0.9421	0.6145	0.7414	1.271	0.2038
LOGSIZE	1.6059	1.3069	1.6317	0.984	0.3250

Relative variable importance:	STAB	LOGRES	LOGSIZE
	0.58	0.10	0.04

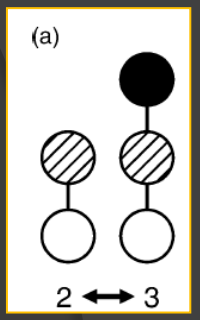






Proximate mechanisms of FCL

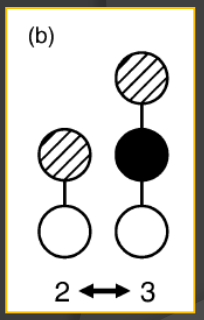
- Additions? ✗
  - Are changes in top predators composition related to changes in FCL?
  - Distance-based LM: community of top predators ~ FCL



SEQUENTIAL TESTS

Variable	AICc	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+FCL	71,339	4166,3	2,2787	0,089	0,24559	0,24559	7

- Insertions? ✗
  - Are changes in predators composition related to changes in FCL?
  - Distance-based LM: community of predators ~ FCL



SEQUENTIAL TESTS

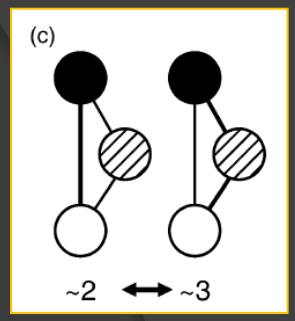
Variable	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+FCL	71,105	2661,1	1,4937	0,123	0,17586	0,17586	7

  - Are changes in consumers composition related to changes in FCL?
  - Distance-based LM: community of consumers ~ FCL

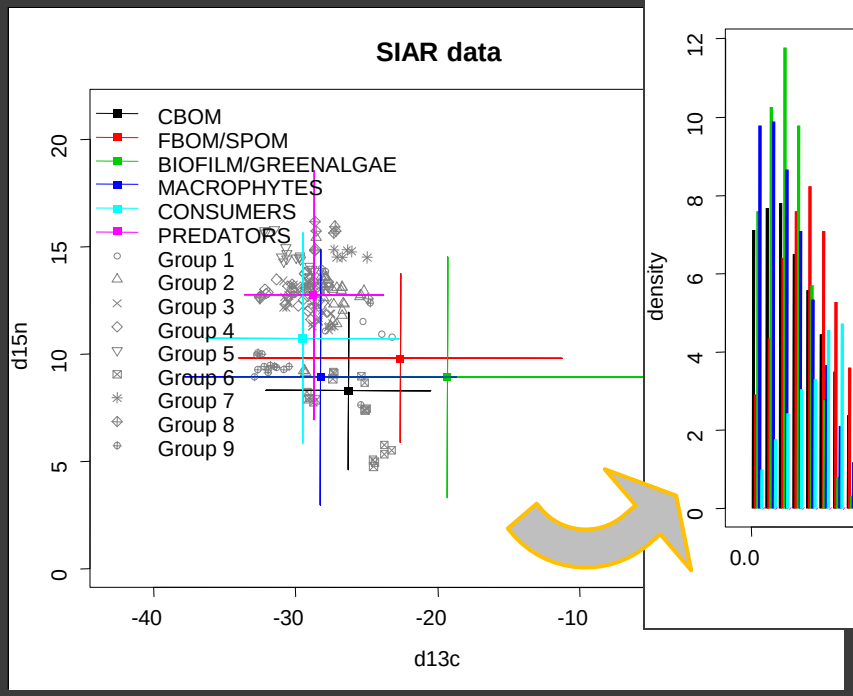
SEQUENTIAL TESTS

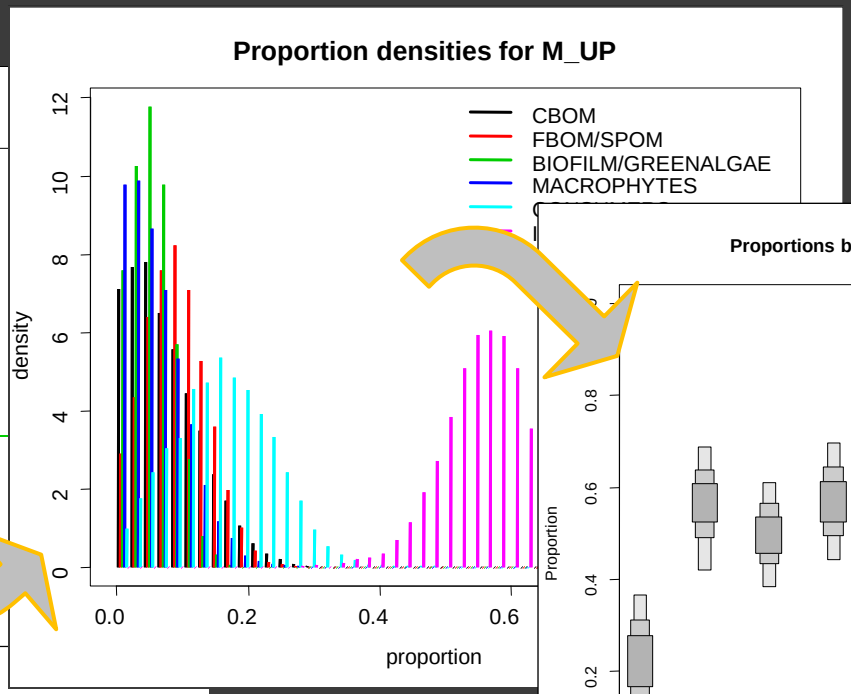
Variable	AICc	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+FCL	75,052	5178,1	1,8747	0,051	0,21124	0,21124	7

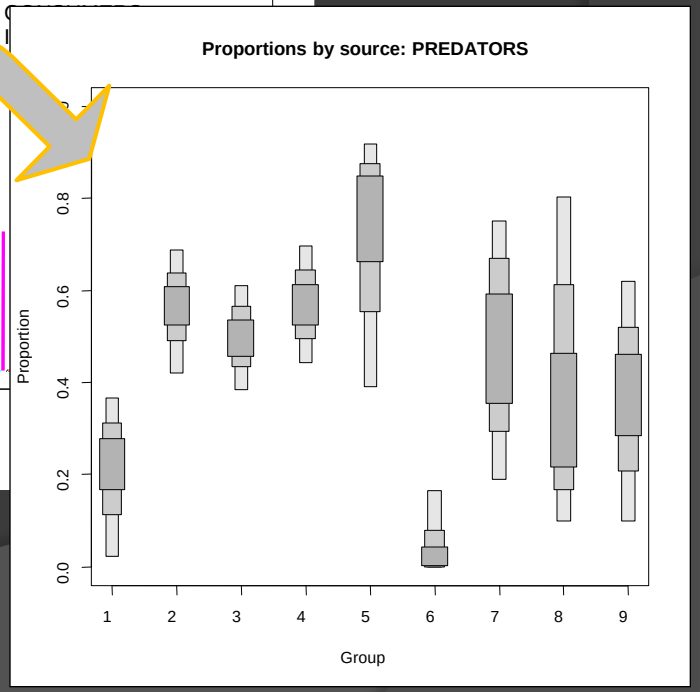
Proximate mechanisms of FCL



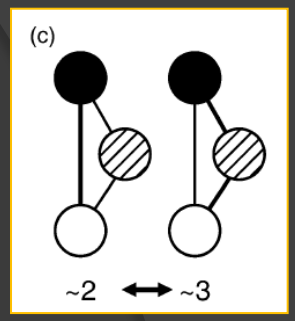
- Changes in multitrophic omnivory?
  - Are changes in top predators diets related to changes in FCL?
  - Are changes in predators diets related to changes in FCL?
    - ➔ Bayesian mixing models (SIAR package in *R*) [uncertainty and variation in input parameters]
      - ➔ Relative contributions of each trophic compartment to the predator diets





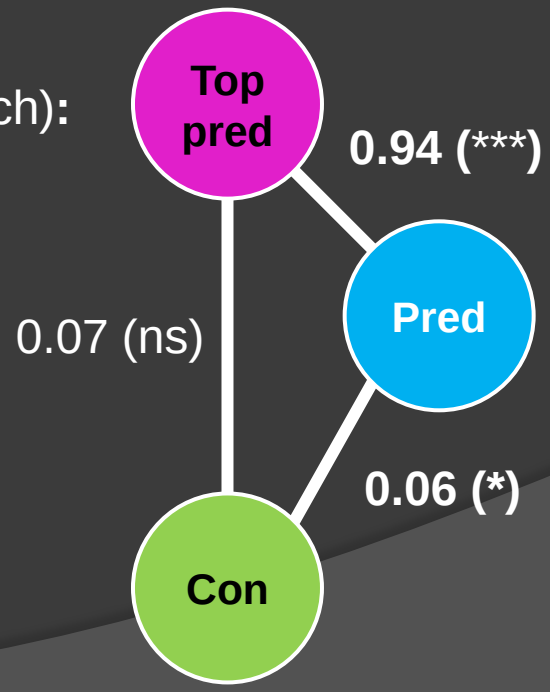


Proximate mechanisms of FCL

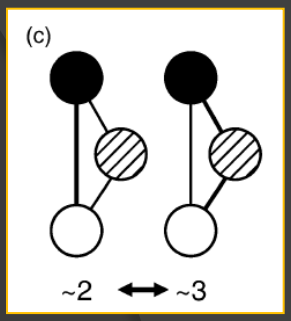


- Changes in multitrophic omnivory:
  - Are changes in top predators diets related to changes in FCL? ✓
  - Are changes in predators diets related to changes in FCL? ✓

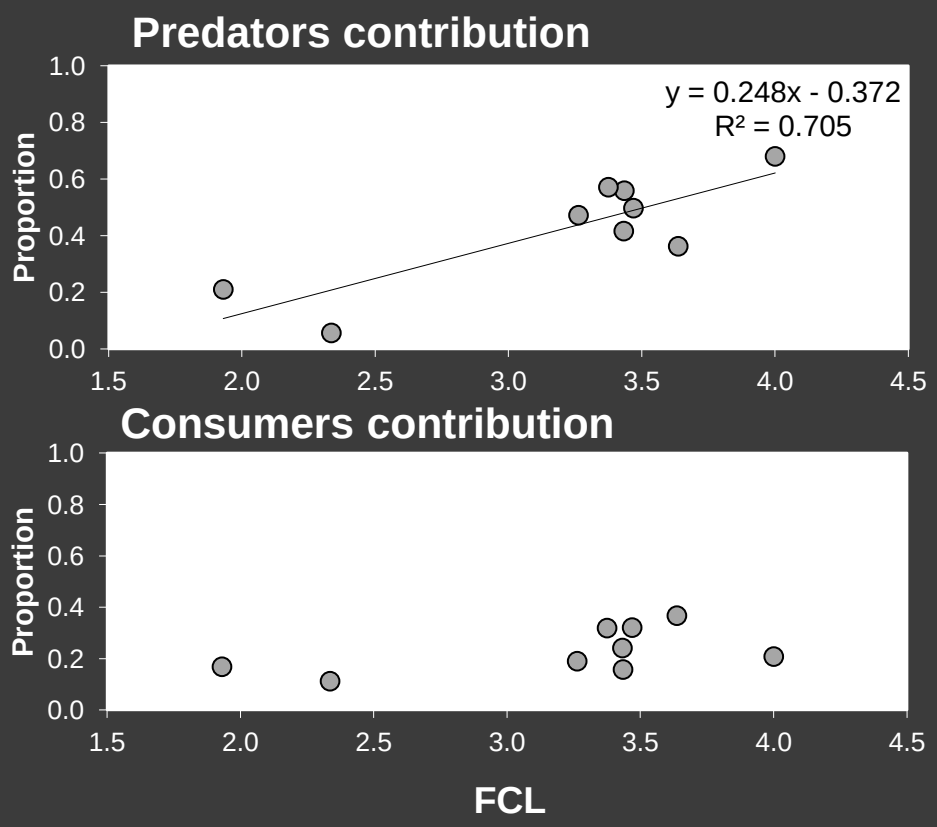
Relative variable importance
(information-theoretic model-selection approach)**:**



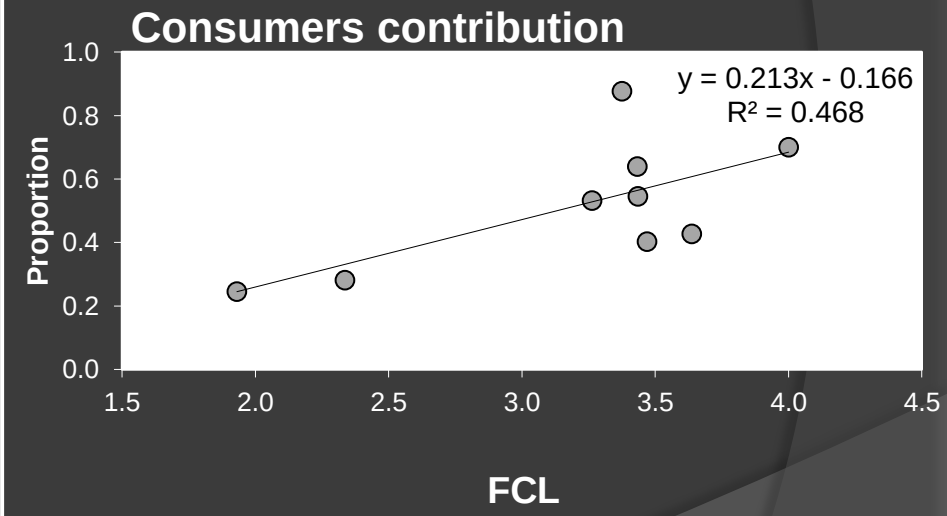
Changes in multitrophic omnivory:



Top predators' diet



Predators' diet



Conclusions

- Hydrological stability appears to be the main environmental control of FCL in Mediterranean rivers
  - Flashy reaches, with frequent floods and droughts, present shorter FCL than stable reaches.

- Neither ecosystem size, nor resource availability, appear to play a relevant role in controling FCL.

- The proximate (biological) mechanism of FCL changes is a shift in top predators' diets:

  ➔ **Stability increases FCL in streams by reducing top predators' omnivory**

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