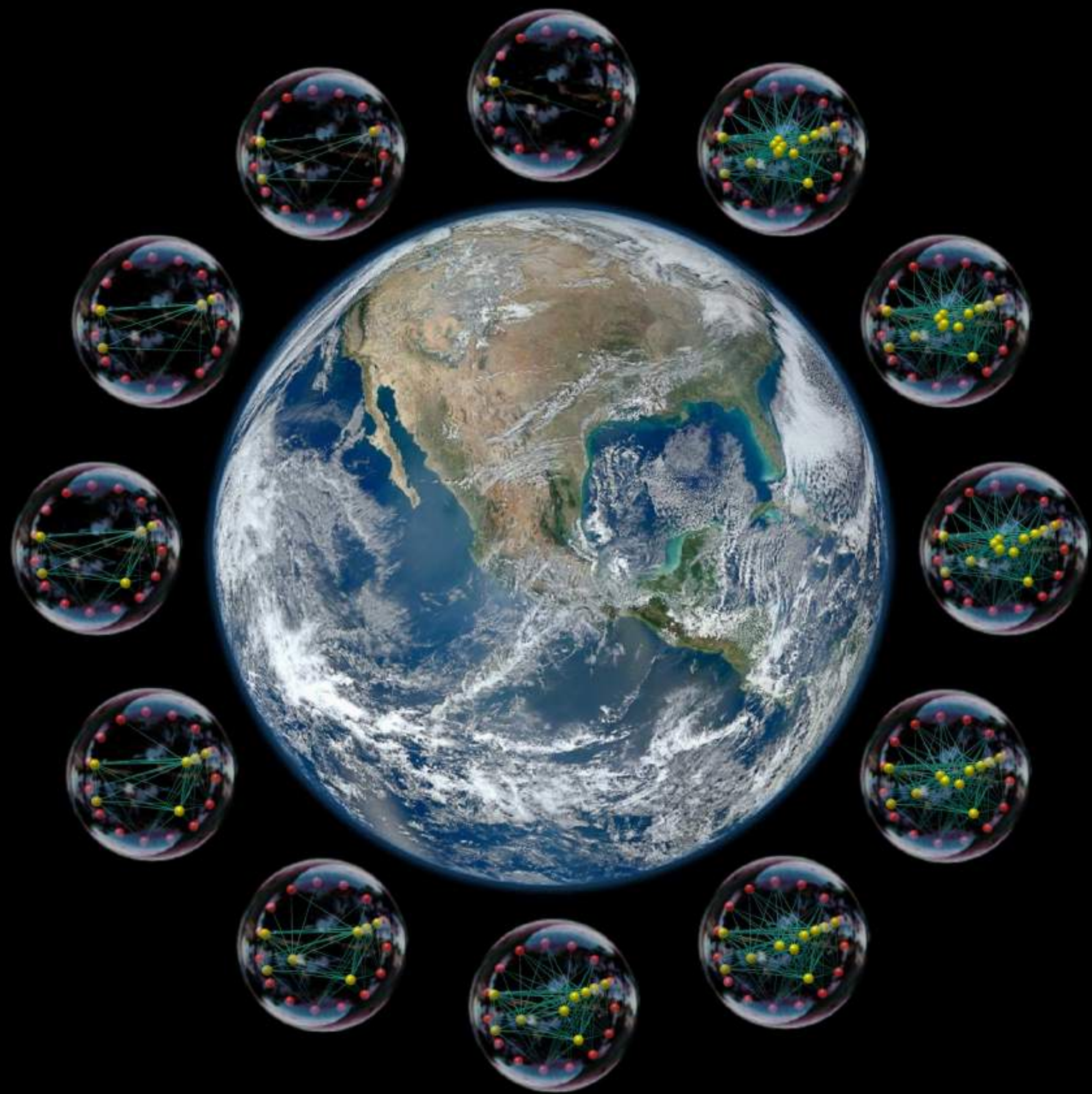
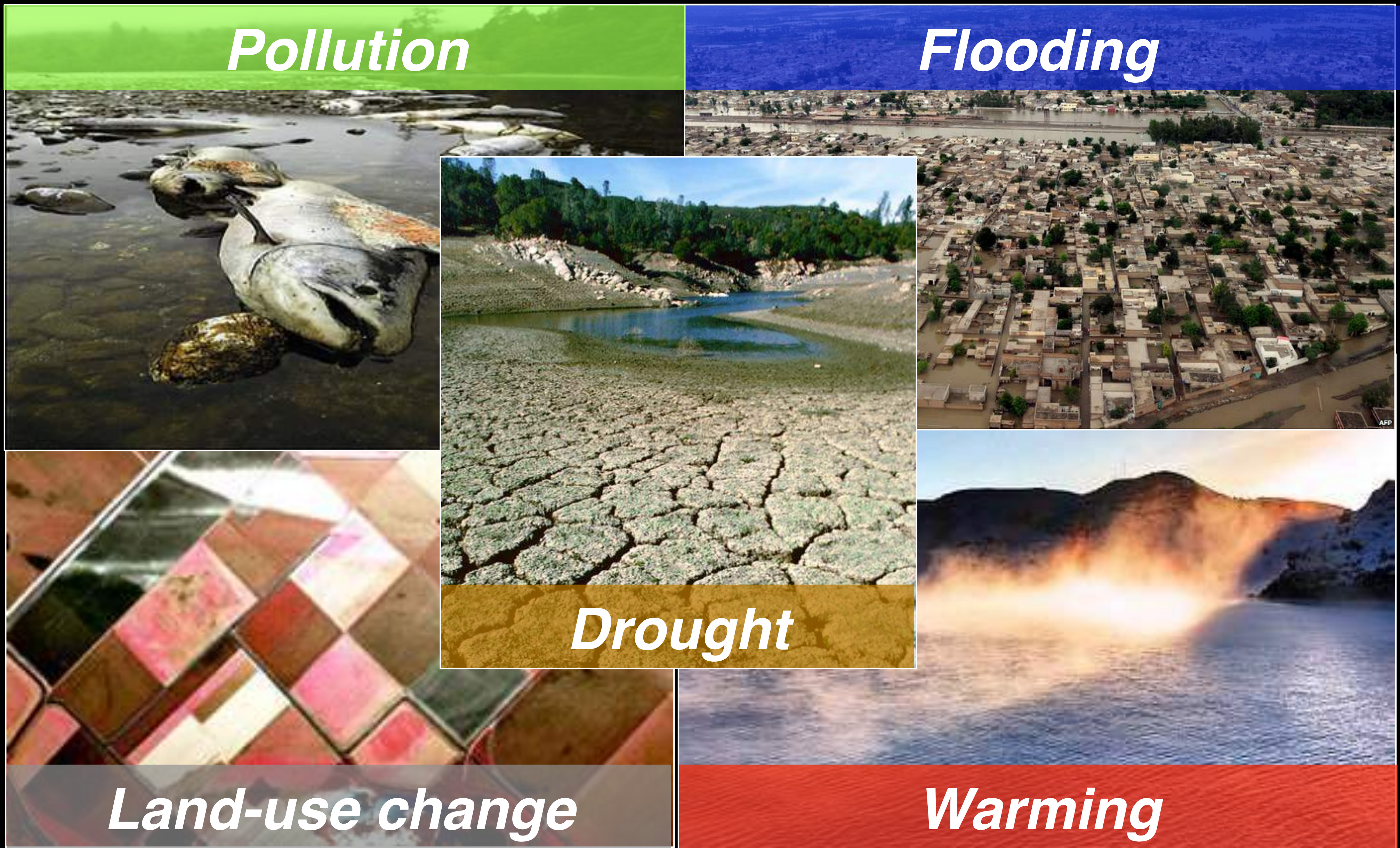
Network-based Approaches to the Grand Challenges of 21st Century Ecology



Guy Woodward (Imperial College London)

Core research focus: freshwaters are exposed to a cocktail of stressors in the 21st century

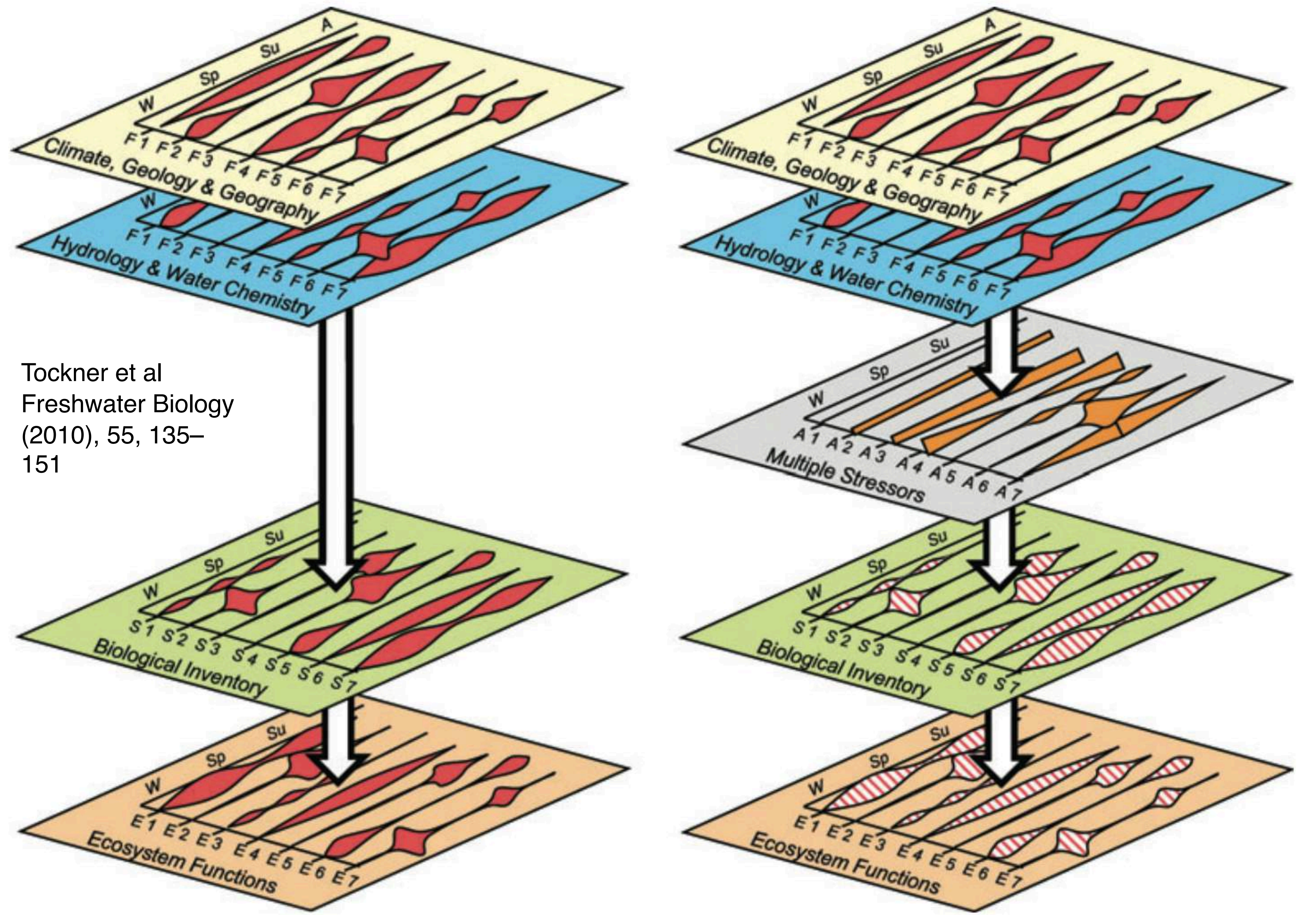


Current research grants (6 postdocs, 10 PhD students)

Title	Funding Body	£	Start
Pesticides — Catastrophic f[illegible]e	N.E.R.C.	£65,000	2013
Habitat Restoration — River restoration: large-scale experiments	Private	£120,000	2013
Drought — Fragility of stream ecosystem functioning in response to drought: an experimental test	N.E.R.C.	£701,000	2012
Land-use — Diversity of Upland Rivers for Ecosystem Service Sustainability (DURESS)	N.E.R.C.	£3,200,000	2012
Warming — Using individual metabolism and body size to predict climate warming impacts on aquatic food webs	N.E.R.C.	£511,000	2011
Warming — The temperature dependence of biogeochemical cycles	AXA Insurance	£90,000	2011
Warming — Predictable feedbacks between warming, community structure and ecosystem functioning	N.E.R.C.	£468,000	2010
Nutrients — Manipulating the chemosynthetic and photosynthetic support of river food webs	N.E.R.C.	£531,000	2010

£5,686,000

Environmental filters can "reshape" ecosystems



Tockner et al
Freshwater Biology
(2010), 55, 135–
151

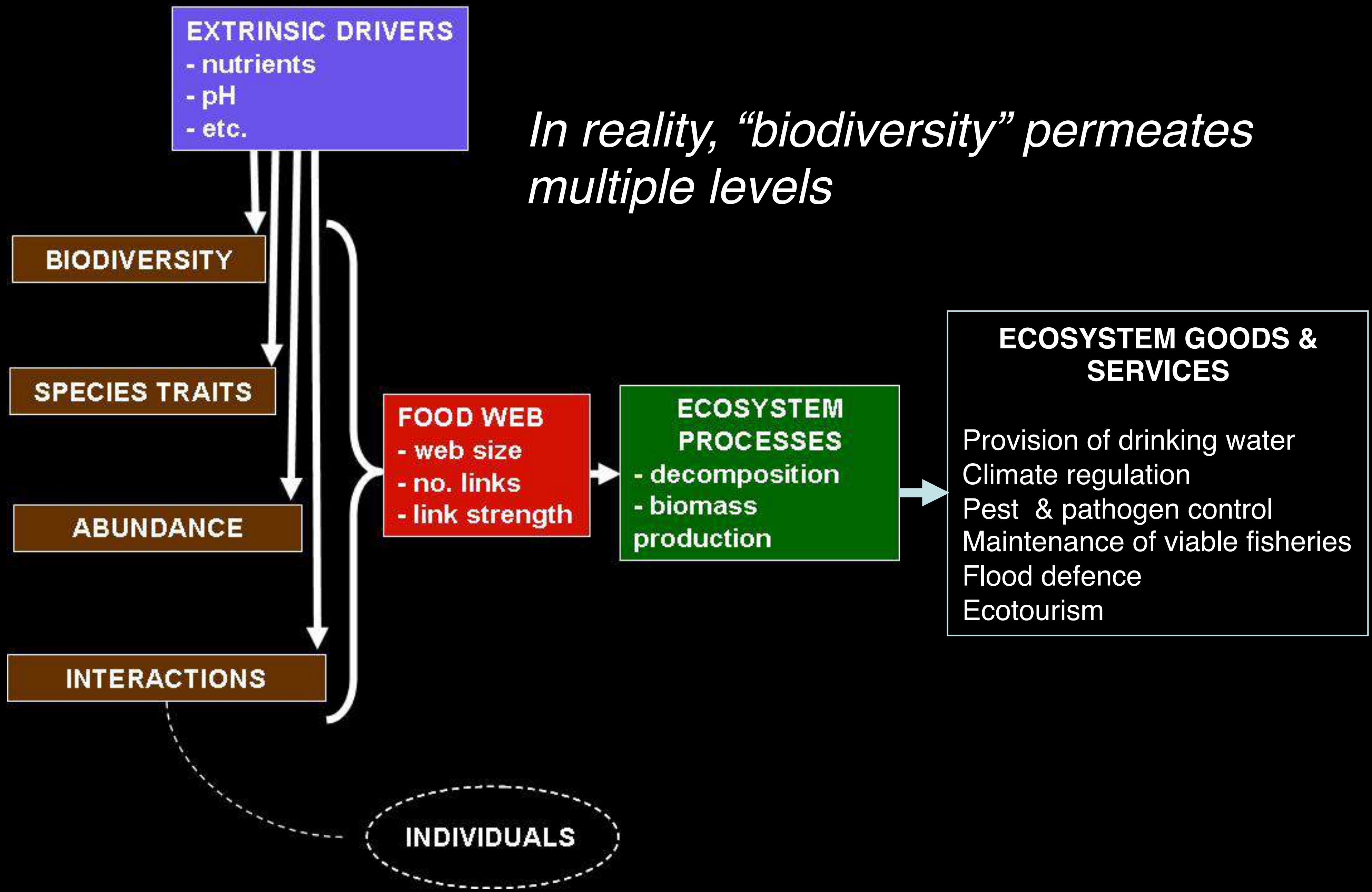
Before we can fix something, we need to understand how it works...

Biodiversity-ecosystem functioning research – what are we really measuring?

So far: a narrow focus on species richness and single process rates – we need to get closer to the true meaning

Linking across levels of organisation: from structure to function and back again...

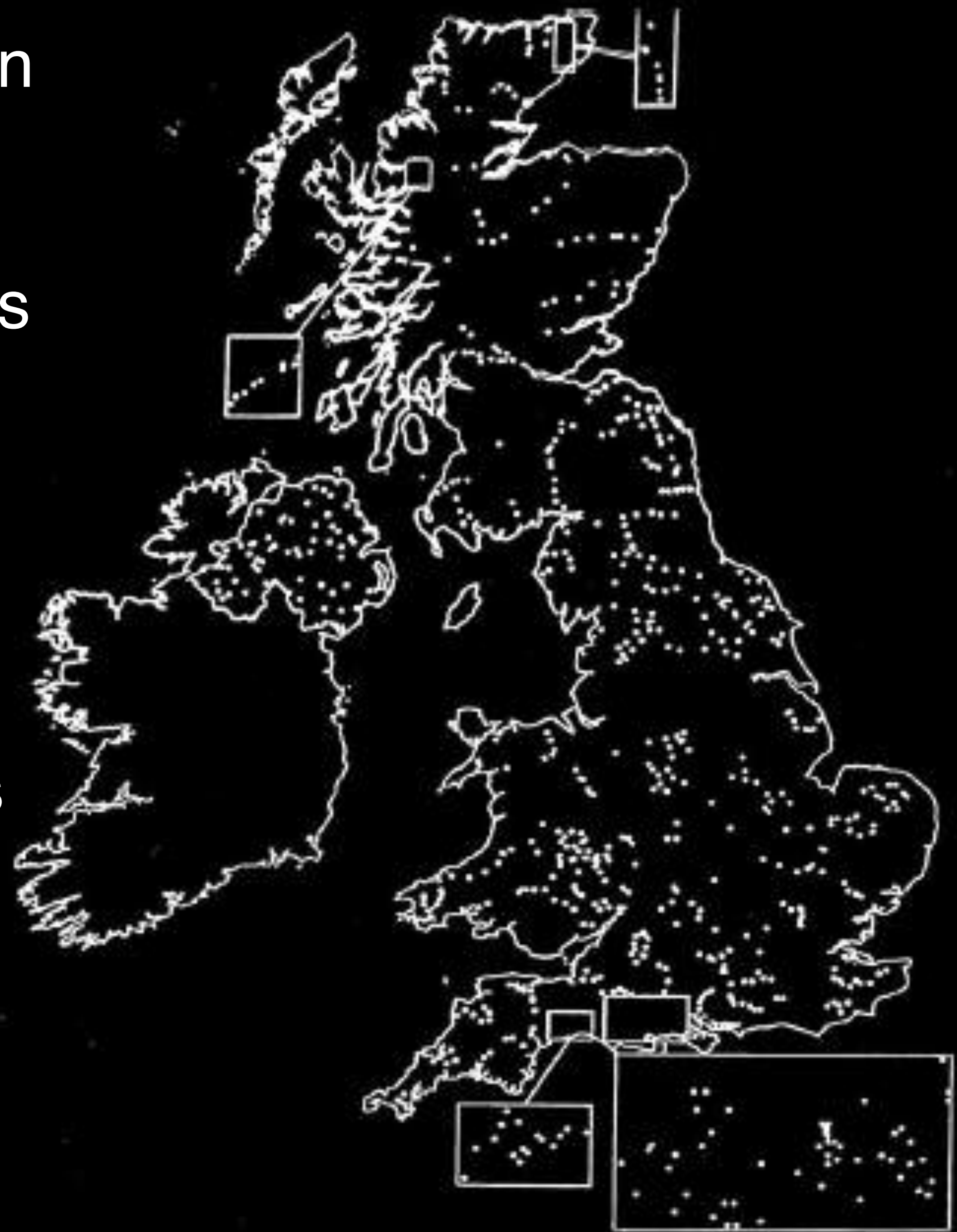
In reality, "biodiversity" permeates multiple levels



Biodiversity and ecosystem functioning: what do we know?

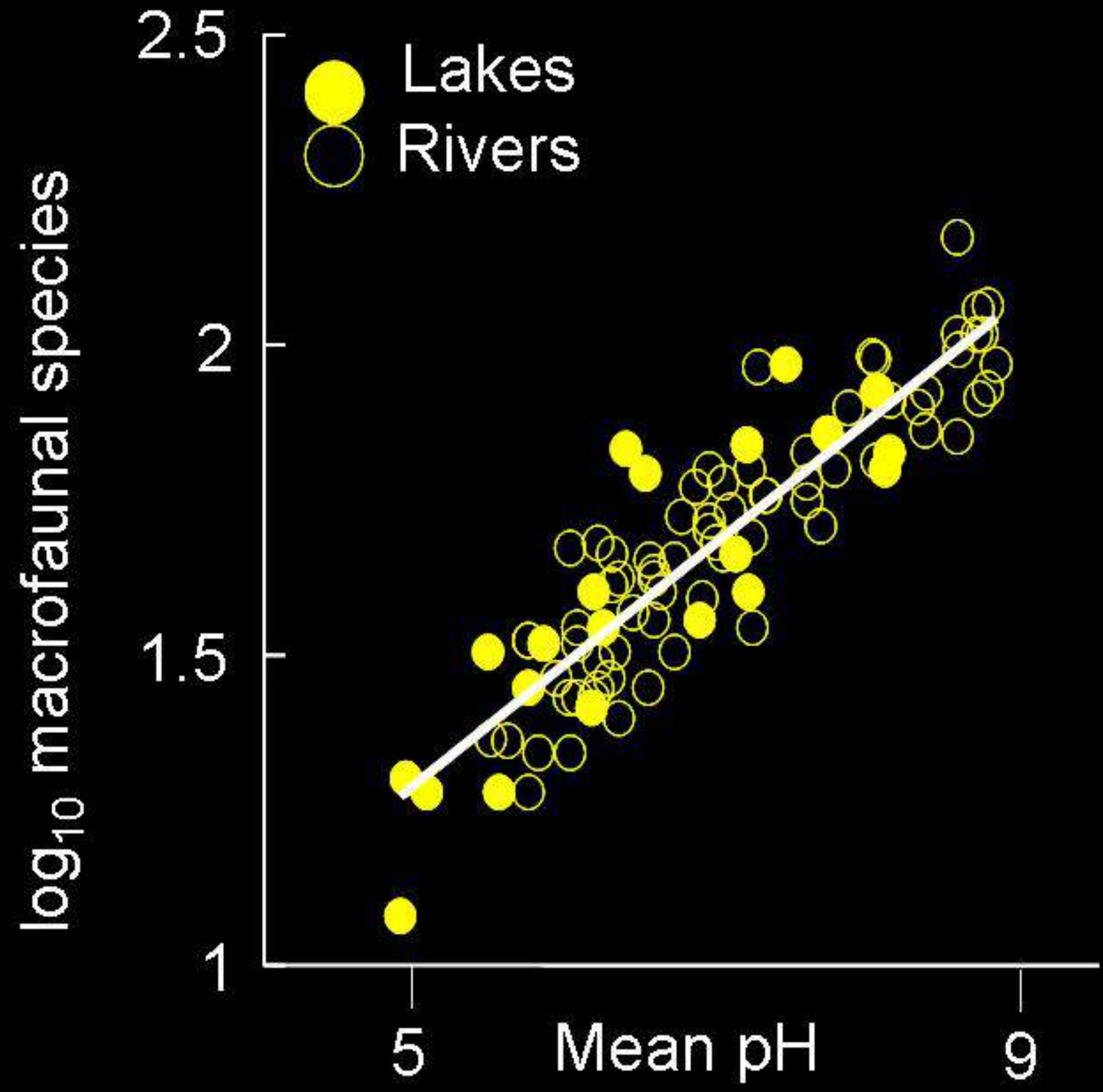
Huge volumes of data exist on community structure – for instance in UK freshwaters alone we have data from 100s of sites over many years..... (e.g. RIVPACS, UKAWMN, ECN sites) .

We know far less about how these are linked to processes and the provision of ecosystem services

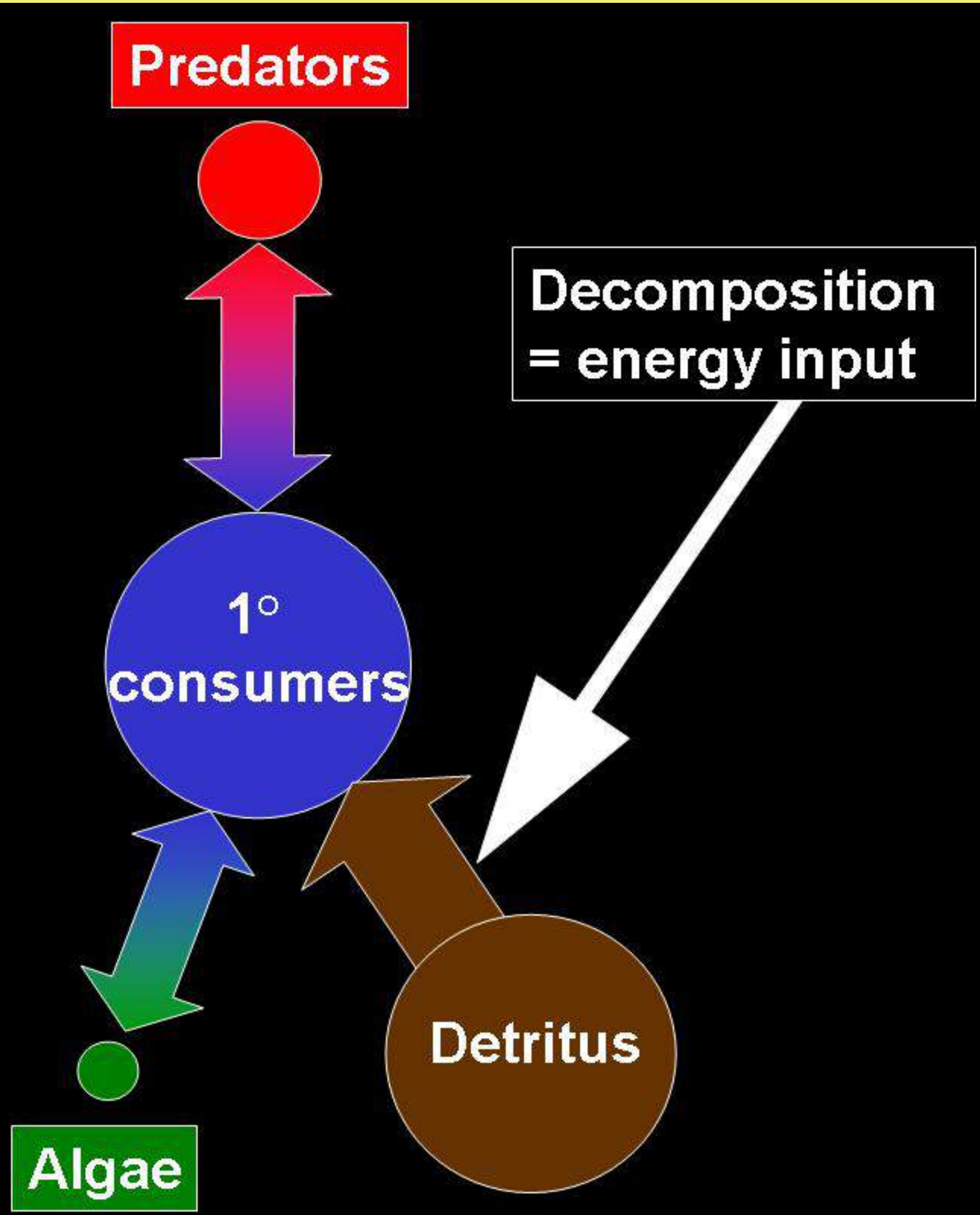


Long-term data are scarce and increasingly valuable for predicting future impacts of environmental change in real systems

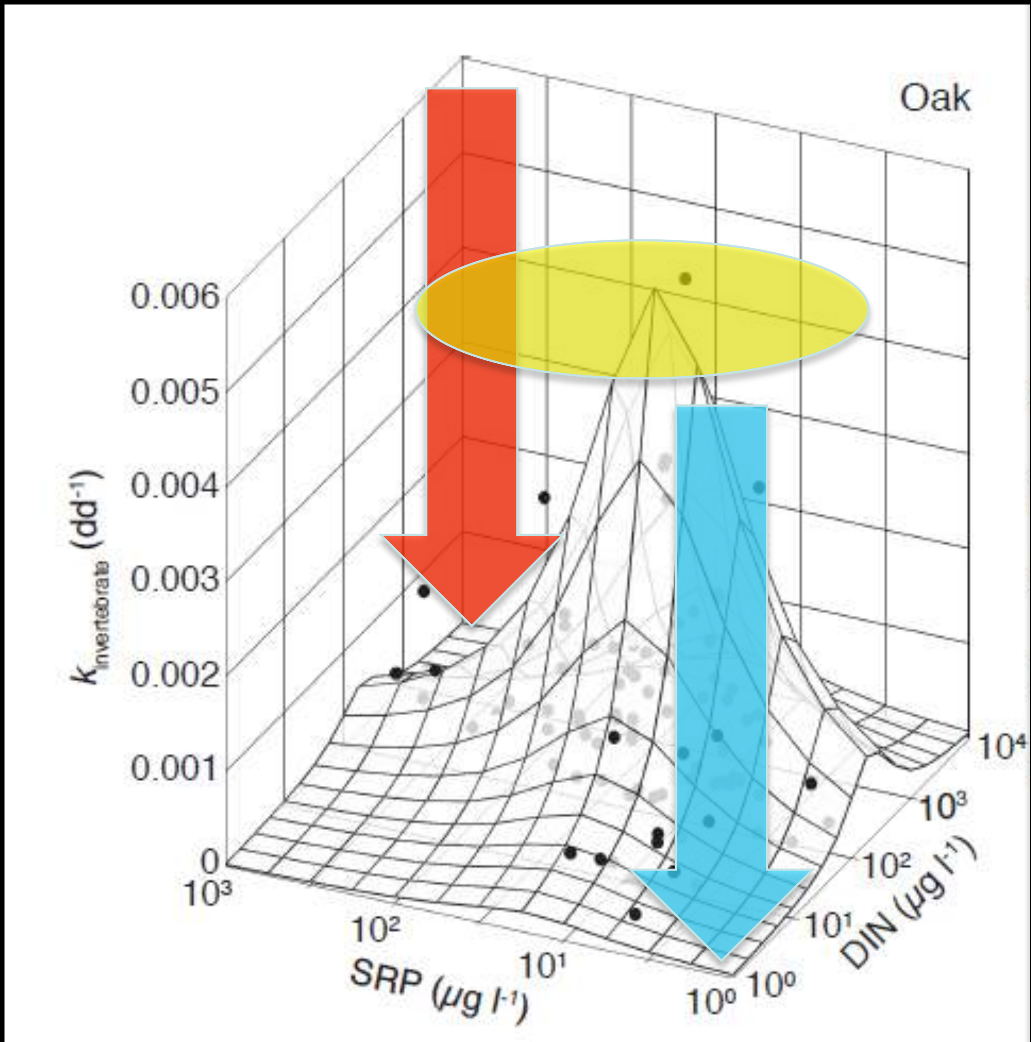
Environmental stressors alter biodiversity (nodes in the food web)…



…stressors also impact ecosystem functioning (e.g. detrital processing in streams)



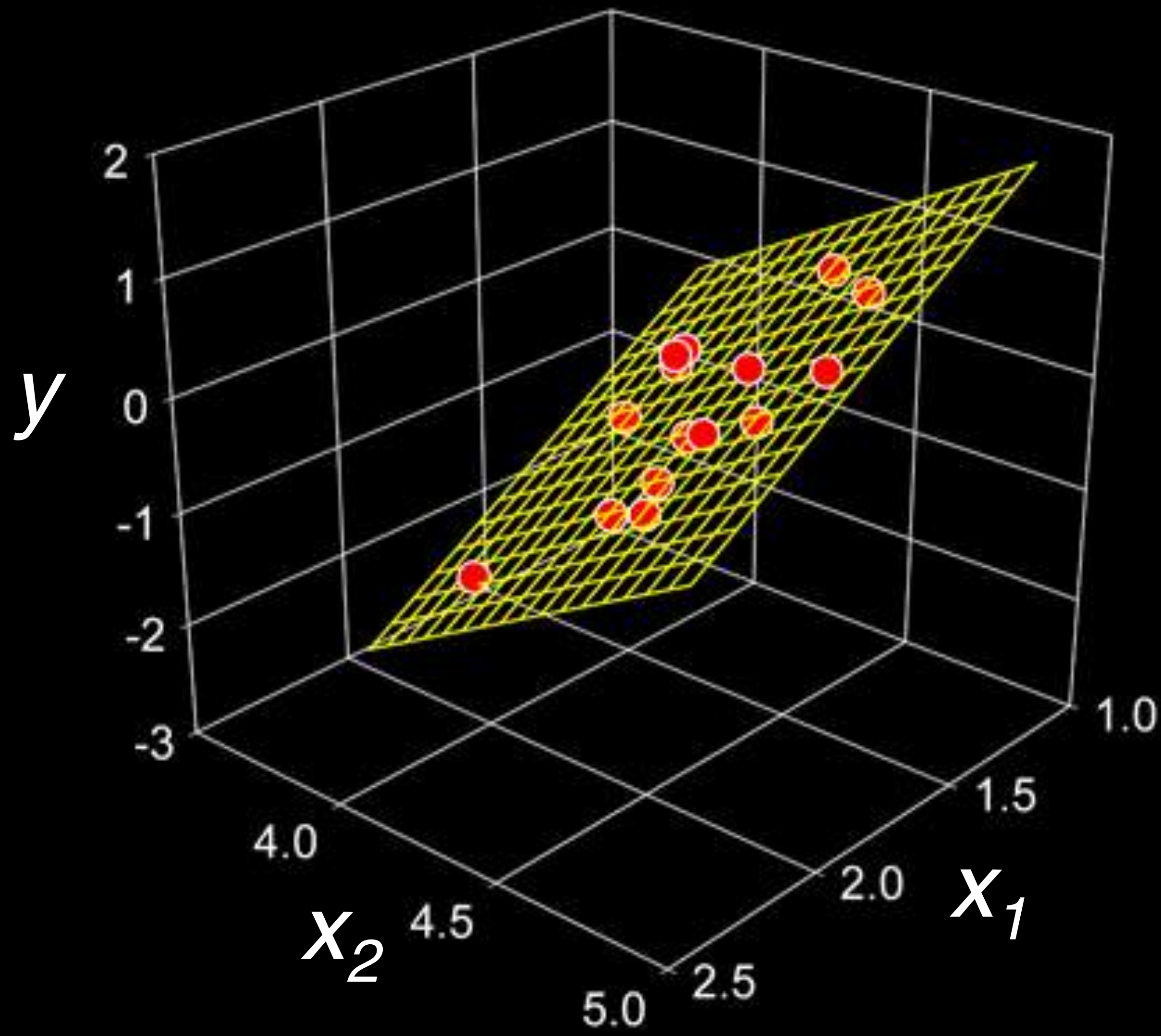
Ecosystem functioning in response to multiple stressors



Woodward et al (2012) *Science*

Decomposition rates across Europe are constrained by nutrient limitation and toxic effects at either end of the nutrient gradient. The "just-right" Goldilocks zone lies in the middle….other drivers (e.g. community composition) are at play here

Resource quality drives consumption rates



y = log % mass loss d^{-1}

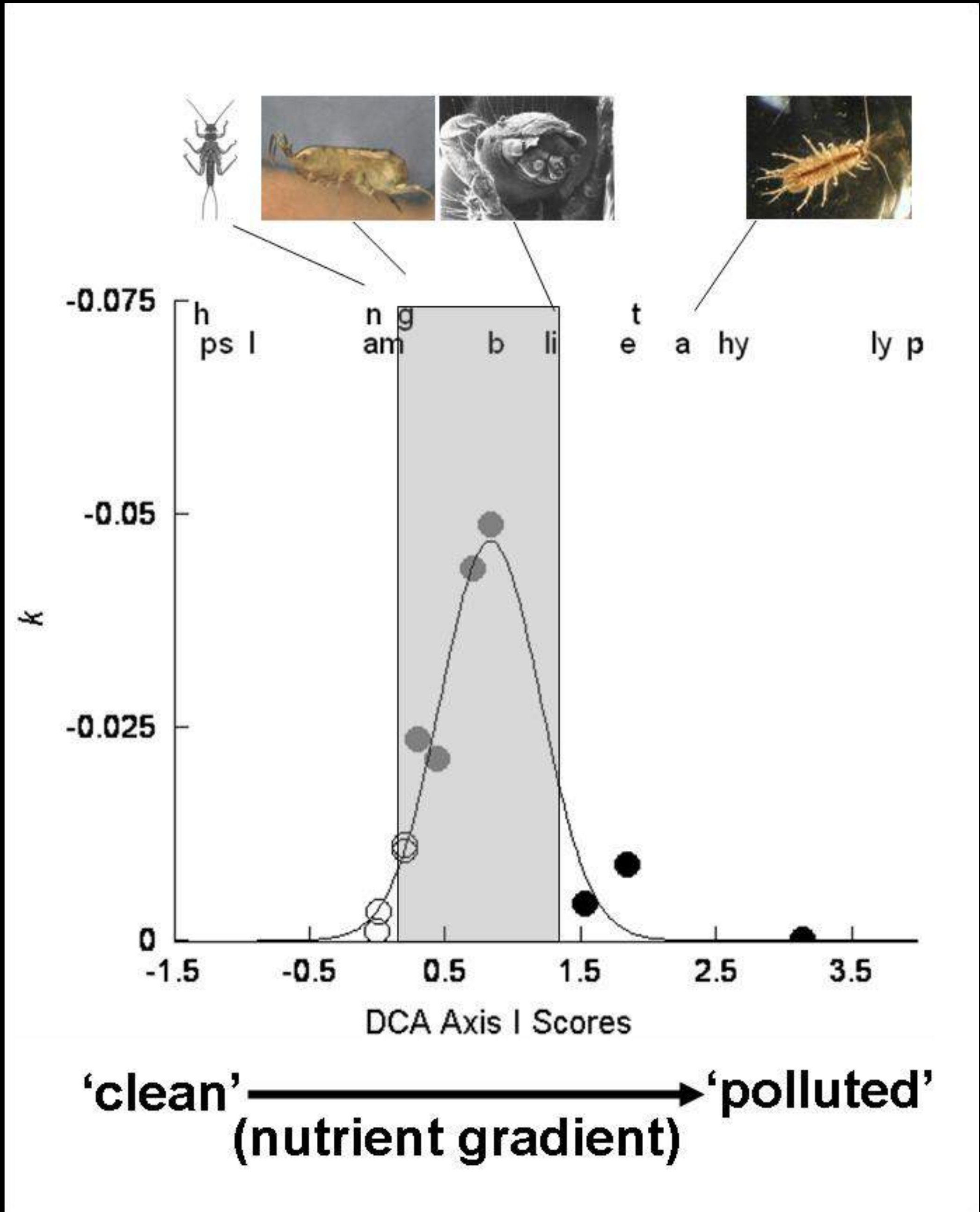
x_1 = log litter C:N

x_2 = log fungal mass

r^2 0.97

Hladyz et al (2009) *Freshwater Biology*

Structure is linked to functioning



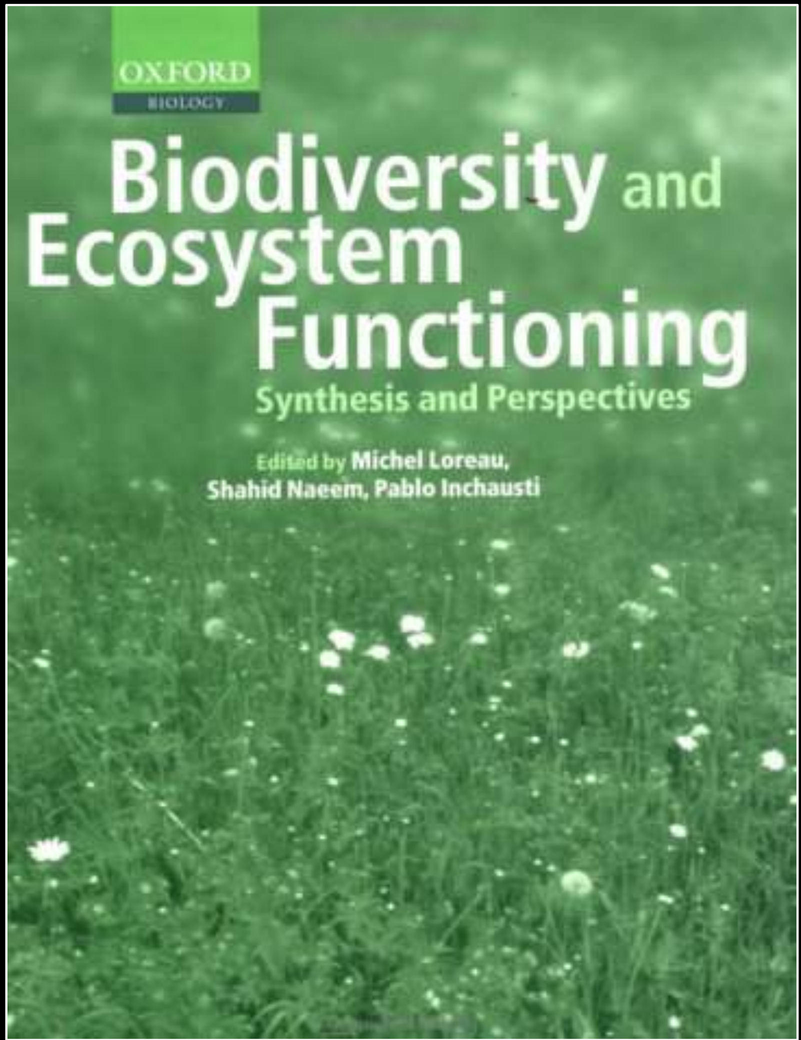
Decomposition rates follow a unimodal curve across a eutrophication gradient – rates are fastest where large consumers ("shredders") predominate

We need to address BOTH structure and functioning

Patterns: diversity, identity, abundance

Processes: decomposition, nutrient cycling etc.

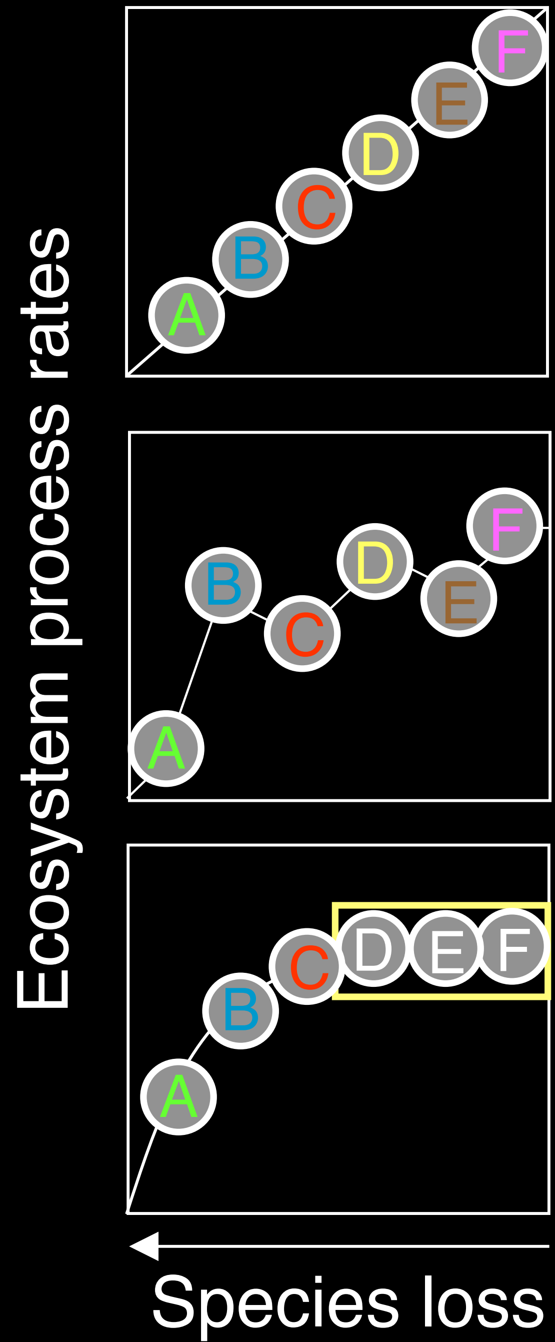
Three biodiversity-ecosystem functioning models



Linear

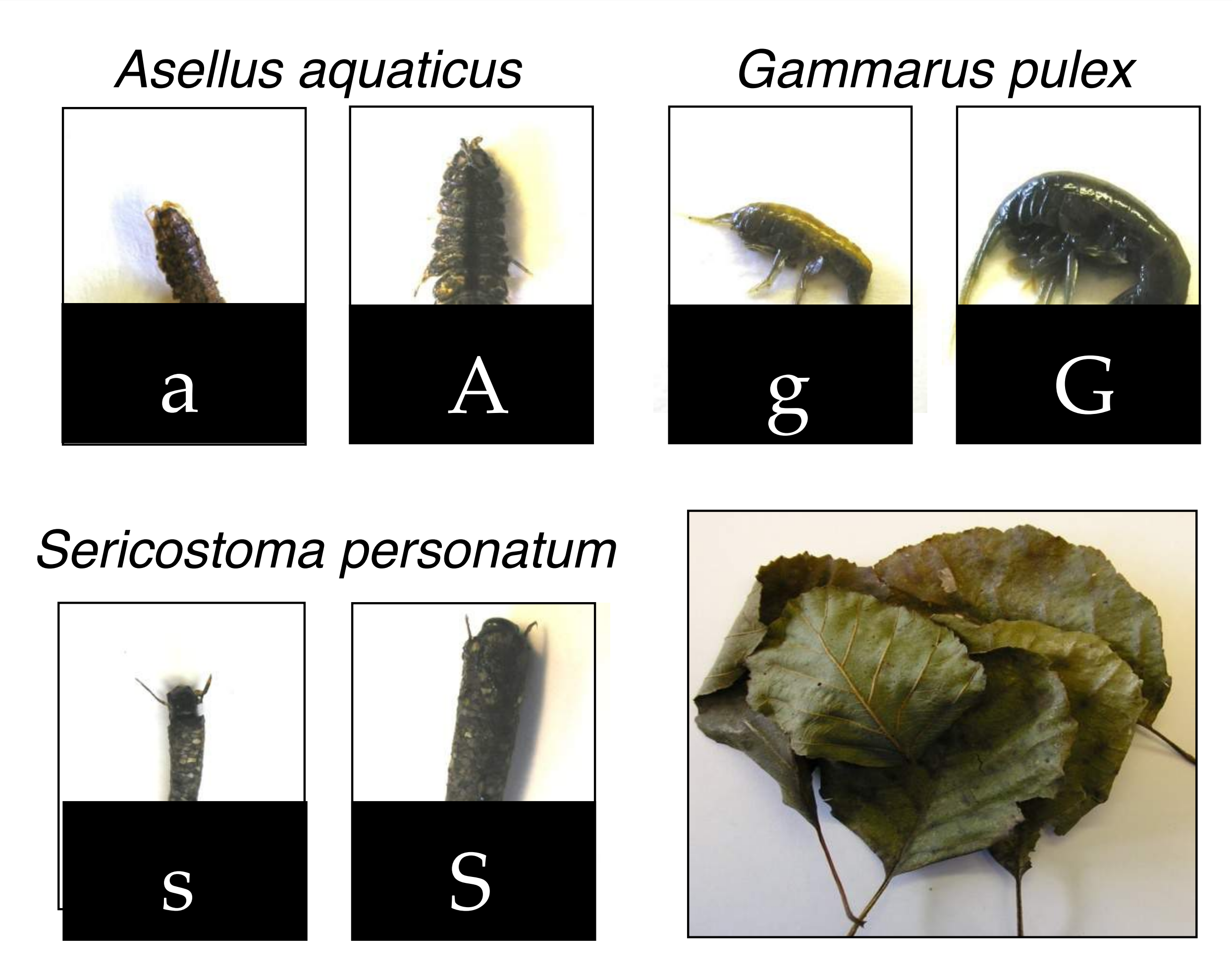
*Idiosyncratic

*Redundancy



*most evidence supports these 2 models

Body size or taxonomic diversity as a key driver of ecosystem processes?



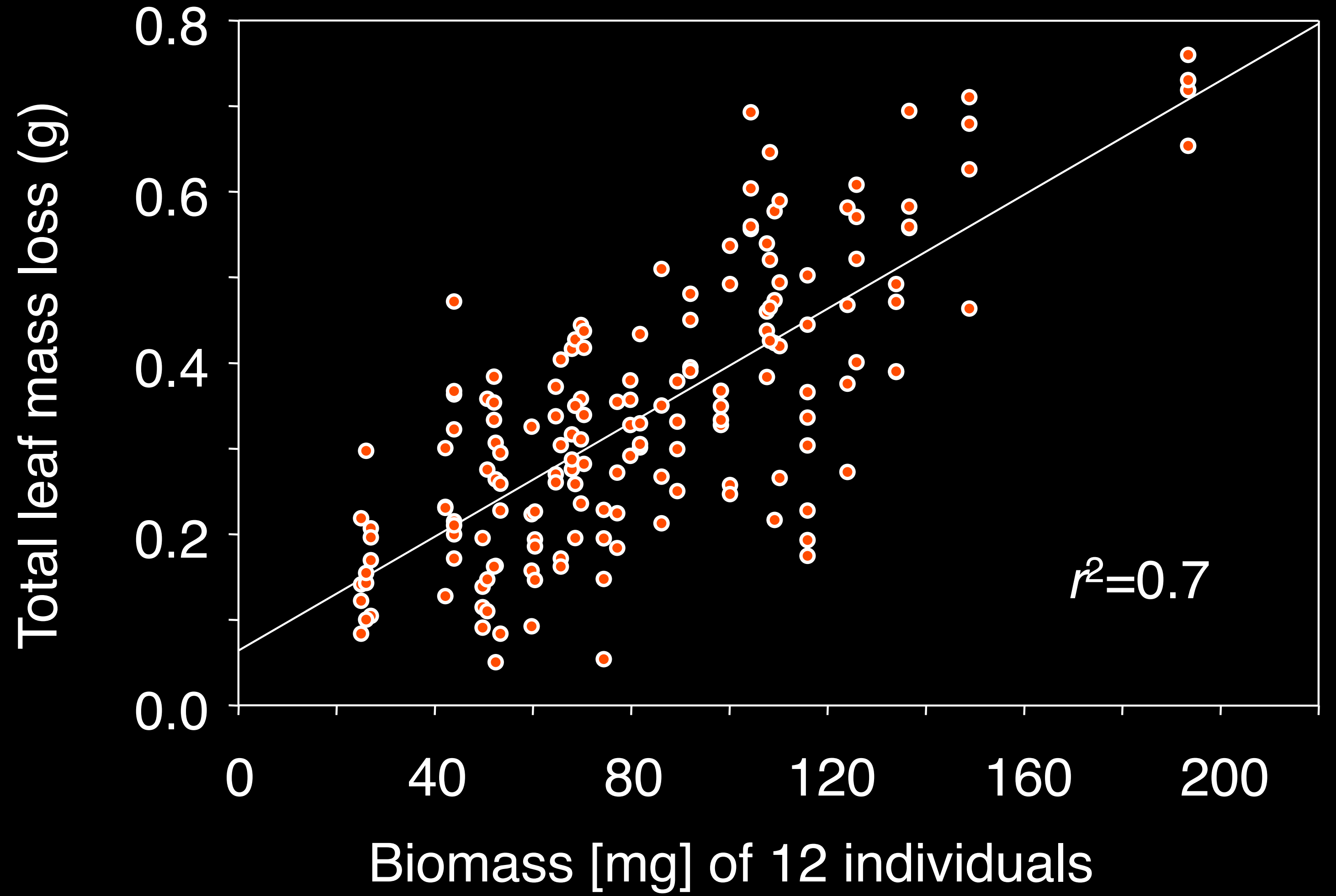
S=1
a A g G s S

S=2
ag as gs AG AS GS
aA gG sS etc…

S=3
ags AGS aAG aAS aGS
sGS agA agG agS etc…

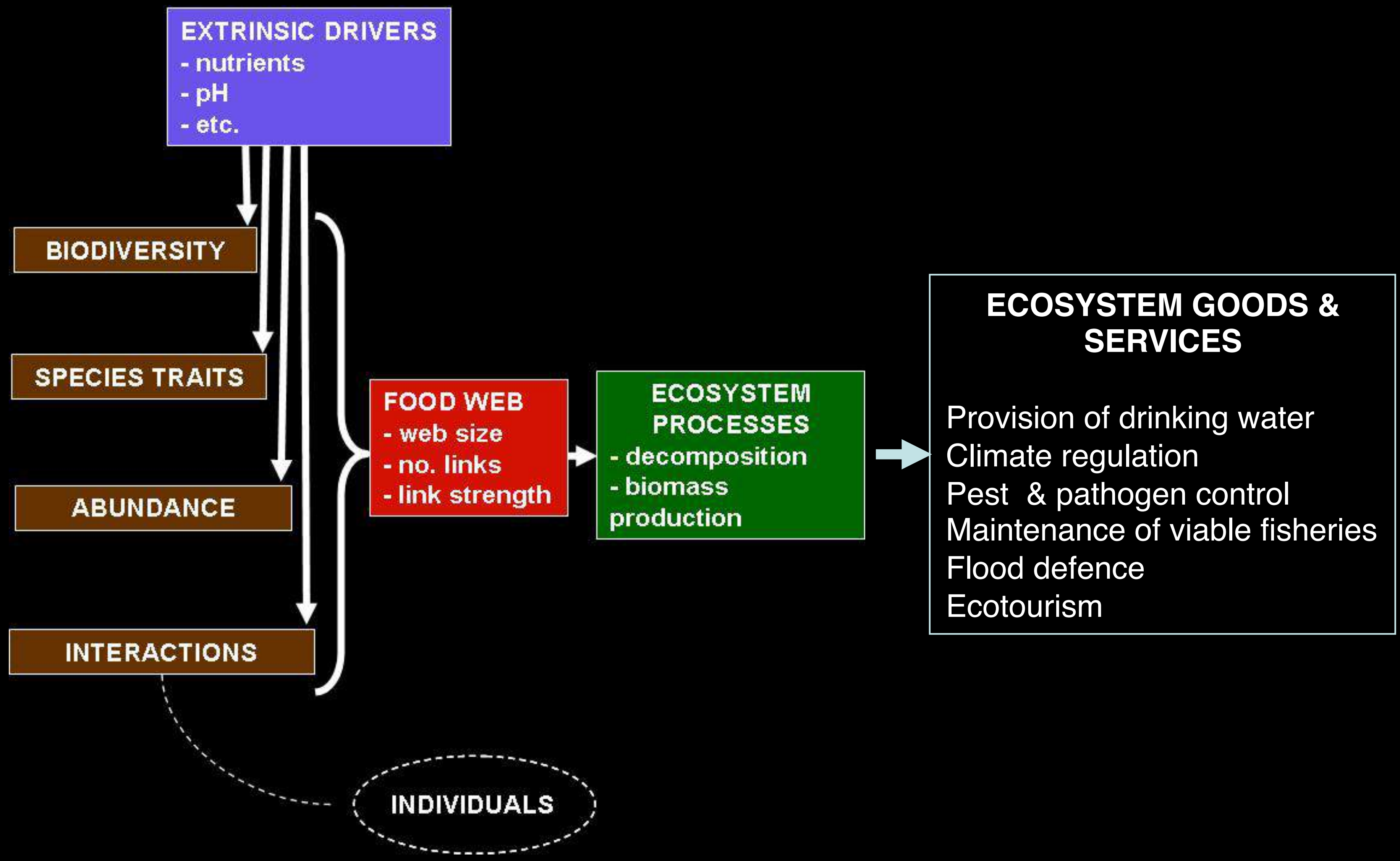
Reiss et al (2011)

Size explained 70% of variation in these experiments…i.e., no effect of species diversity

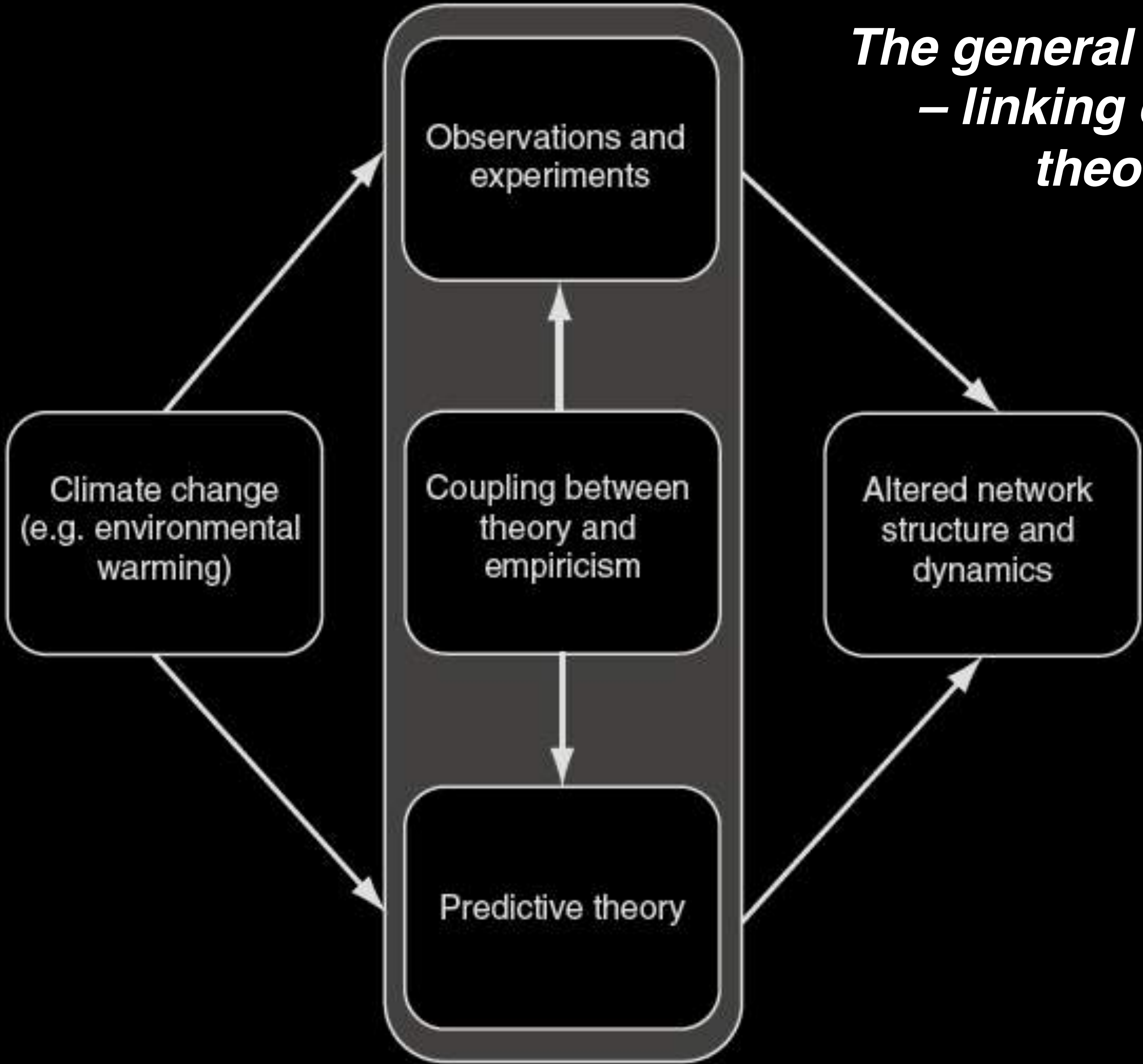


Reiss et al. (2011) *Journal of Animal Ecology*

Biodiversity is more than just species richness: understanding individuals and their size distribution allows us to link across organisational levels...



The general approach – linking data to theory



Prioritising biotic measures...from structure to function

Biomass (*B*) and body mass (*M*)

Numerical abundance (*N*)

Diversity (species richness, *S*, is not the only measure!!)

Feeding links (introducing interactions) (*L*)

Functional attributes (*F*) (e.g. ecosystem process rates)

Most ecological studies measure just one or two of these variables, giving an incomplete view

Different combinations can address different questions (and require different expertise)

N + M + B + S + L + F: The "Rolls-Royce" can address multiple questions relating to energy flux, community stability, functioning, redundancy & "emergent properties"

N + M + S + L: food web dynamics & stability

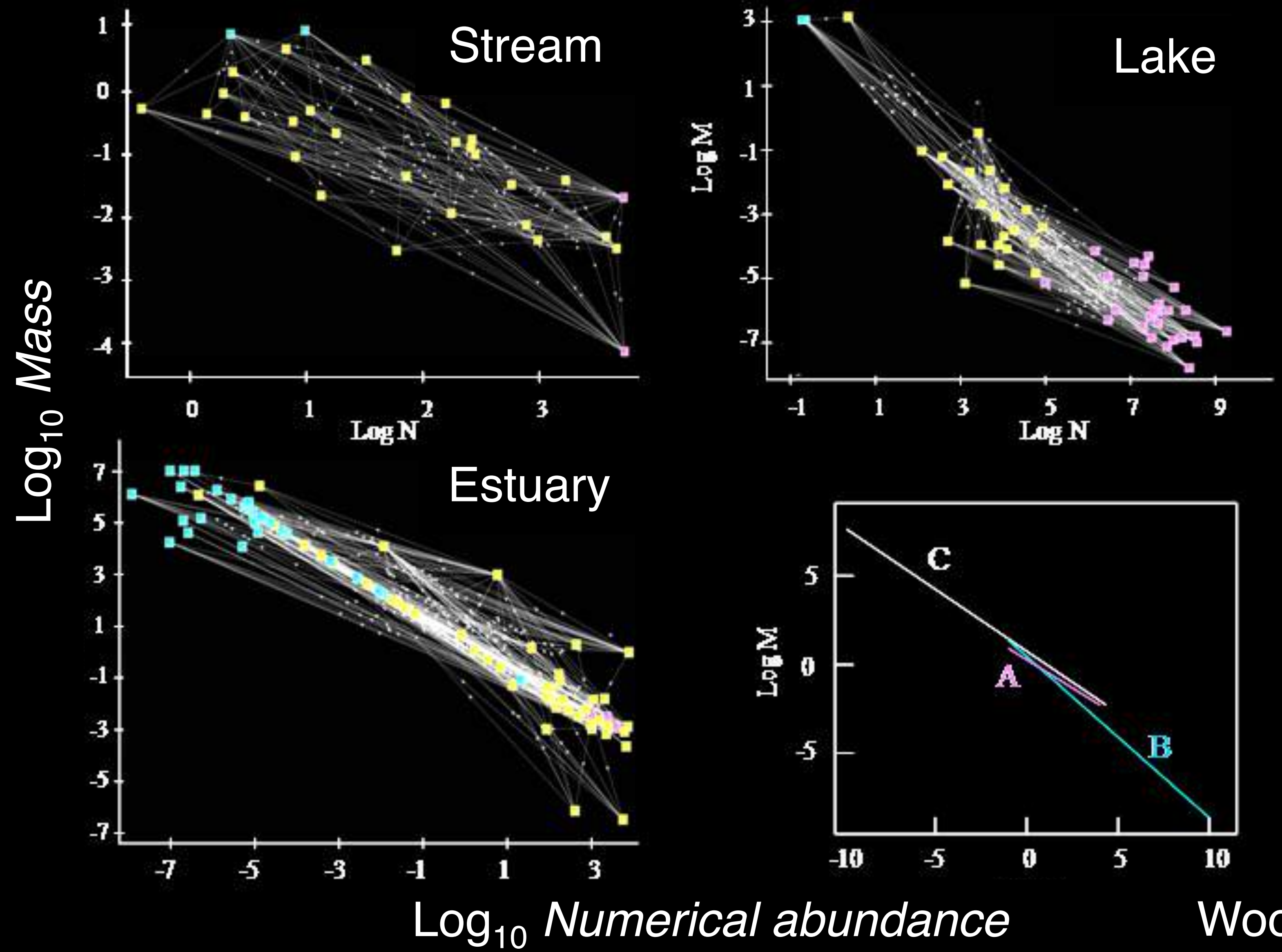
N + M (B = NM): community energy flux, size spectra

B + S + F: weighting of key functional species

S + F: functional diversity

S: .....relatively little!

Recurrent patterns in aquatic food webs: energy flows from many small, abundant species to a few large, rare species



Woodward et al. (2005) *TREE*

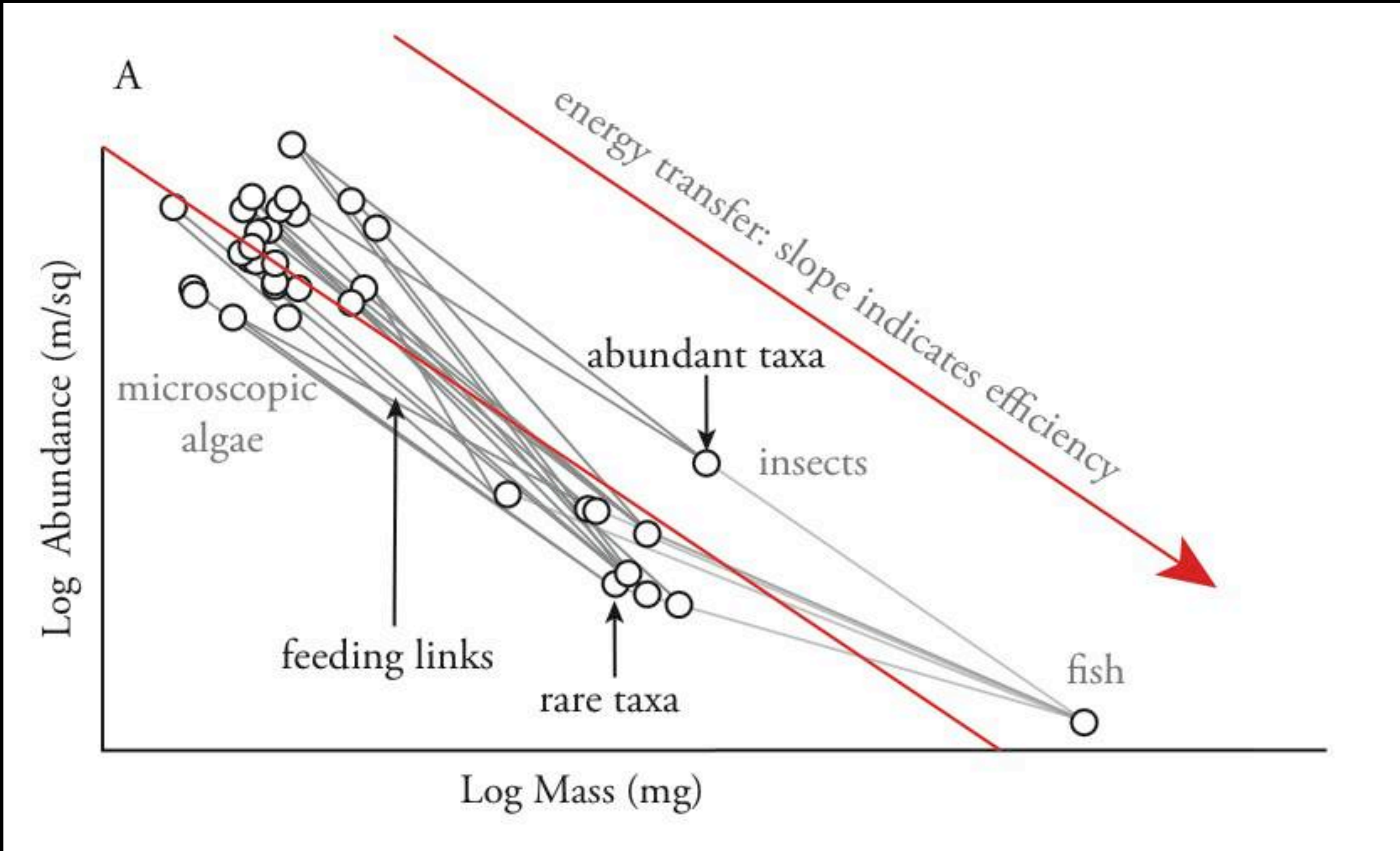
Collecting the data…(it’s not rocket science)

Stones scrapes: algal community

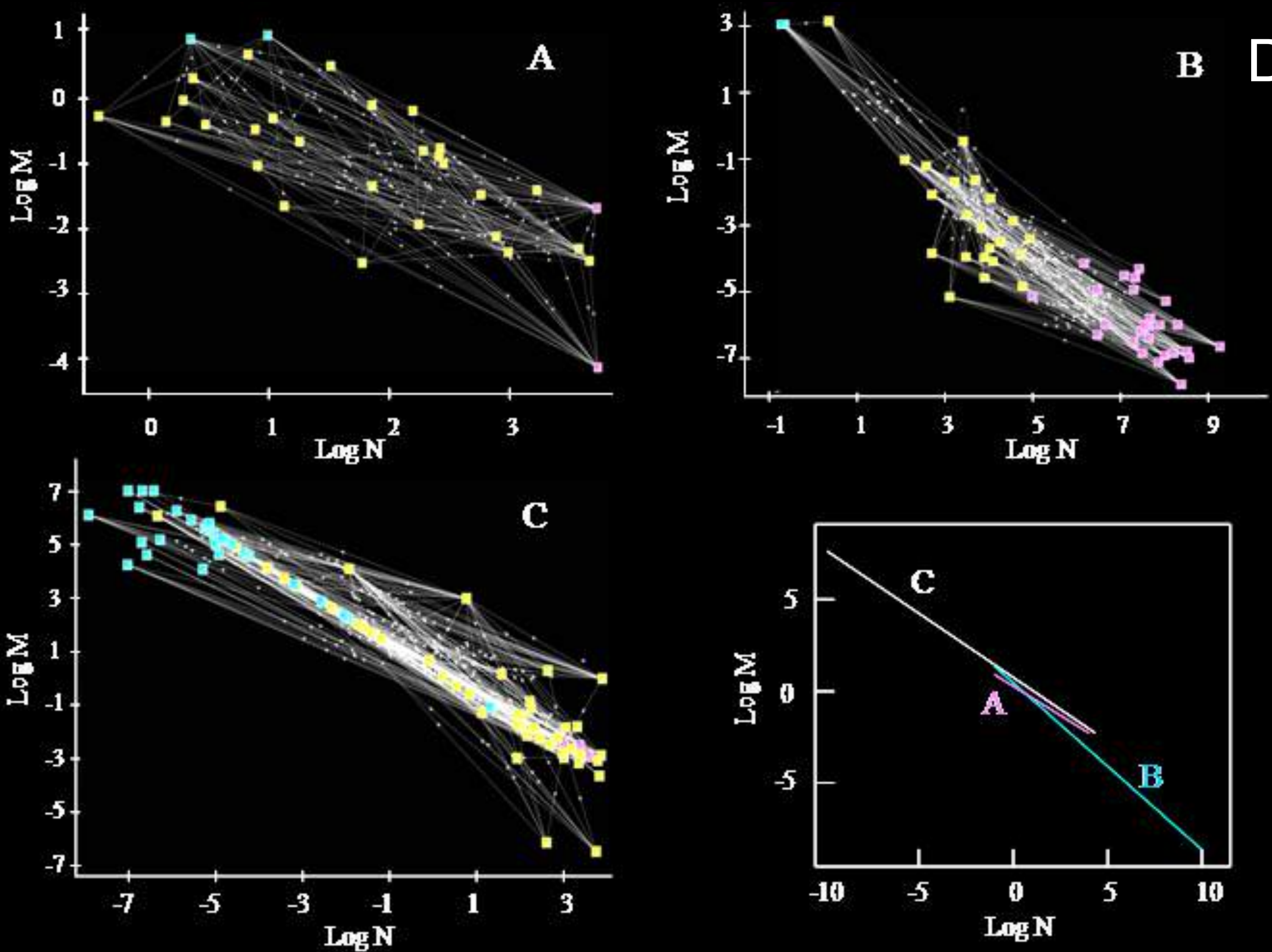
Hess sampler: invertebrates

Electrofishing between stop nets

The food web provides multiple levels of biosensing the environment (Gray et al 2014 J. Anim. Ecol.)



Searching for patterns: complex systems can be predictable



Data: *N, M, S, L*

Woodward et al. (2005) *Trends in Ecology & Evolution*

Non-random species loss affects ecosystem functioning

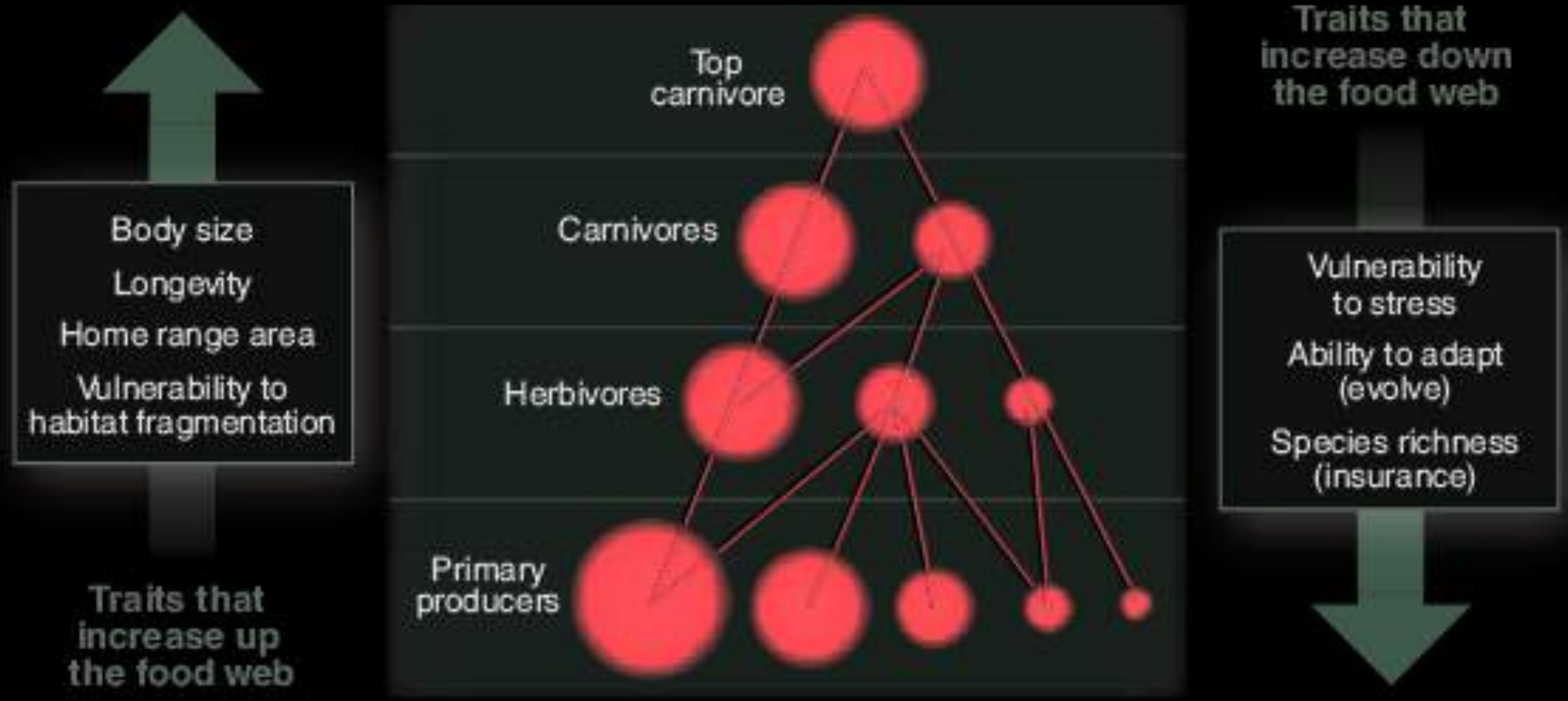
ECOLOGY

SCIENCE VOL 306 12 NOVEMBER 2004

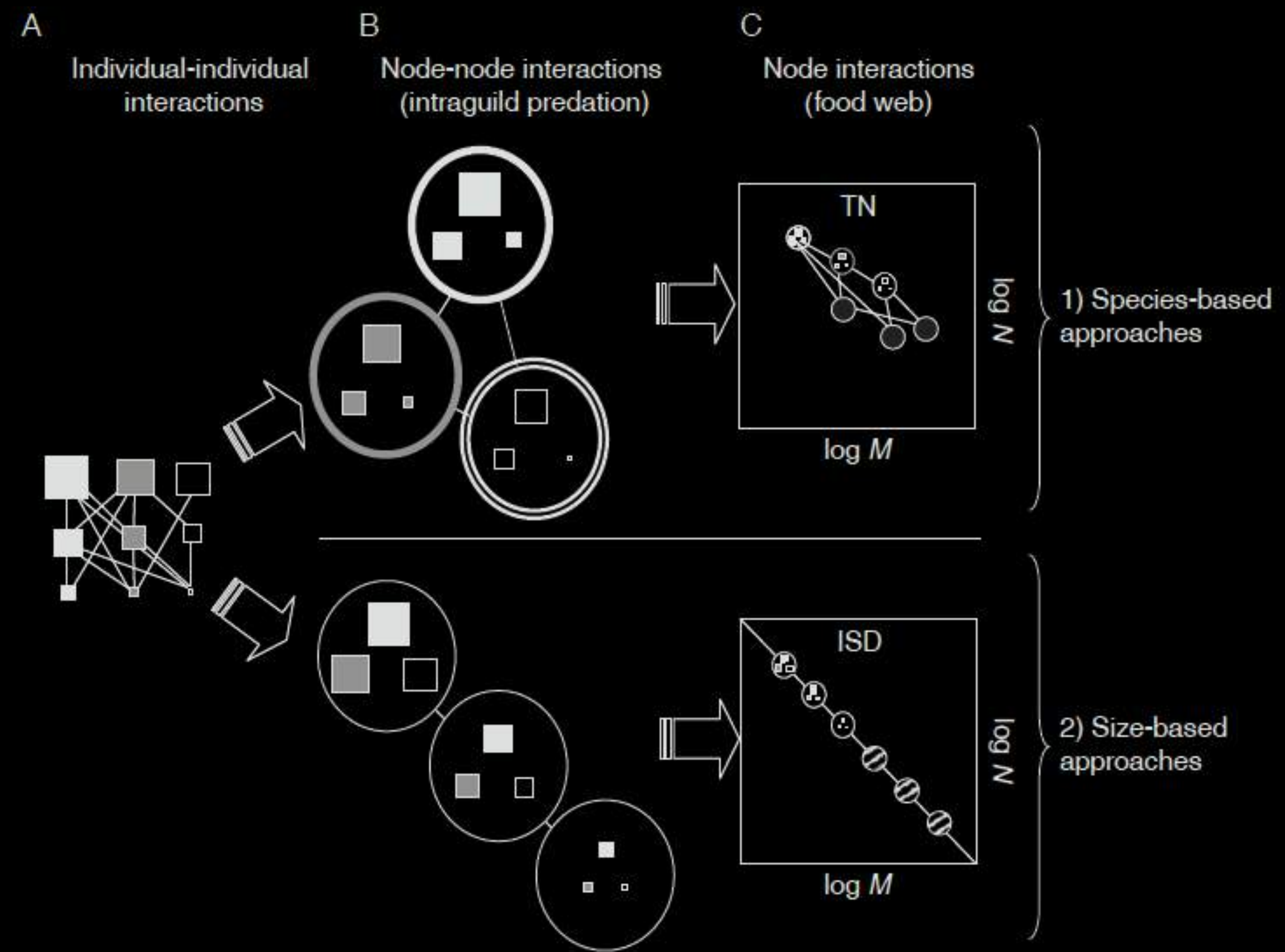
How Extinction Patterns Affect Ecosystems

David Raffaelli

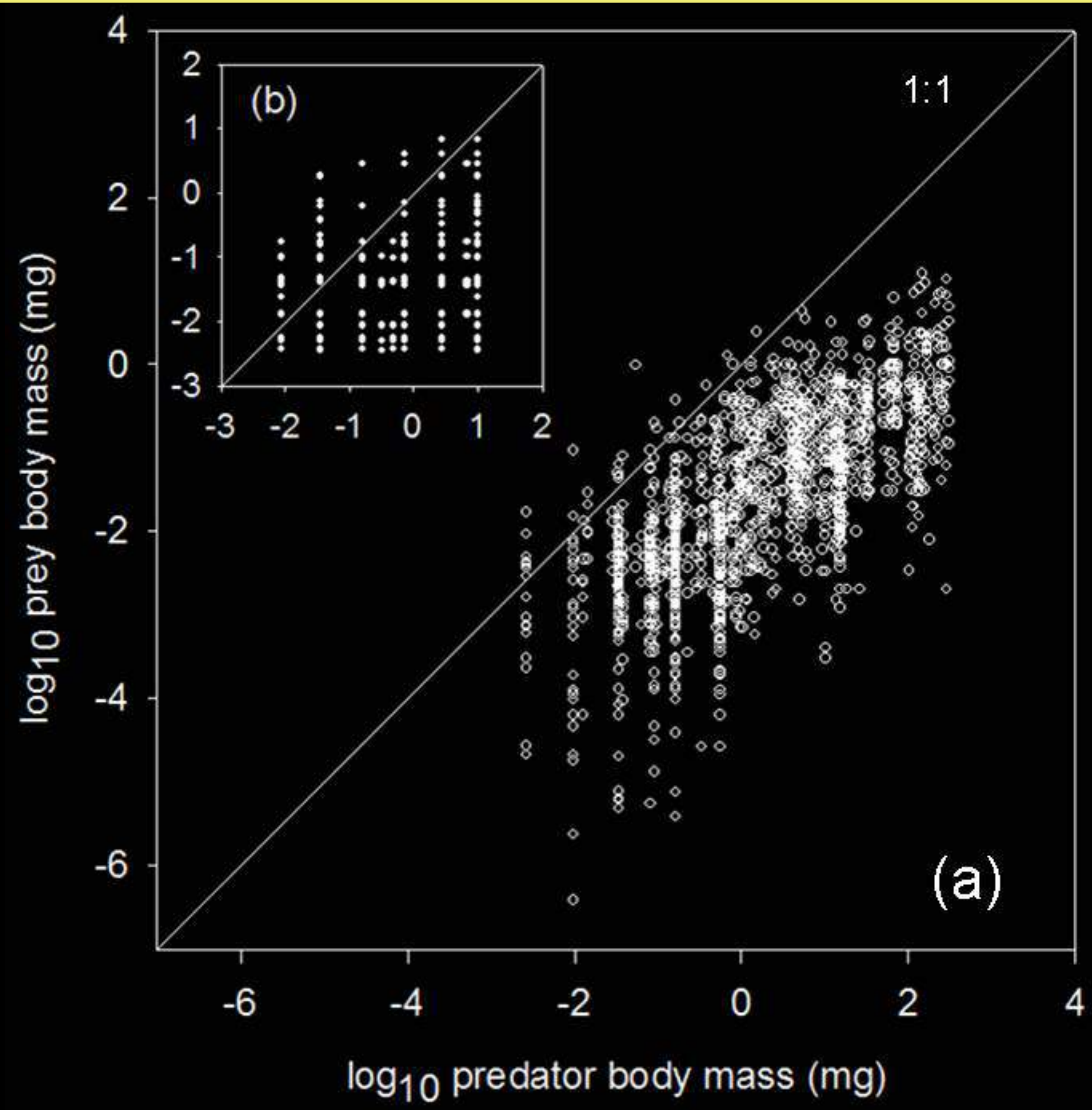
"…effects of biodiversity loss… will depend largely on the order in which species are lost, which in turn is determined by the susceptibilities of ecosystems to different types of stresses"



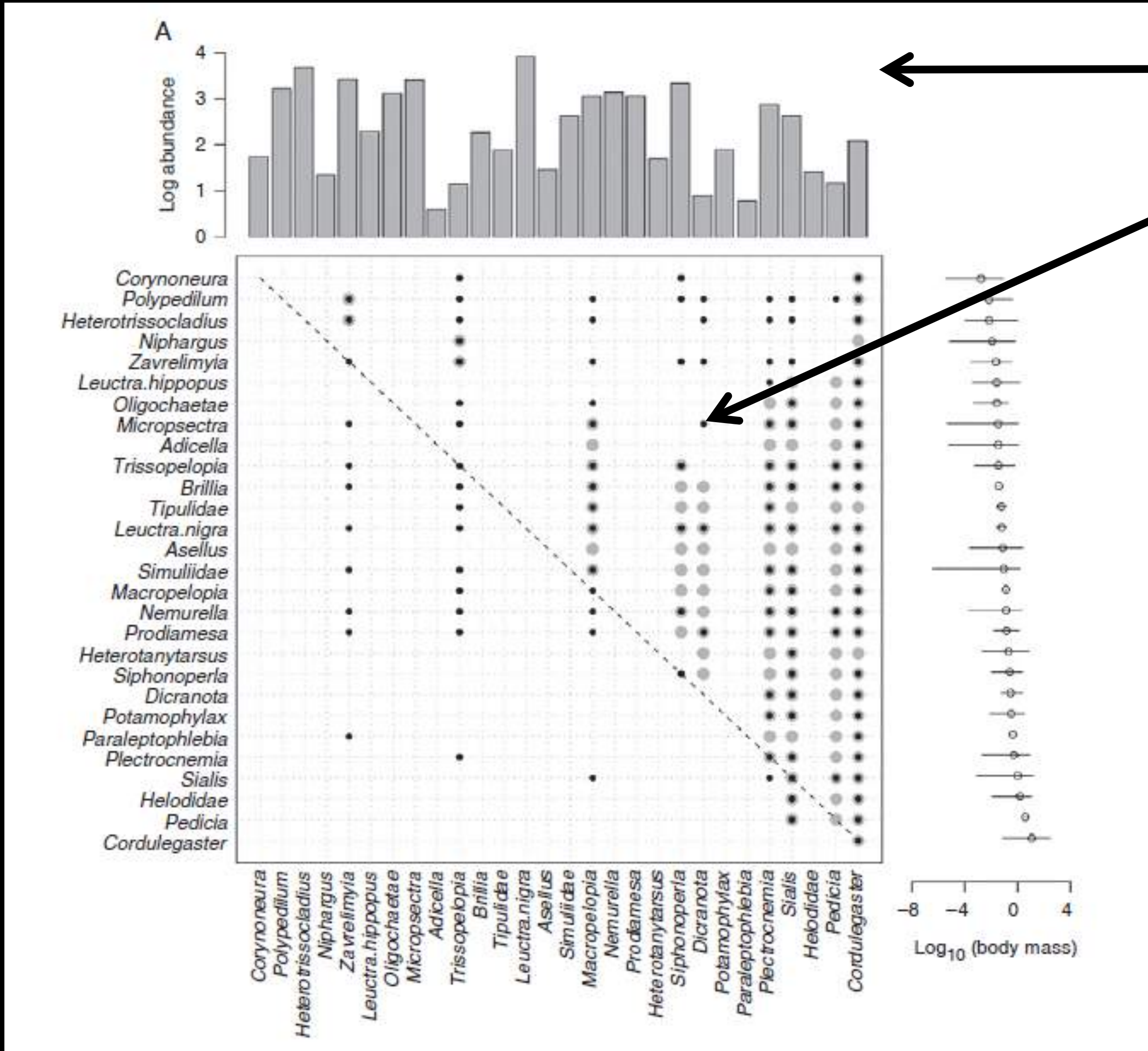
Individuals in food webs?
Species and size as two sides of the same coin



Individual-based feeding matrix differs markedly from species-averaged version



Species-averaged food web size structure and fit to model predictions

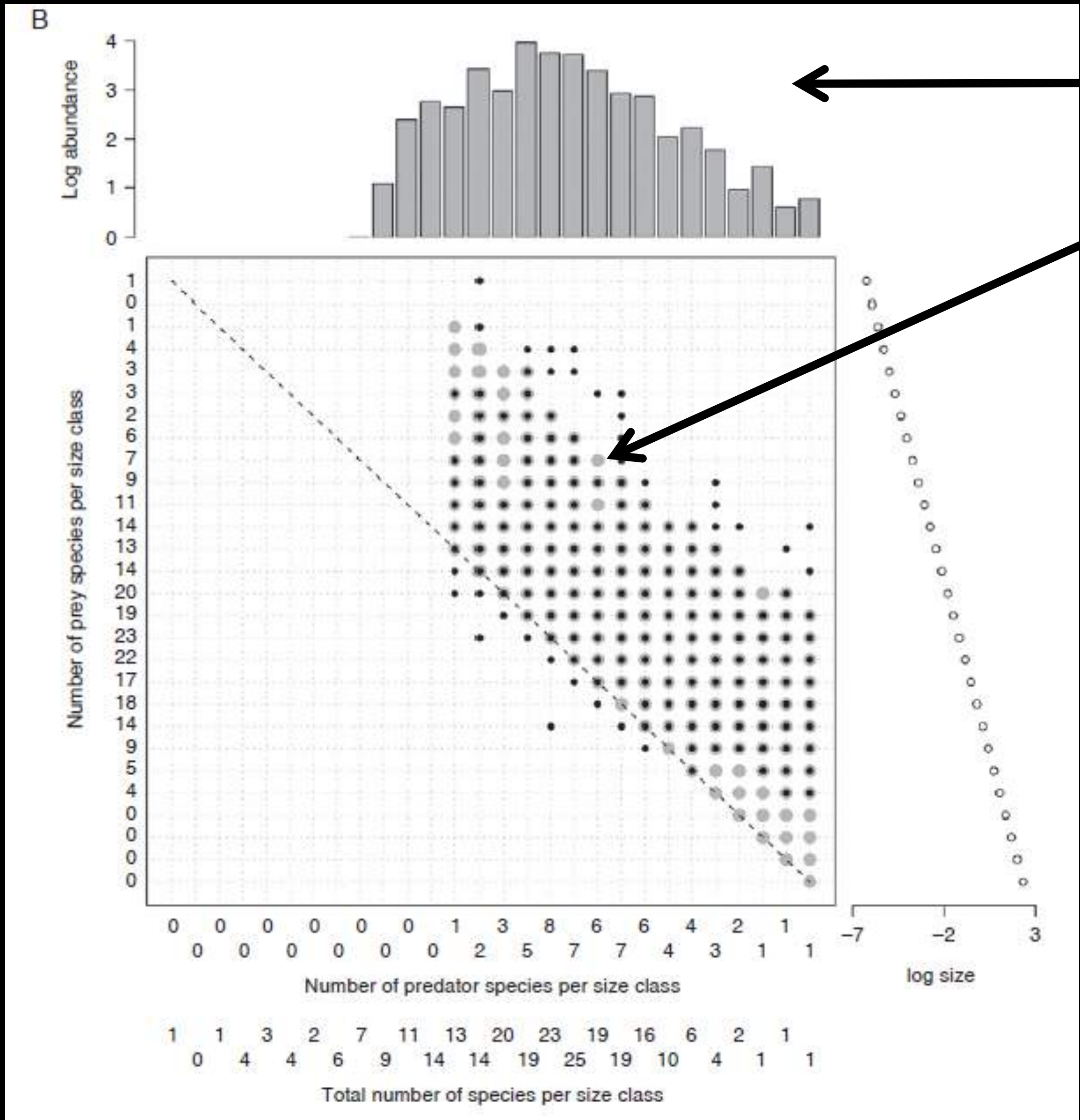


Size-abundance spectrum

Model (grey dots) versus real data (black dots)

Consumers x resources (both ranked by size)

Individual-based food web size structure and fit to model predictions

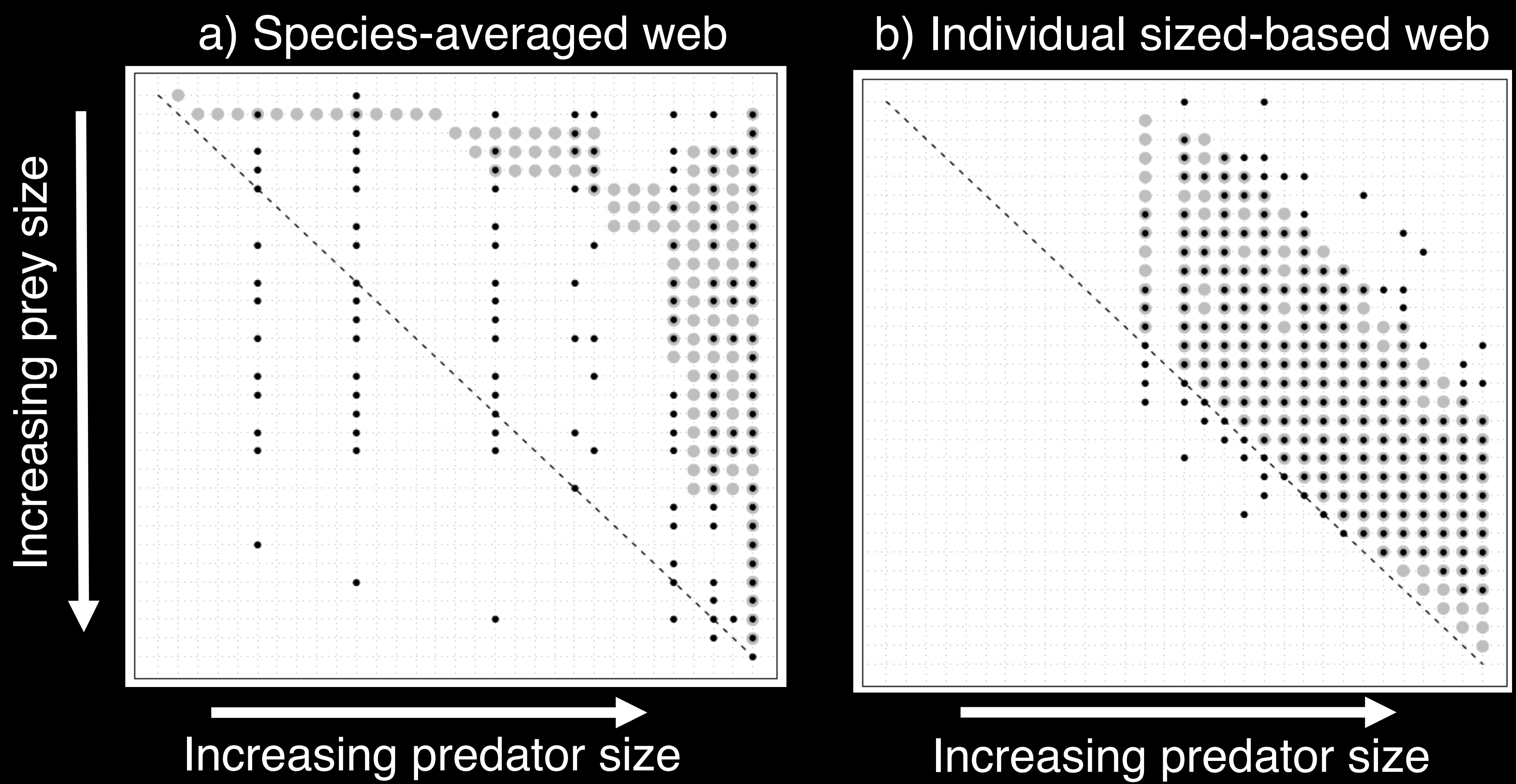


Size-abundance spectrum

Model (grey dots) versus real data (black dots)

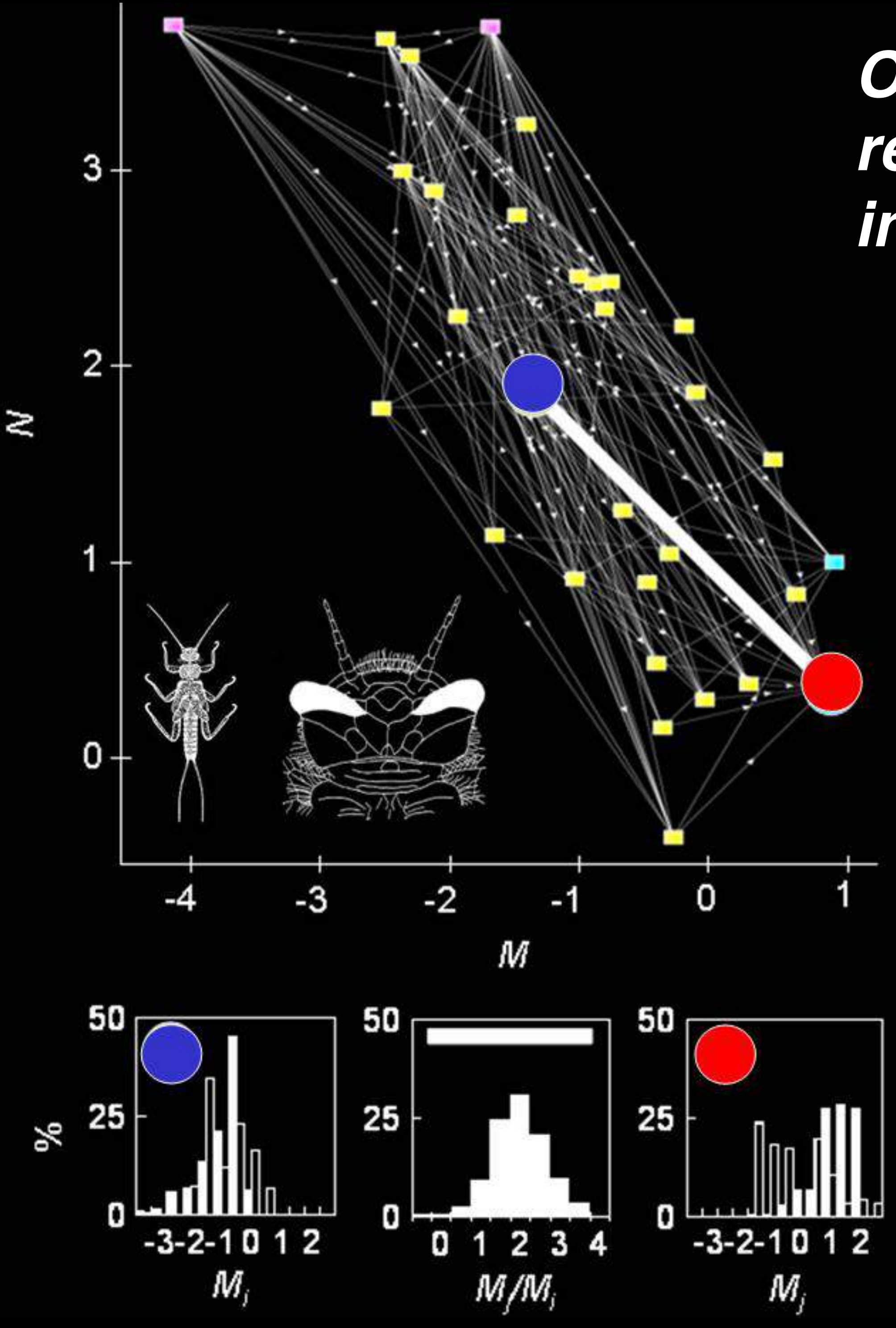
Consumers x resources (both ranked by size)

Size structure in food webs is hidden by species-averaging



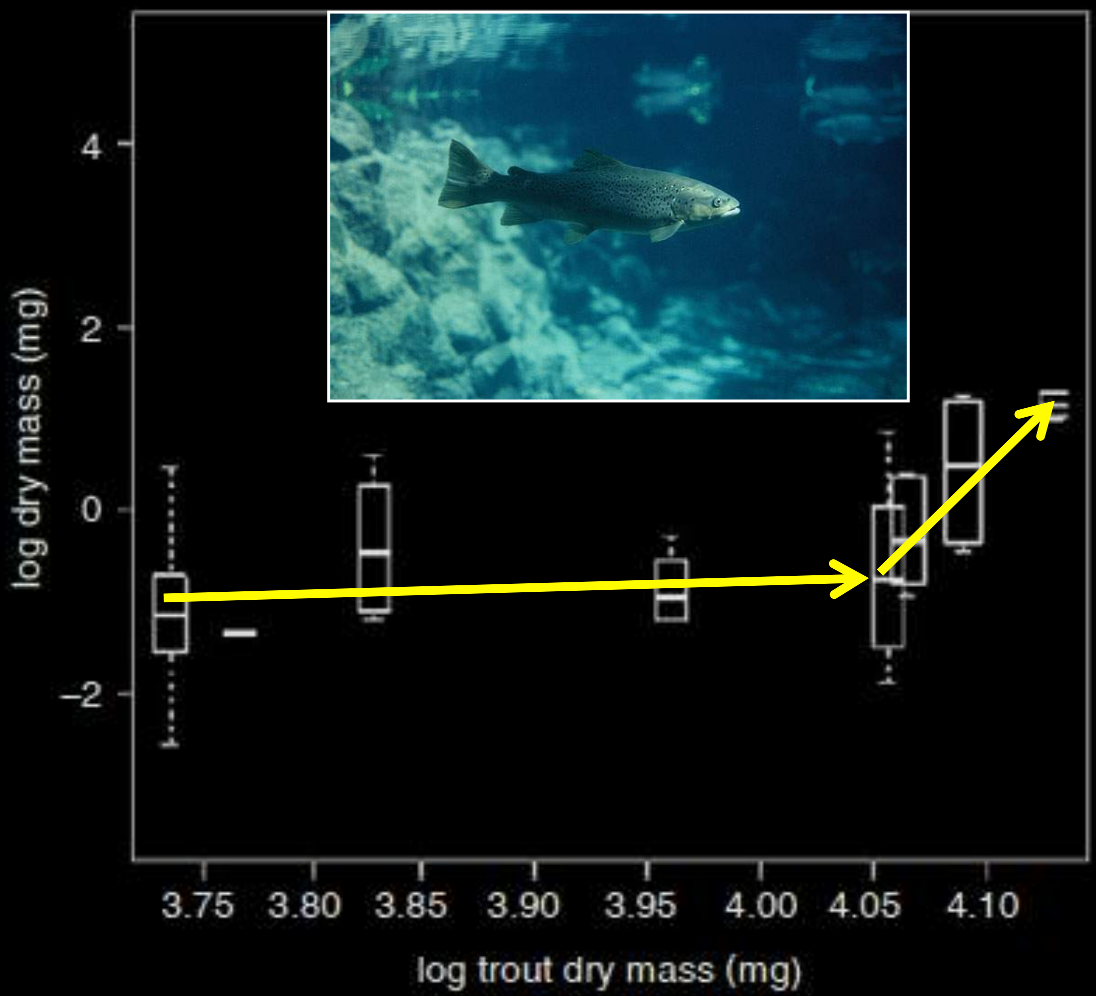
Feeding matrix for 31 entities as either a) species or b) size classes. Black dots = observed links, grey dots = ADBM predicted links (a = 47% fit; b = 83% fit). (Woodward et al 2010b *Advances in Ecological Research*)

Only portions of consumer-resource populations interact…

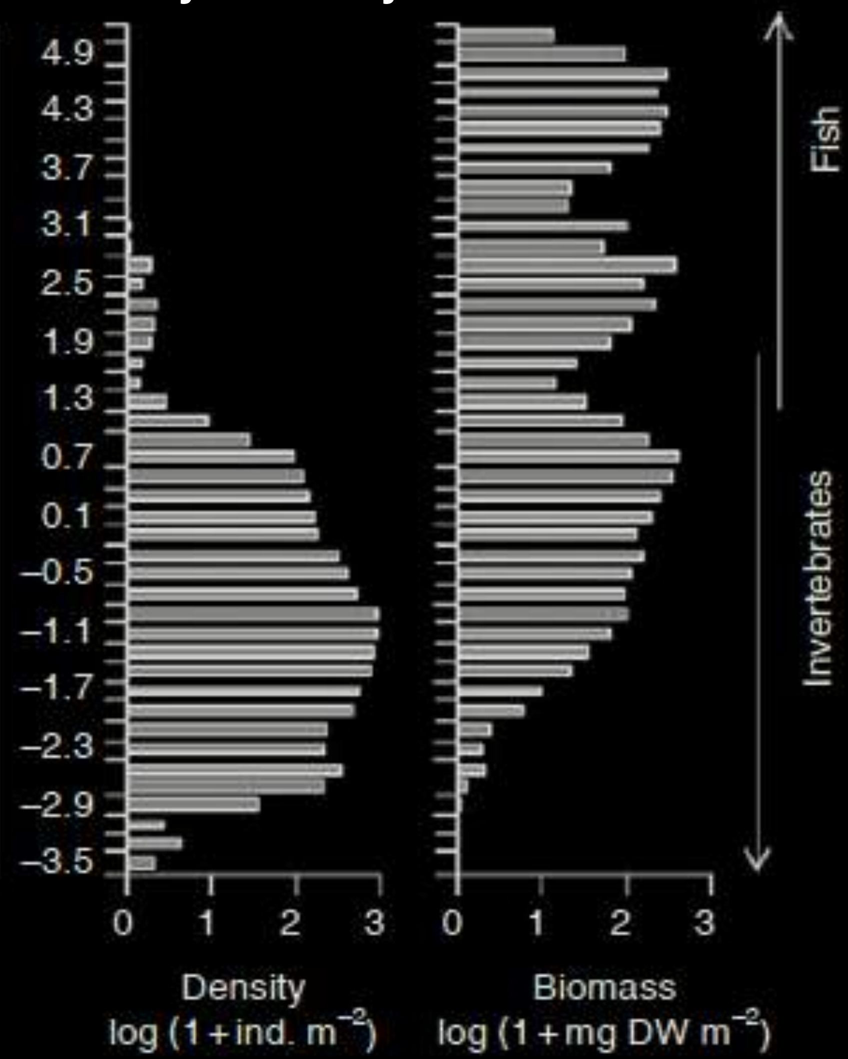


Tracking individuals over time – as they move up the food web

Size of prey eaten on 8 dates



Prey density & biomass



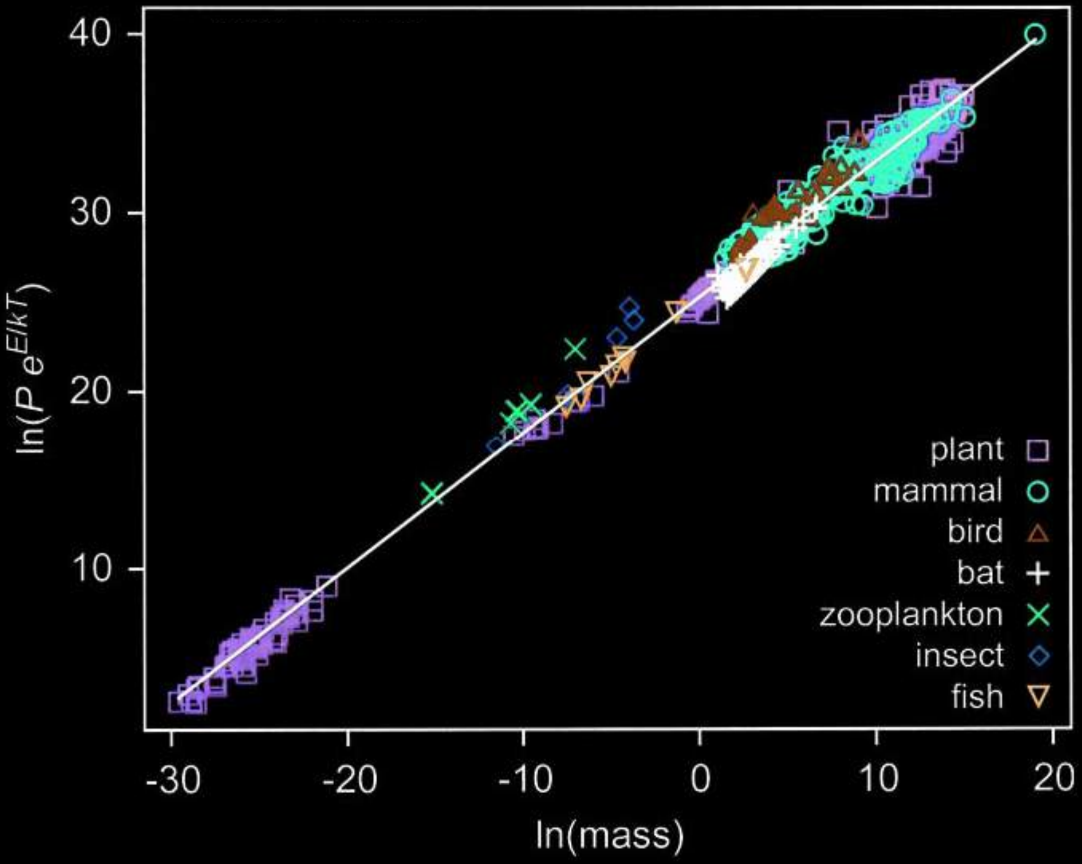
Temperature and body mass determine metabolic rates

$$\mathrm{MR} = a\boxed{M}^{3/4}e^{-E/(\boxed{kT})}$$

These drivers operate at individual through to ecosystem levels...

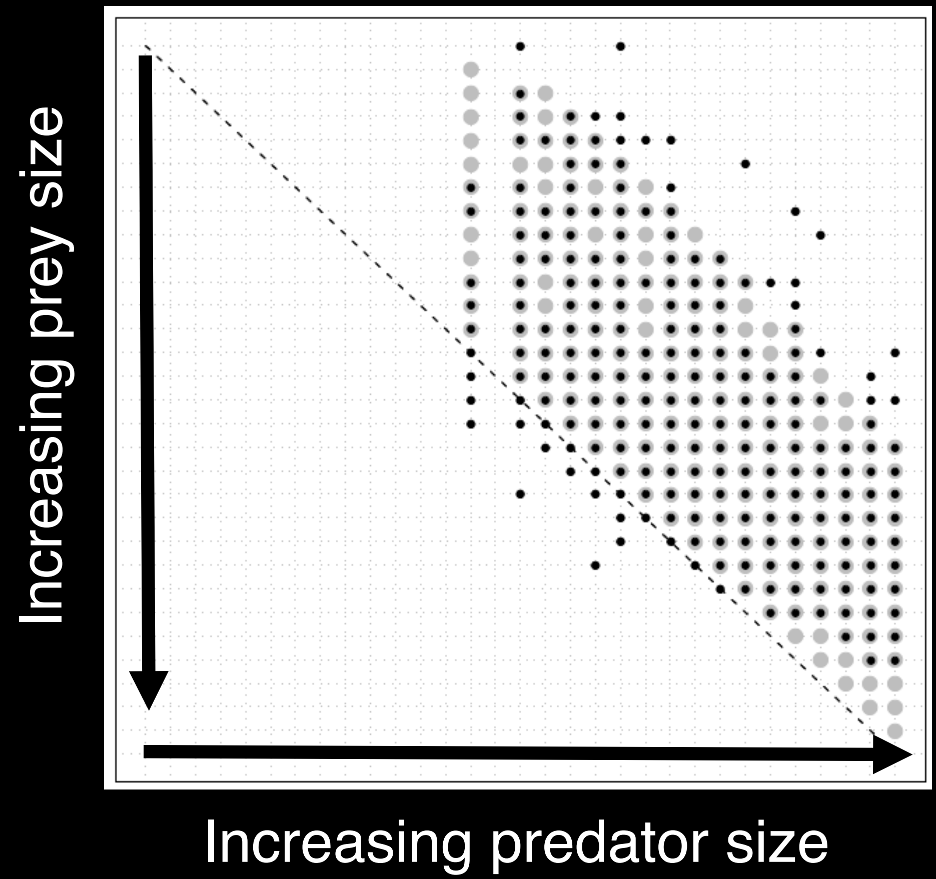
Body size determines an individual's metabolism in aquatic systems and its place in the food web

Metabolism v mass



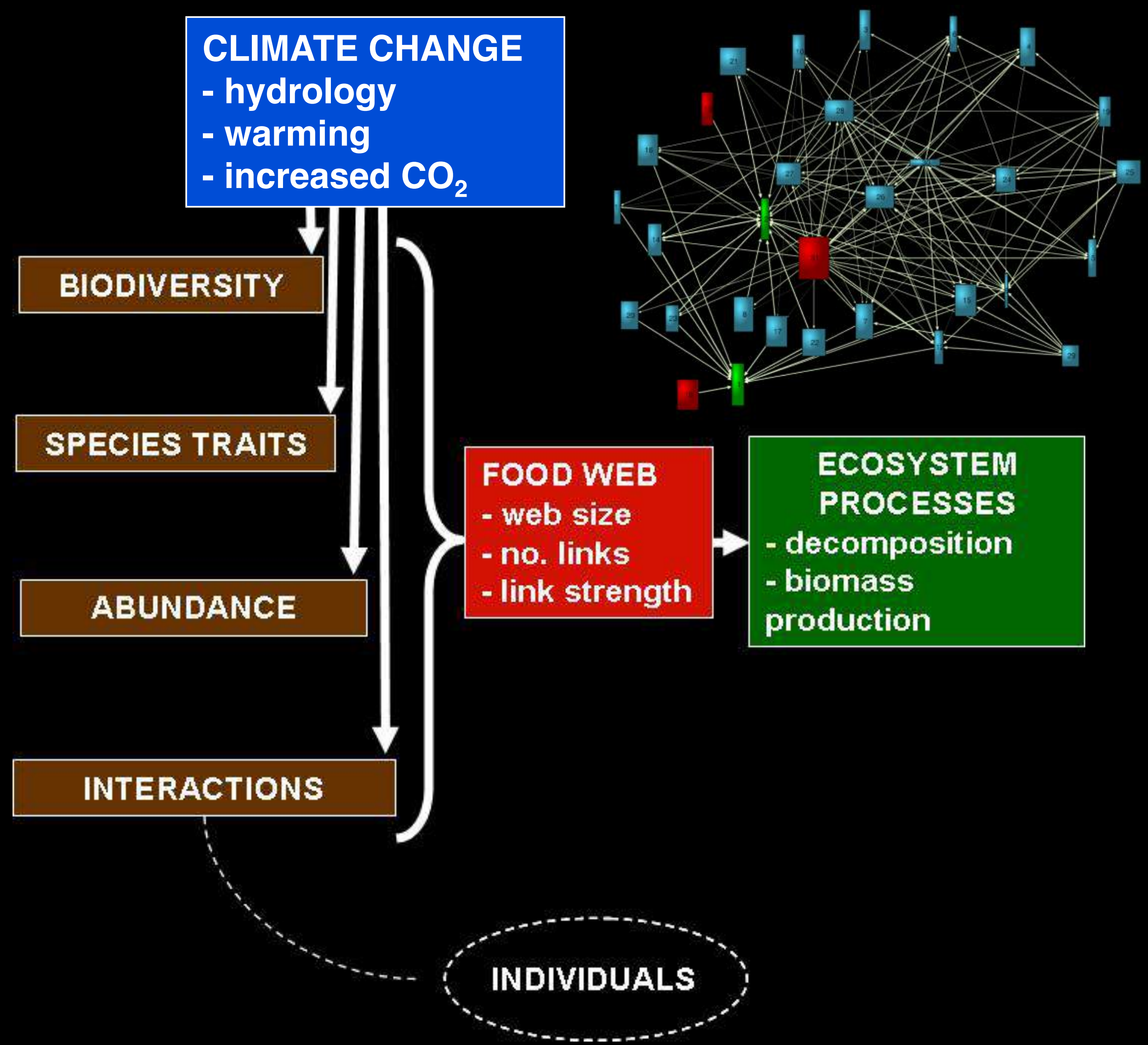
Brown et al 2004

Individual-based food web



Woodward et al 2010

Climate change.....the 21st Century problem



Climate change is a compound stressor – we need to examine its component parts before addressing synergies

COMPONENT	ECOLOGICAL CONSEQUENCE
Hydrology	**Habitat fragmentation by droughts**
Temperature	**Elevated metabolic demands**
Phenology	Consumer-resource mismatches
Wildfires	Manifold effects of riparian vegetation loss
Atmospheric change	Altered consumer-resource stoichiometry
Invasive species	Emergence of novel food webs

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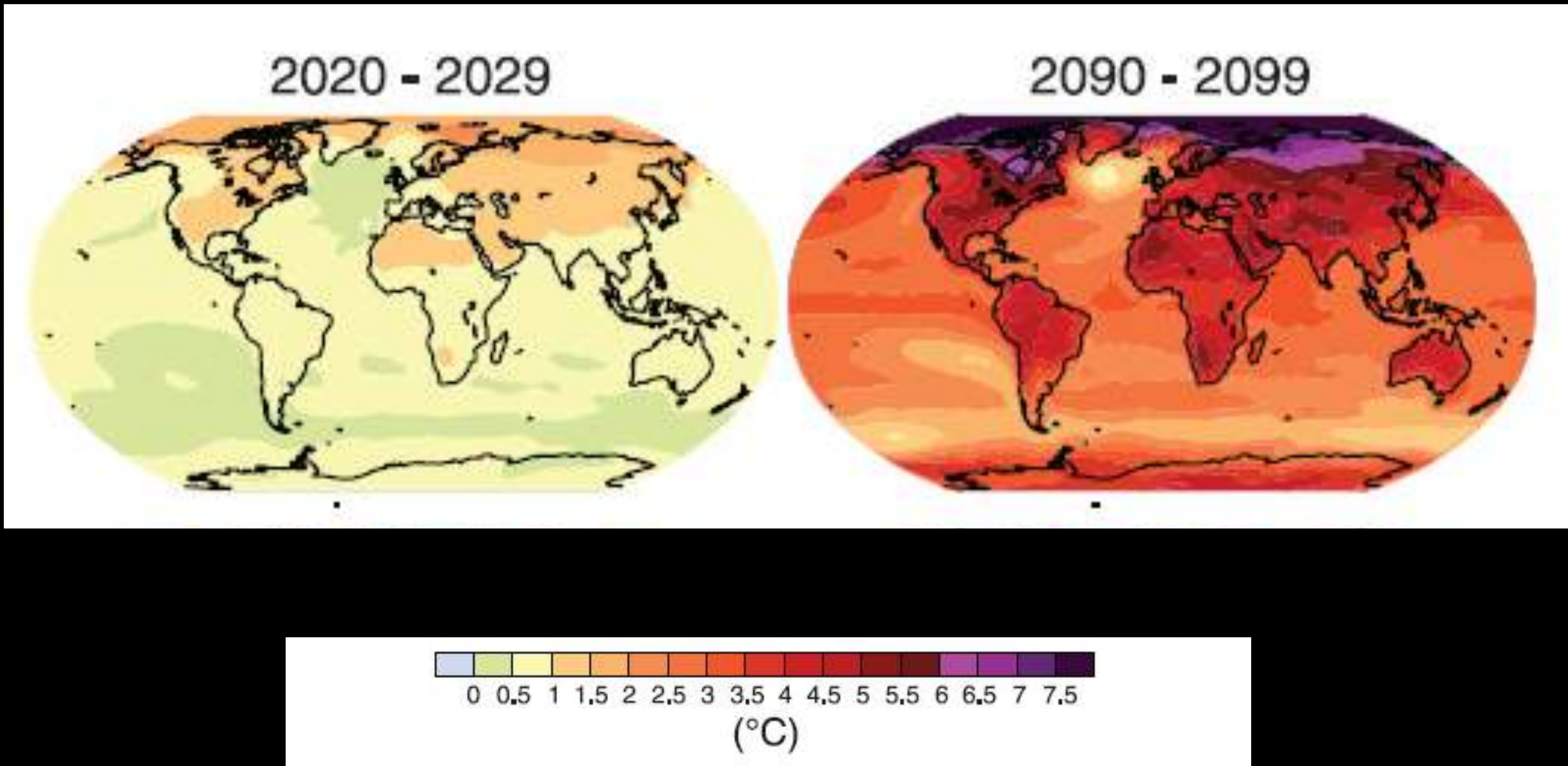
Global climate change - into the 21st Century



IPCC: Projected surface temperature changes for the 21st century relative to the period 1980-1999.

Ecosystems in a changing climate….?

Current focus on lower levels of organisation (individuals, species populations)

Effects on higher levels & ecosystem services still poorly understood...

Searching for simple rules in complex systems...

Surveys **Natural experiments** **Field experiments**

Woodward et al 2010 *Advances in Ecological Research*

The tools at our disposal – none are perfect, so we need to combine them

	Pros	Cons
Surveys	Realism	Inferential, confounded
Natural experiments	Realism	Limited replication, few sites
Field experiments	Some realism	Often small-scale
Lab experiments	High control	Limited realism, small-scale
Modeling	Predictive	Limited realism, lack of data

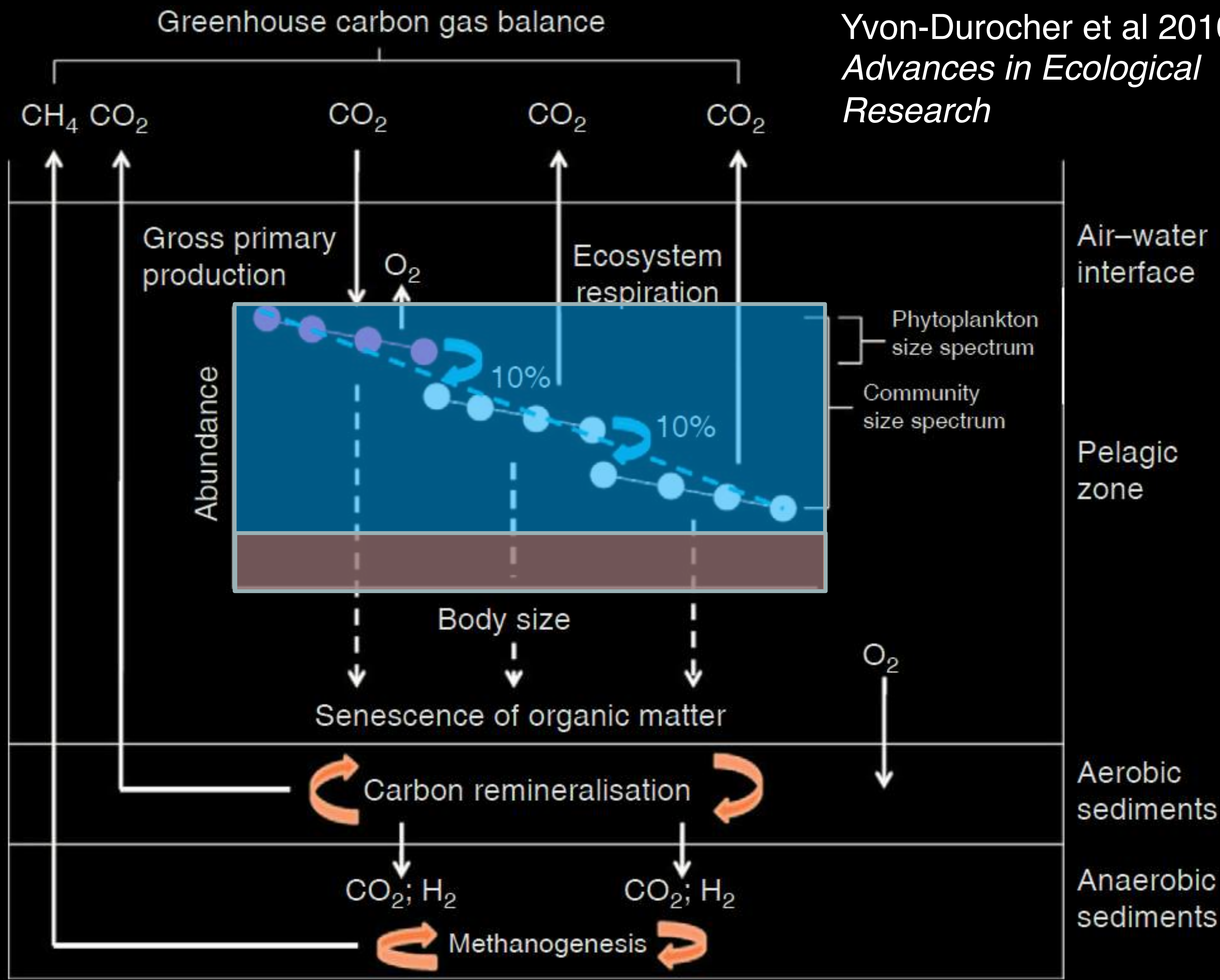
Trade-off : "Replication – Realism – Control"

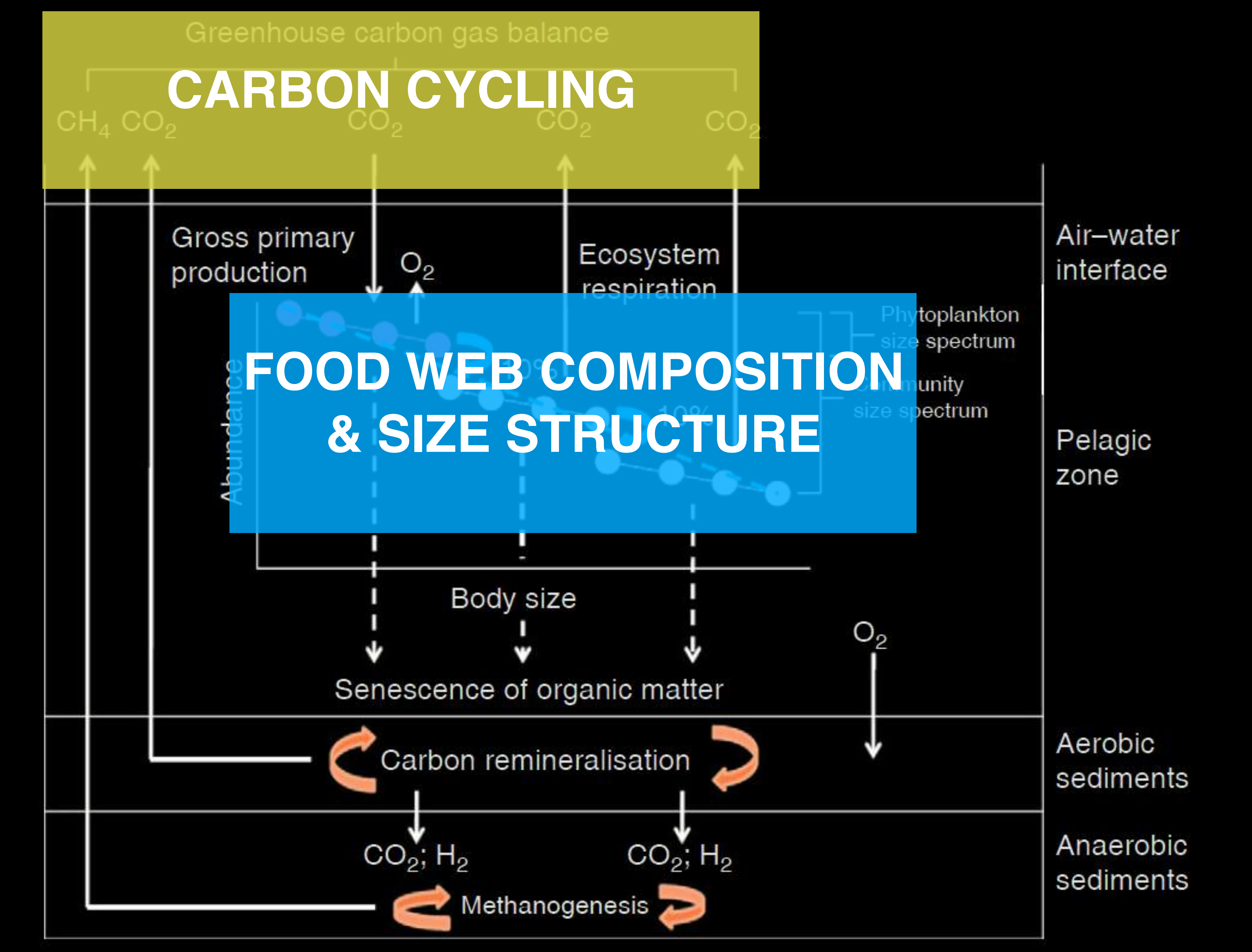
Mesocosm experiments: warming impacts in freshwaters

Using mesocosms to test a priori theoretical predictions

Long-term mesocosm experiment at FBA River Lab
4°C warming above ambient since 2006

Yvon-Durocher et al 2010 *Advances in Ecological Research*





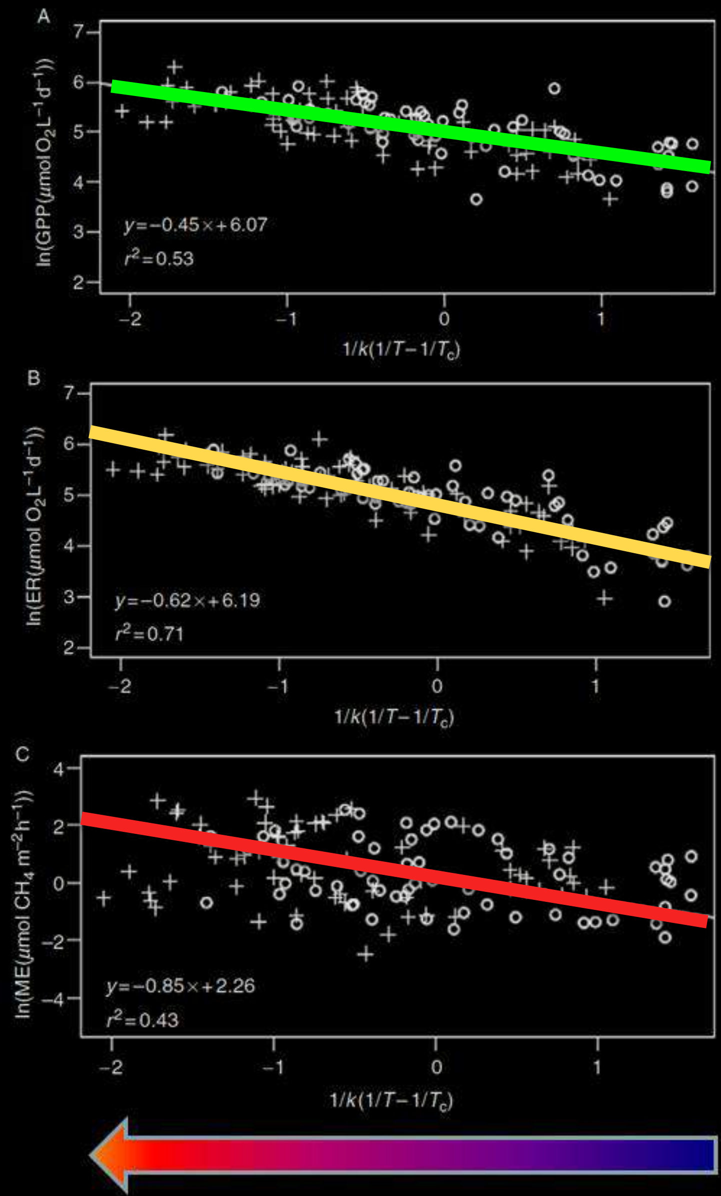
CARBON CYCLING
FOOD WEB COMPOSITION & SIZE STRUCTURE
Greenhouse carbon gas balance
CH_4 CO_2
CO_2
CO_2
CO_2
Gross primary production
O_2
Ecosystem respiration
Phytoplankton size spectrum
size spectrum
Abundance
Body size
Senescence of organic matter
O_2
Carbon remineralisation
CO_2; H_2
CO_2; H_2
Methanogenesis
Air–water interface
Pelagic zone
Aerobic sediments
Anaerobic sediments

Each component of the carbon cycle has its own activation energy

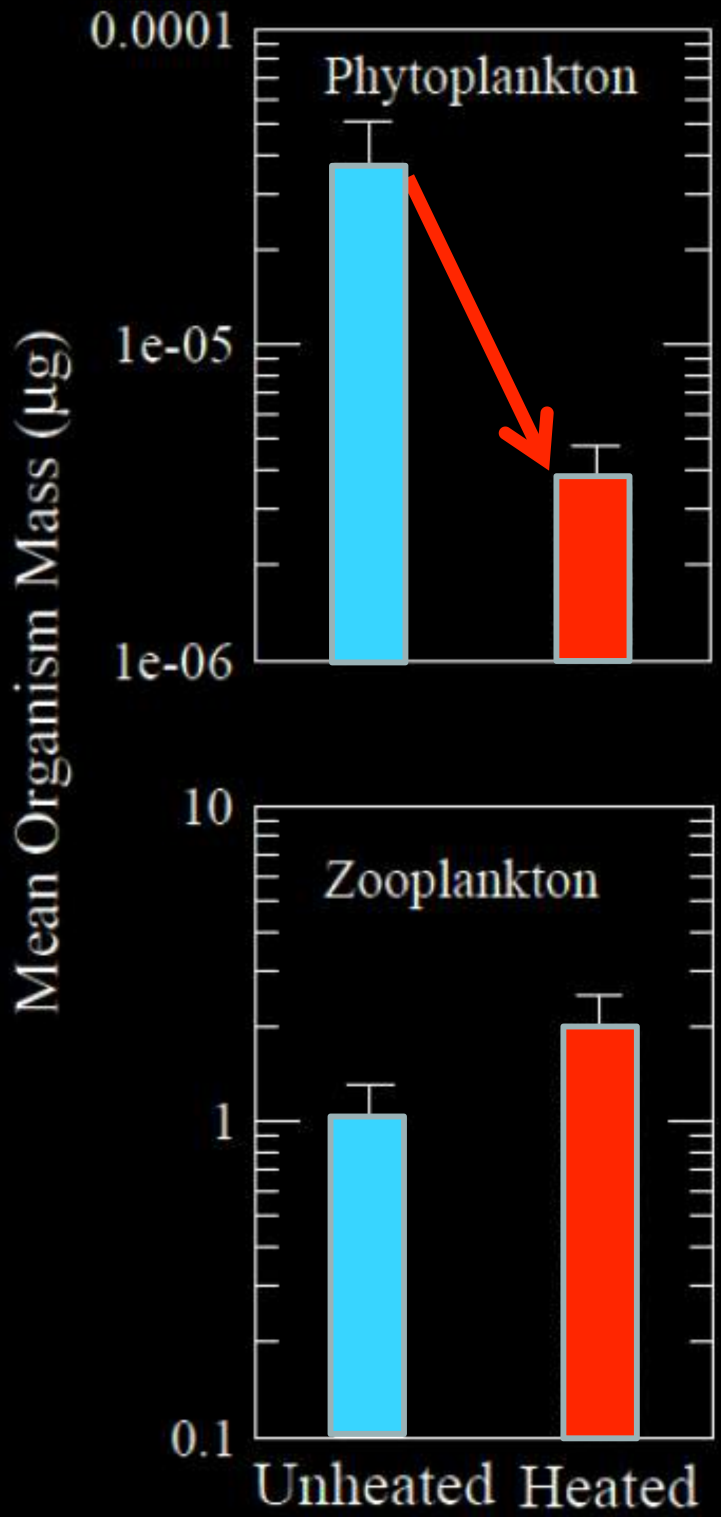
Gross Primary Production
E = 0.45

Ecosystem Respiration
E = 0.62

Methane Efflux
E = 0.85



Yvon-Durocher et al 2010
Advances in Ecological Research



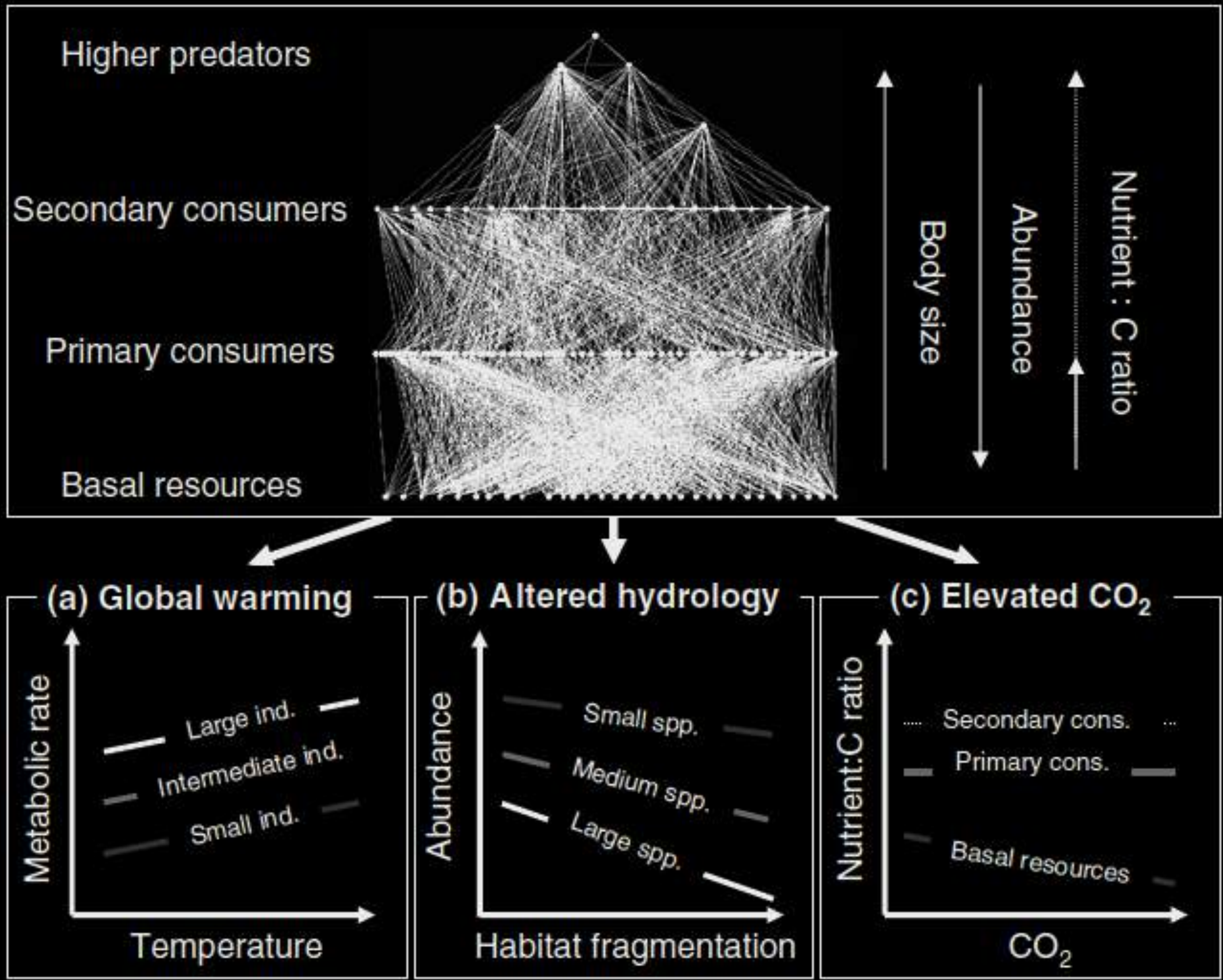
UK mesocosms: mean phytoplankton cell size decreased tenfold in ponds warmed by 4°C - after one year of warming

Yvon-Durocher et al 2011 *Global Change Biology*

Summary of warming experiments (so far...)

- Mesocosms were highly replicable (self-similar) and broadly realistic (similar to natural webs)
- Long-term, intergenerational warming (since 2006)
- Carbon cycle components responded strongly to warming – but at different rates - in line with theoretical predictions
- Community structure responded strongly to warming, with shifts in size spectrum as predicted by theory
- Small organisms benefited – as reported from correlational surveys

Body size and metabolism offer a means to predict climate change impacts across organisational levels



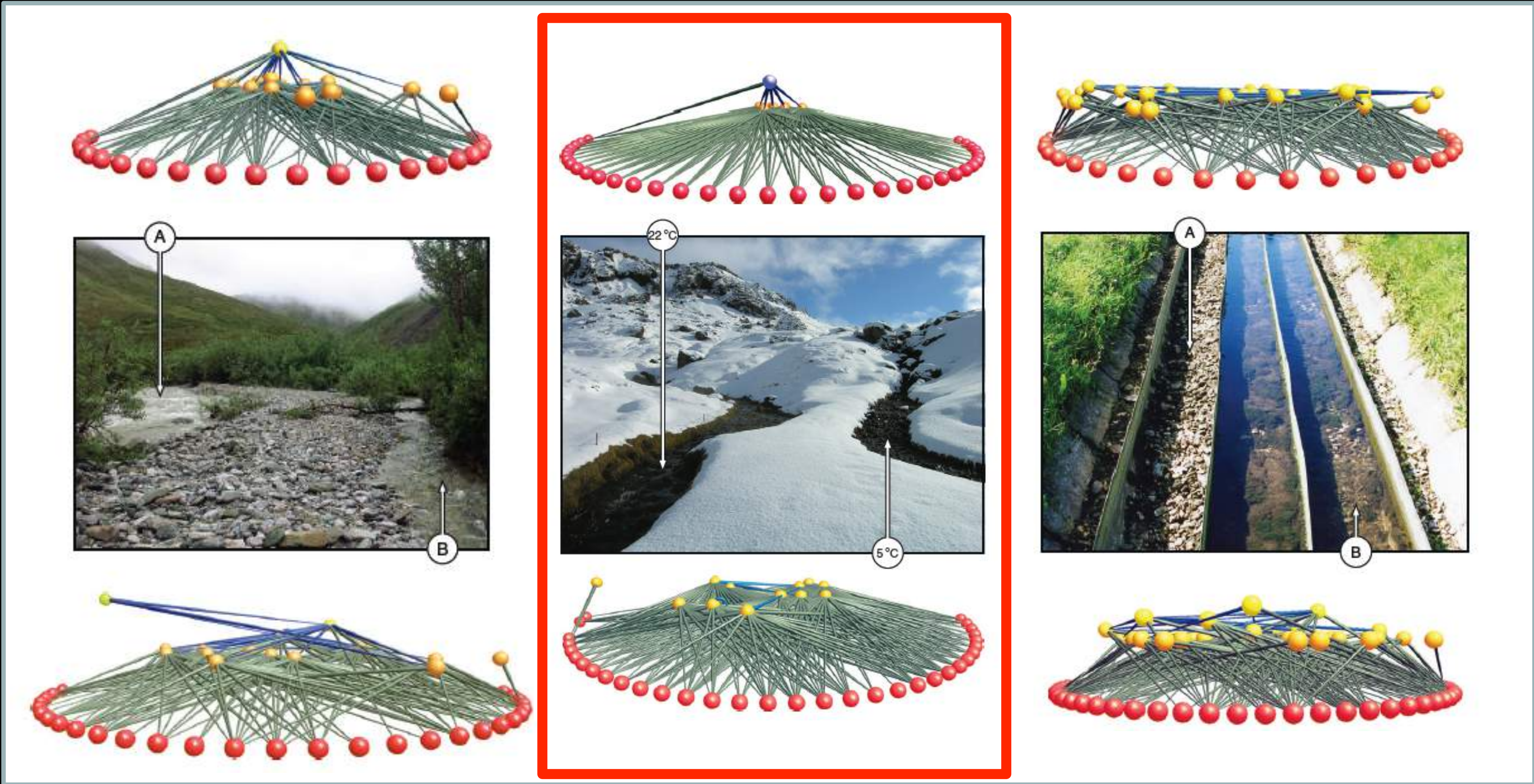
Perkins et al 2010 *Hydrobiologia*

We can use ecological theories to help develop a more predictive framework

THEORY		ECOLOGICAL RELEVANCE
MT:	Metabolic Theory	Thermal sensitivity of nutrient cycles
FT:	Foraging Theory	Encounter rates and food web linkages
ES:	Ecological Stoichiometry	Carbon:nutrients at base of food webs

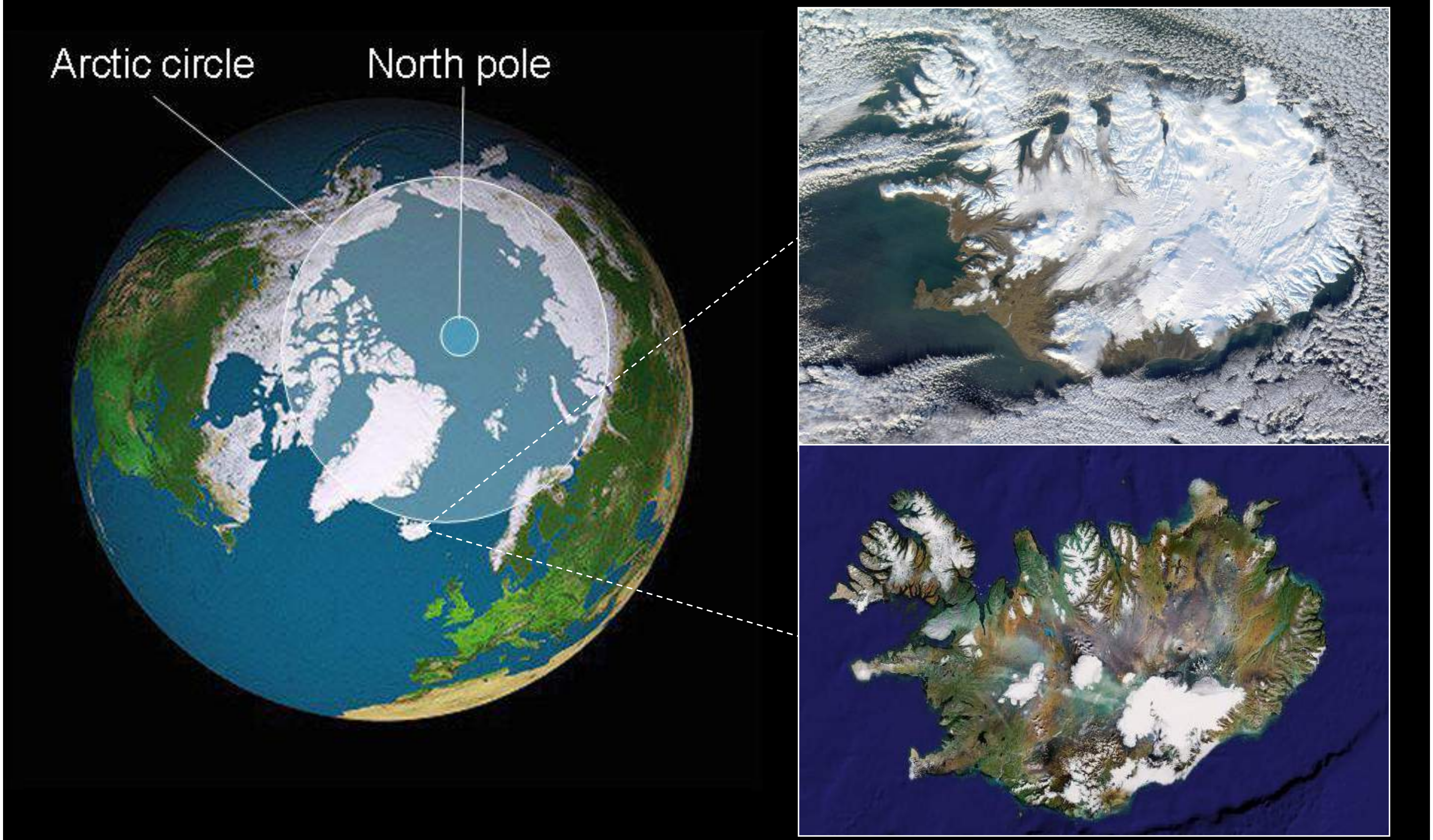
Woodward et al 2010 *Philosophical Transactions of the Royal Society B*

Empirical approaches in complex systems



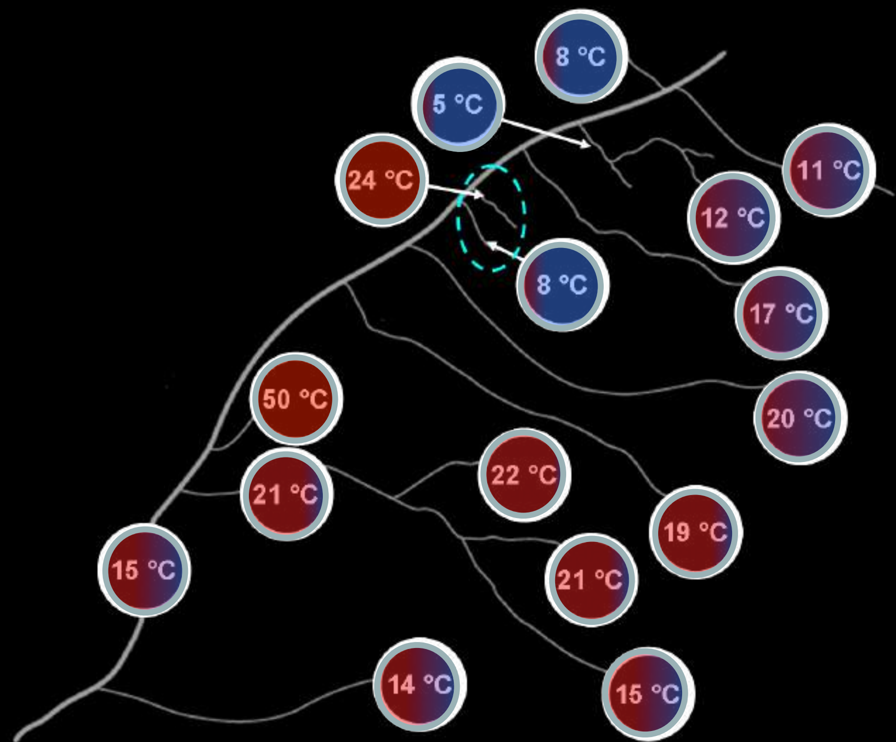
Surveys | Natural experiments | Field experiments

Studying "sentinel systems" at high latitudes can help us to anticipate climate change impacts



A natural experiment in Iceland - isolating the effects of temperature in multiple food webs

- Geothermal catchment
- 15 streams - 2m-2km apart
- Linked to main river
- Alike in phyisico-chemistry
- No dispersal constraints
- 5-25°C thermal gradient



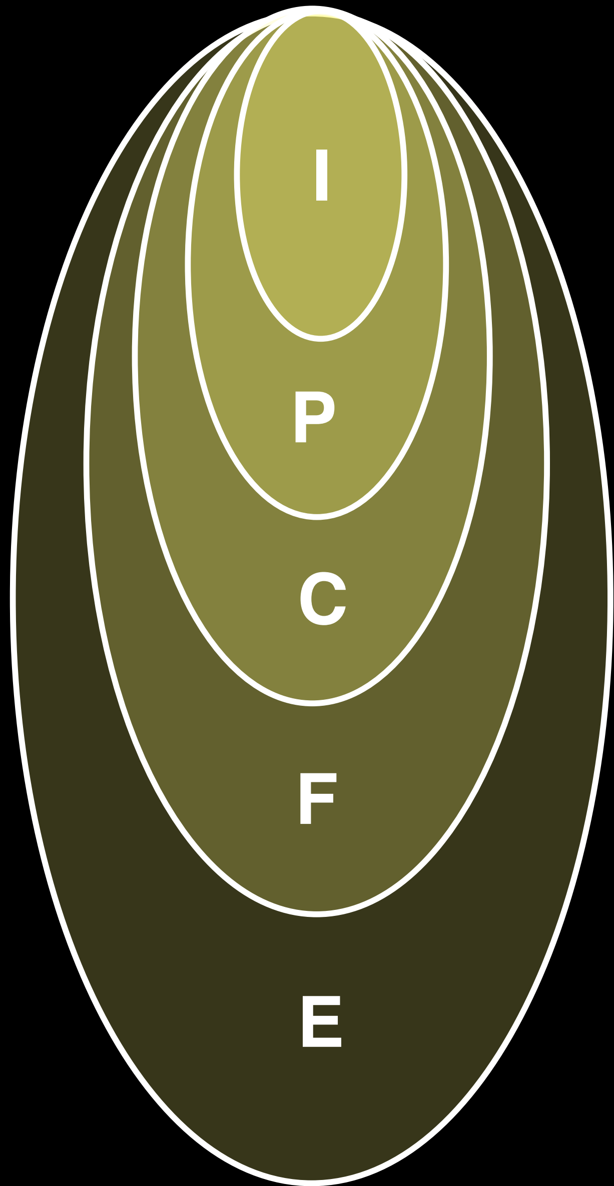
Key questions - how does temperature affect...

Population abundance?

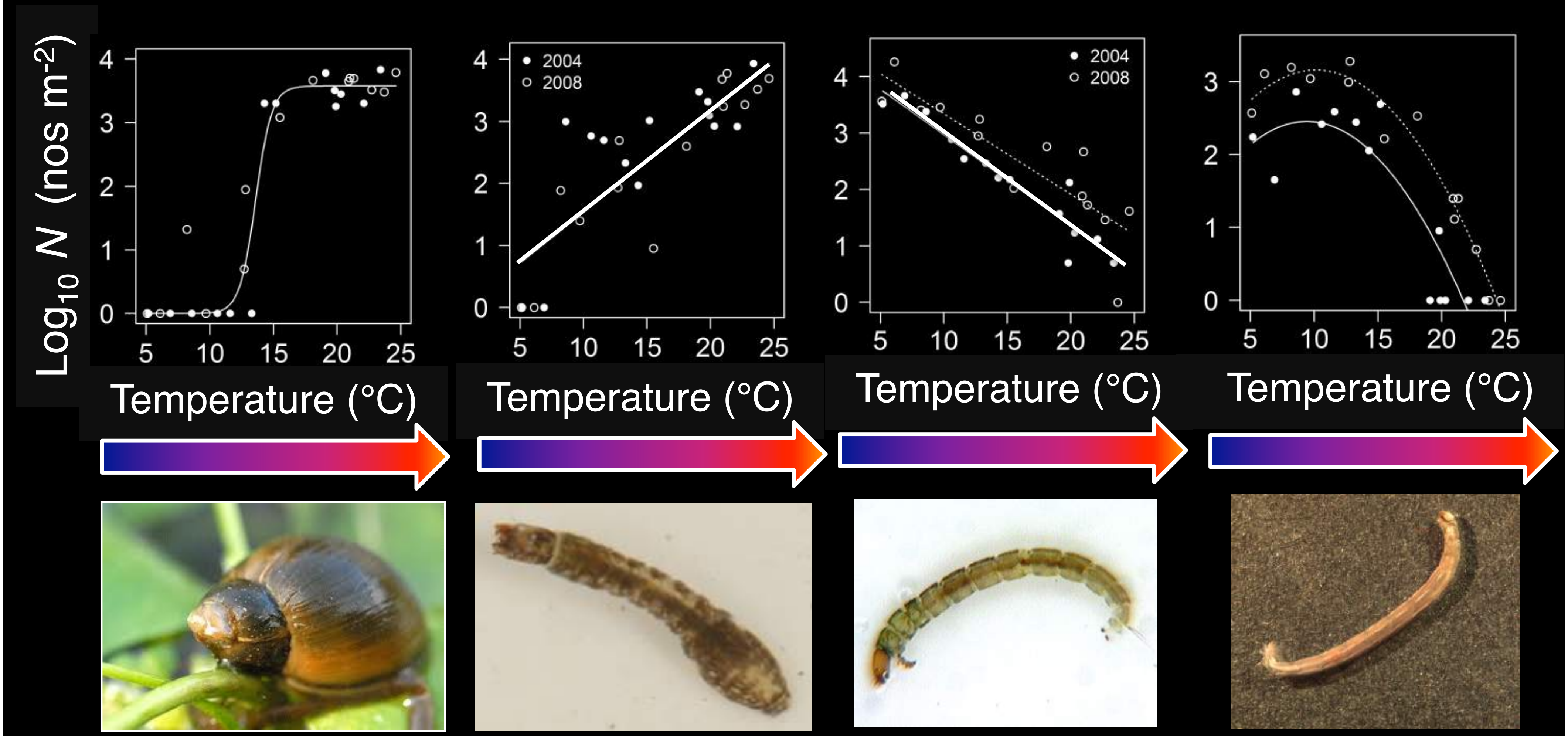
Community composition?

Food web structure and dynamics?

Ecosystem functioning?

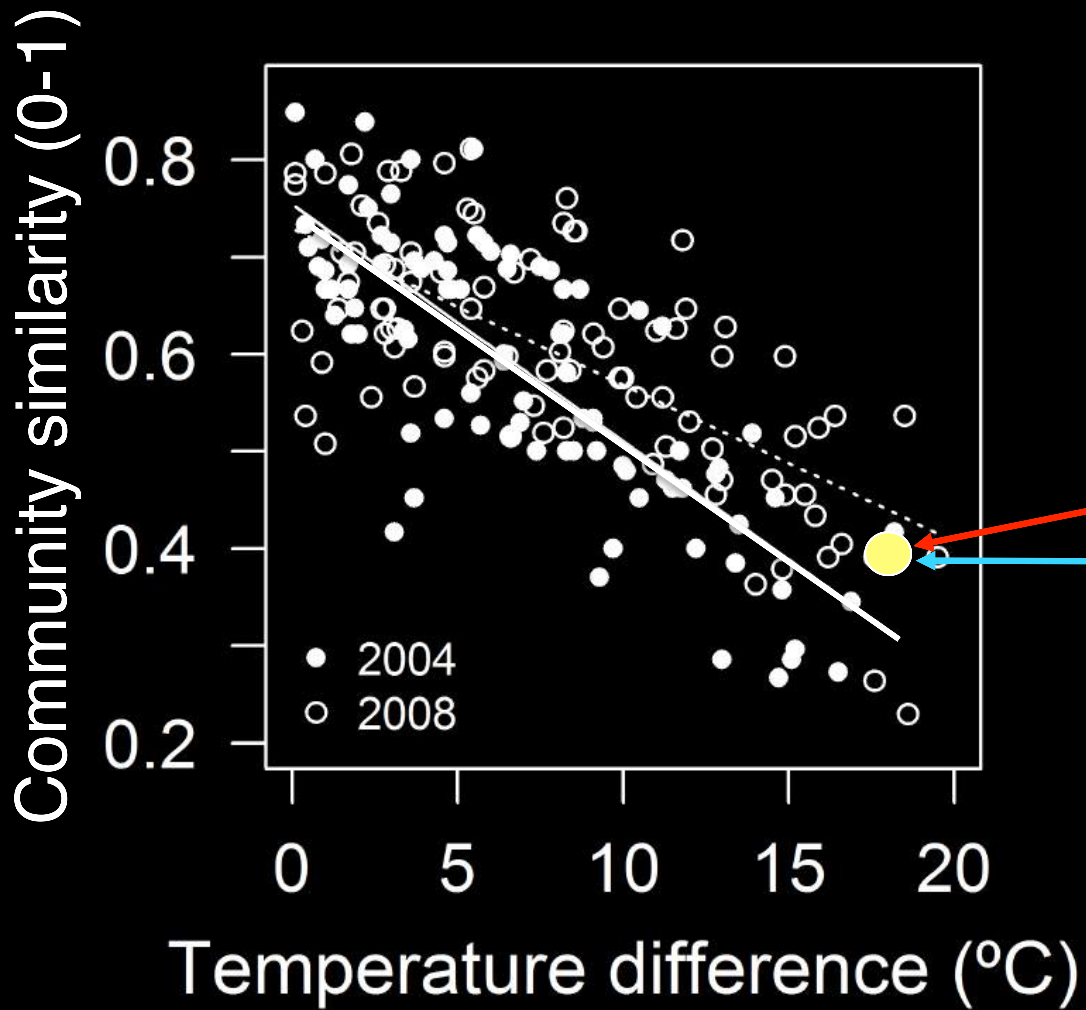


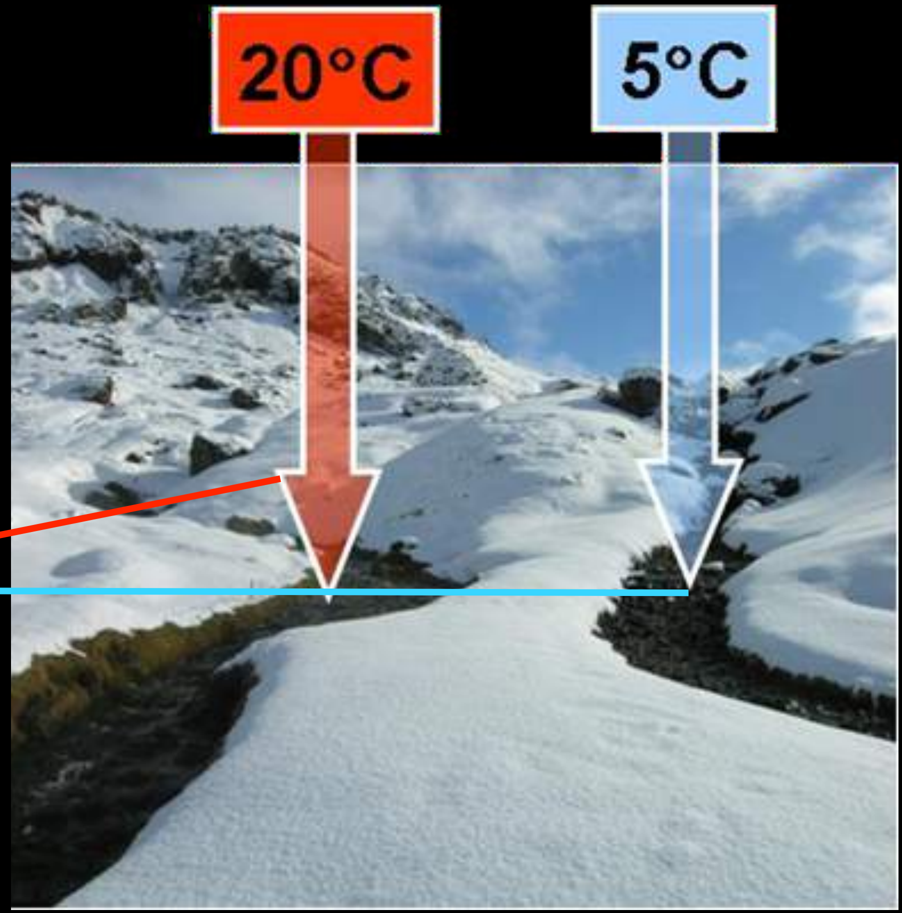
Population responses: winners…and losers



Pichler *et al.* (*in prep*)

Temperature drives community composition



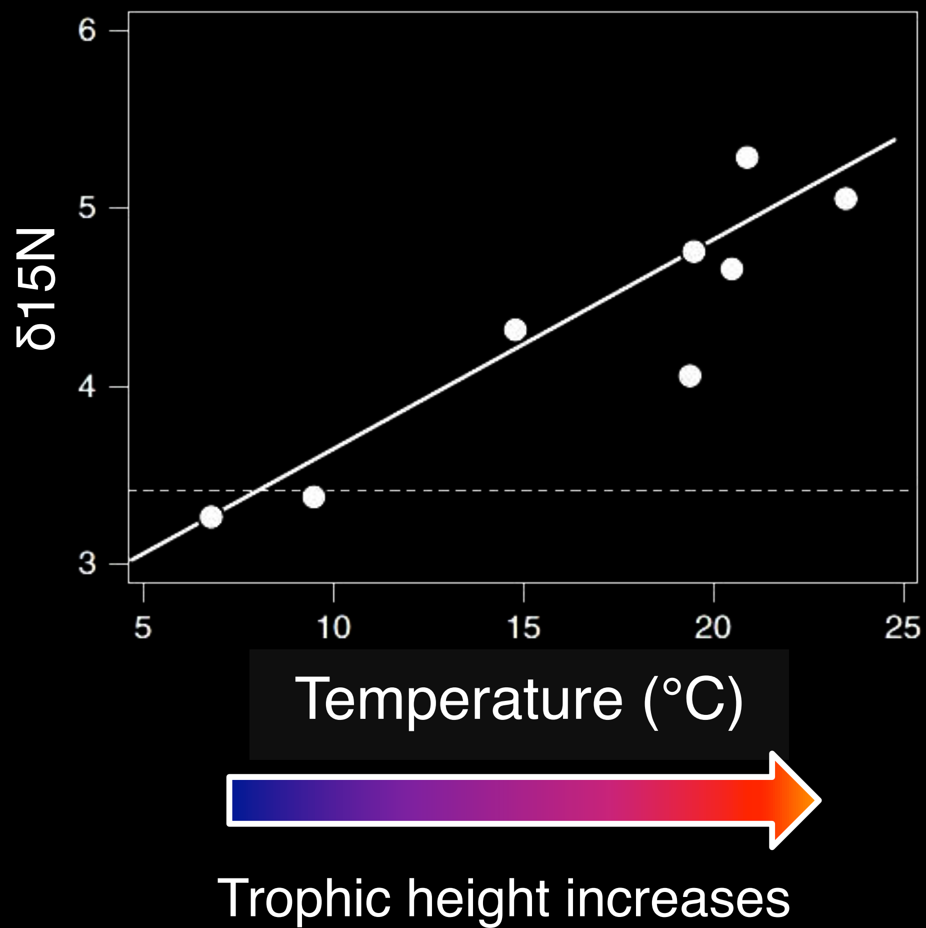


As temperature difference increases, community similarity decreases

Consistent intergenerational effect

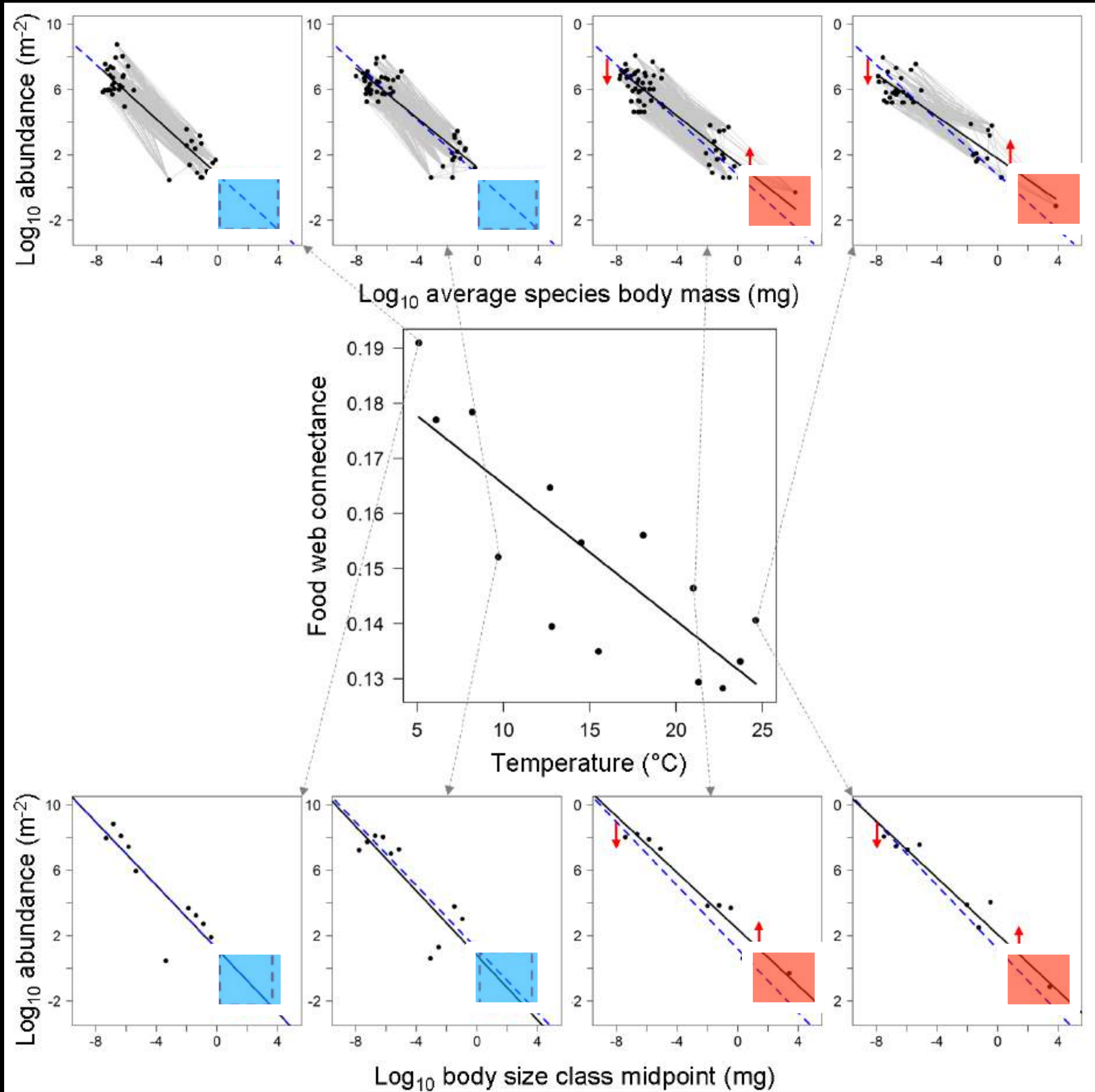
Pichler *et al.* (*in prep*)

Food chains lengthen as temperatures increase



Woodward *et al*. (2010) *Global Change Biology*

Temperature also alters food webs and size structure

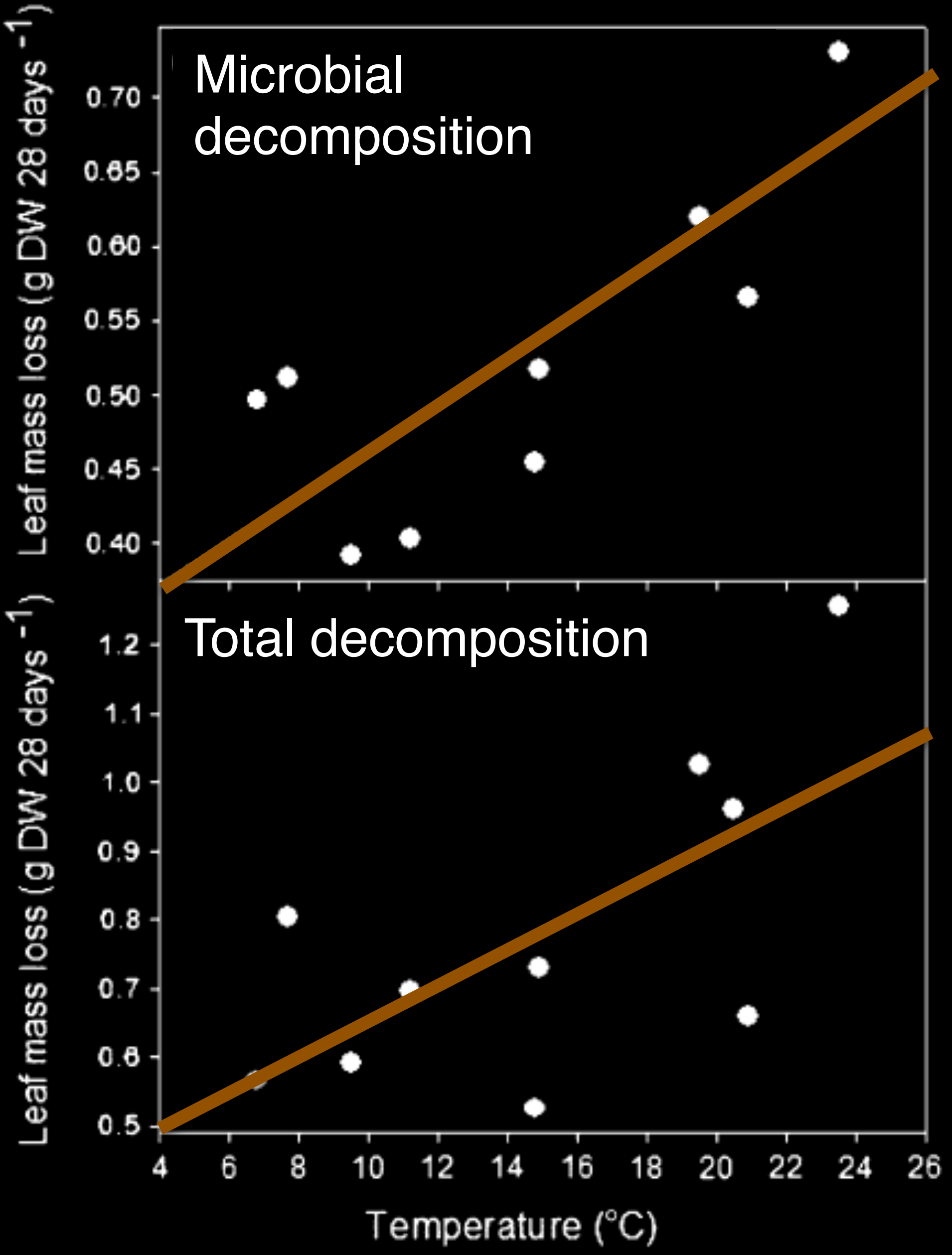


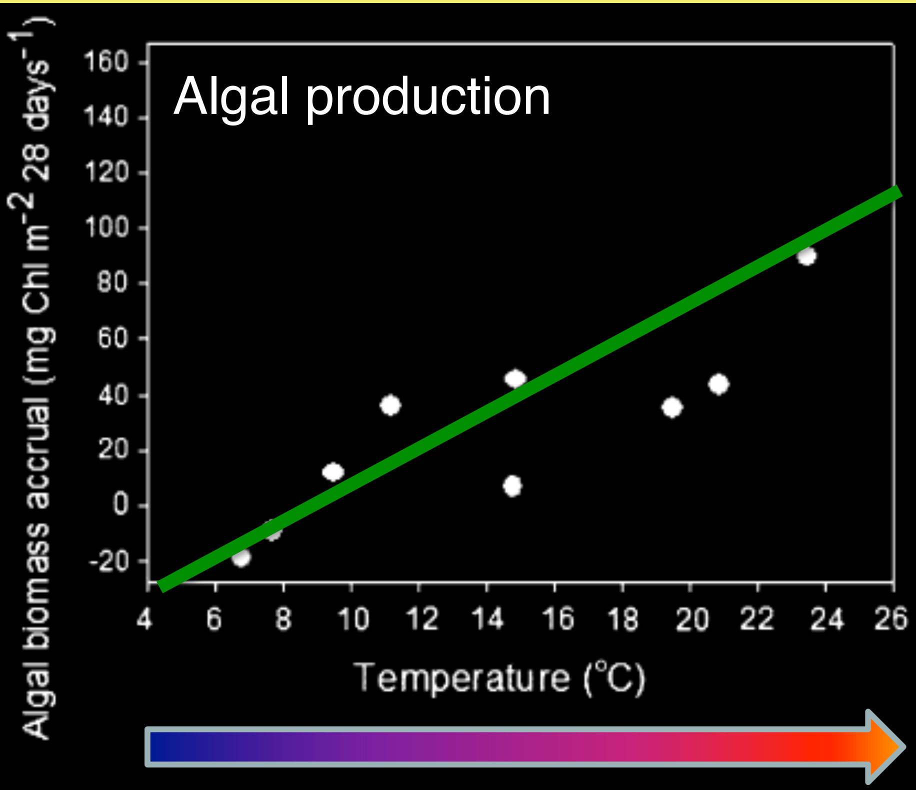
Network complexity declines….as size spectrum expands (fish invasion)

O'Gorman et al (in prep)


Warming impacts on ecosystem respiration?

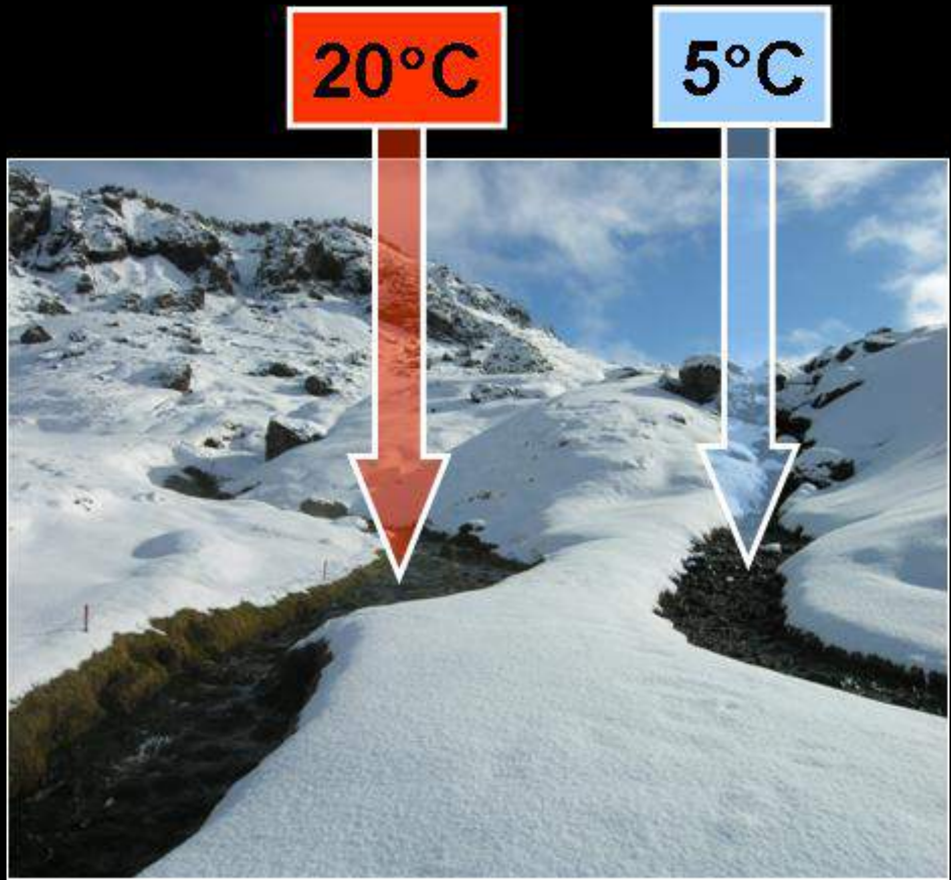
Ecosystem process rates increase with temperature in field assays

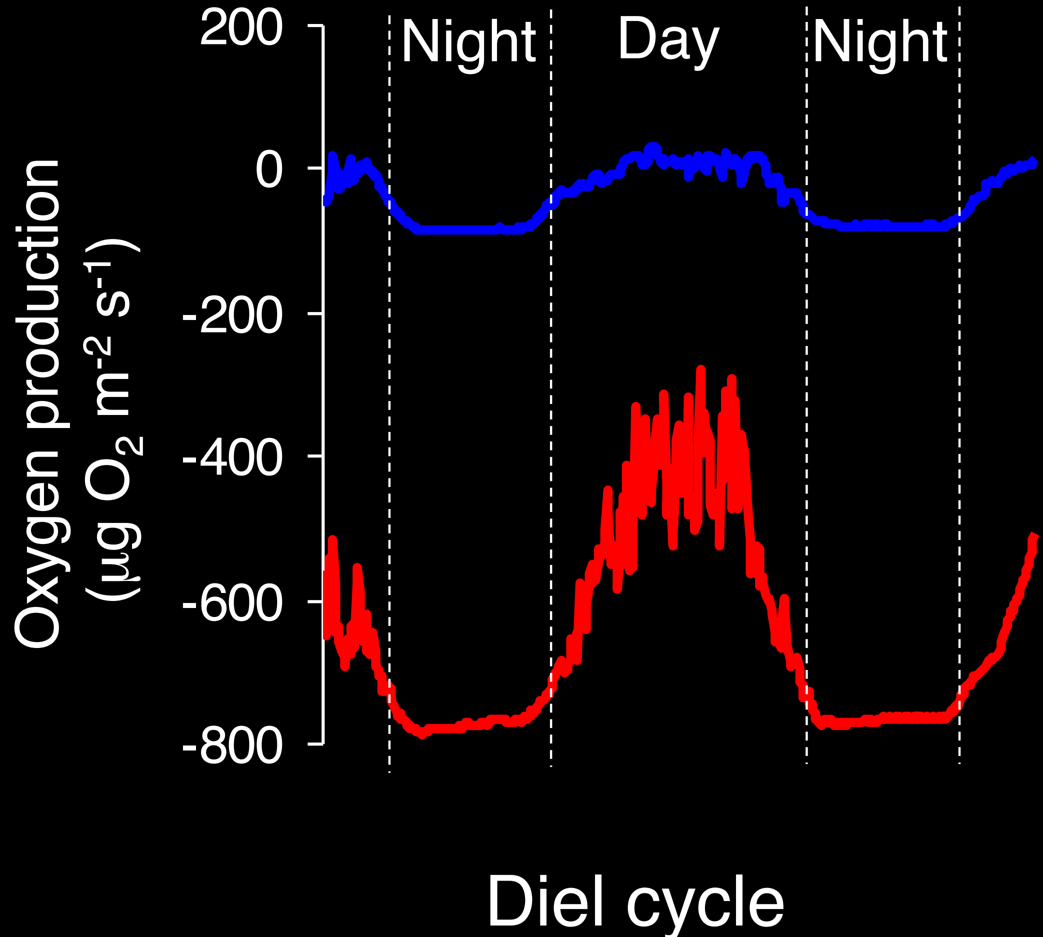




Friberg et al 2009 *Freshwater Biology*

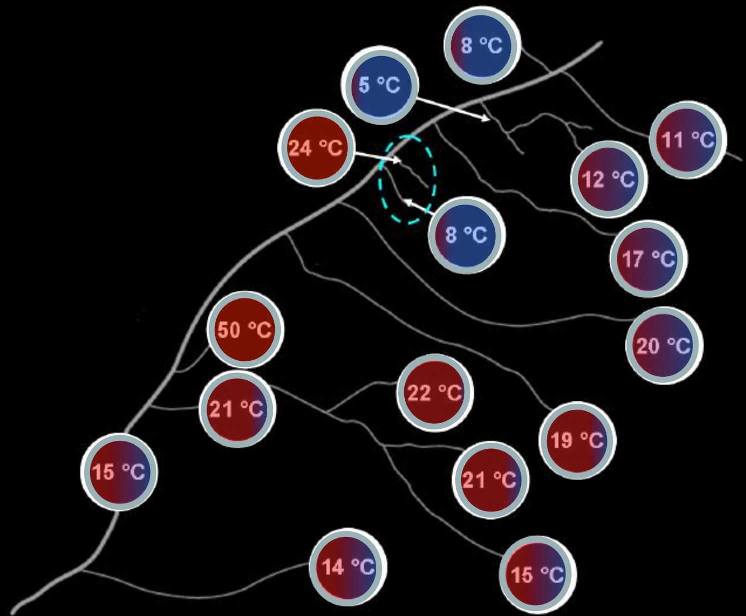
Watching the food web breathe…



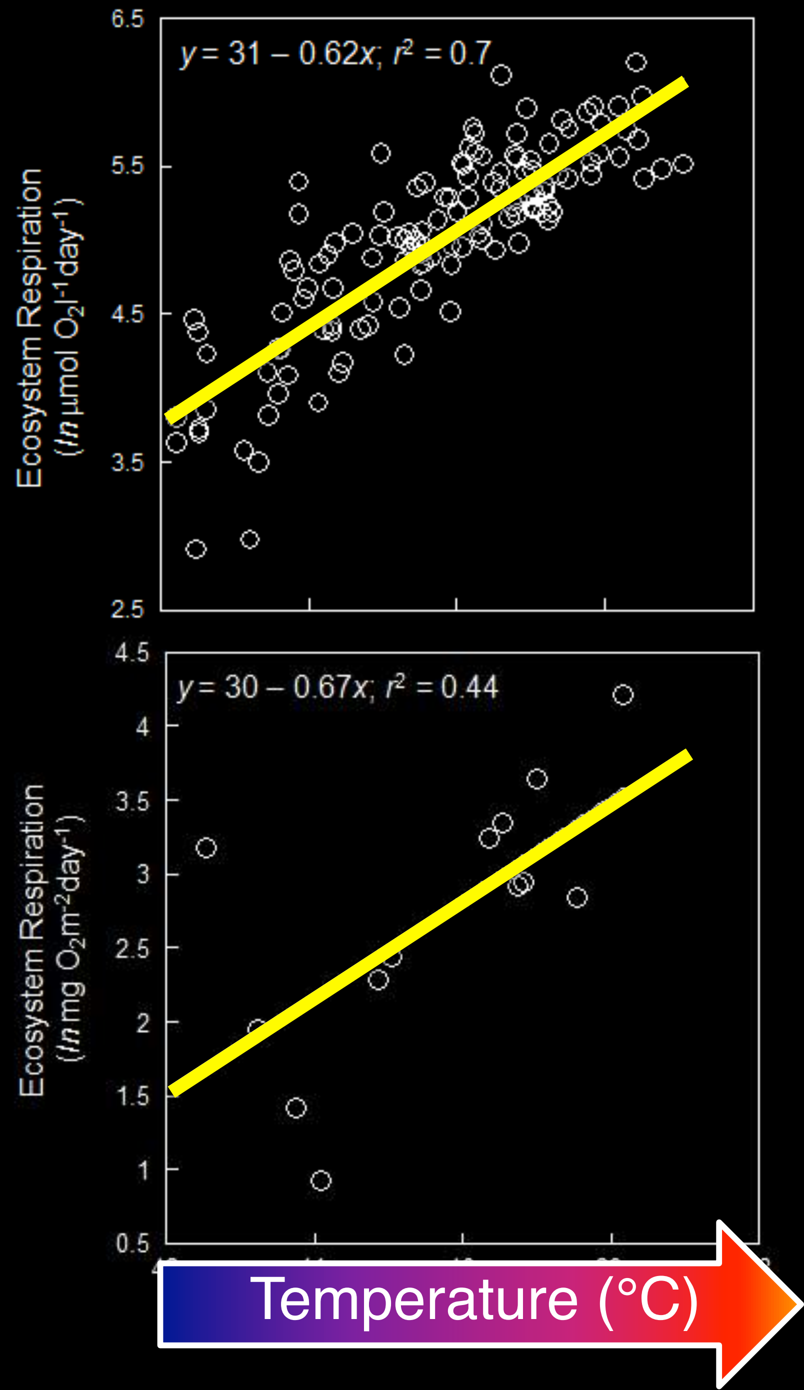


Demars et al 2011 *Freshwater Biology*

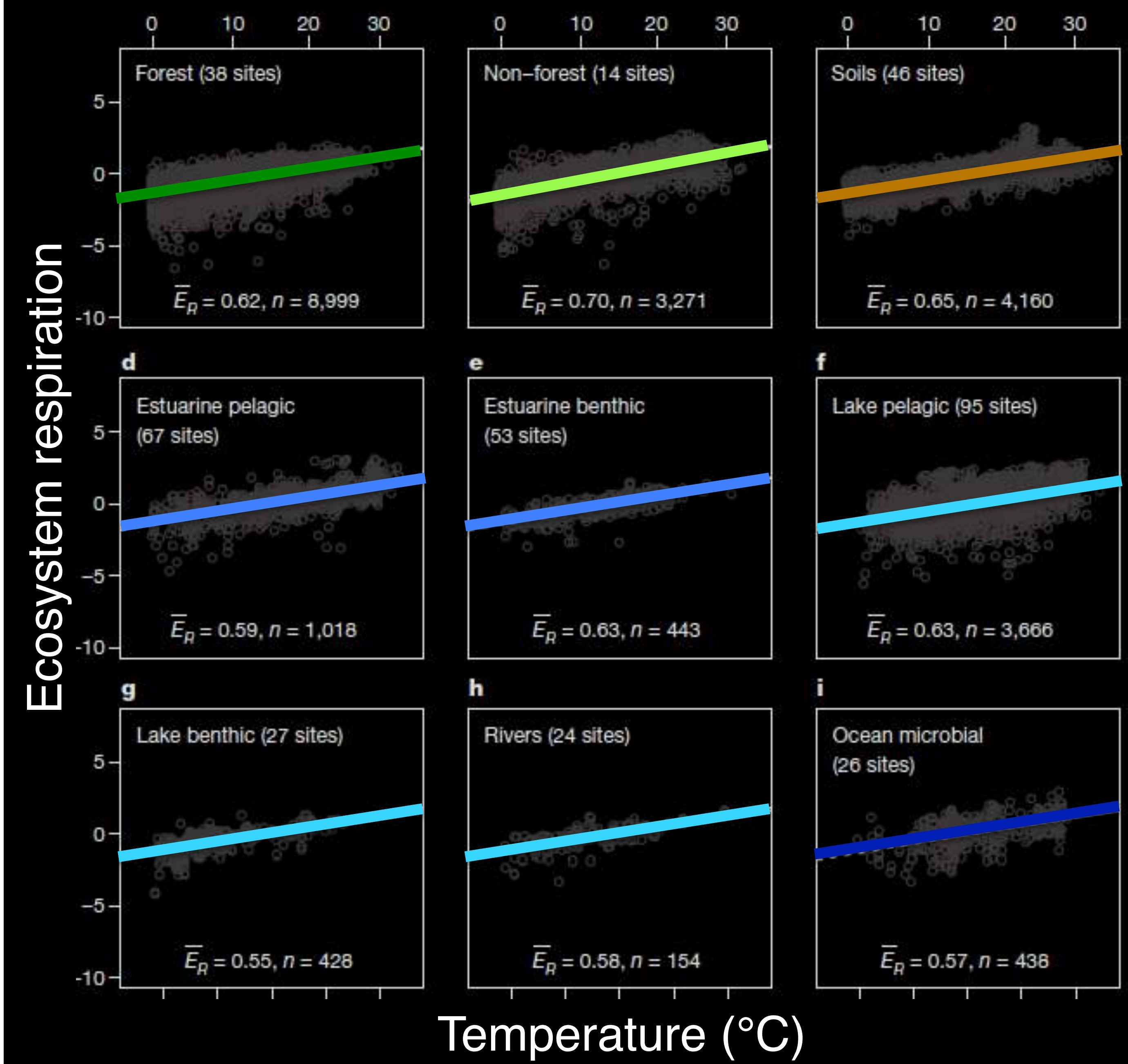
Congruence in Icelandic streams & U.K. mesocosms...



Friberg et al (2011) *Adv Ecol Res*



...and with the wider world

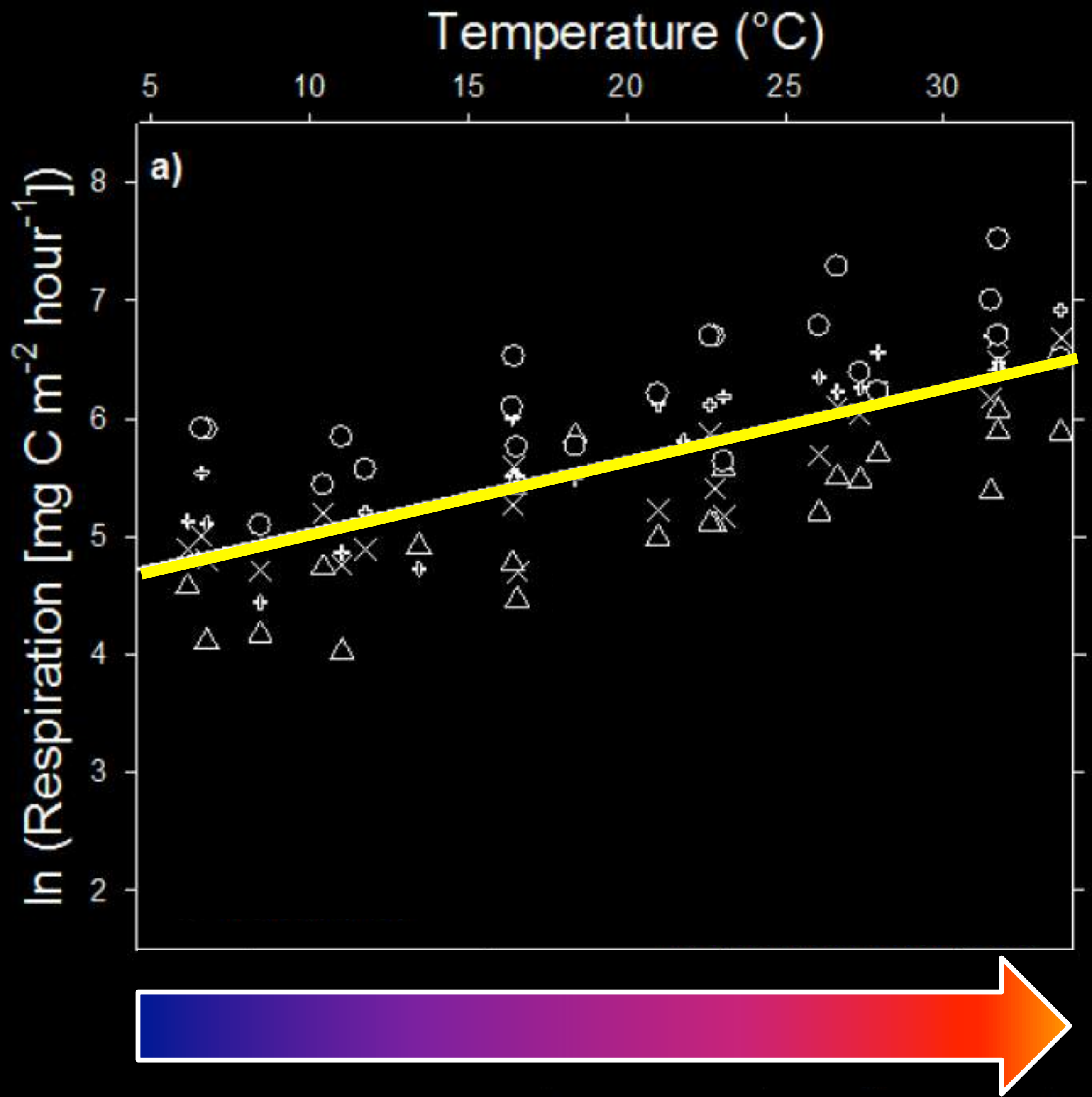


Consistent whole-system respiration responses to temperature across 100s of aquatic and terrestrial ecosystems

Yvon-Durocher et al (2012) *Nature*

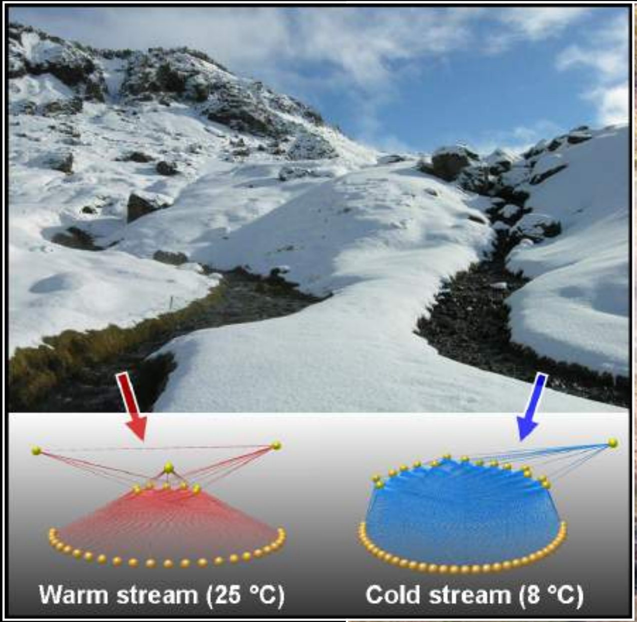
Ecosystem responses in Iceland are resilient, despite huge species turnover

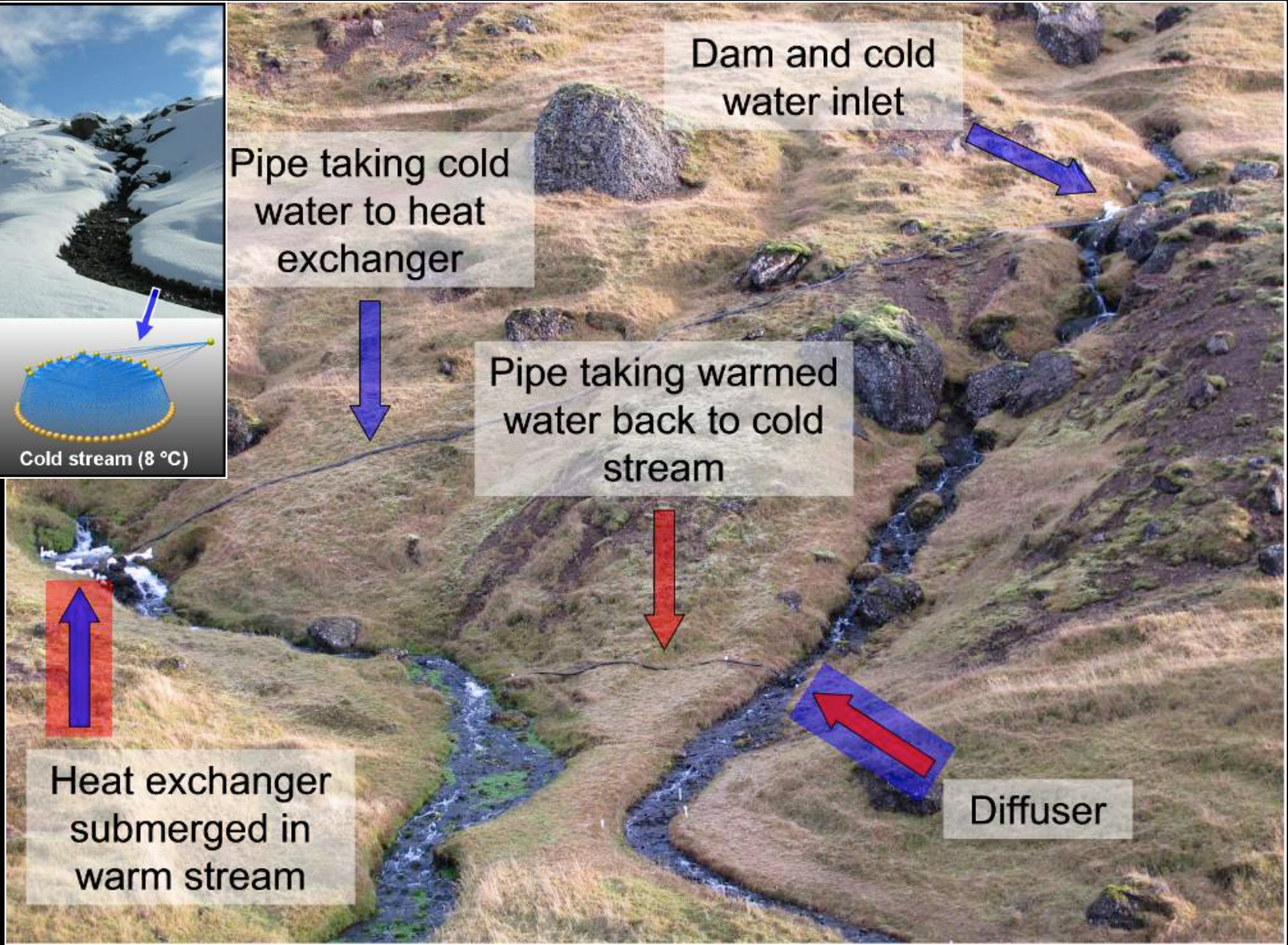
Lab incubations of biofilm from 4 streams (6°C, 12°C, 20°C and 25°C) - slopes are identical



Perkins et al (2012) *Global Change Biology*

Transient vs equilbrial dynamics?
1st year of stream warming experiment (+4°C) now completed



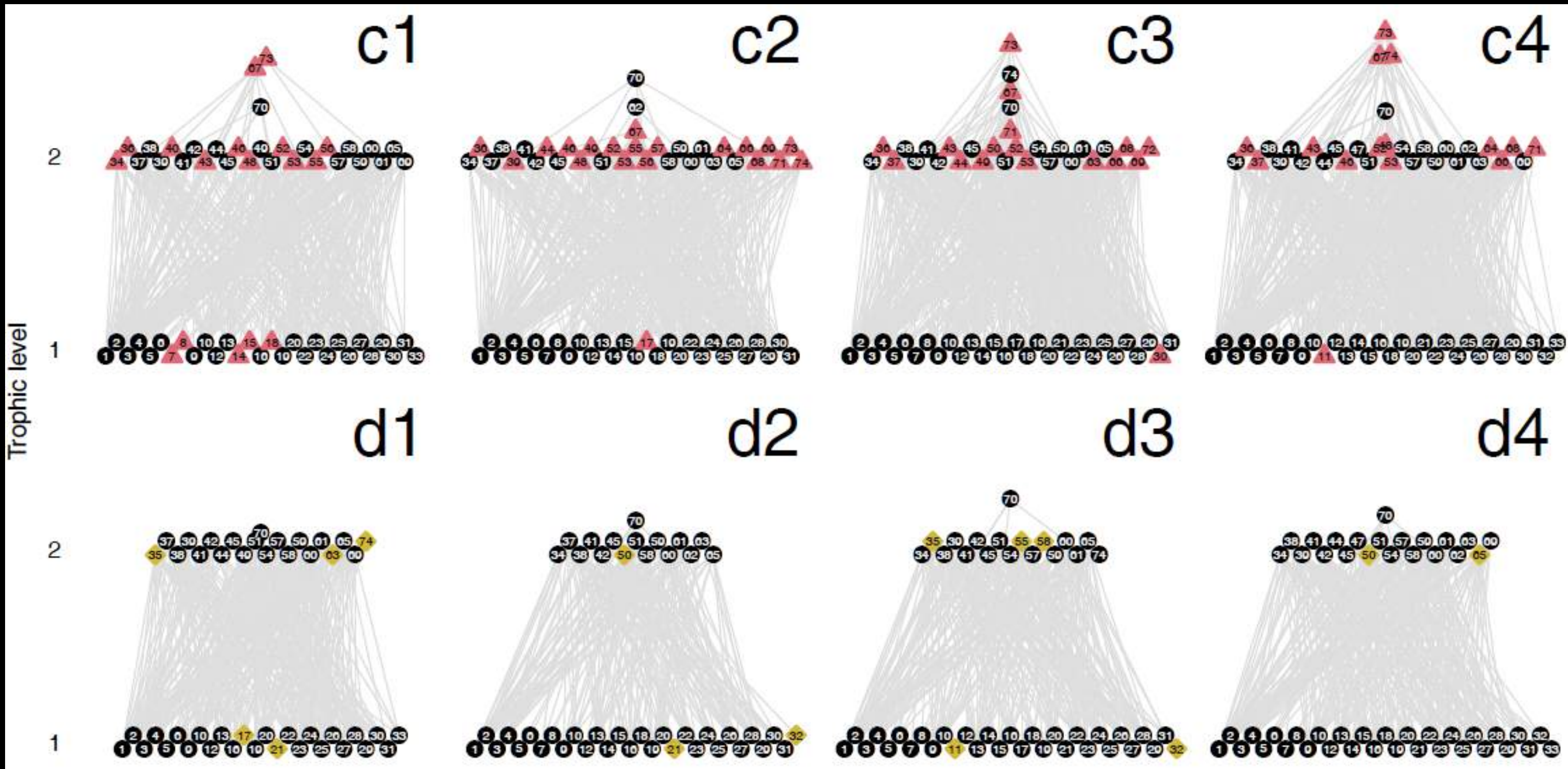


Climate change is a compound stressor – we need to examine its component parts before addressing synergies

COMPONENT	ECOLOGICAL CONSEQUENCE
Hydrology	**Habitat fragmentation by droughts**
Temperature	**Elevated metabolic demands**
Phenology	Consumer-resource mismatches
Wildfires	Manifold effects of riparian vegetation loss
Atmospheric change	Altered consumer-resource stoichiometry
Invasive species	Emergence of novel food webs

Mesocosm experiments: drought impacts on stream food webs

Replicable responses: large, rare consumers and their links are lost under repeated drought events over 2 yrs

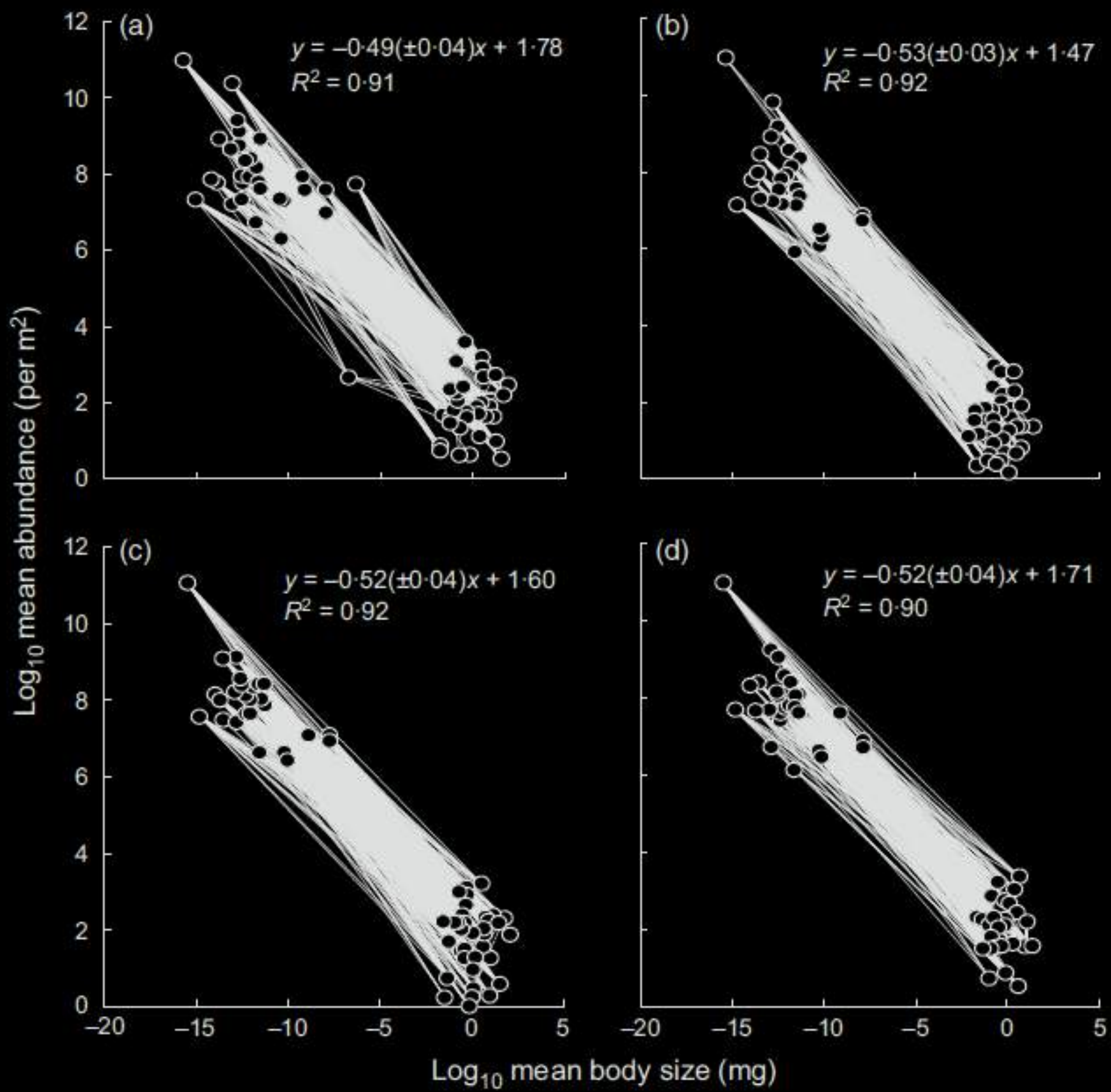


Only in control treatment

Only in drought treatment

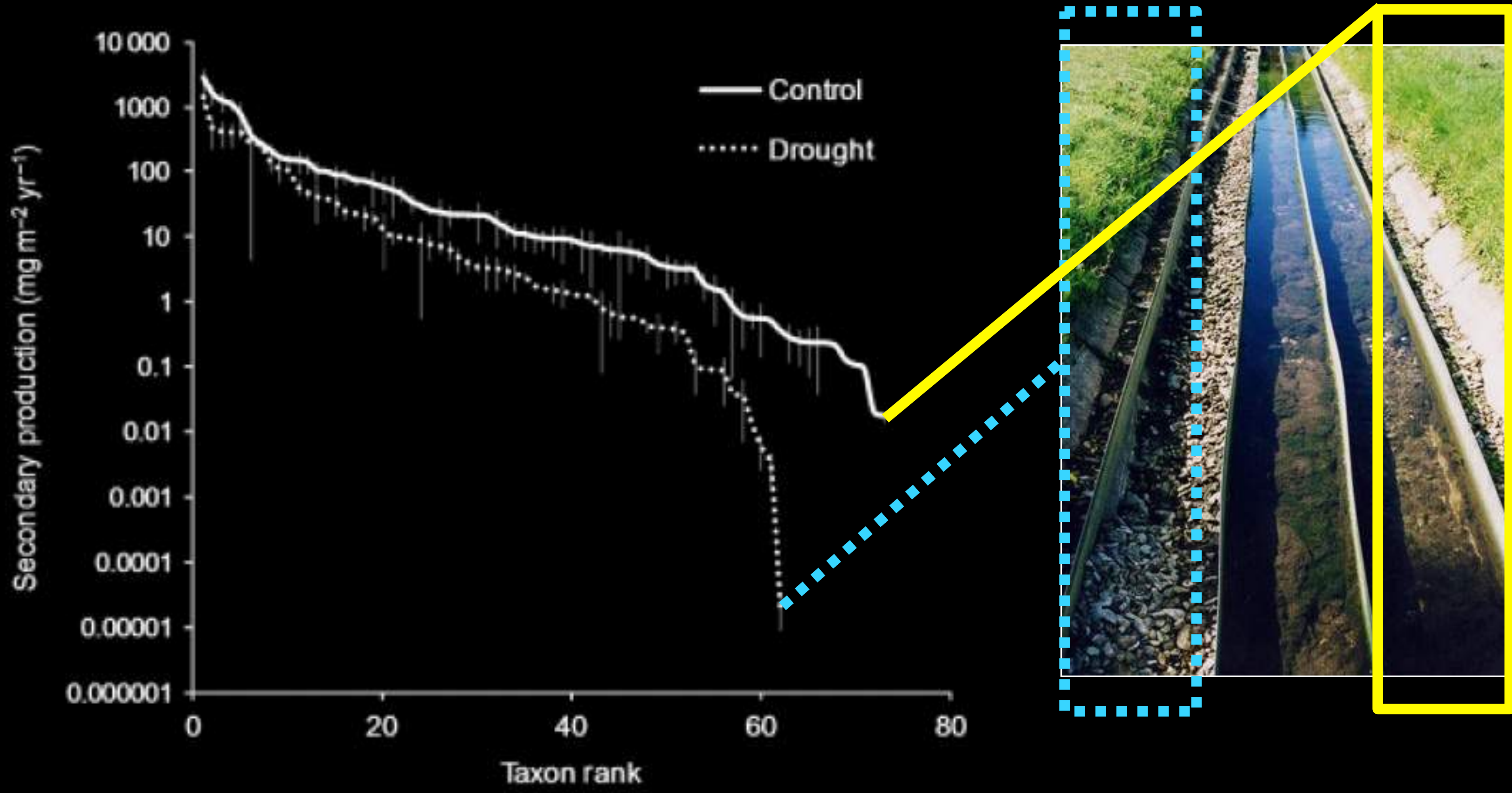
Woodward et al (*Phil. Trans Roy Soc B,* 2012)

Replicability and realism – trivariate food webs



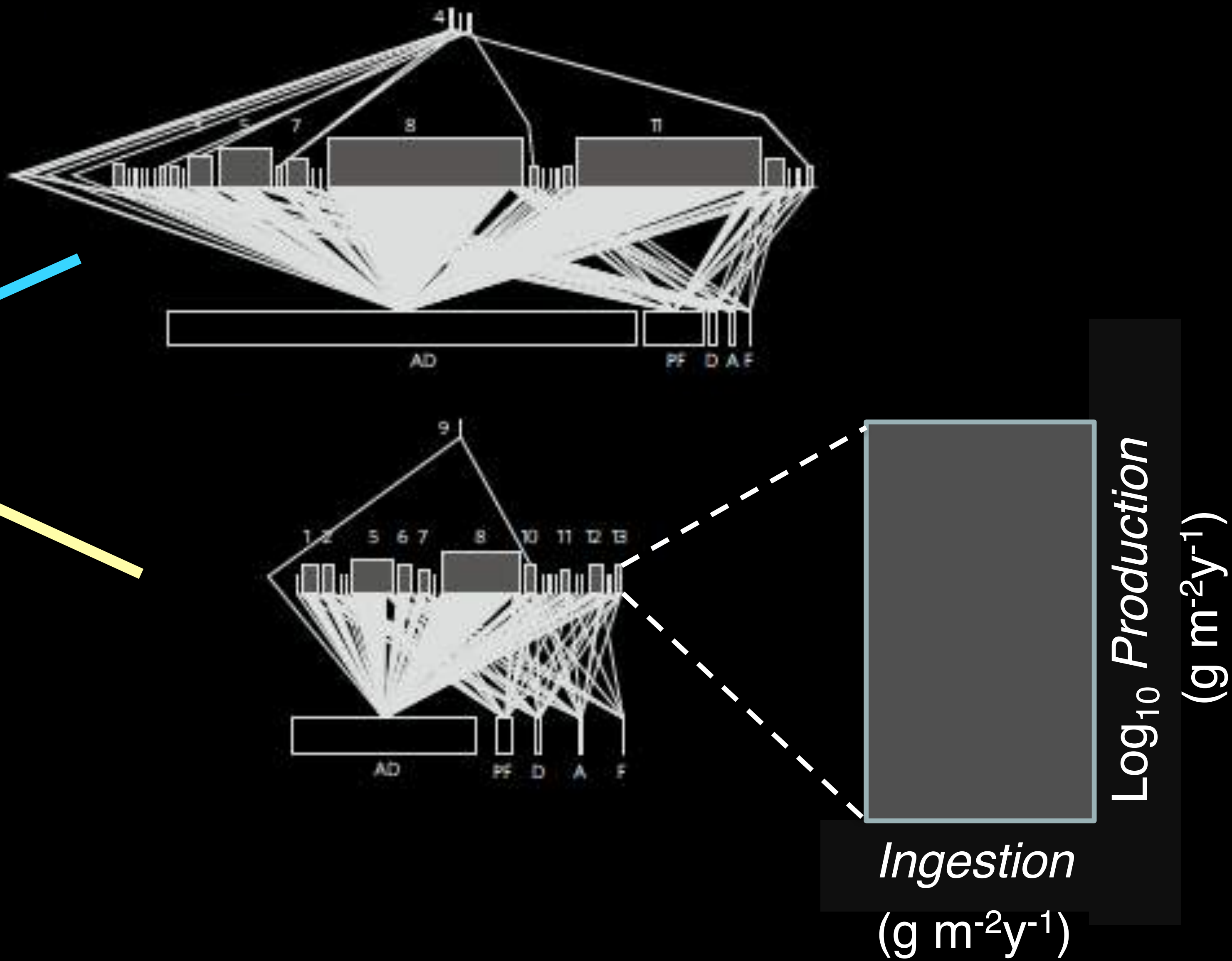
Brown et al. 2011
Journal of Animal Ecology

Drought reduces biodiversity and secondary production



Ledger et al. 2011 *Global Change Biology*

Drought simplifies food webs and suppresses secondary production by ½ an order of magnitude: resilience is eroded



Ledger et al (*Nature Climate Change*, 2012)

The DRI-STREAM Project – extreme events and ramped stressors (led by Birmingham)

Work in progress, but we are “highly confident” P will be <0.05!!

Summary of drought experiments (to date)

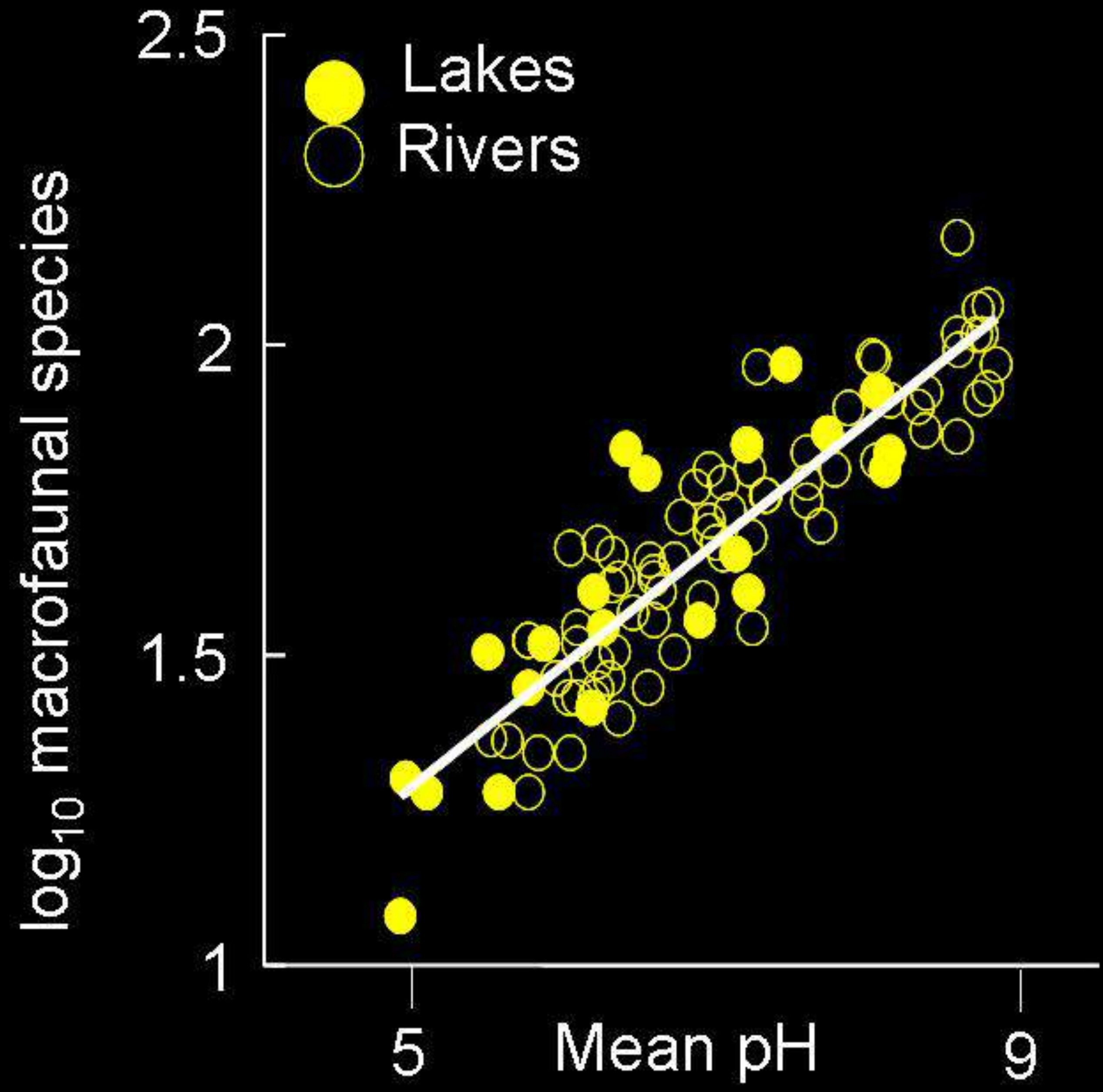
- Mesocosms were highly replicable (self-similar) and broadly realistic (similar to natural webs)
- Simulated patch-scale drought over intergenerational timescale (approx 2-years)
- Food webs simplified as links and species lost
- Ecosystem functioning (biomass production) was impaired – but effects were skewed in food web
- Large organisms (esp. predators) strongly impacted

Freshwaters are exposed to a cocktail of stressors in the 21st century

Acidification caused widespread species losses in the 1970s – acidifying emissions have been reduced since then

Fisheries collapse and loss of biodiversity and ecosystem services

Species richness (= food web size) increases with pH across >100 UK freshwaters



Chemical impacts, recovery and ecological resilience

Biological recovery is evident but has lagged behind chemical recovery and not been a simple reversal of responses to acidification - why?

1. **Dispersal constraints?**

(fragmentation of freshwater habitats in the landscape)

2. Species interactions?

(e.g. if acid webs are dominated by generalist consumers prey (re)colonisation may be slowed)

nb: ***not*** mutually exclusive hypotheses...

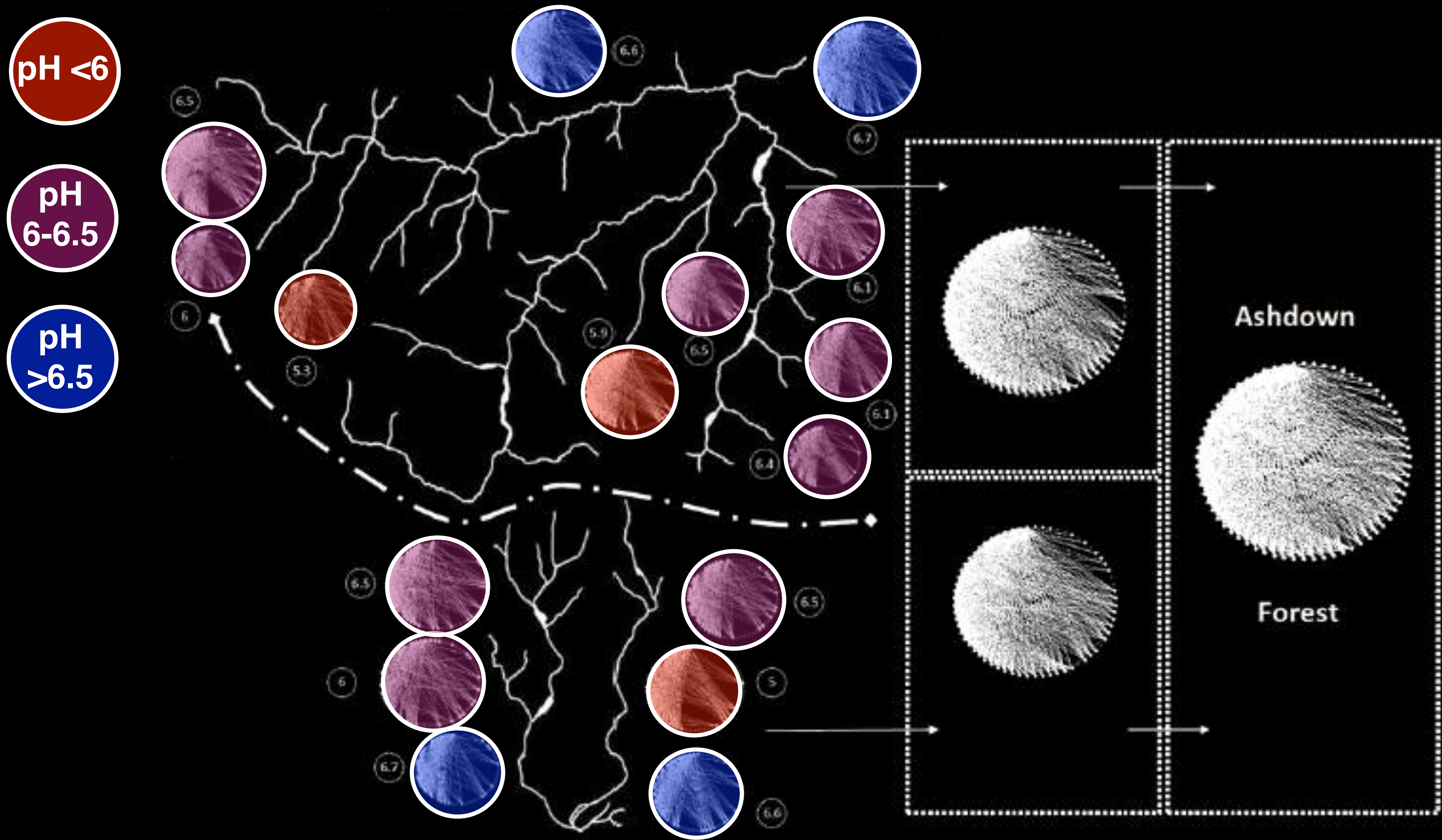
Fish have recently started returning to some systems, but biological recovery has lagged far behind chemical recovery – why?

1990s – *Cordulegaster* invasion

2000s – trout invasion

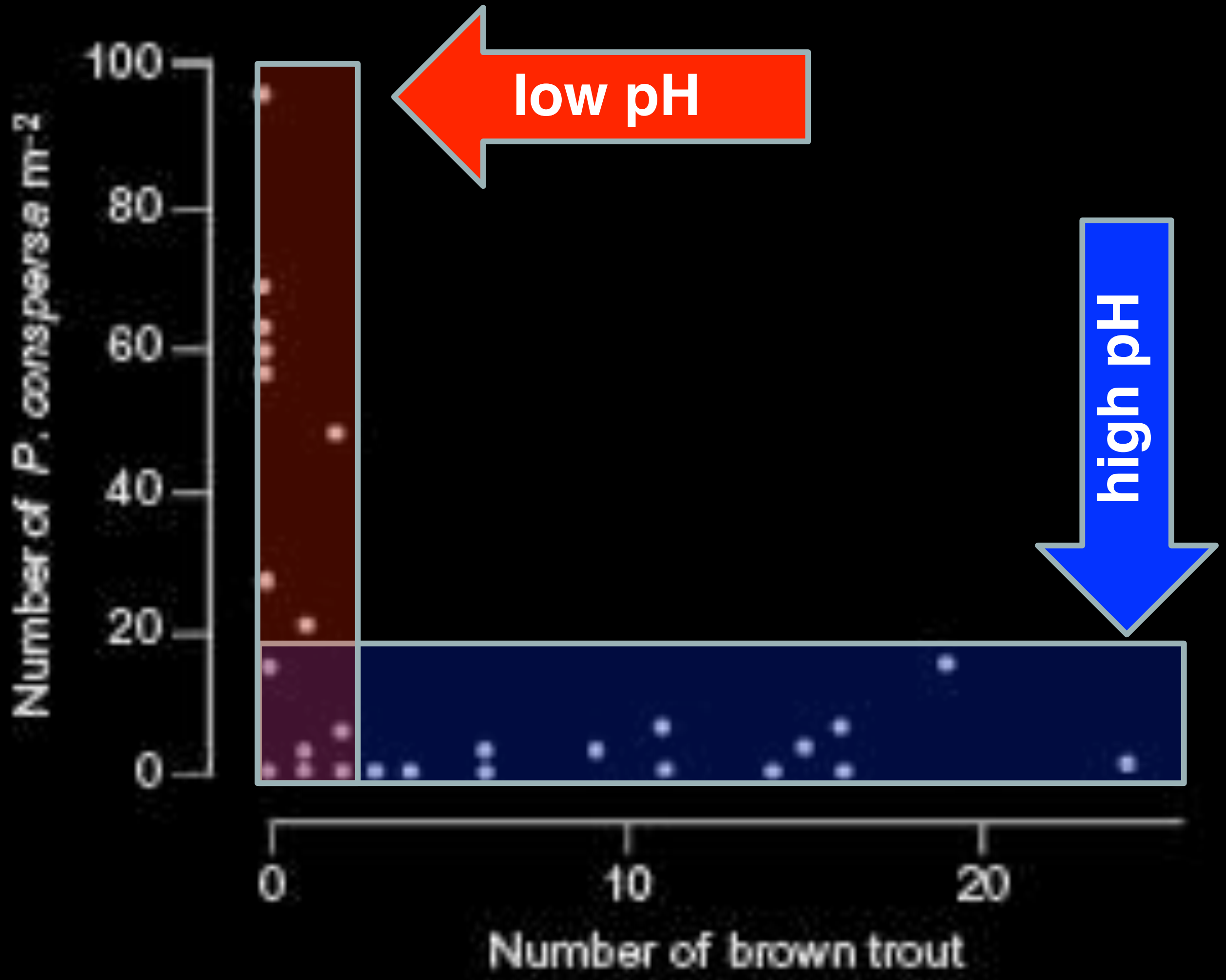
New top predators in the Broadstone Stream food web

Freshwater food webs are spatially fragmented but dispersal is <u>not</u> limiting recovery rates for many taxa



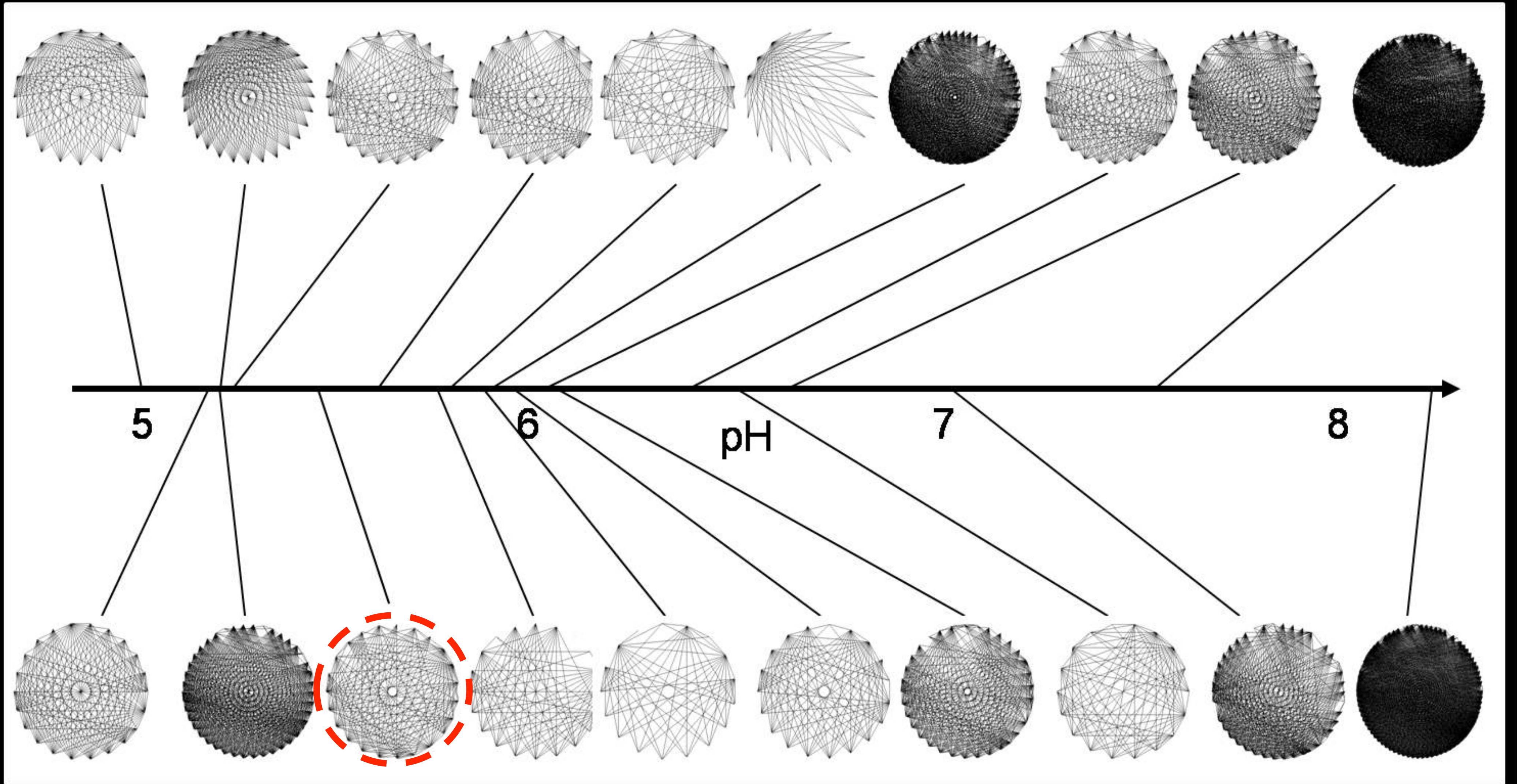
Hagen et al Adv. Ecol. Res. 2012

Negative relationships between fish and large invertebrate predator populations – "either/or" scenarios across spatial pH gradients



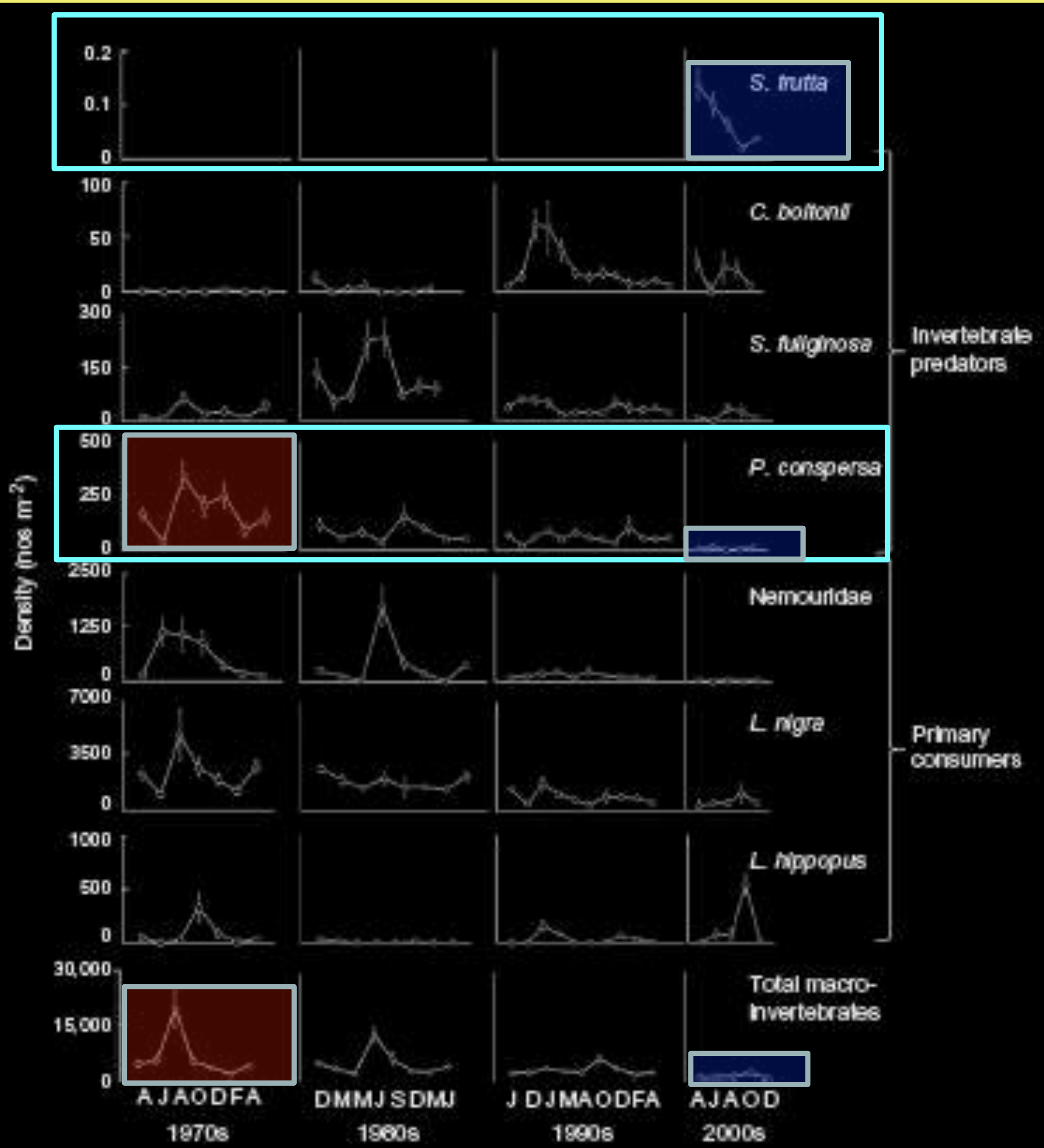
Layer et al (2011)

Is food web structure and functioning the key? 20 stream food webs across a spatial pH gradient (Layer et al. 2010)

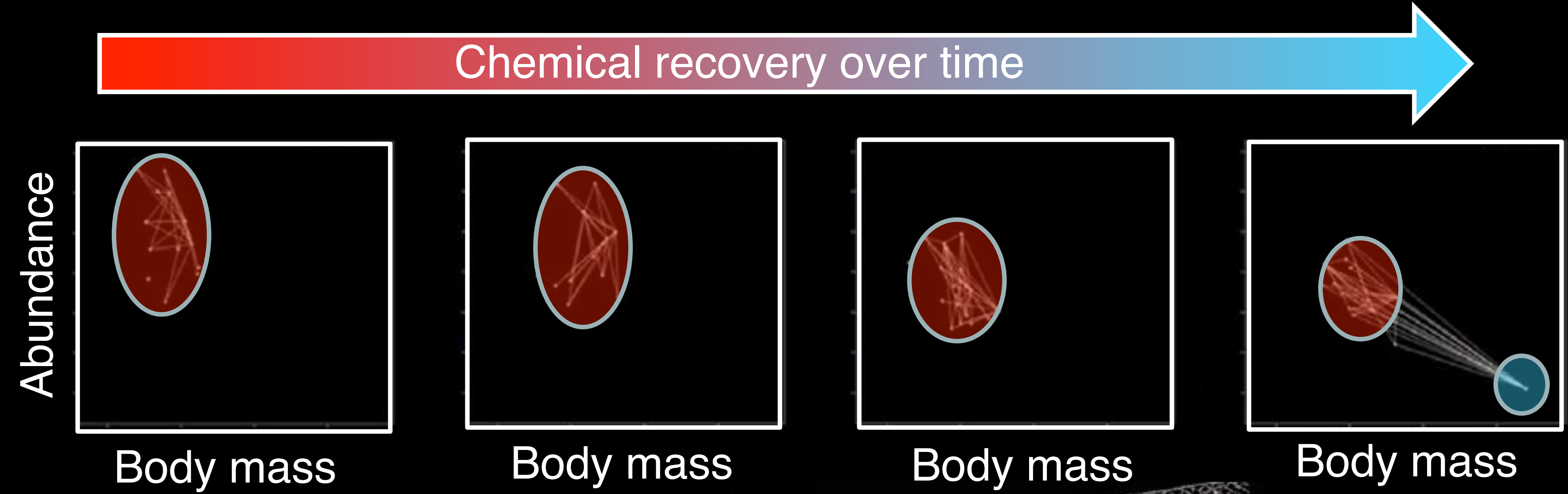


Broadstone Stream

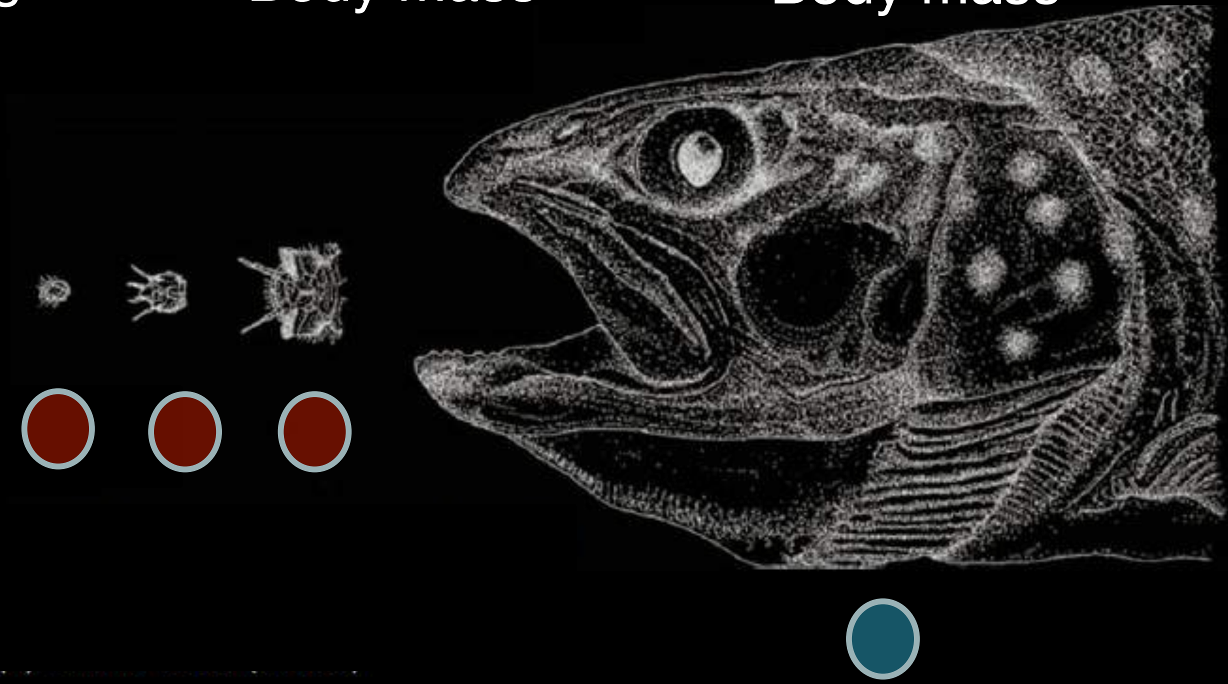
Negative relationships between fish and large invertebrate predators across temporal pH gradient in a single system



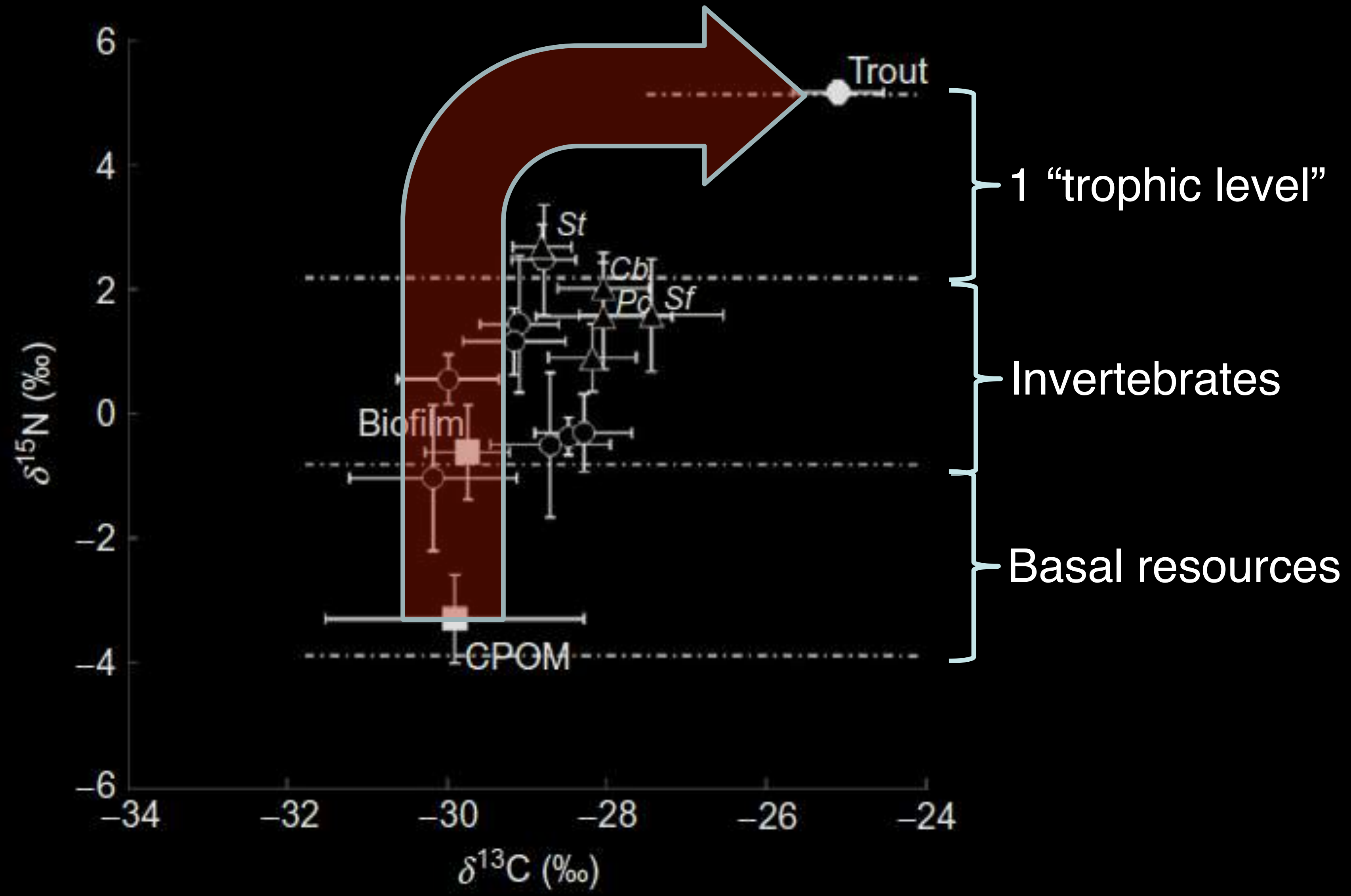
Case Study: declining invertebrate numbers <u>BUT</u> return of trout as food web recovers from acidification



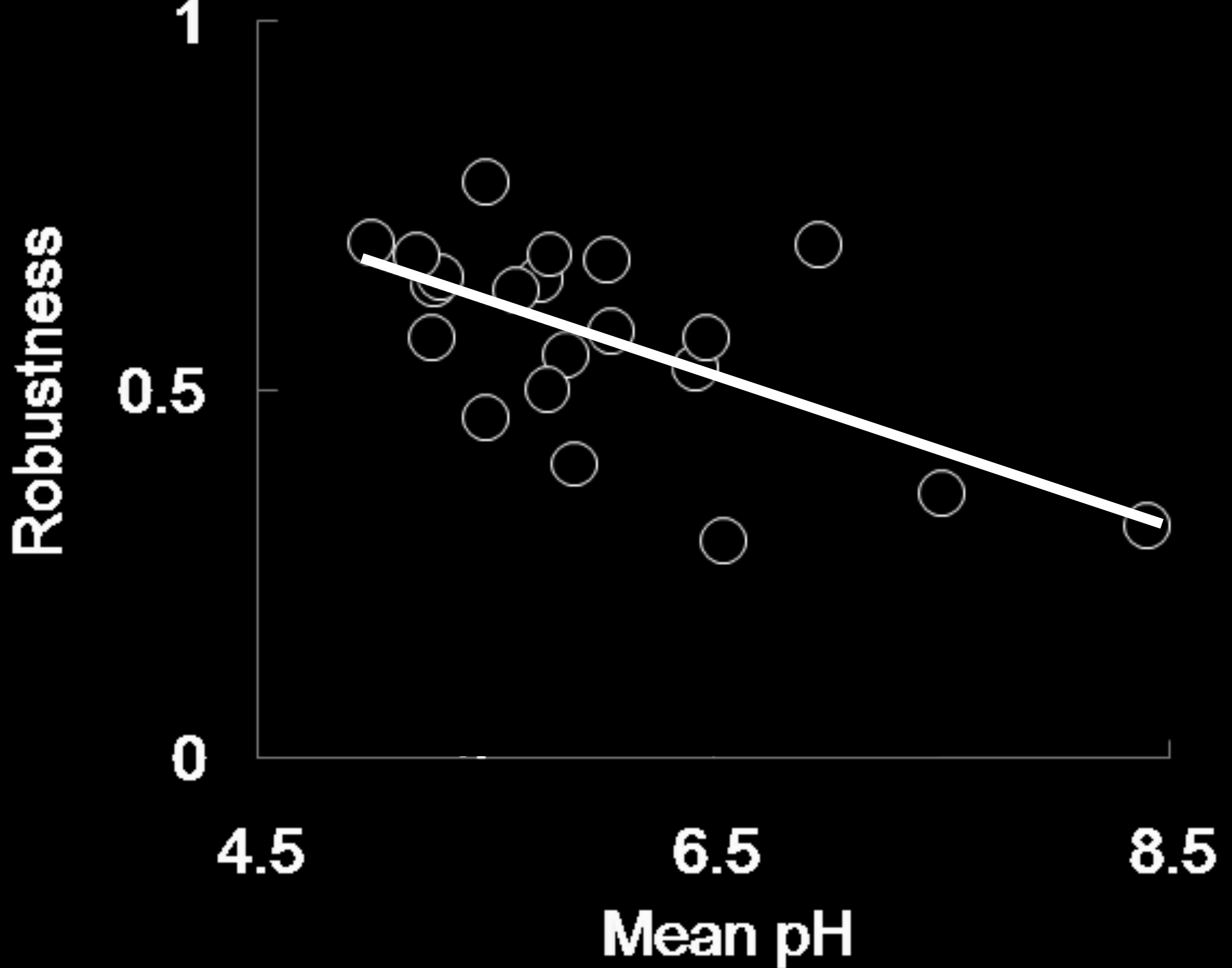
“Top predators” in each web drawn to scale:



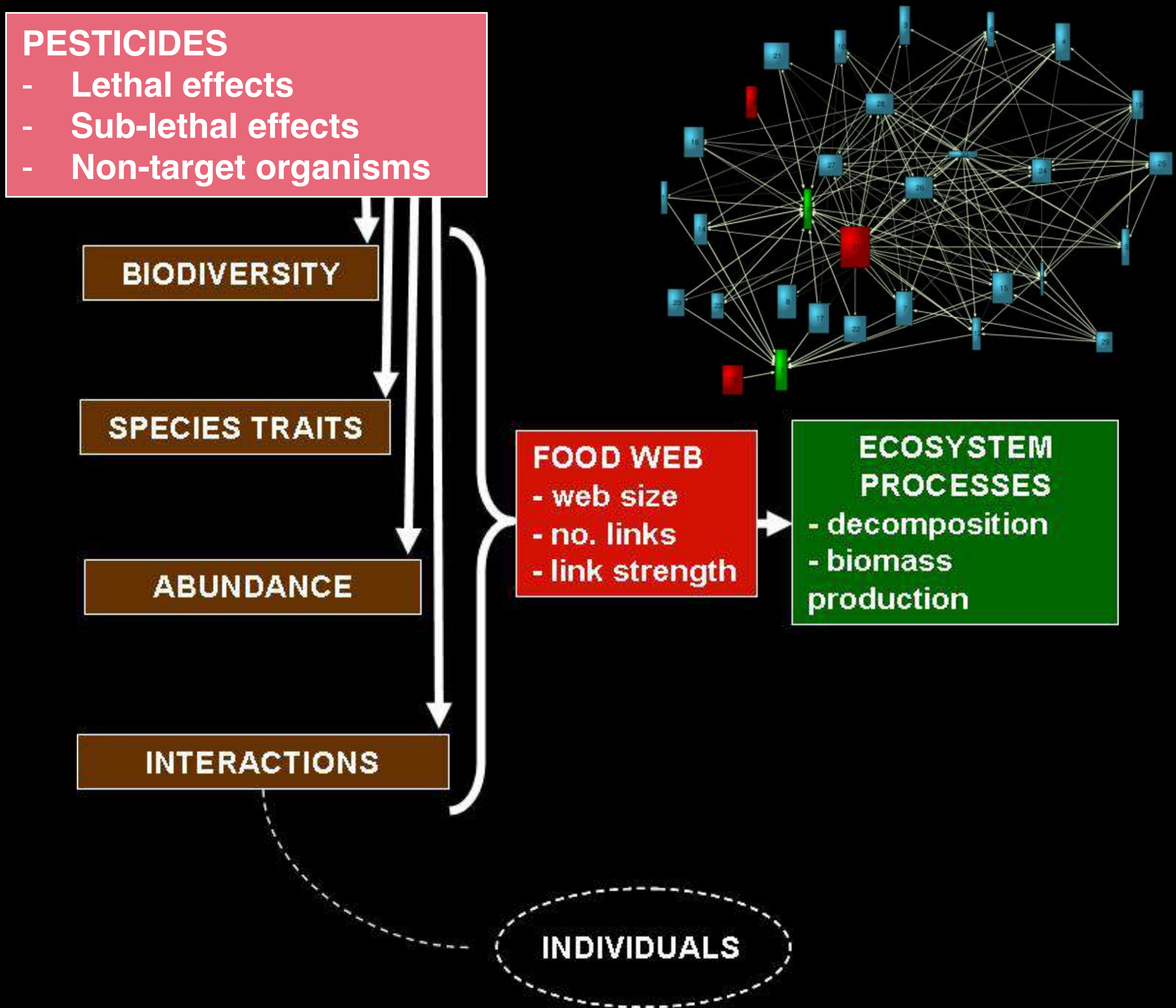
Stable isotope analysis: a full trophic level is added as the food web recovers



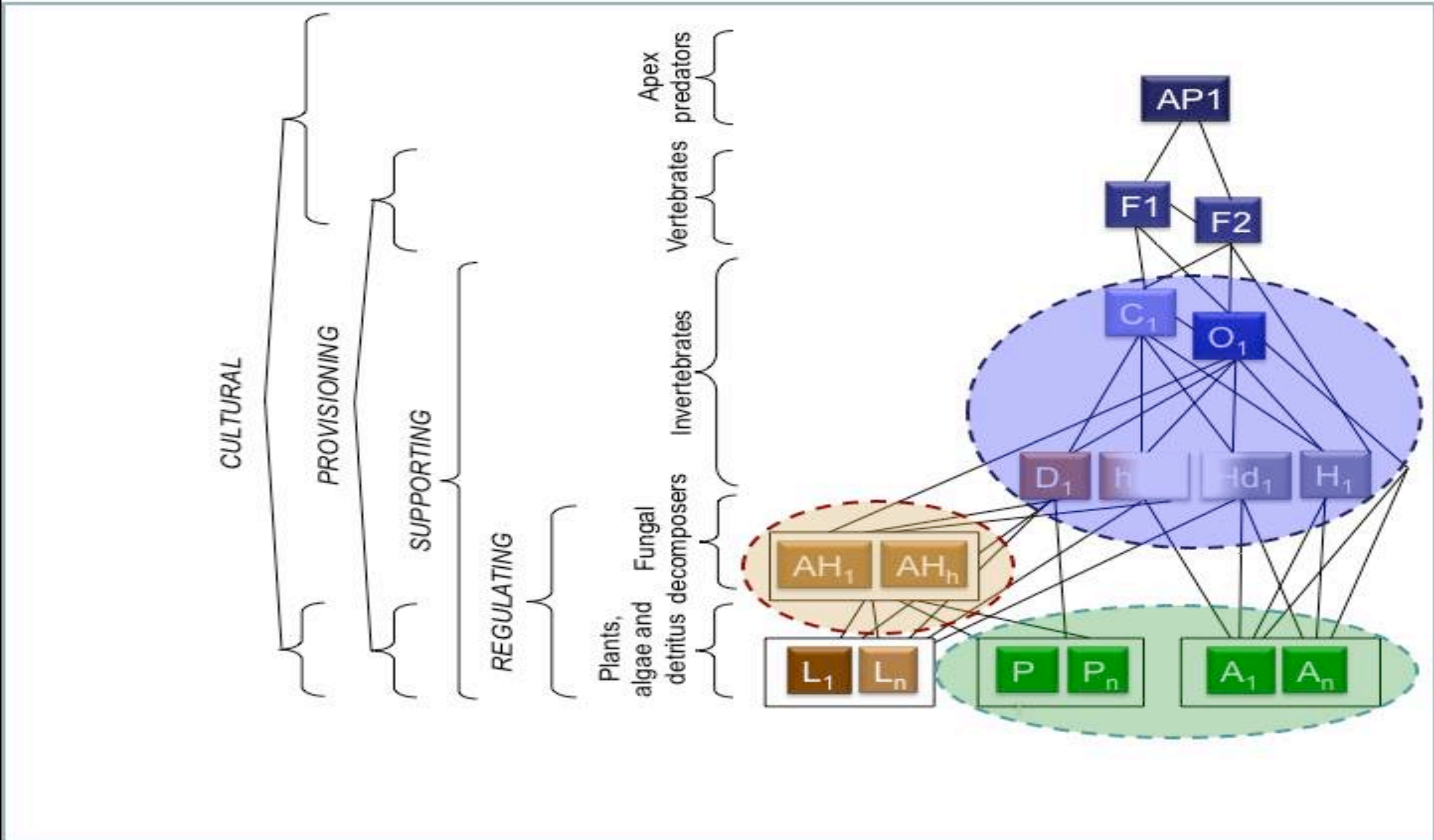
Acid webs are more stable…is ecological inertia slowing biological recovery?



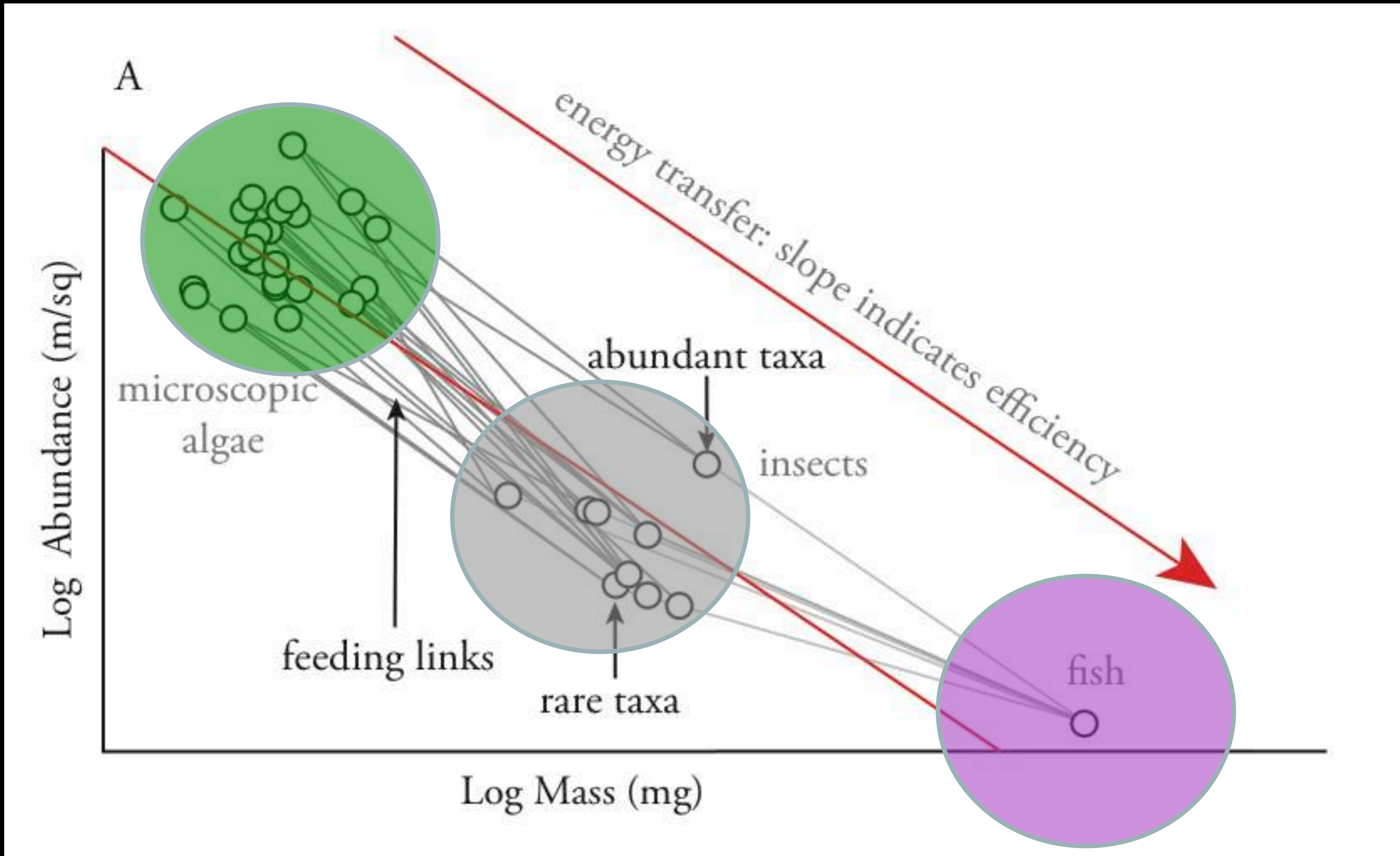
Pesticides – paying the “agricultural debt”



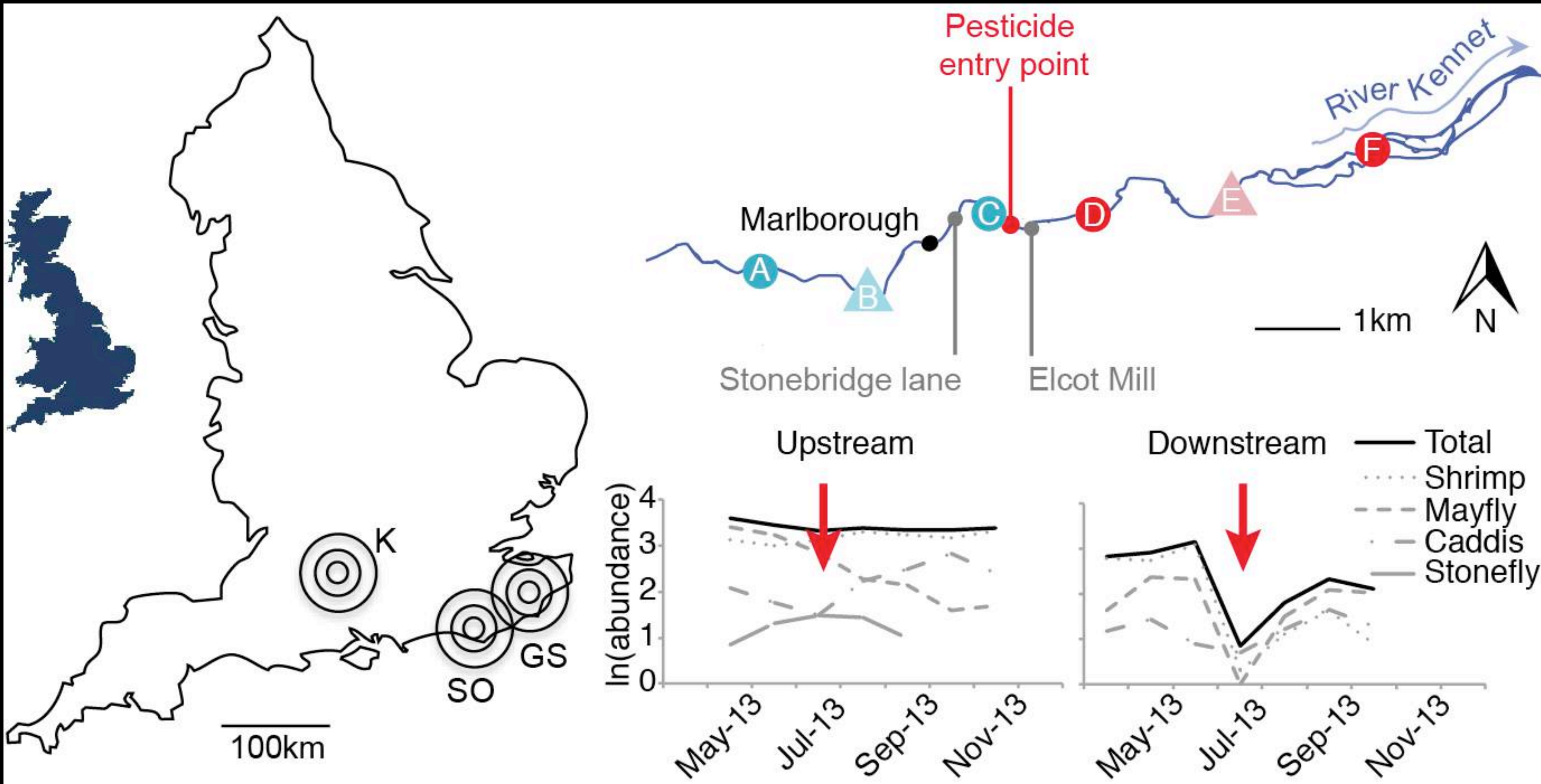
Society's Faustian Pact: trading ecosystem services with agrochemical-based food production



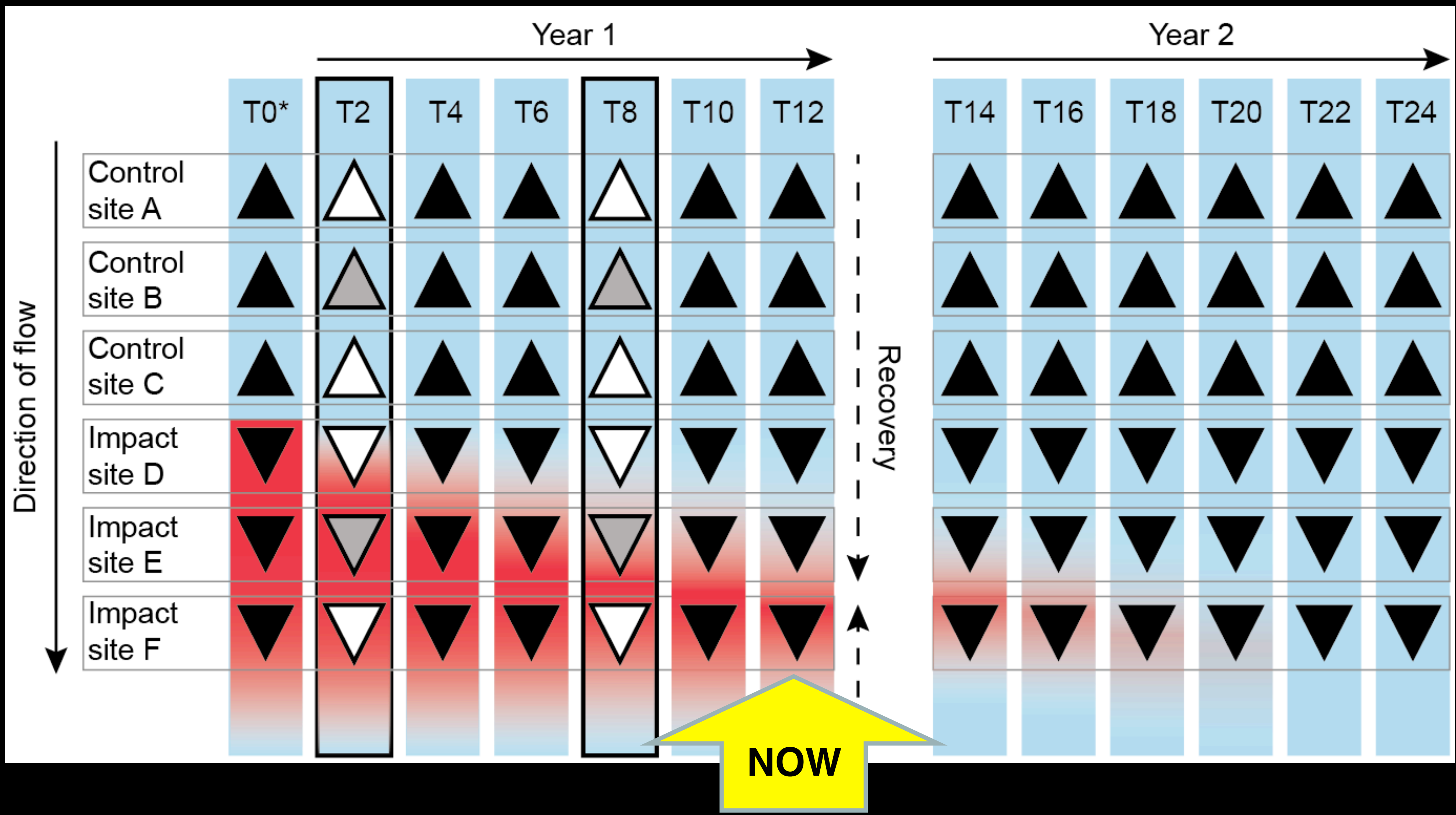
Pesticides as models for understanding targeted food web perturbations

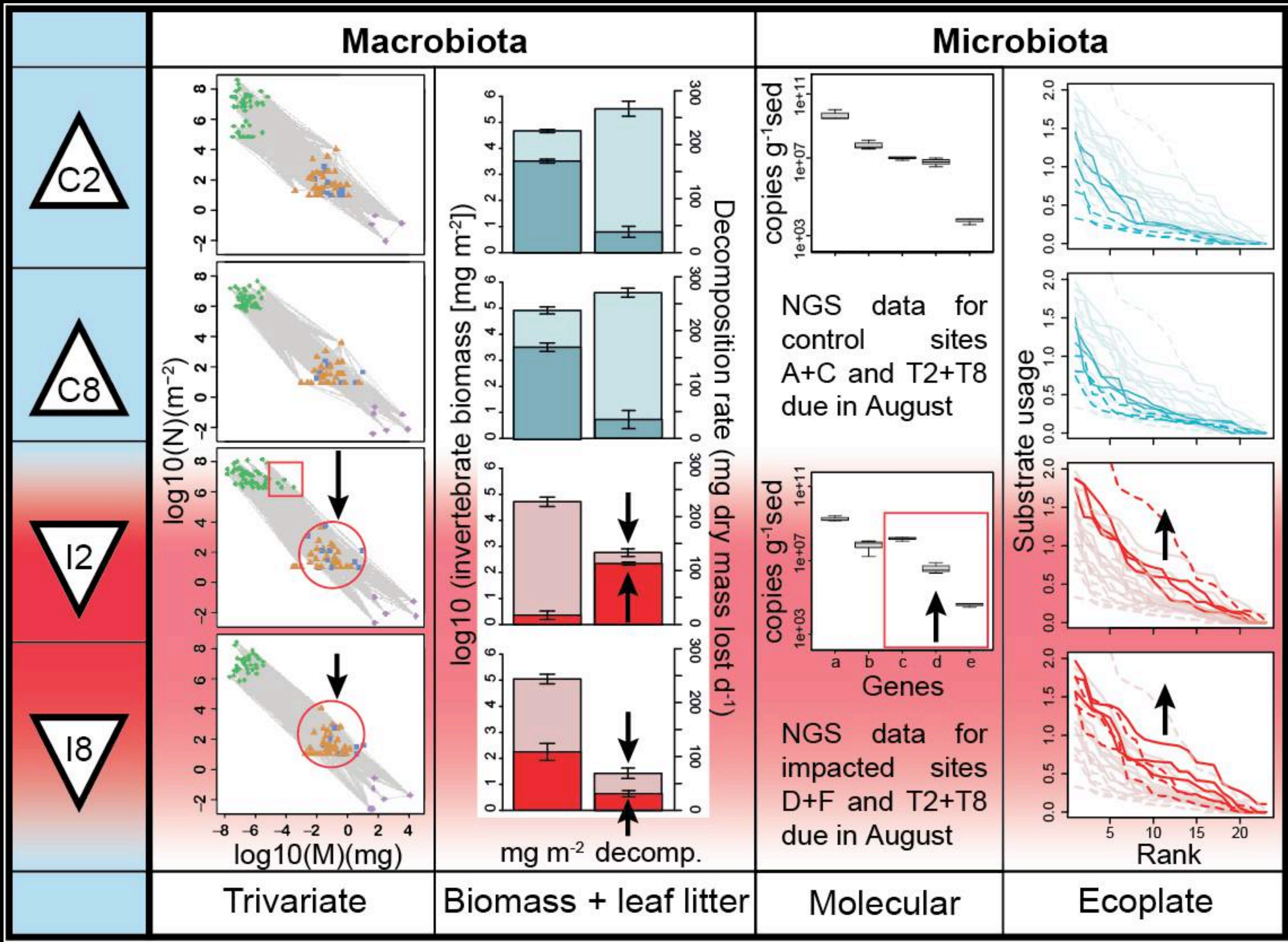


Linking across levels and scales in natural experiments – gene-to-ecosystem responses in the the River Kennet food web following a pesticide spill (2013)

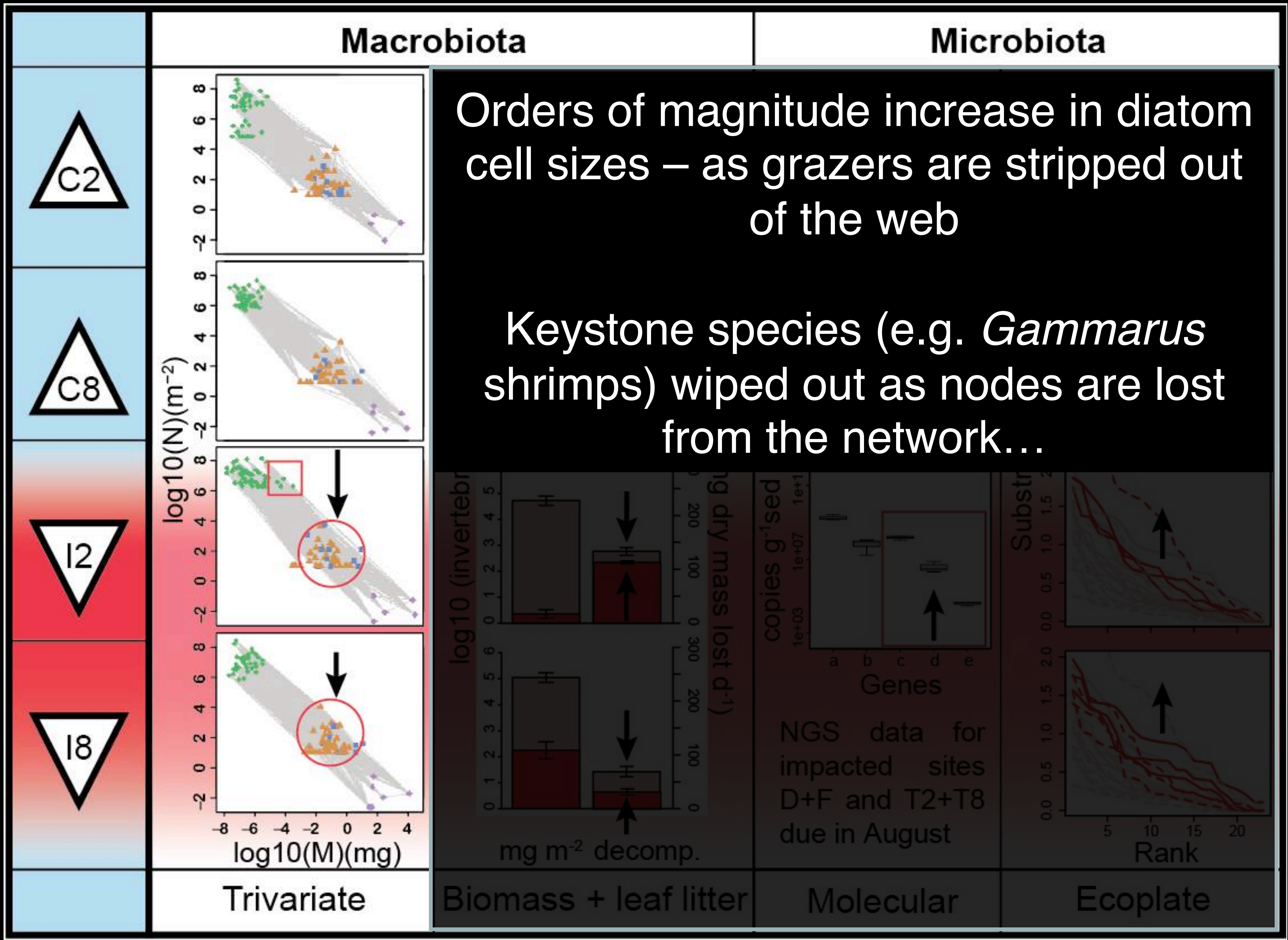


Tracking impact and recovery to quantify multilevel resilience

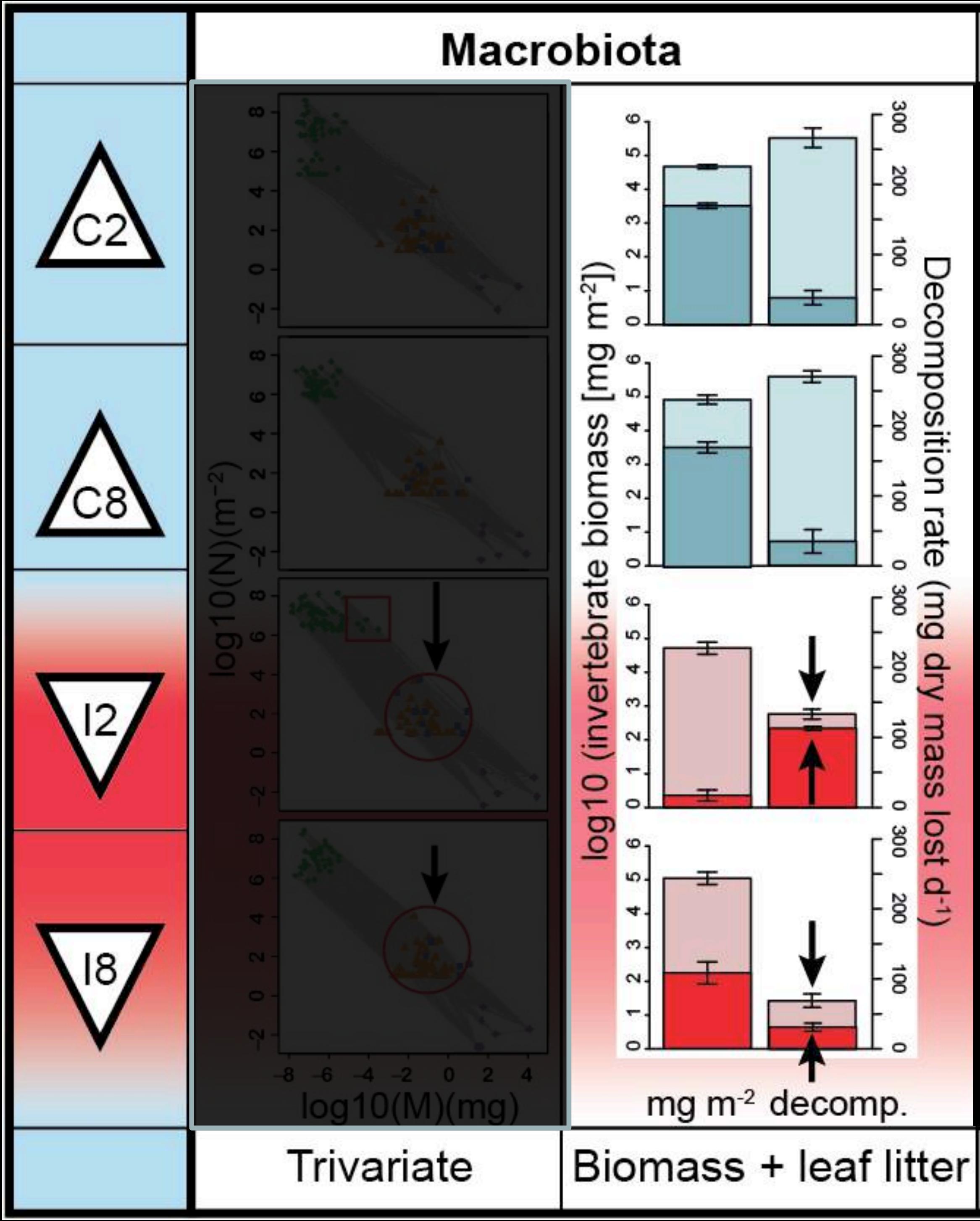




Macrobiota
Microbiota
C2
C8
I2
I8
log10(N)(m^-2)
log10(M)(mg)
log10 (invertebrate biomass [mg m^-2])
Decomposition rate (mg dry mass lost d^-1)
mg m^-2 decomp.
copies g^-1sed
Genes
NGS data for control sites A+C and T2+T8 due in August
NGS data for impacted sites D+F and T2+T8 due in August
Substrate usage
Rank
Trivariate
Biomass + leaf litter
Molecular
Ecoplate



Macrobiota
Microbiota
C2
C8
I2
I8
log10(N)(m^{-2})
log10(M)(mg)
Trivariate
Orders of magnitude increase in diatom cell sizes – as grazers are stripped out of the web
Keystone species (e.g. *Gammarus* shrimps) wiped out as nodes are lost from the network…
mg m^{-2} decomp.
Genes
NGS data for impacted sites D+F and T2+T8 due in August
Rank
Biomass + leaf litter
Molecular
Ecoplate



System shifts towards r-selection & key detritivores that dominate biomass are lost (e.g. *Gammarus* shrimps)……

Microbial processes dominate detrital processing….structure recovers faster than process – small *Gammarus* functionally less effective

The NERC BESS – Biodiversity & Ecosystem Services Sustainability – Research Programme

biodiversity & ecosystem service sustainability

Living With Environmental Change

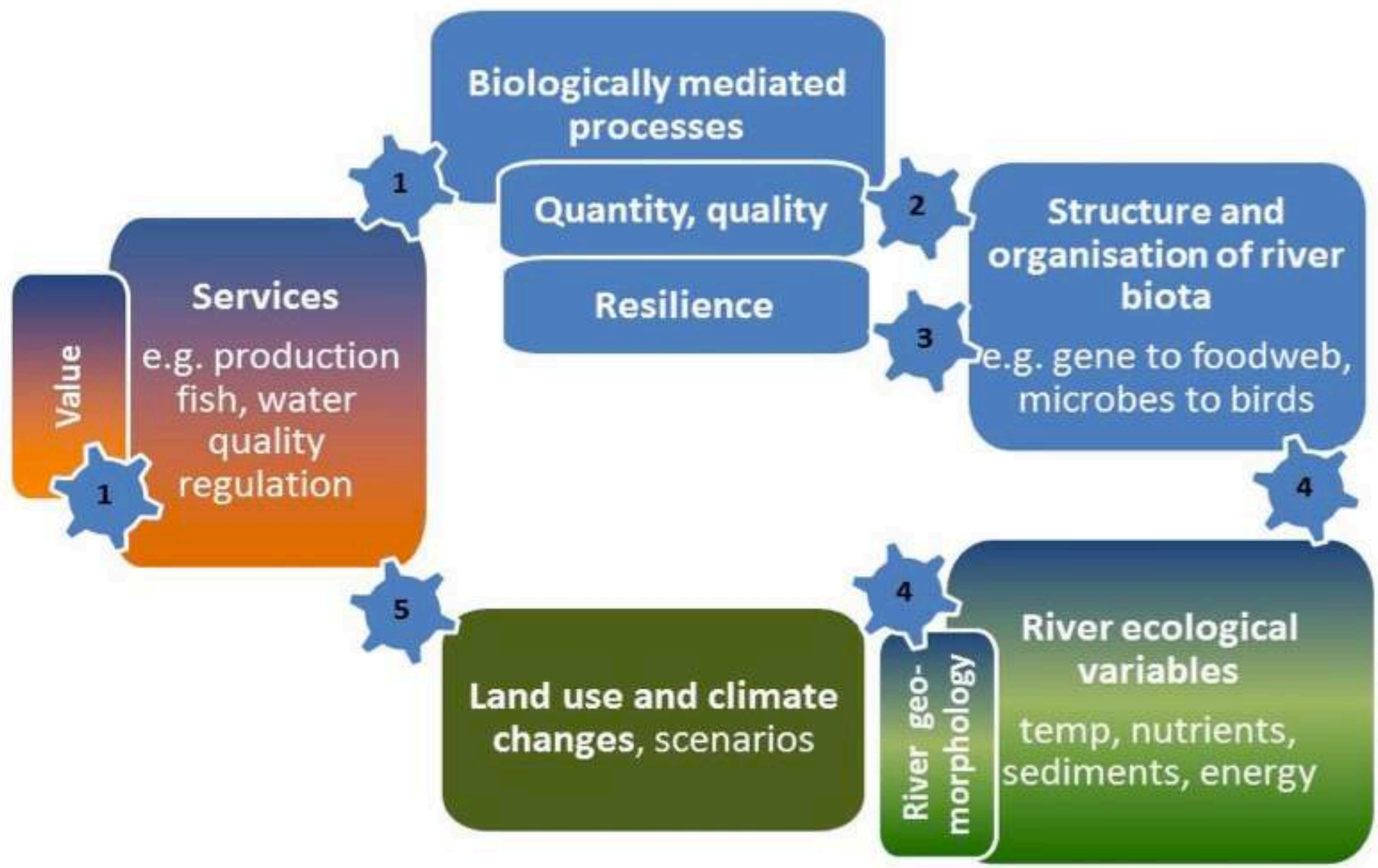
BBSRC bioscience for the future

NATURAL ENVIRONMENT RESEARCH COUNCIL

DURESS

Diversity in Upland Rivers for Ecosystem Service Sustainability

The NERC Duress Project (part of the BESS Programme)



The NERC Duress Project (£3.7m) - new biodiversity & ecosystem service resilience study in >400 upland streams…

EA catchments:
More than 400 catchments for which large scale data on invertebrates, fish, birds and land use are available for the past 20 years

Historical sites:
A set of 99 sites across upland Wales from which land use and historical invertebrate, fish and bird data are available. Used for resilience analysis

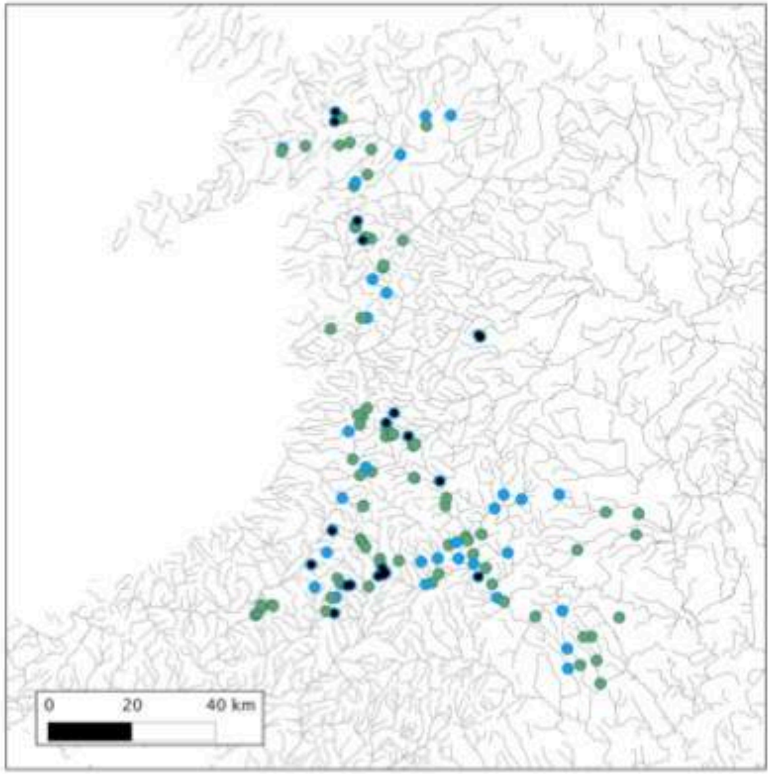
Extensive food web sites:
A subset of 50 sites across upland Wales along a gradient of water quality, land use, altitude where food web, fish and genetic analysis will take place

Intensive food web sites:
A subset of 20 sites where detailed food web and fish population analysis will be performed

Dynamic sites:
A subset of 8 sites to test the resilience of invertebrate and biofilm communities under different land uses

Experimental sites:
A subset of 6 replicate streams, 3 moorland streams and 3 conifer streams, to test the impact of N, C and litter addition

Duress
Diversity in Upland Rivers for Ecosystem Service Sustainability



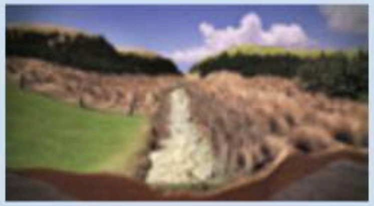
We are now starting to model alternate future scenarios…

The 4 alternate scenarios – from intensification to abandonment

From an analysis of drivers of change, and a review of historic changes in the uplands since World War 2, we have considered four possible scenarios to 2050:

Agricultural Intensification

Maximising food and fibre production becomes crucial to meet the challenges of food security and increasing global demand.



Managed Ecosystems

Ecosystem integrity is pro-actively enhanced to safeguard water, carbon and nature through either public funding of agri-environment schemes or because the market value of these services increases.

Business as Usual

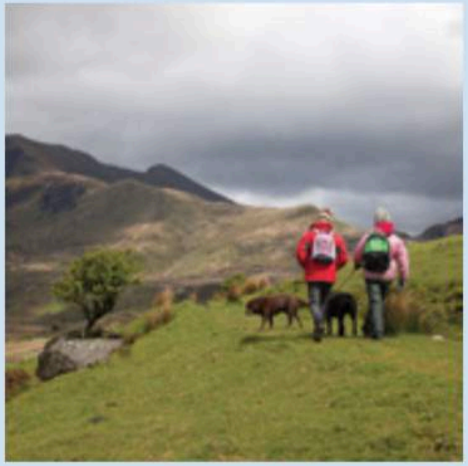
Publically funded agri-environment continues to deliver social benefits and ecosystem services.

Abandonment

Land becomes abandoned as a result of market or regulatory failure of the other three scenarios, leading to rapid decline in production and unmanaged development of quasi-natural habitats.

We can then start to model likely impacts of these alternate futures on ecoservices

Food



Biodiversity and Cultural Value

Fibre

Carbon Sequestration and Water

These "options" will be presented to the general populace and political bodies

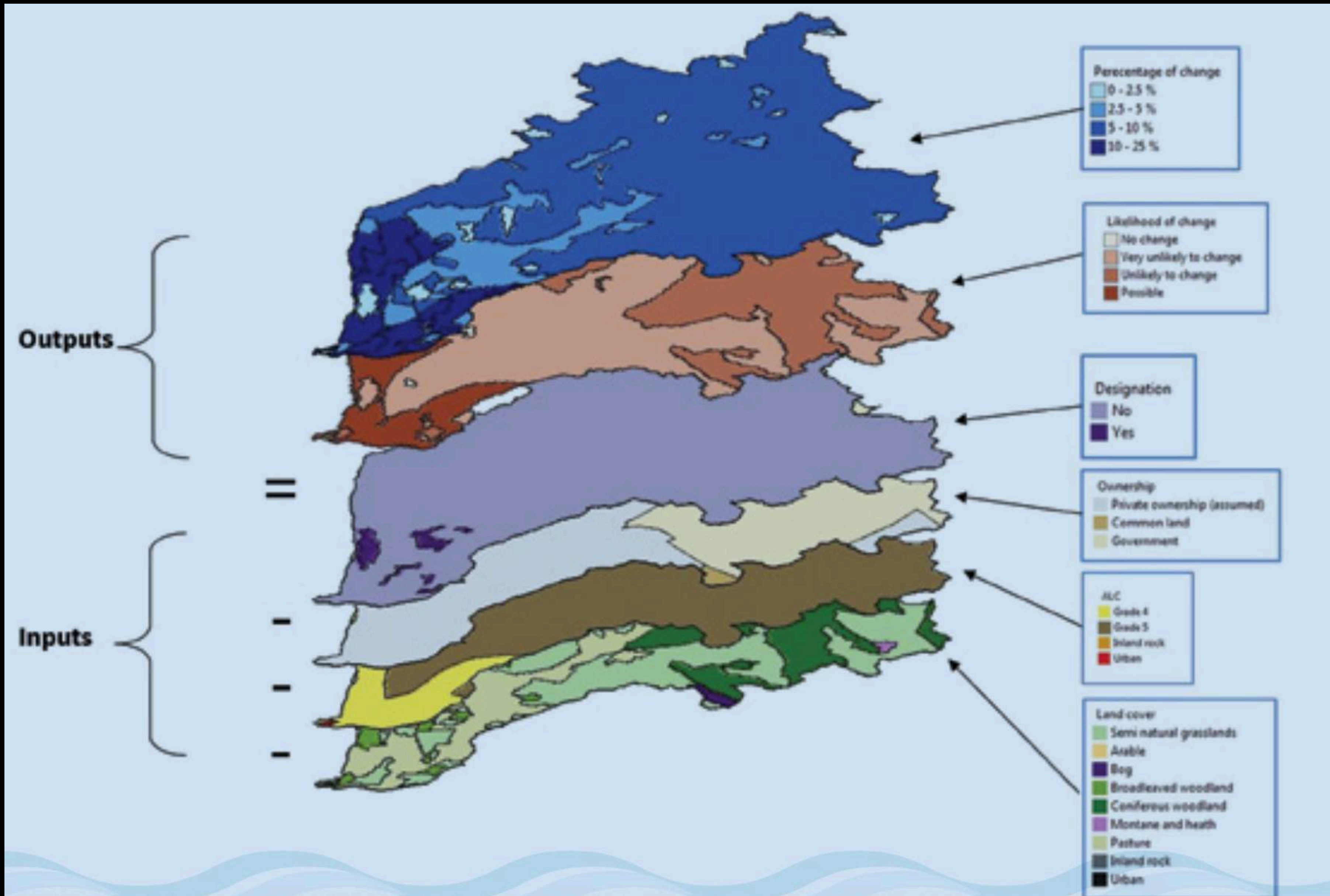
Scenario A: Agricultural intensification in the uplands

Scenario B: Managed ecosystems

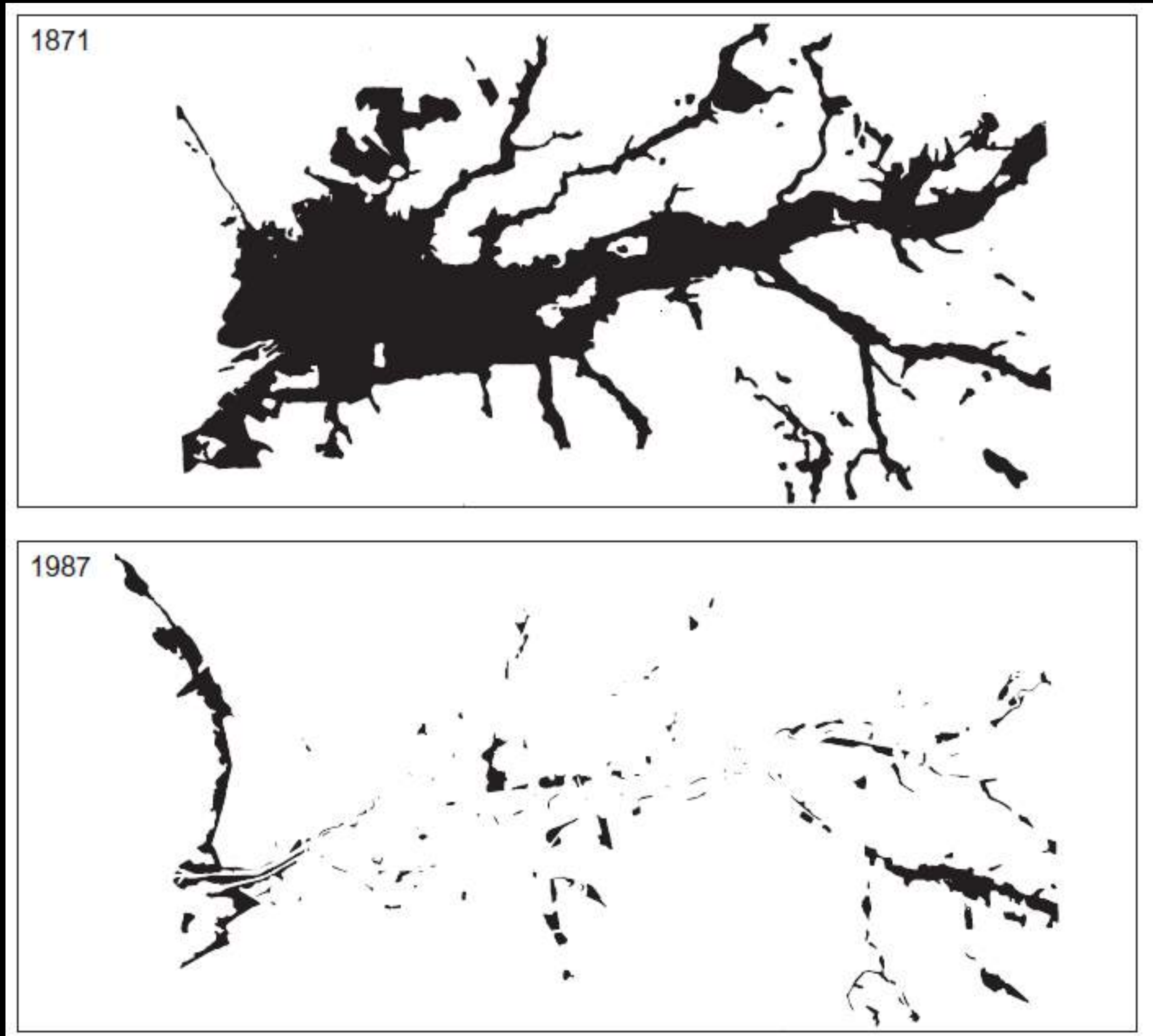
Scenario C: Business-as-usual

Scenario D: Abandonment

Connecting ecoservices to policy – a multilayered, spatially explicit modelling approach



Drought will amplify the effects of historic anthropogenic fragmentation of freshwaters



New stream mesocosm facilities under construction….and robots for new high-throughput B(M)EF experiments

The 96-well-plate approach….new facility at Imperial

Summing up...thanks for listening

Freshwater ecosystems:

1. Size-structured food webs
2. Highly dynamic - impacts are expressed rapidly
3. Communities are predictable in space-for-time surveys...*BUT* recovery is not simply reversal of response to impacts
4. Top-down effects, hystereses and “inertia” in the food web
5. Ecosystem processes are highly resilient to species loss or turnover - high redundancy....
6. Need for longer-term, larger-scale , whole-system and translocation experiments....especially to disentangle transient and equilibrial responses