



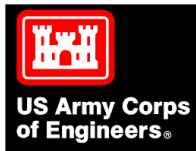
Fast, slow, short, long, green, and brown

The importance of spatial resource subsidies and drying for food webs in semi-arid riverscapes

Dr. Weston Nowlin

Department of Biology

Texas State University

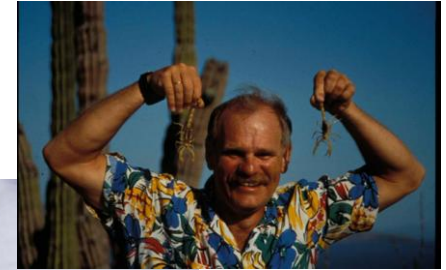


Ecosystems are “open”

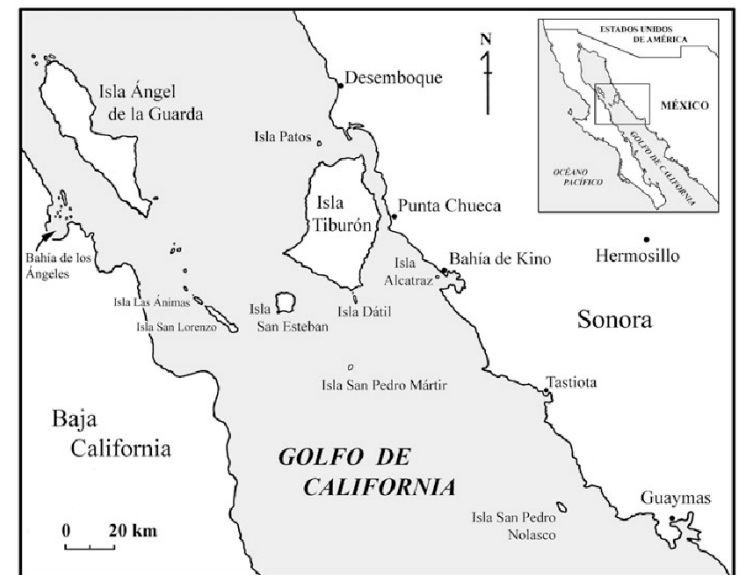


# Spatial Subsidies

- Movement of nutrients, energy, or organisms from one area to another
  - Enhance local productivity
  - Cross-boundary subsidies



- Allochthonous
  - Originate from outside
- Autochthonous
  - Originate from within



# Modeling Allochthonous Subsidies

## Rosenzweig. 1971

### Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time

Abstract. Six reasonable models of trophic exploitation in a two-species ecosystem whose exploiters compete only by depleting each other's resource supply are presented. In each case, increasing the supply of limiting nutrients or energy tends to destroy the steady state. Thus man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance.

Schemes for increasing primary productivity by enriching an ecosystem's energy or nutrient flow are much in evidence today and are probably a reflection of the increasing demands of the world's population. Such schemes may end in catastrophe.

In 1963, Huffaker, Shea, and Her-

29 JANUARY 1971

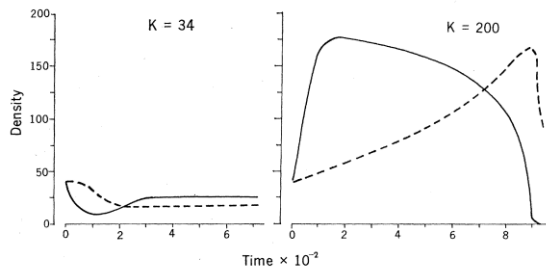


Fig. 2. Iteration of the model 4 exploitation at  $K=34$  and  $K=200$ . Solid curve is  $V$ ; dashed curve is  $P$ . Enrichment causes the simulated extinction of both species. The exploiter equation used was  $dP/dt = AKP(e^{-eV} - e^{-eV})$ . Time units are in calculator cycles (10).

## Loss of stability

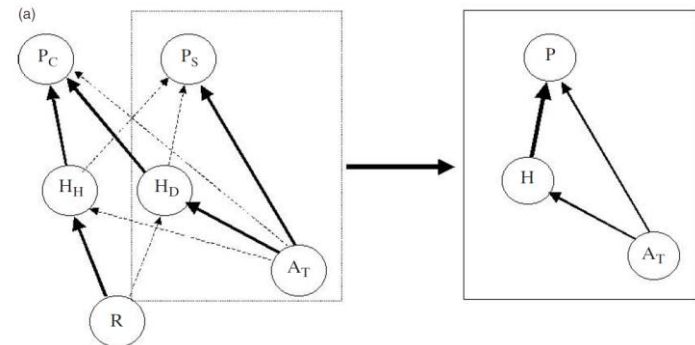
## Huxel, McCann and others

*Ecological Research* (2002) 17, 419–432

### Effects of partitioning allochthonous and autochthonous resources on food web stability

GARY R. HUXEL,\* KEVIN MCCANN† AND GARY A. POLIS

*Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA*



## Increase stability

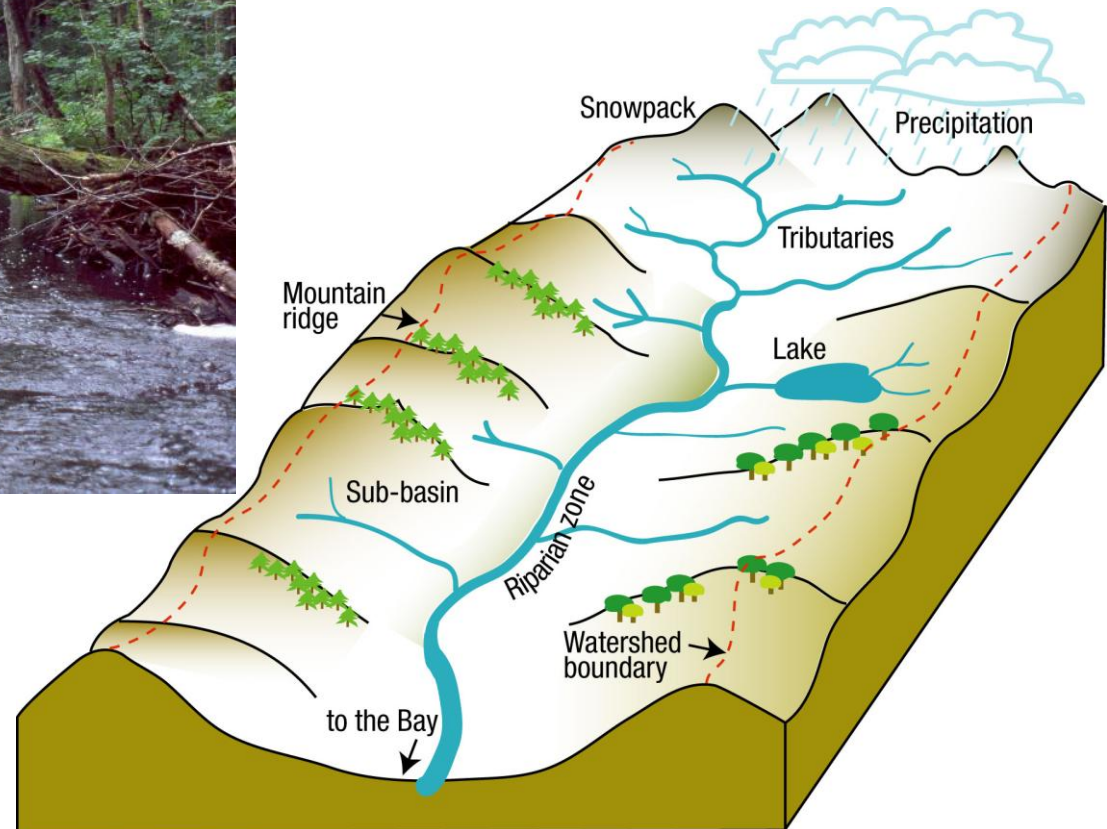
- Food web structure
- Magnitude of inputs
- Link strengths

# Lotic Ecosystems and Allochthony

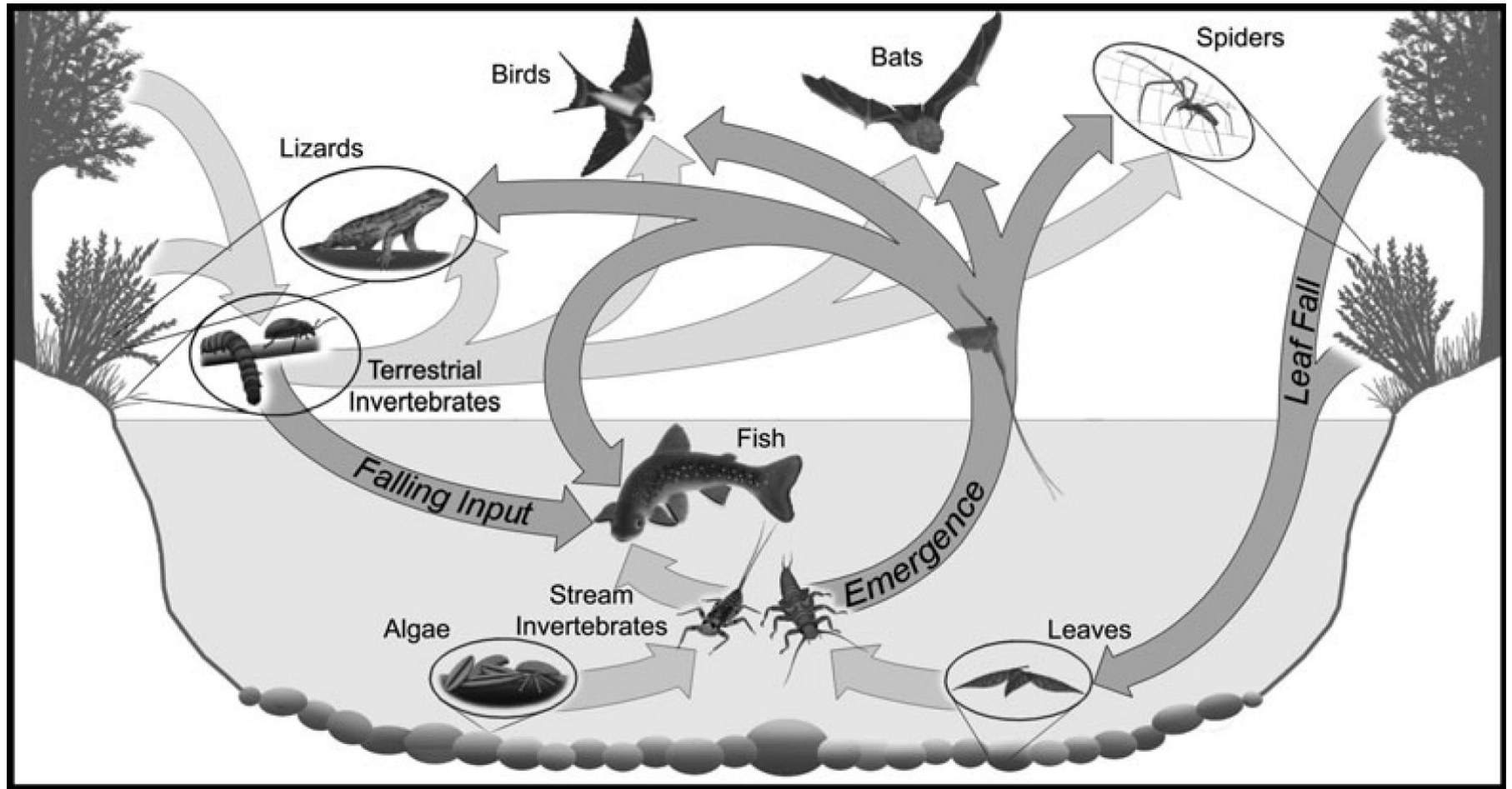
## Local Scale: Stream – Riparian



## Watershed Scale

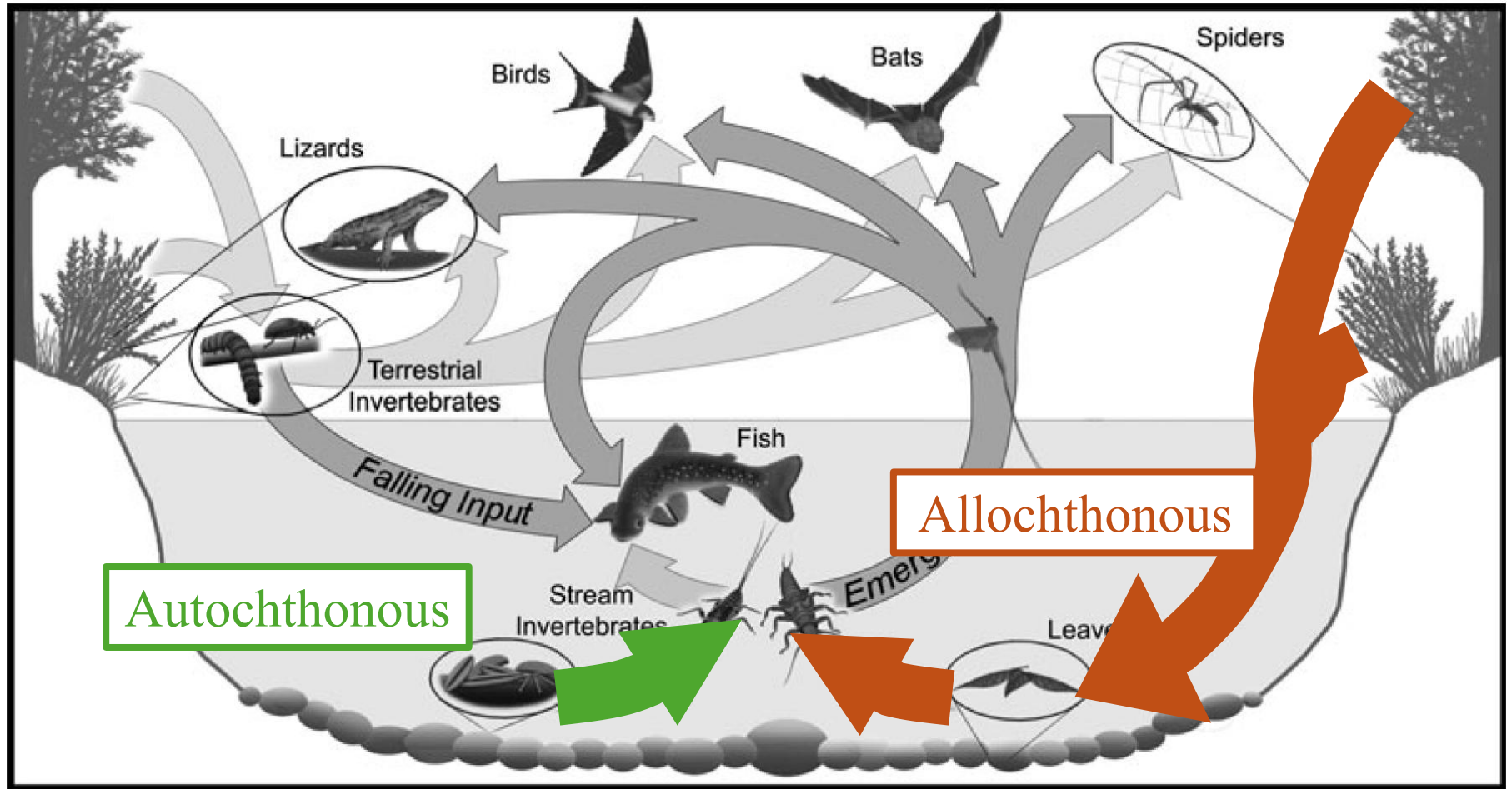


# “Tangled Web” Meta-ecosystem



**Fig. 1** A generalised diagram showing reciprocal flows of invertebrate prey and inputs of plant material (dark arrows) that have direct and indirect effects in stream and riparian food webs.

# “Tangled Web” Meta-ecosystem



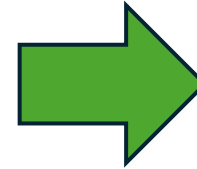
**Fig. 1** A generalised diagram showing reciprocal flows of invertebrate prey and inputs of plant material (dark arrows) that have direct and indirect effects in stream and riparian food webs.

# “Green” versus “Brown”

- Differences in quality, lability, speed, and efficiency

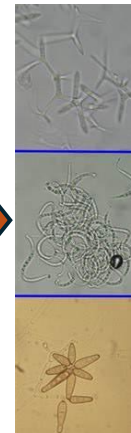
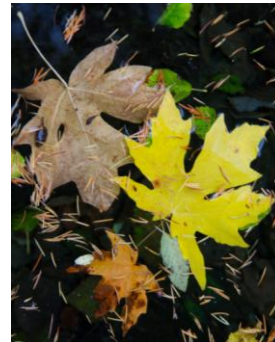
- **Autochthonous sources**

- Algae – Grazer
- Higher quality
- Greater efficiency
- Faster responses



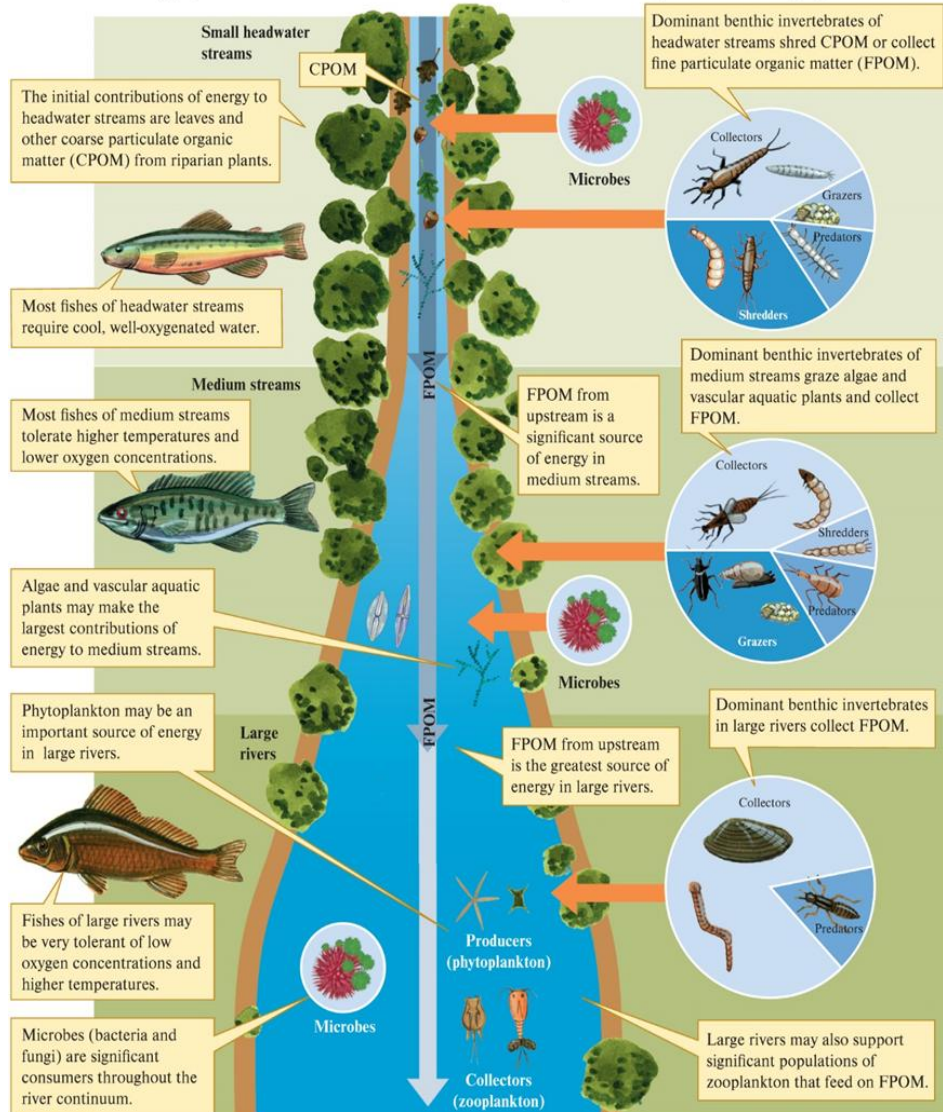
- **Allochthonous sources**

- Detritus – Decomposer
- Microbial alteration
  - Litter – Microbes - Shredders
- Lower quality
- Lower efficiency
- Slower responses



# Allochthony in Conceptual Models

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- River Continuum Concept
  - Vannote (1980)
- Allochthonous sources
  - Shredders (CPOM – FPOM)
- Autochthonous sources
  - Collectors (FPOM) and Grazers
- Geographic bias
  - Temperate zone
- Hydrology
  - Perennial flows

# Importance of Allochthony in Other Settings?



- Conceptual models informed by temperate (and tropical) ecosystems



- Arid and semi-arid (sub-humid) contexts?

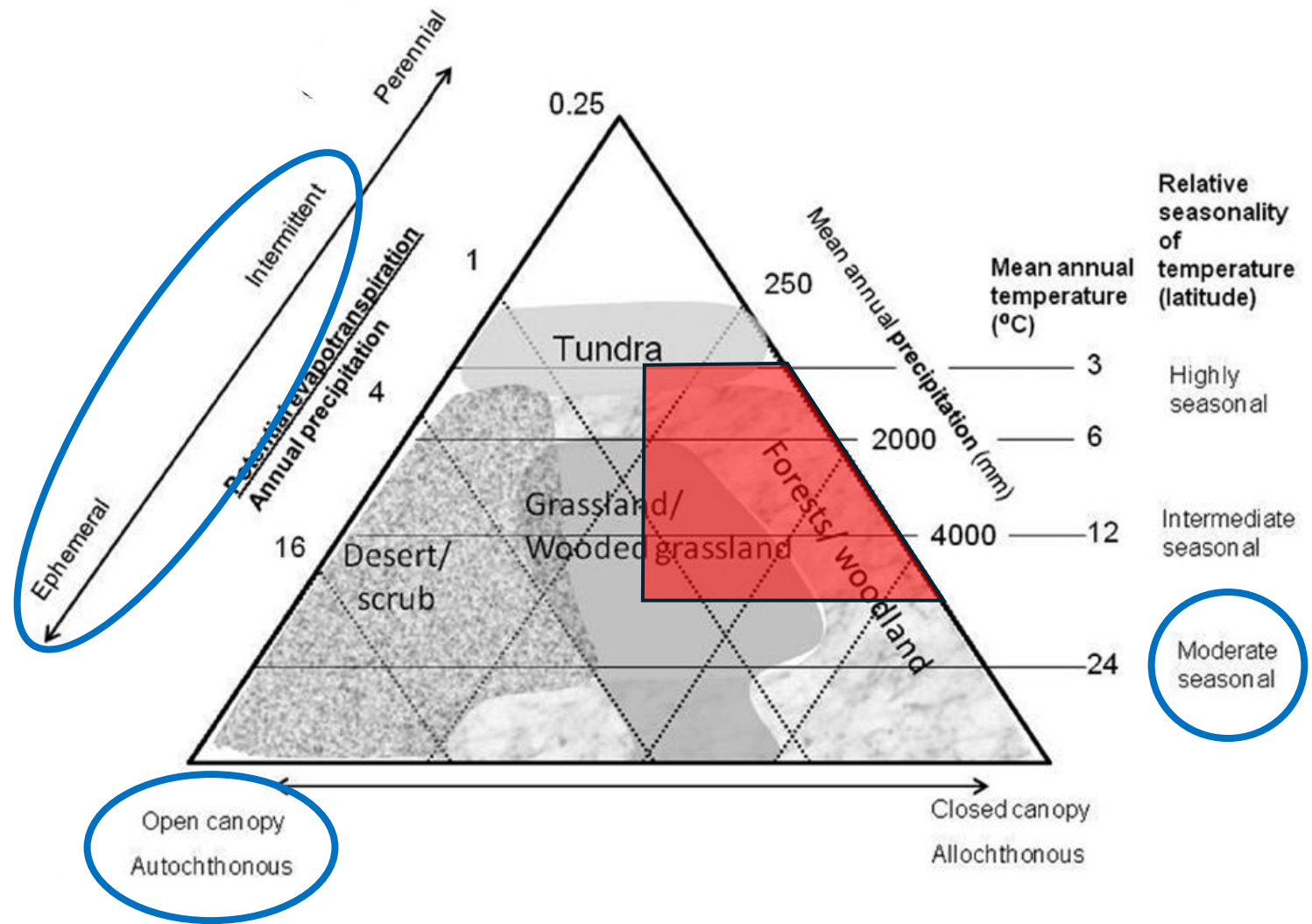
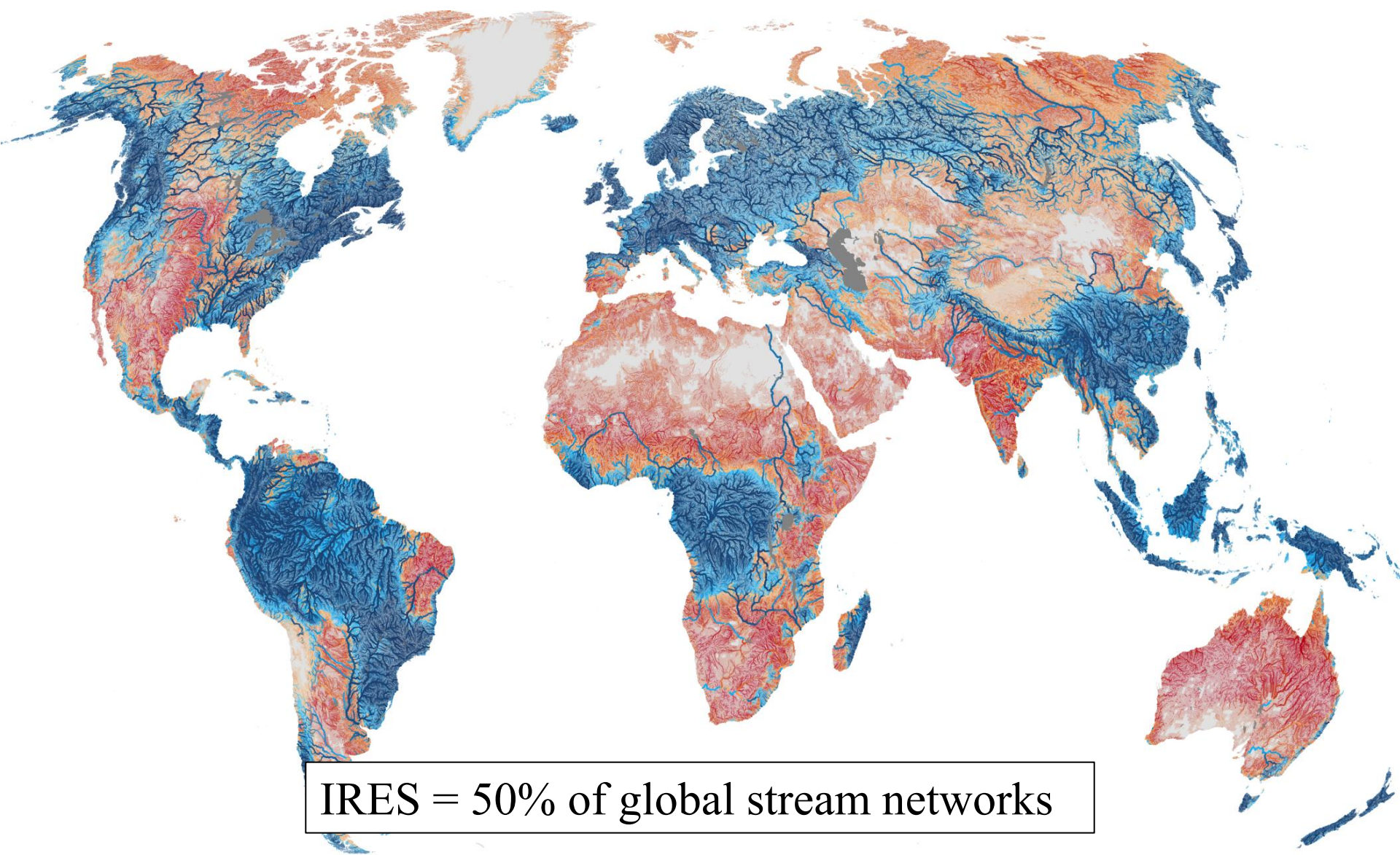


Figure 1. Climate zones, vegetation types, and relationship to stream characteristics (modified from Holdridge 1947).

Modified from Dodds et al. (2015). *Freshwater Science*

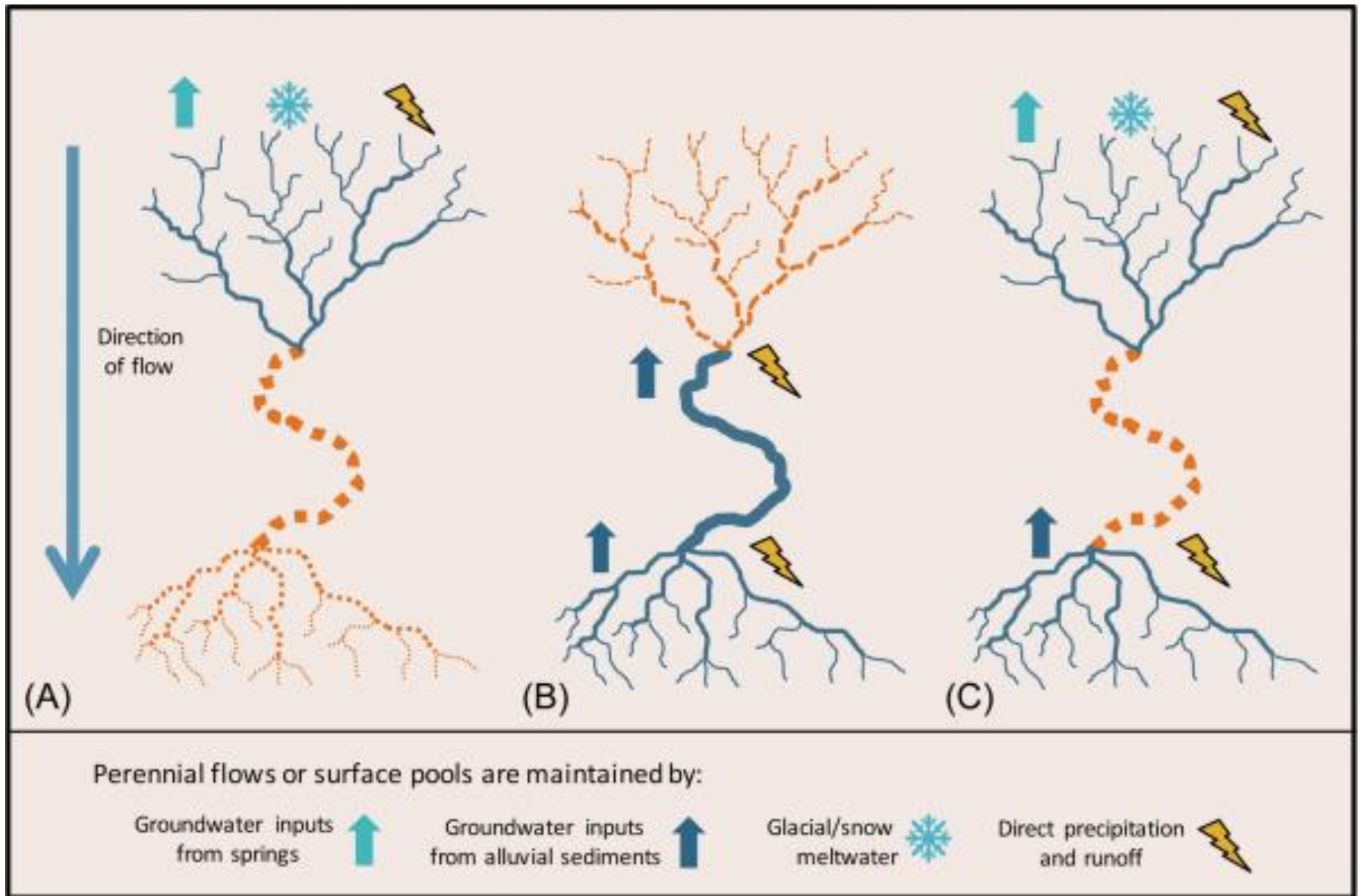


IRES = 50% of global stream networks

Mean annual discharge  
(line width and transparency)  
 $10^{-1}$   $10^0$   $10^1$   $10^2$   $10^3$   $10^4$   $\text{m}^3 \text{s}^{-1}$

Probability of flow intermittence  
Non-perennial 1.00 0.75 0.50 0.25 0 Perennial

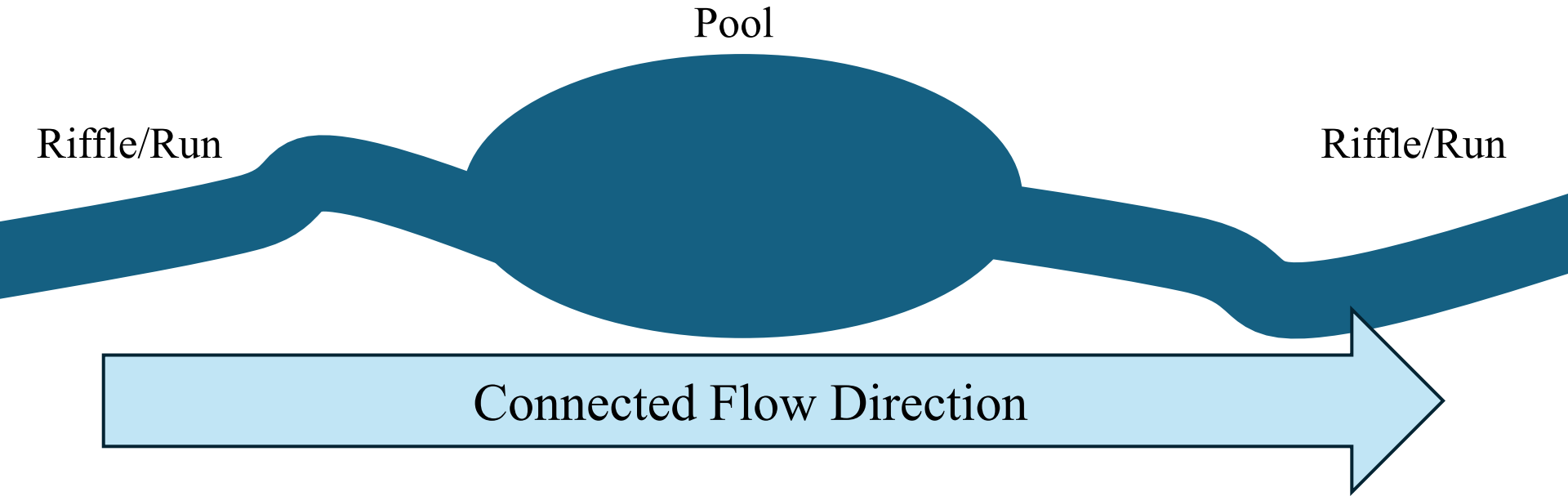
■ Lake or reservoir  
■ No flow



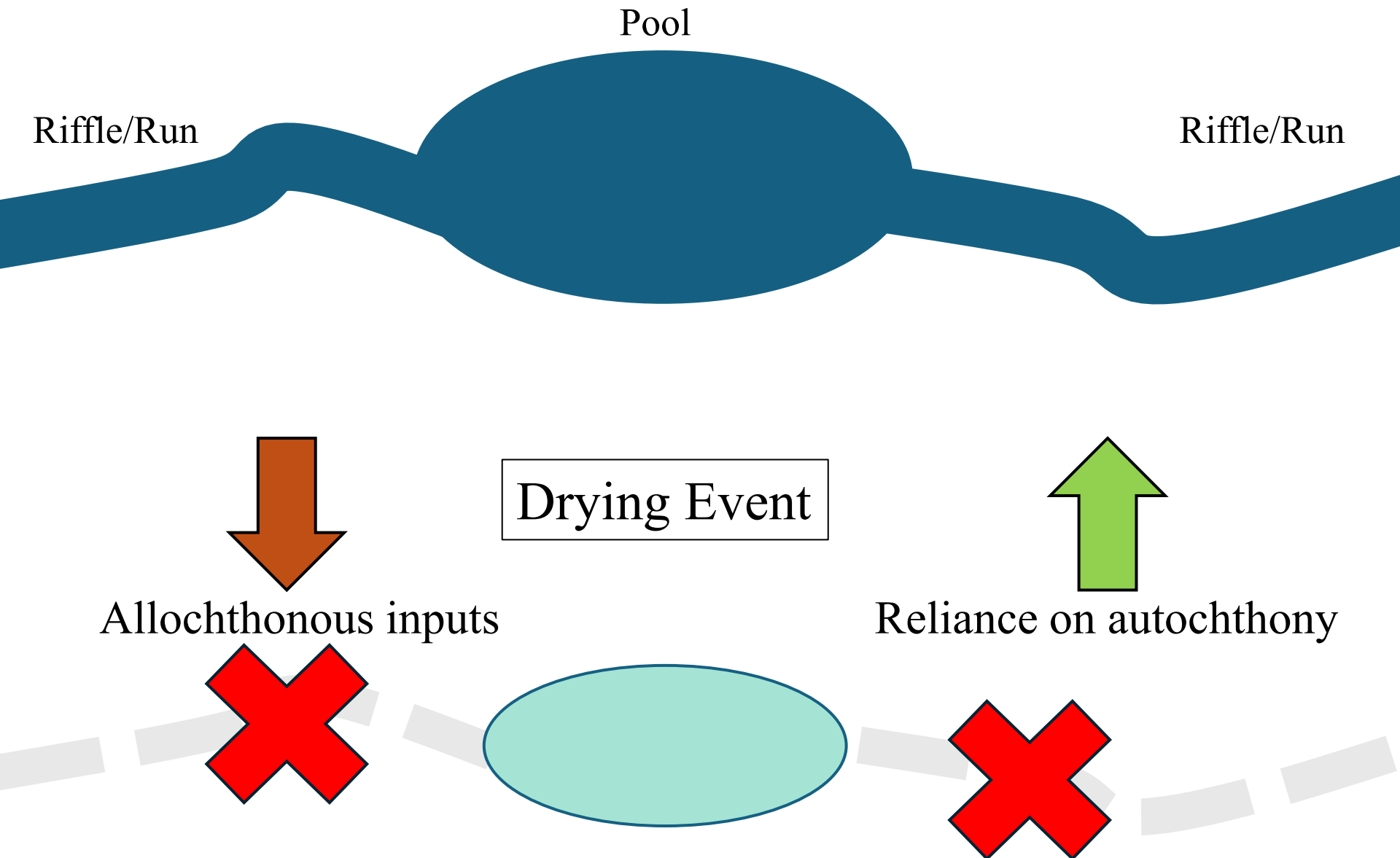
Boulton et al. (2017)

*In: Intermittent Rivers and Ephemeral Streams: Ecology and Management*

# Disconnection and Allochthony

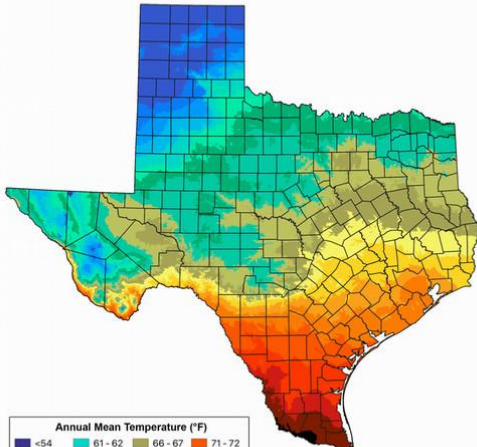


# Disconnection and Allochthony



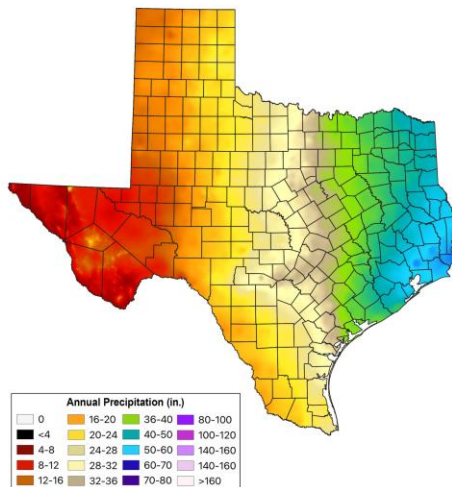
# Allochthony and Semi-Arid Rivers

30-yr Normal Temperature: Annual  
Period: 1991-2020



- Role of decreased seasonal variation?
  - Regional rivers = Semi-arid

30-yr Normal Precipitation: Annual  
Period: 1991-2020



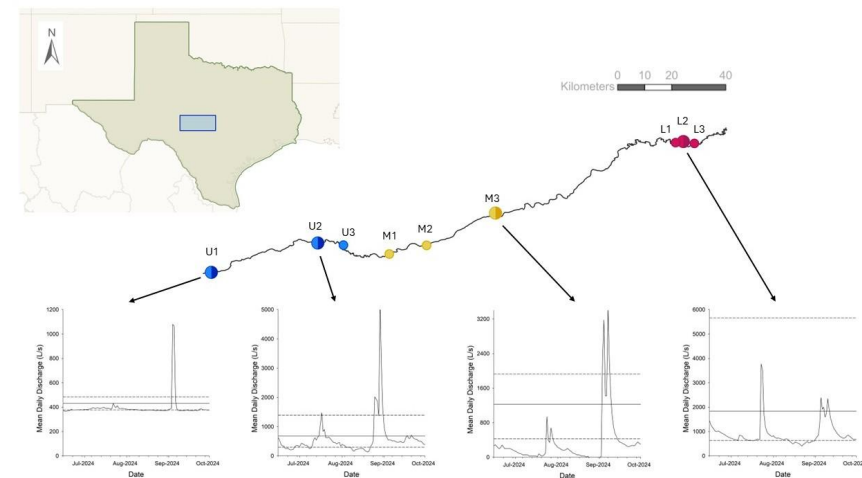
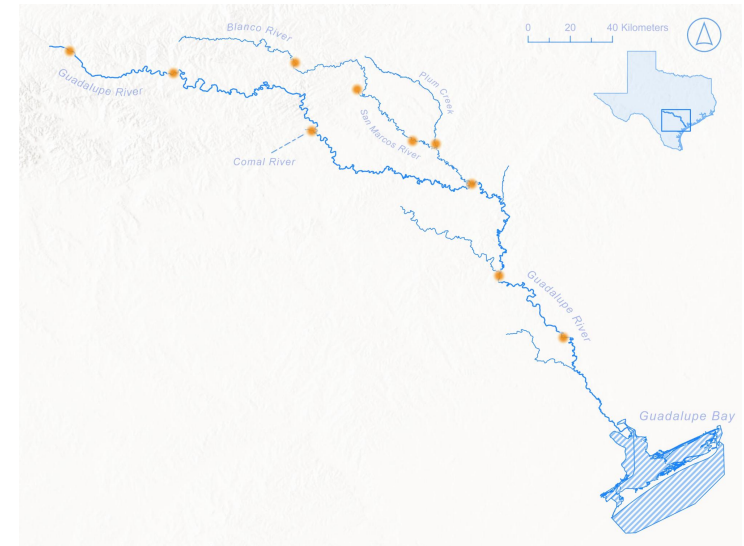
- Role of flow intermittency?
  - Spatiotemporal variation in flow loss

# Main Questions for Today

- What is the importance of allochthonous resources in lower latitude semi-arid rivers?
  - Are allochthonous resources important in two semi-arid rivers?
  - Does the importance of allochthonous resources vary over space and time?
- What is the role of intermittency in determining the influences of allochthonous resources on riverine communities?

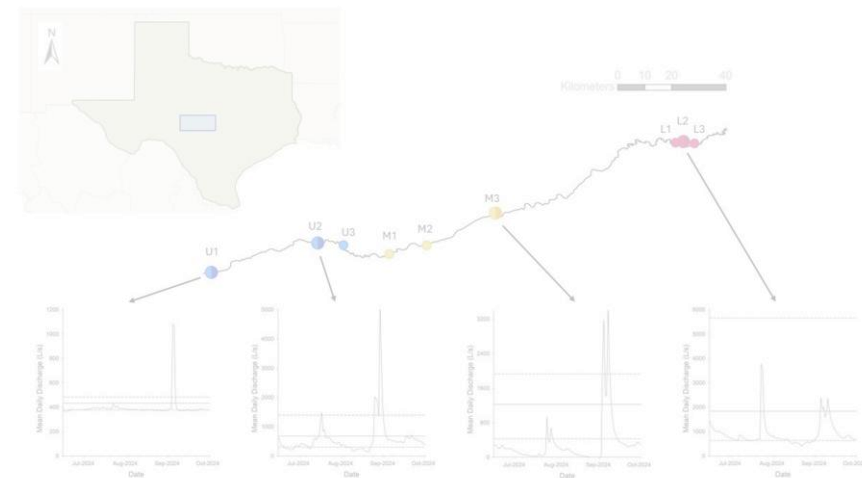
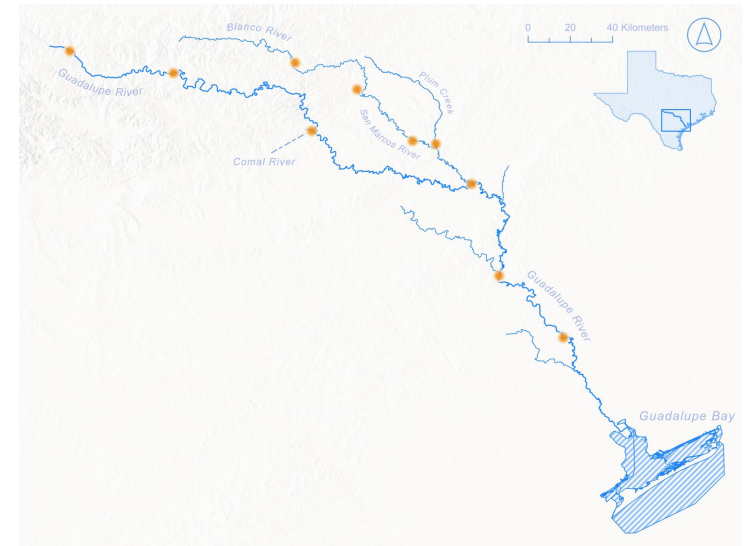
# Two Studies on the Menu

- Seasonal dynamics of terrestrial leaf litter decomposition across a flow and environmental gradient within a single drainage basin
  - Importance of seasonality (phenology), environmental conditions, and intermittency
  
- Effects of spatial (longitudinal) variation in intermittency on the importance of allochthonous *versus* autochthonous resources and food chain length in a river



# Two Studies on the Menu

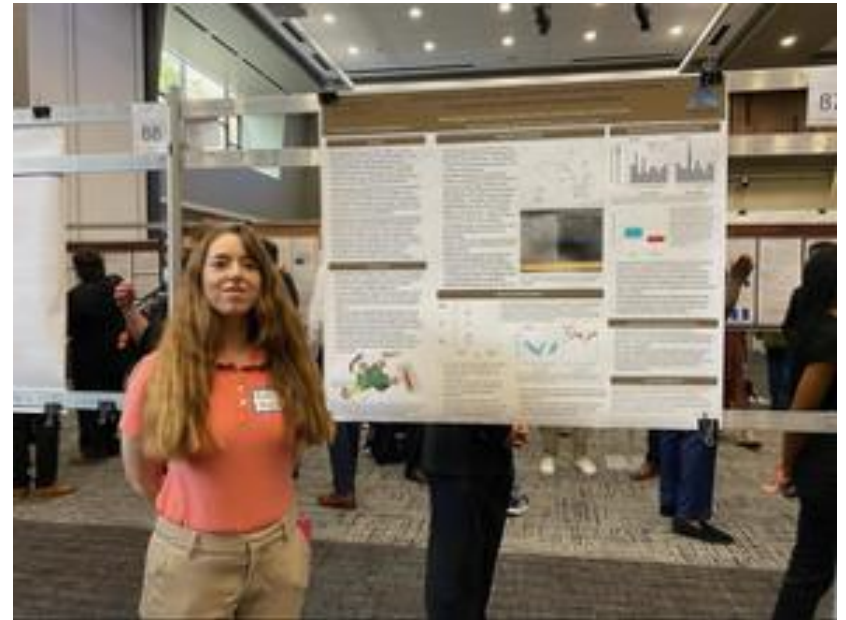
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# Acknowledgements



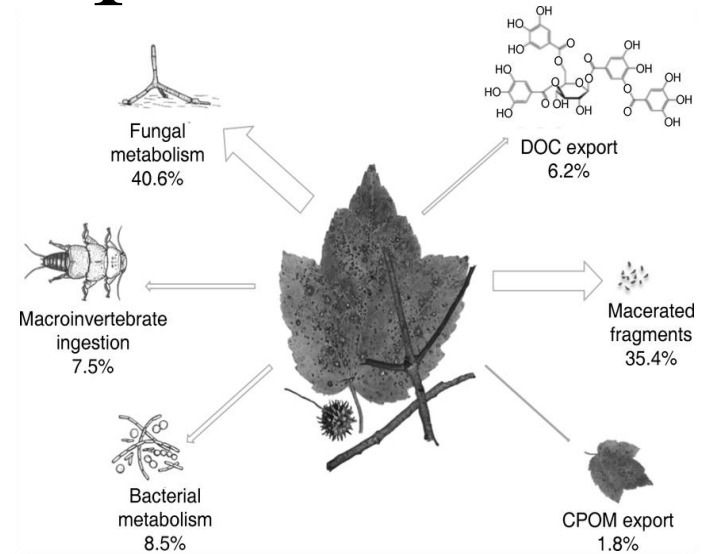
Dr. Tonya Ramey



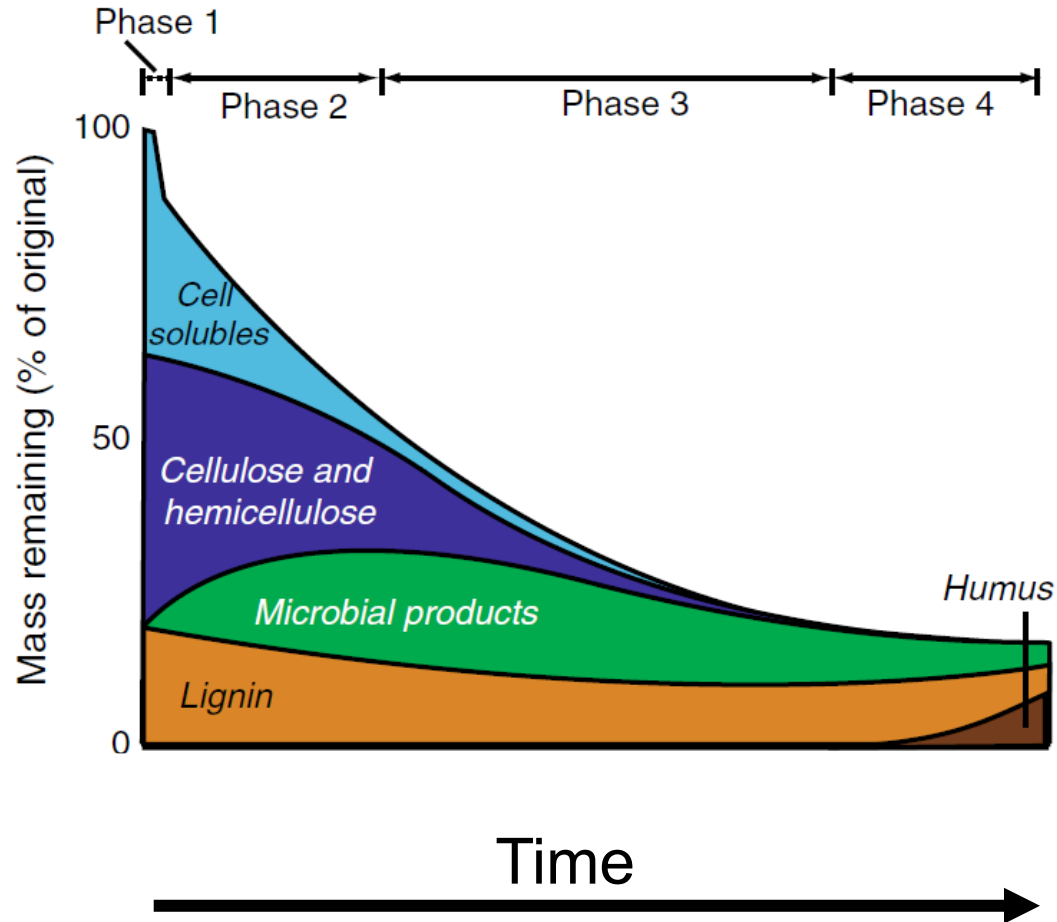
Hannah Madler

# Why Leaf Litter Decomposition?

- OM decomposition is a central ecosystem function
  - Responds to changing environmental conditions
  - C cycling
- Terrestrial litter is a major basal allochthonous resource input
  - Microbial communities and benthic invertebrates
- Microbes use litter as *energy source*
- Invertebrates use “conditioned” litter as *energy source*
  - Flow refuge, attachment, predation refuge



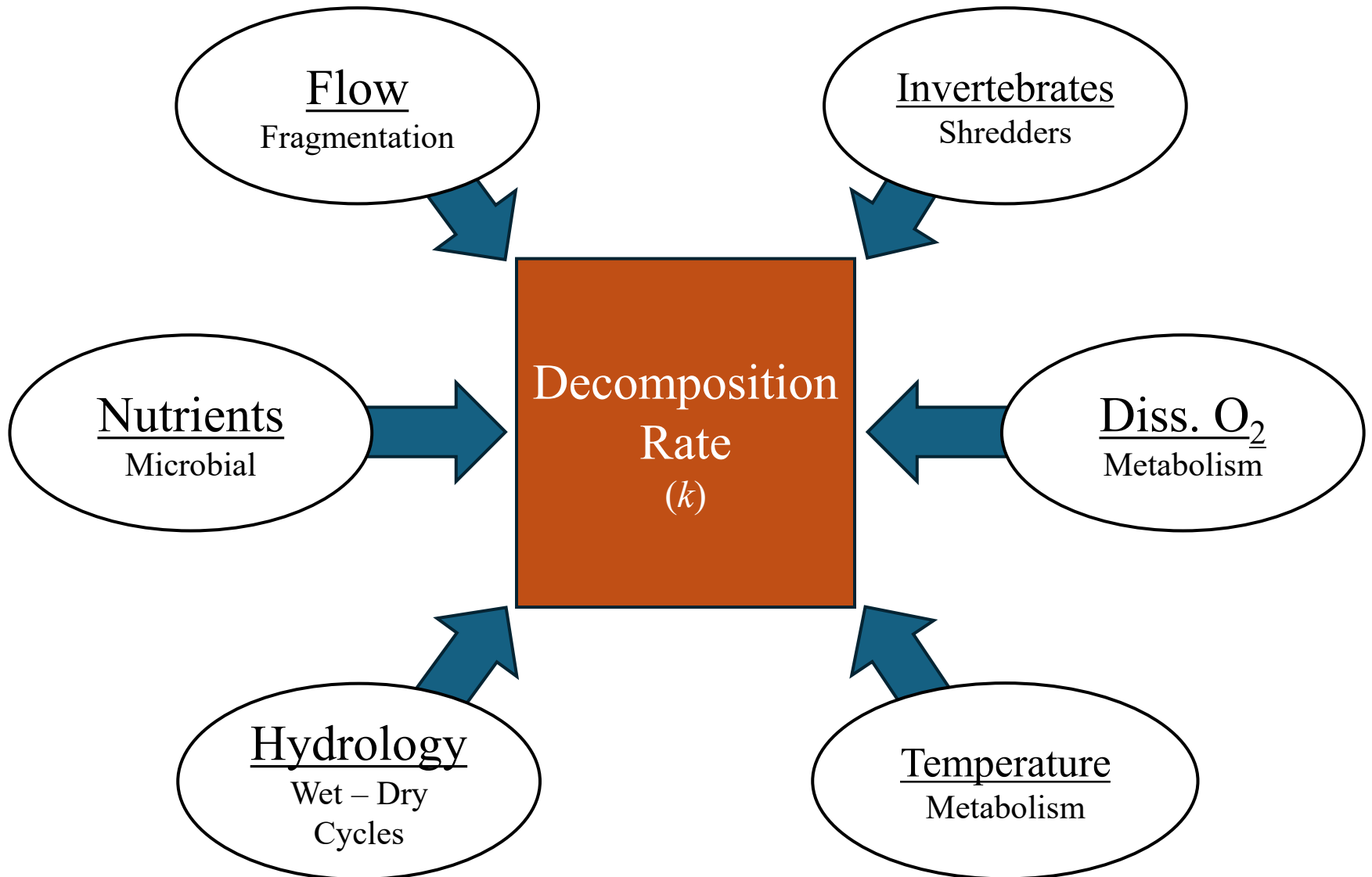
# Factors Affecting Decomposition



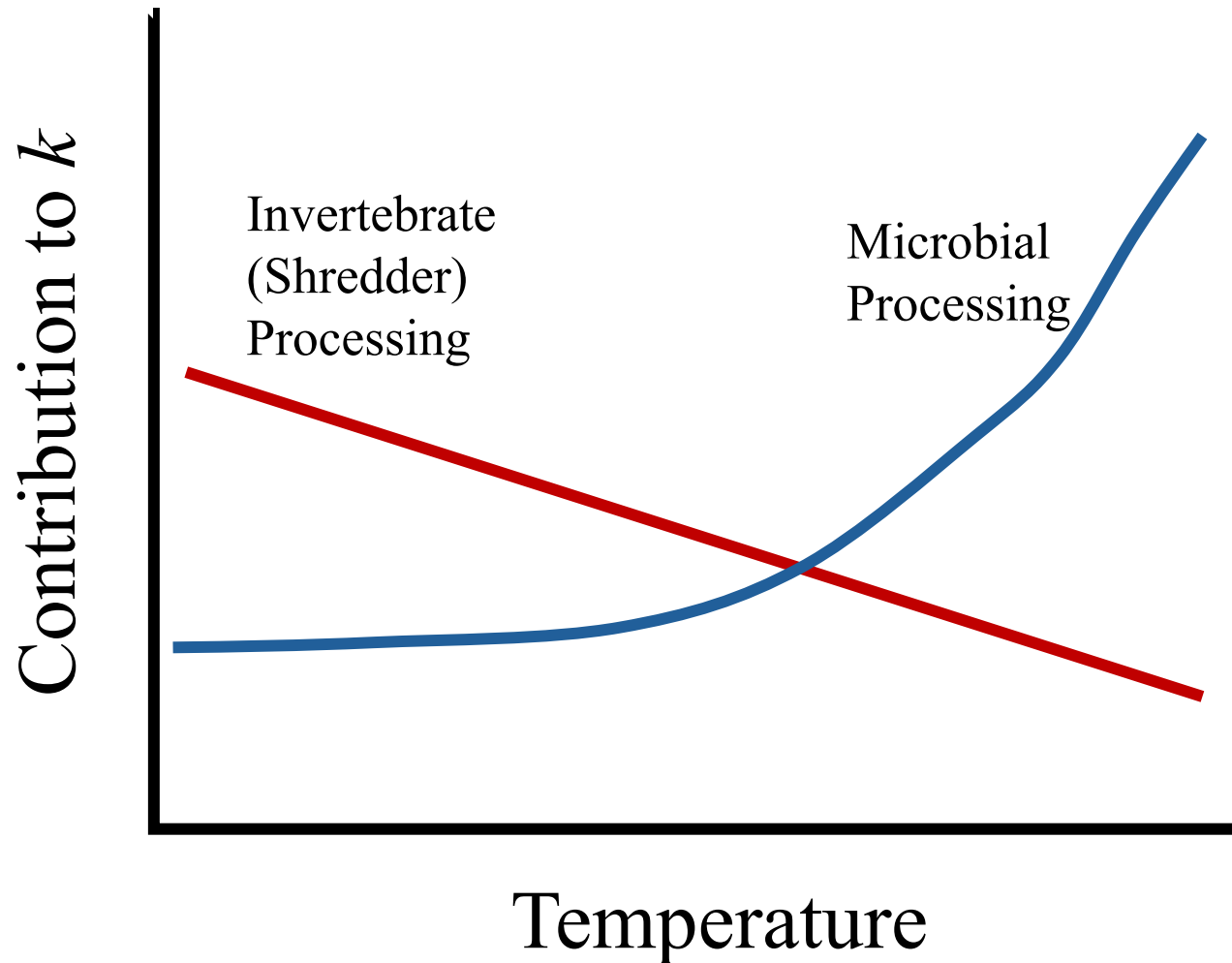
Modified from:

Chapin et al. (2011). *Principles of Terrestrial Ecosystem Ecology*, 2<sup>nd</sup> Edition

# Decomposition – Extrinsic Factors



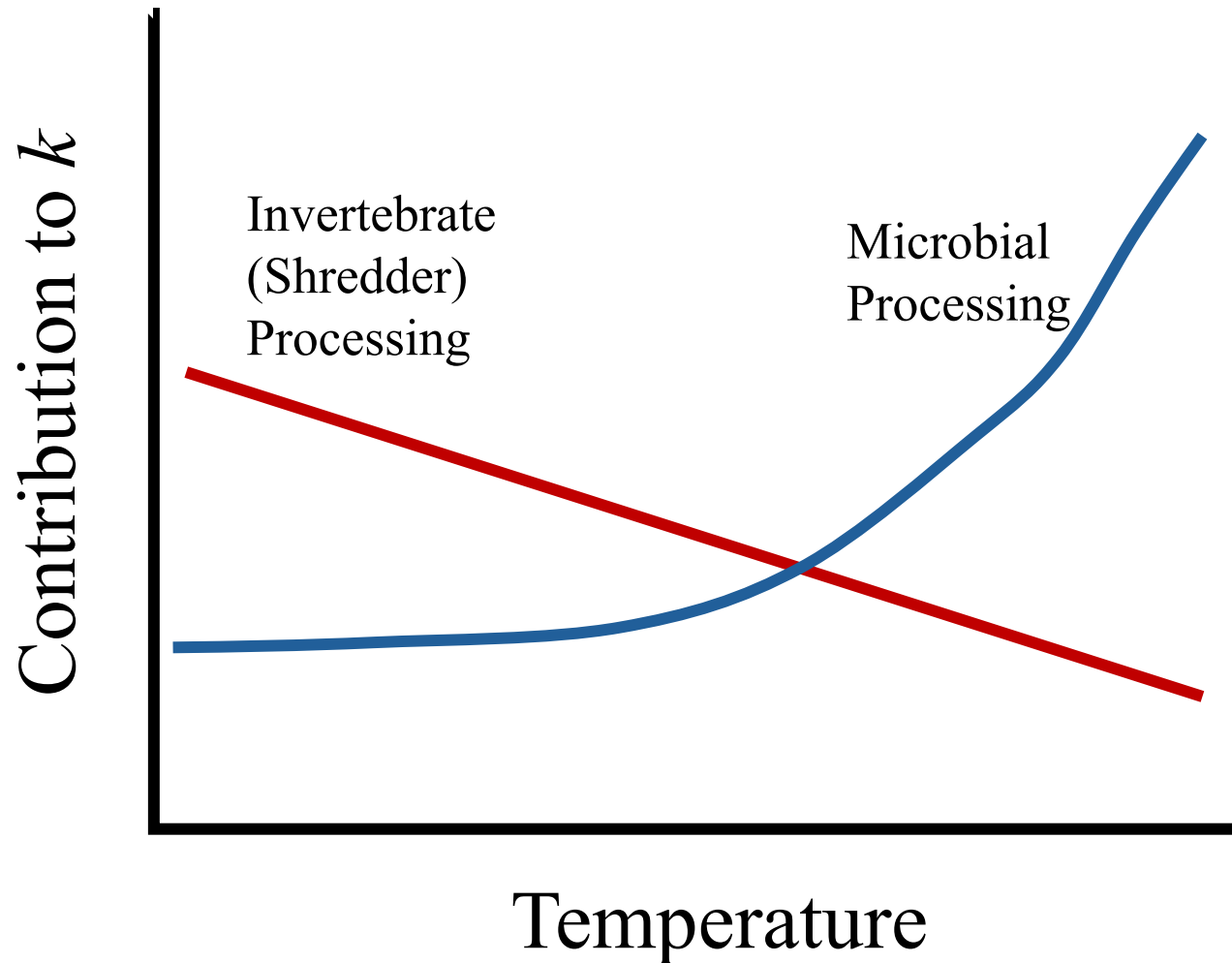
# Invertebrates *versus* Microbes



## Rationale

- Microbial metabolism more sensitive to temperature than invertebrates
- Lower densities of shredding insects
  - Biogeography
  - Diversity of shredders highest in cold water systems

# Invertebrates *versus* Microbes

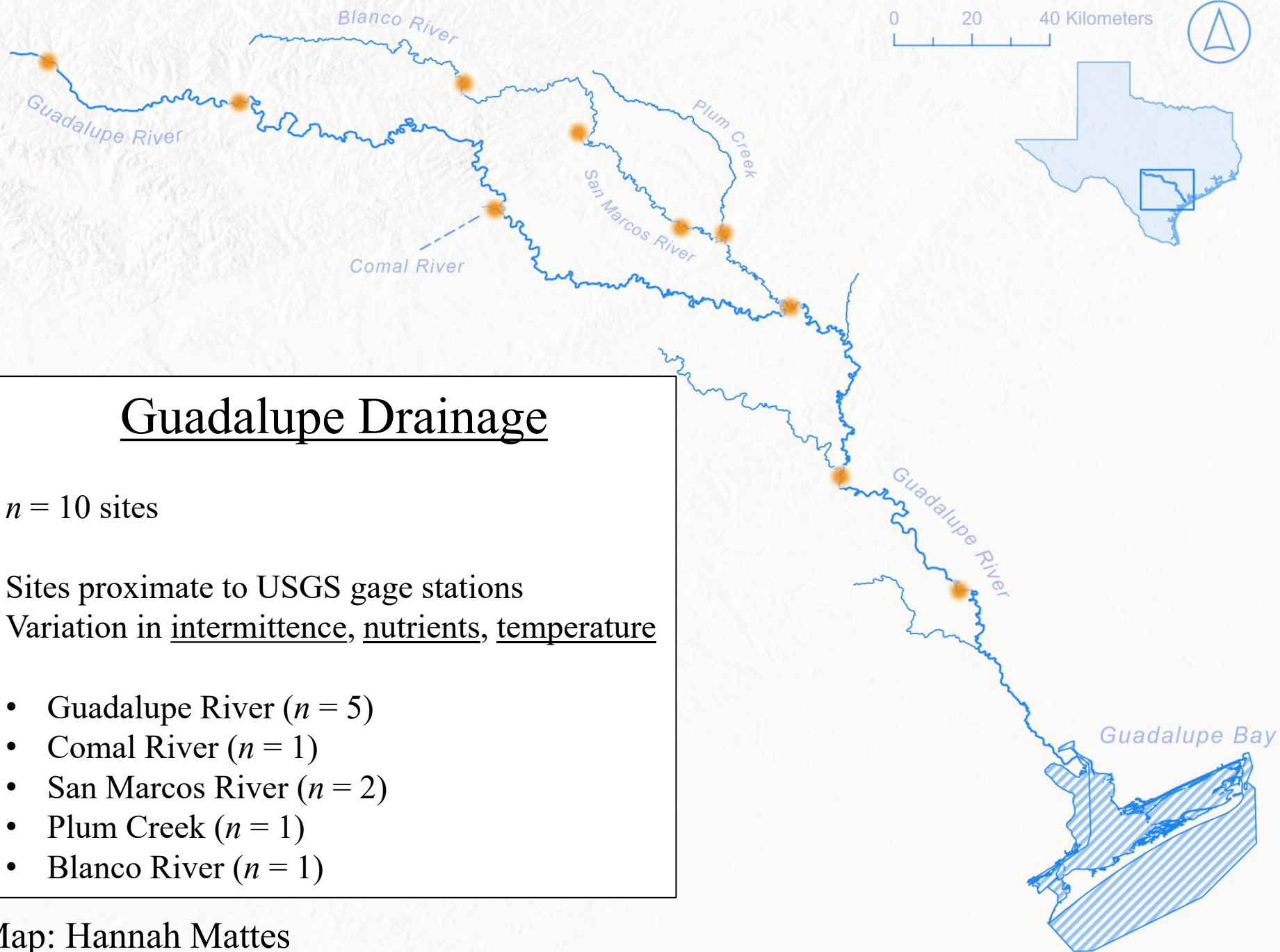


## Time Scales

- Short-term instantaneous changes in metabolism (microbial)
- Longer term climate driven differences in seasonality
  - Phenology (invertebrates)
- Most decomposition studies do not distinguish between these scales

# Study Questions

- Main questions:
  - Does detrital processing in a semi-arid river network vary with spatio-temporal changes in environmental conditions?
    - Longer-term seasonal changes in conditions and biological community composition?
    - Shorter-term responses (monthly)?
  - Are the environmental factors that drive detrital processing by microbes and invertebrates different?
    - Water chemistry, flow conditions/intermittence, temperature?



## Guadalupe Drainage

$n = 10$  sites

Sites proximate to USGS gage stations

Variation in intermittence, nutrients, temperature

- Guadalupe River ( $n = 5$ )
- Comal River ( $n = 1$ )
- San Marcos River ( $n = 2$ )
- Plum Creek ( $n = 1$ )
- Blanco River ( $n = 1$ )

# Field Sampling and Lab Analysis

- Sampled in 2023
  - Sycamore (*Platanus occidentalis*)
  - Fine (1-mm) and Coarse (1-cm) mesh
  - Fall, Winter, Spring, Summer
- $n = 5$  packs of both types per site
  - 35 – 42 d
- Collected water quality and discharge variables
- Invertebrates in packs
  - $n = \underline{386}$  leaf packs
  - 108,077 invertebrates
  - #/ind per g litter remaining
- Mass loss of packs expressed as  $k$  (proportion of mass lost/day)
  - $\text{Ln}(k)$



# Data Analyses

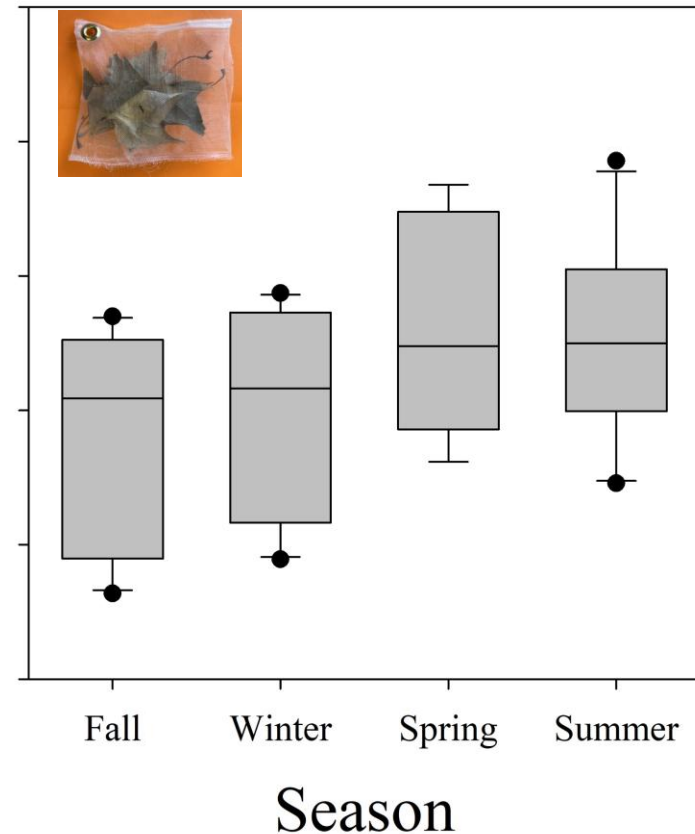
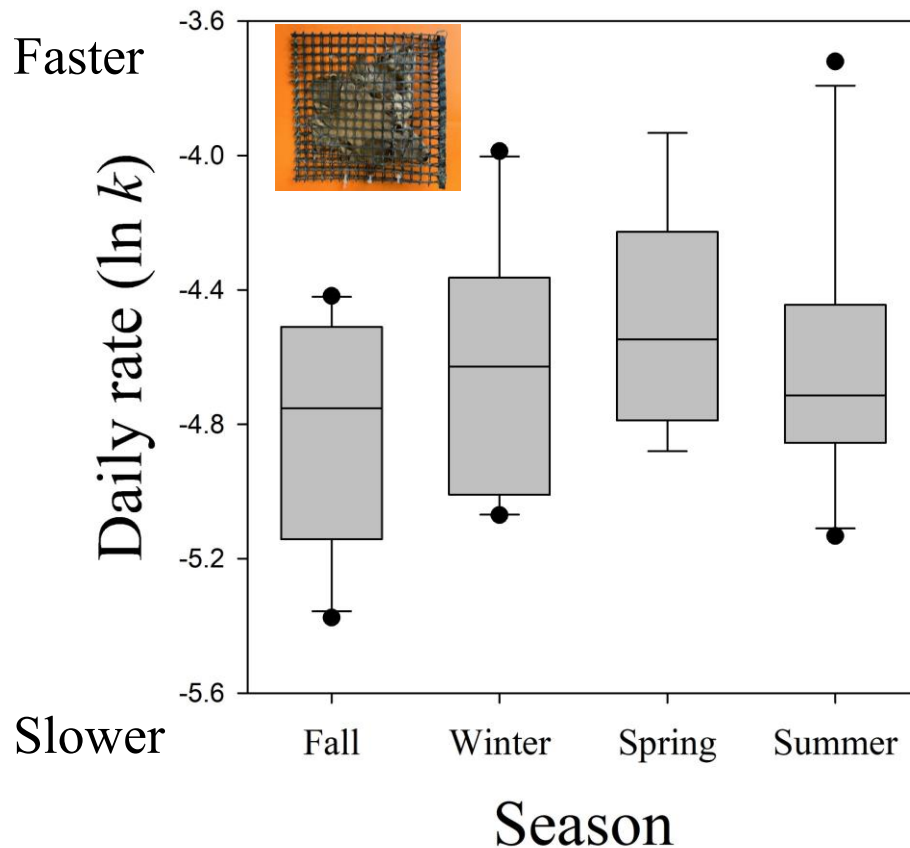
- Differences between coarse and fine leaf packs
  - Invertebrates + Microbes versus Microbes Only
  - Daily  $k$  rates (% mass lost/day)
  - Invertebrate density, taxonomic richness, and FFGs (% Shredders)
  - ANOVA
- Factors affecting daily  $k$  rates
  - Coarse mesh  $k$
  - Fine mesh  $k$
  - Invertebrate mediated  $k$  (Coarse mesh  $k$  – Fine mesh  $k$ )
  - Multicollinearity addressed with VIFs
  - Linear models, best model selection using AICc (*dredge* function in *MuMIn* package)
  - Used standardized  $\beta$  to determine effect sizes
- R platform

Overall Mass Loss:  $40.8 \pm 15.8$  % over deployment period

Mean Daily Mass Loss:  $0.84 \pm 0.27$ % per day

Coarse Mesh

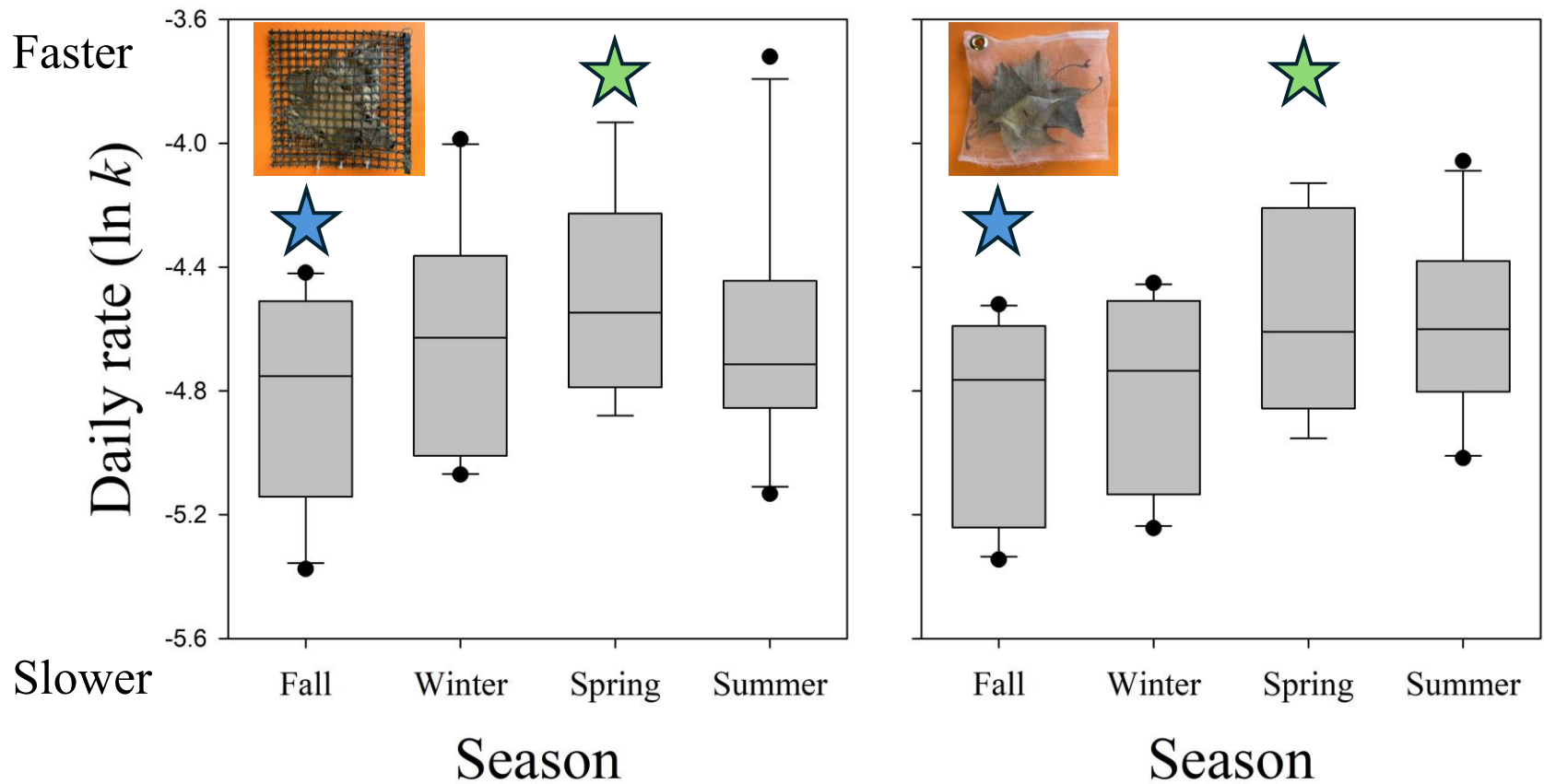
Fine Mesh



Season:  $p = 0.043$   
Mesh Size:  $p = 0.384$   
Season x Mesh Size:  $p = 0.801$

Coarse Mesh

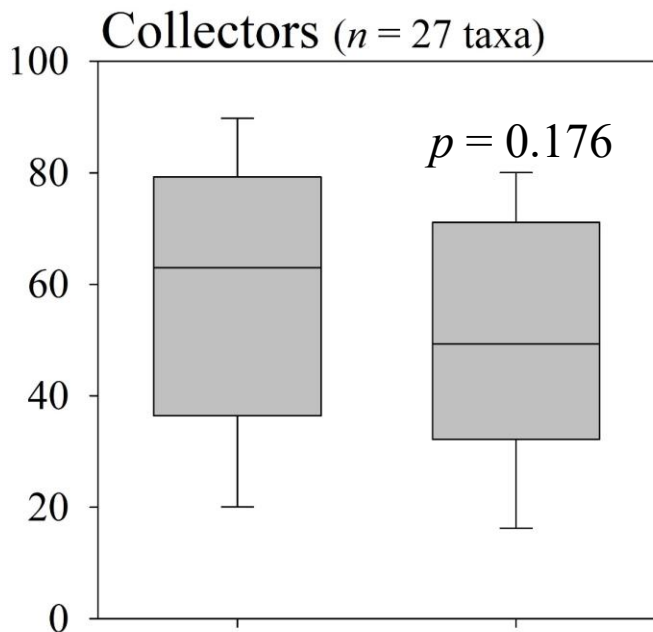
Fine Mesh



Hydropsychidae

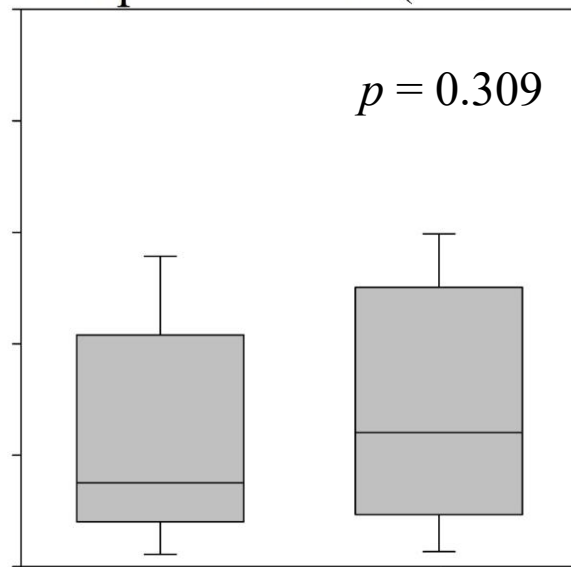


%



Scrapers/Grazers ( $n = 33$  taxa)

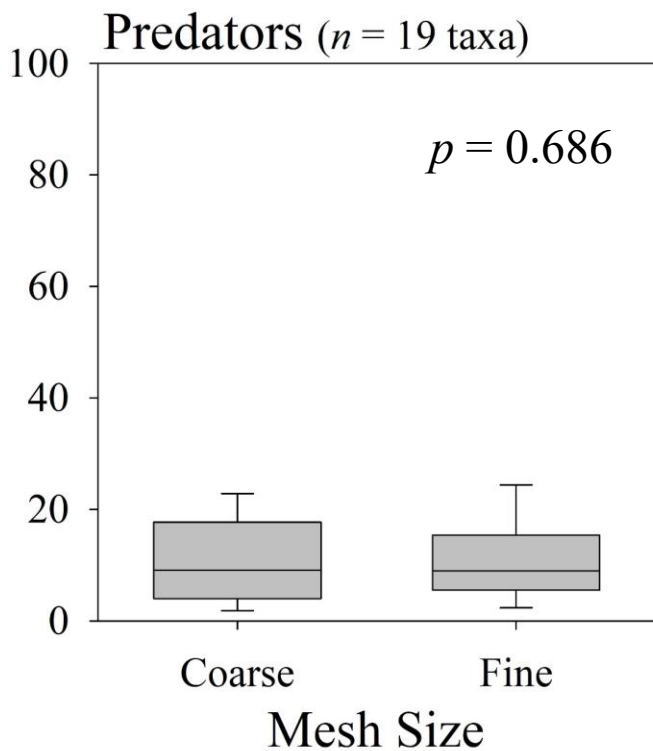
Elmidae



*Argia* sp.

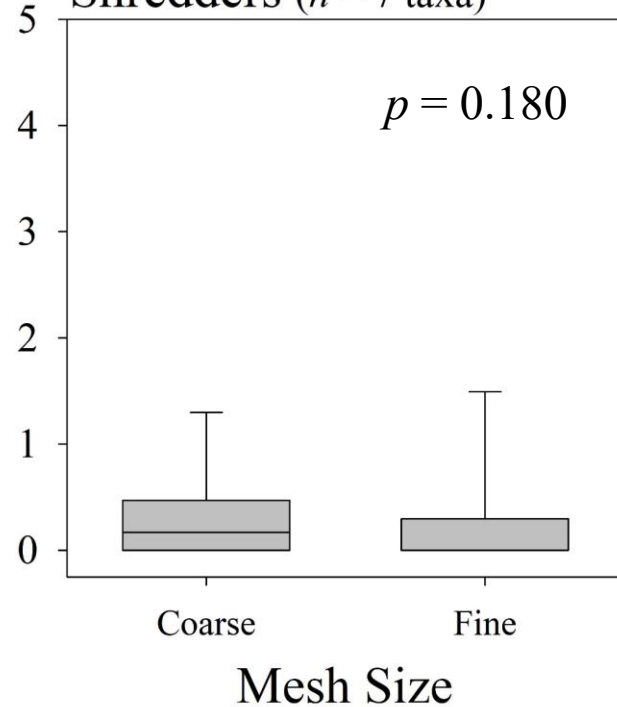


%



Shredders ( $n = 7$  taxa)

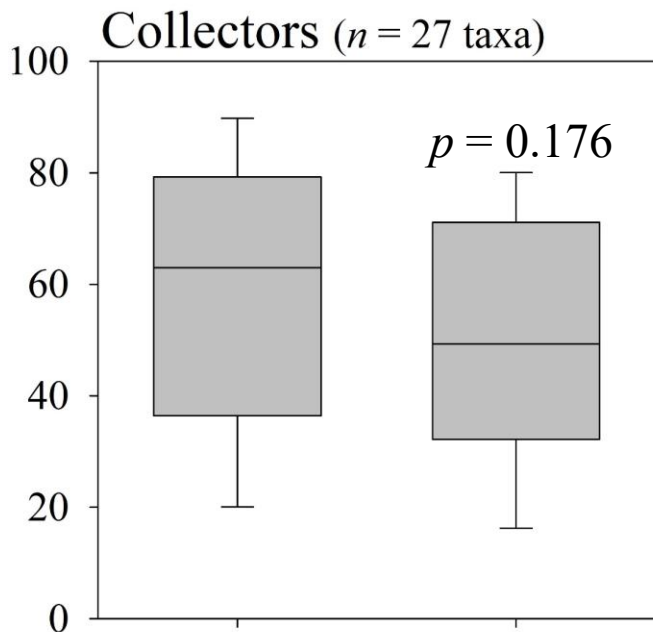
Tipulidae



Hydropsychidae

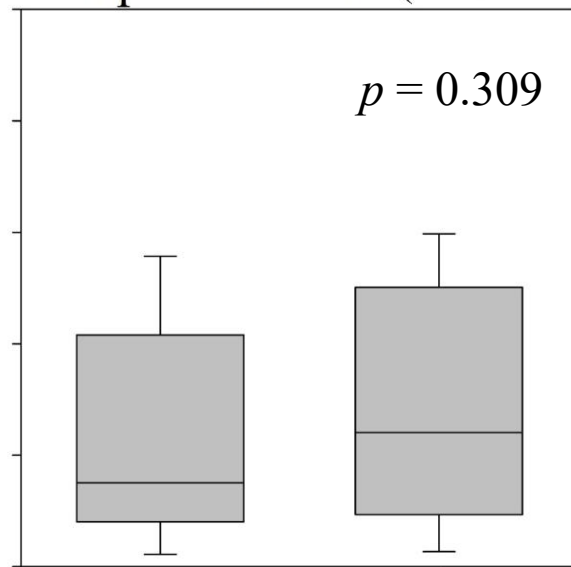


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### Scrapers/Grazers ( $n = 33$ taxa)

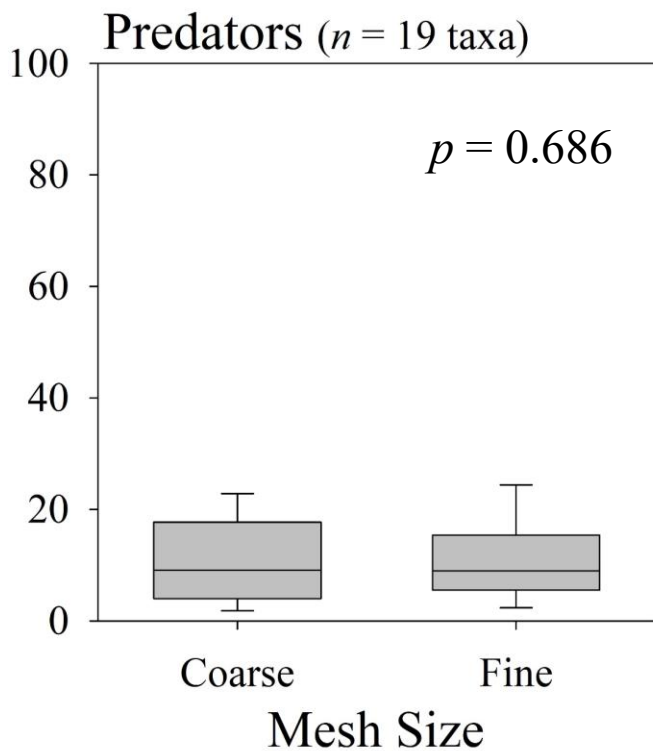
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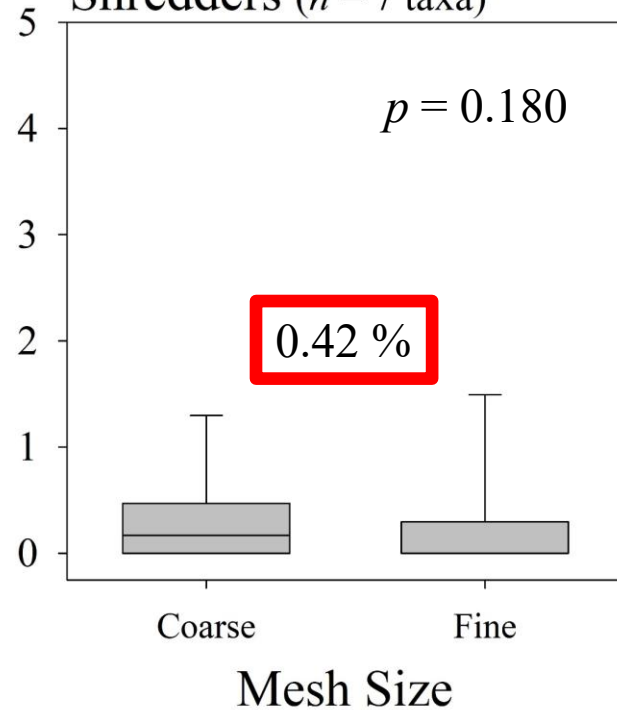


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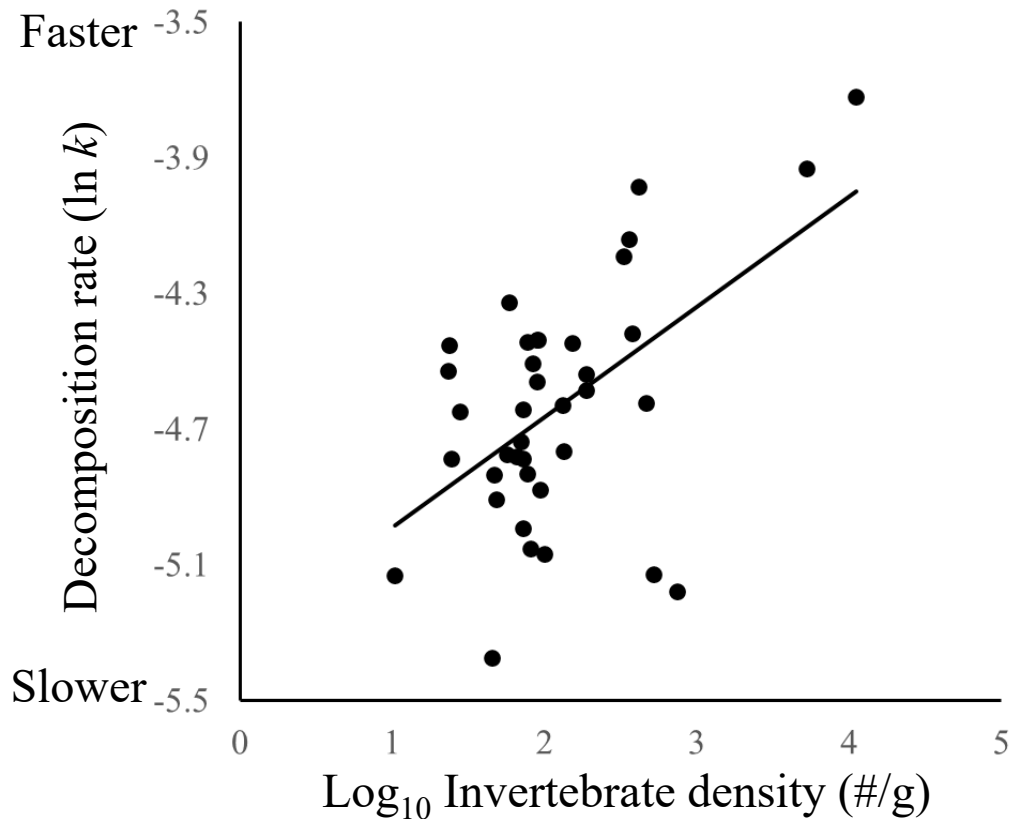
Tipulidae



# Detrital Processing Predictors

- Coarse Mesh

- Invertebrates and microbes
- Coarse Mesh  $k \sim$  Total Invertebrate Density
  - $p < 0.001$ ,  $R^2_{adj} = 0.325$



# Detrital Processing Predictors

- Fine Mesh

- “Only” Microbes

- Fine Mesh  $k \sim$  Temperature + Velocity + Days<5cfs + Conductivity

- $p < 0.001, R^2_{adj} = 0.606$

- 1) Temperature: +

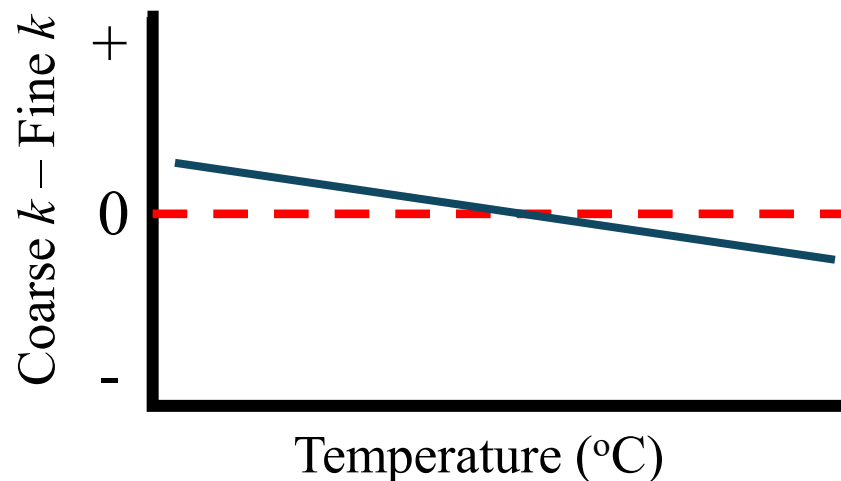
- 2) Velocity: +

- 3) Days < 5cfs: -

- 4) Conductivity: +

# Detrital Processing Predictors

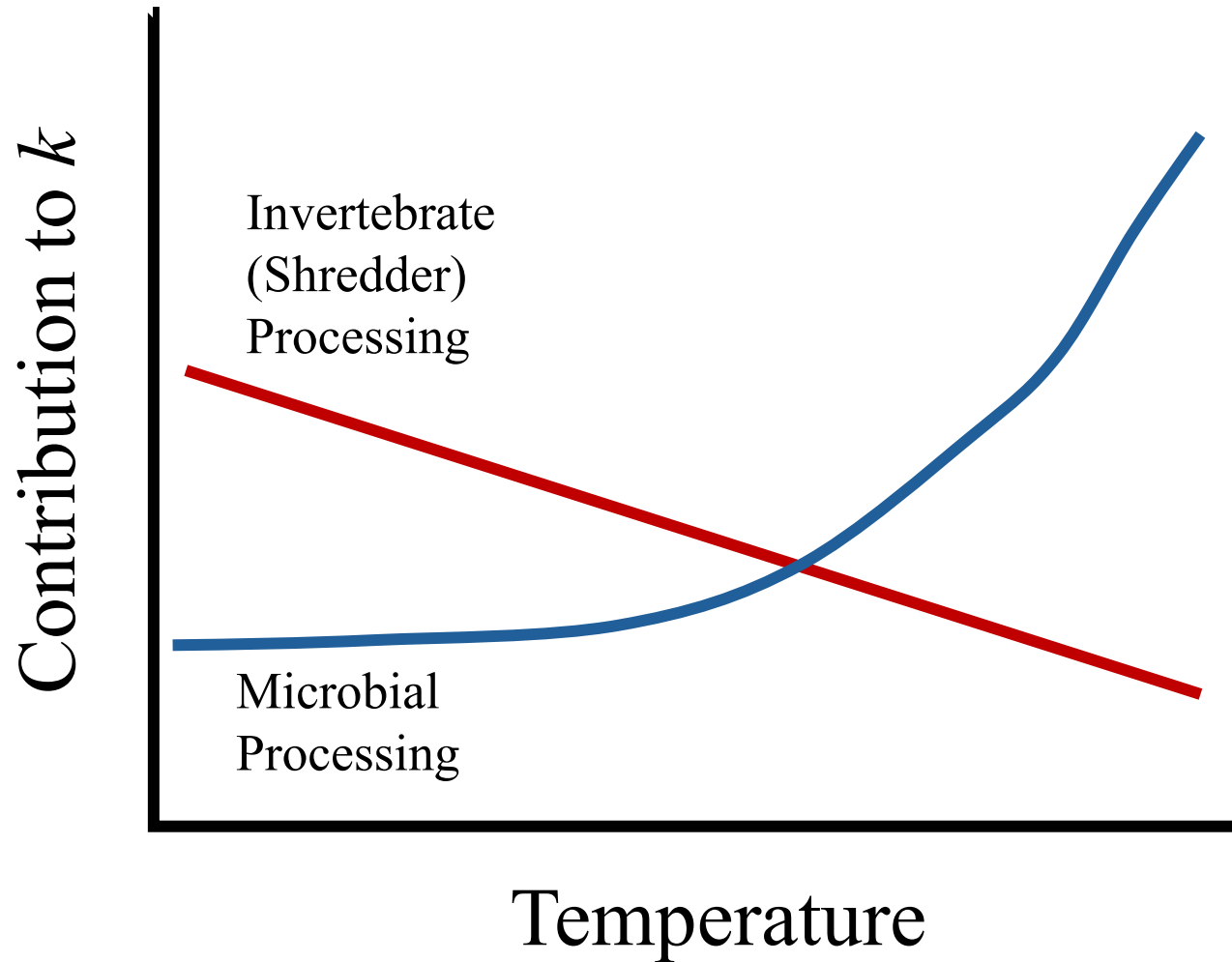
- Invertebrate Mediated Decomposition
  - Coarse Mesh minus Fine Mesh  $k$
  - $Ck$  minus  $Fk \sim$  Temperature + Total Invertebrate Density
    - $p < 0.001$ ,  $R^2_{adj} = 0.361$
    - 1) Temperature: -
    - 2) Total Invertebrate Density: +



# What does this mean?

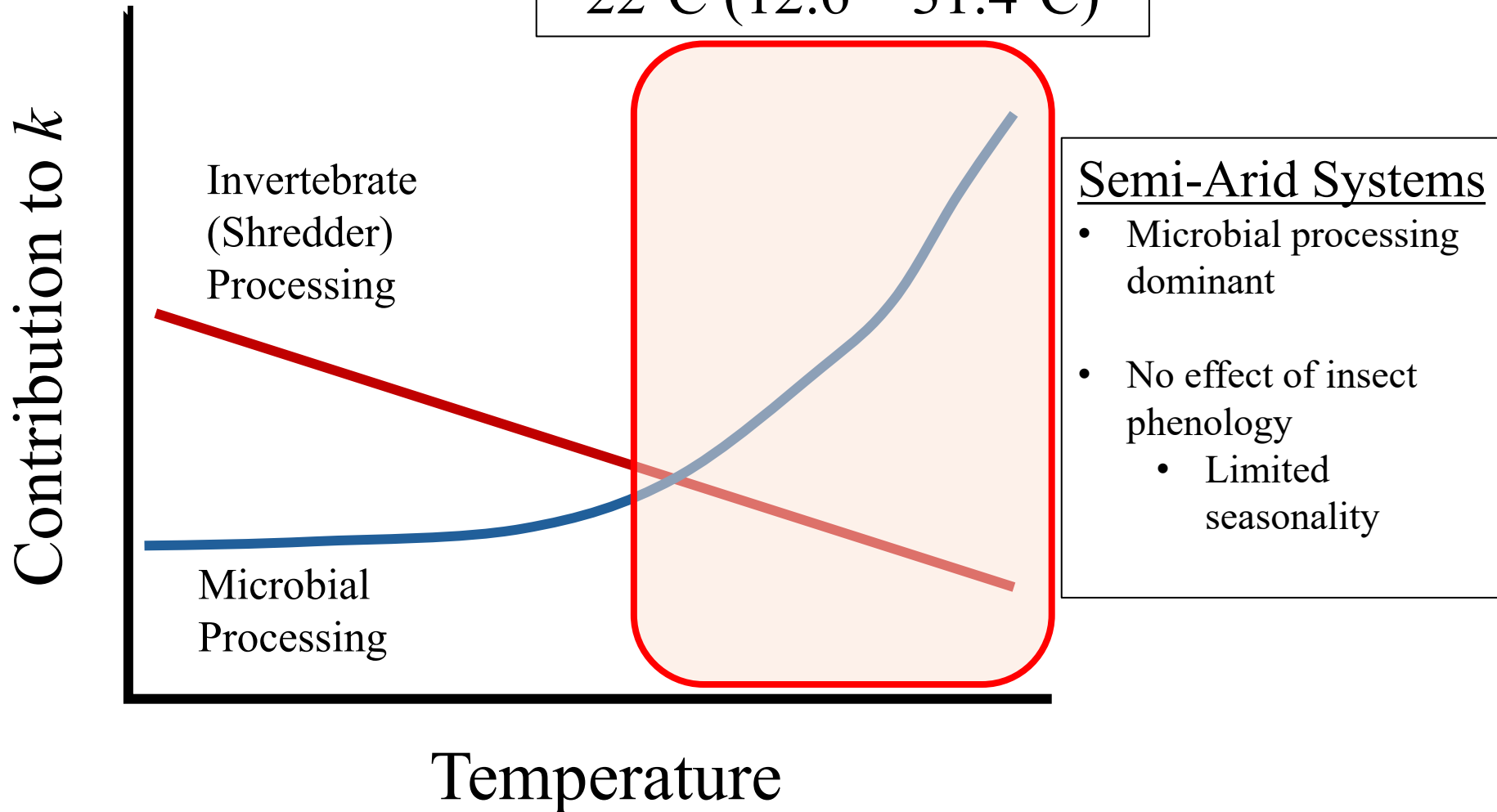
- Microbial processes are important in decomposition
  - Coarse and Fine mesh  $k$  values similar
  - Lack of shredders
- Season was not significant in models
  - Lower seasonal variation and lack of major phenological changes in invertebrate community composition
  - Overall decomposition rates across sites - Fall and Spring
- Fine mesh decomposition
  - Factors that control microbial processing rates
  - Intermittency has an impact (slows decomposition)
  - More invertebrates than expected
- When invertebrates have access to leaf litter, they utilize it and lead to greater decomposition rates
  - Total invertebrate density significant predictor
  - Movement, excretion, literature defined FFGs inaccurate?
  - Non-trophic use is common

# Invertebrates *versus* Microbes

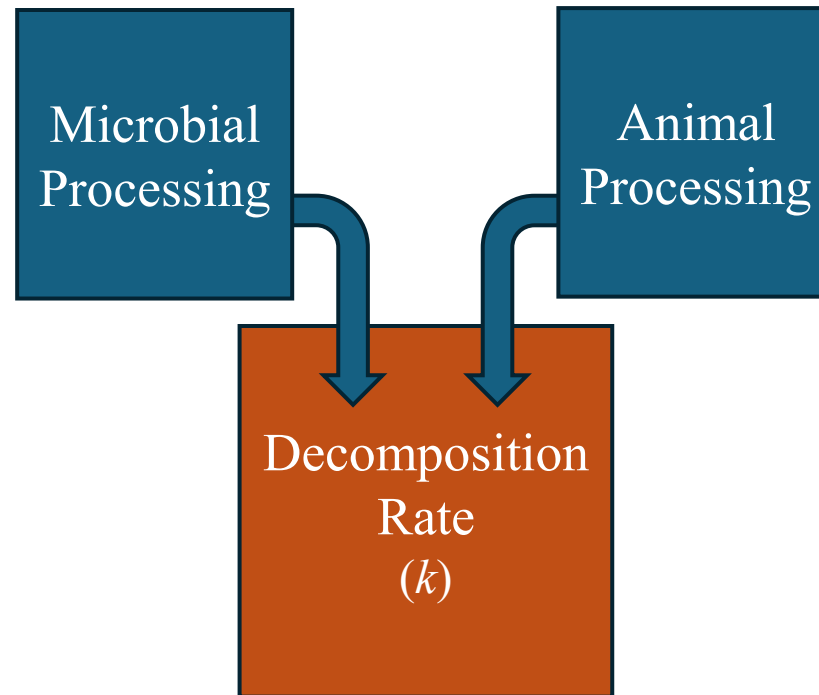


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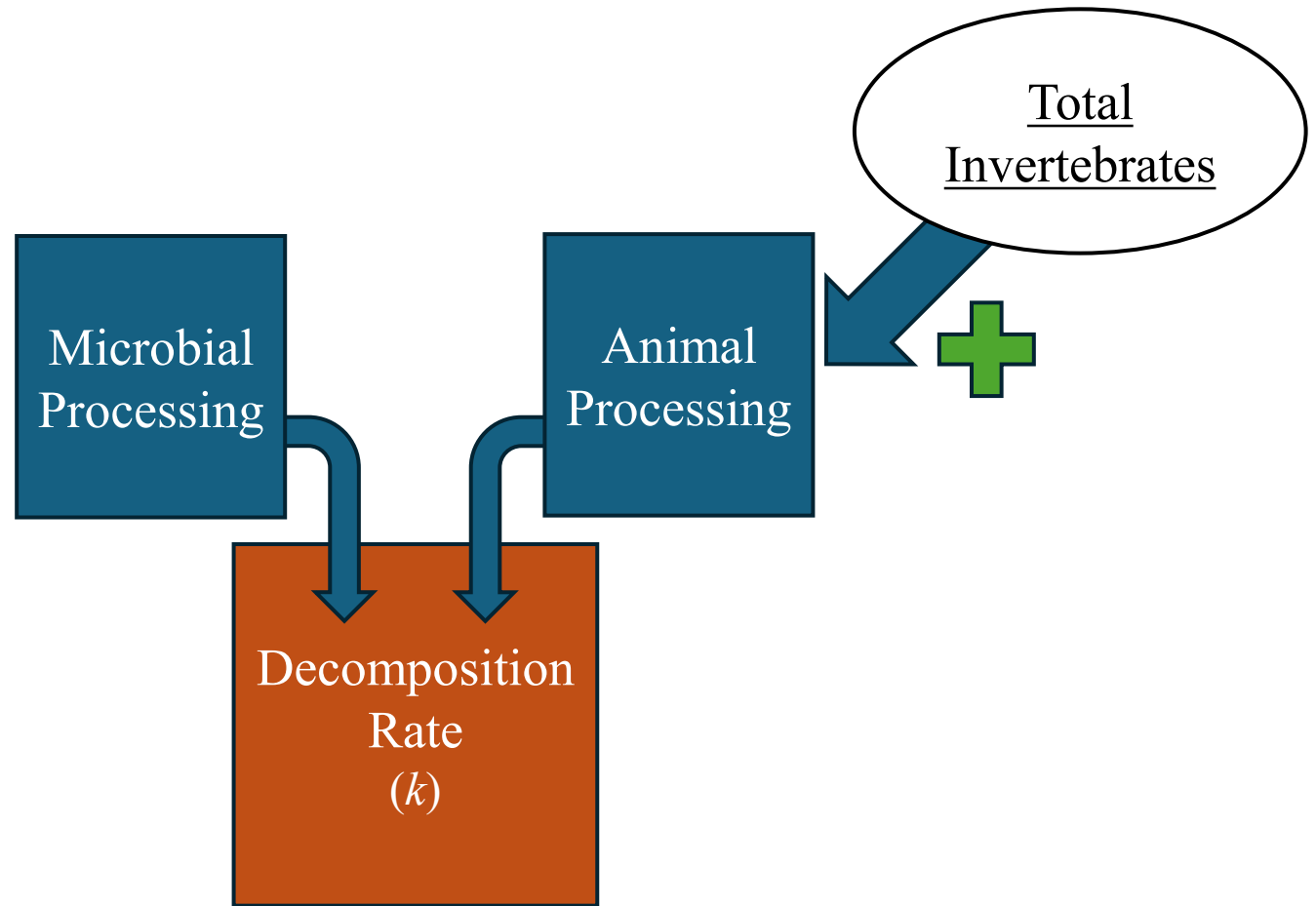
22°C (12.6 – 31.4°C)



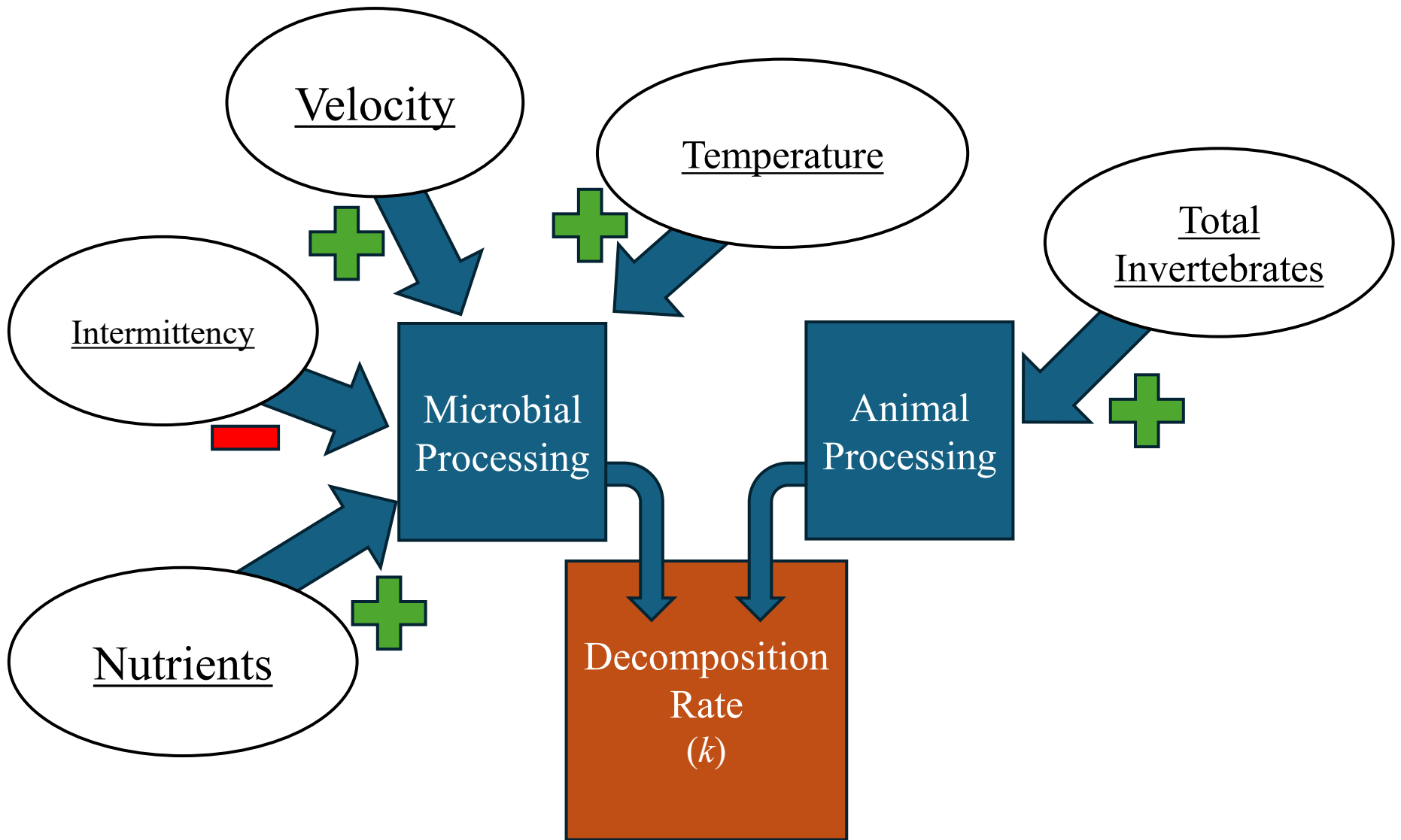
# Decomposition in the Future



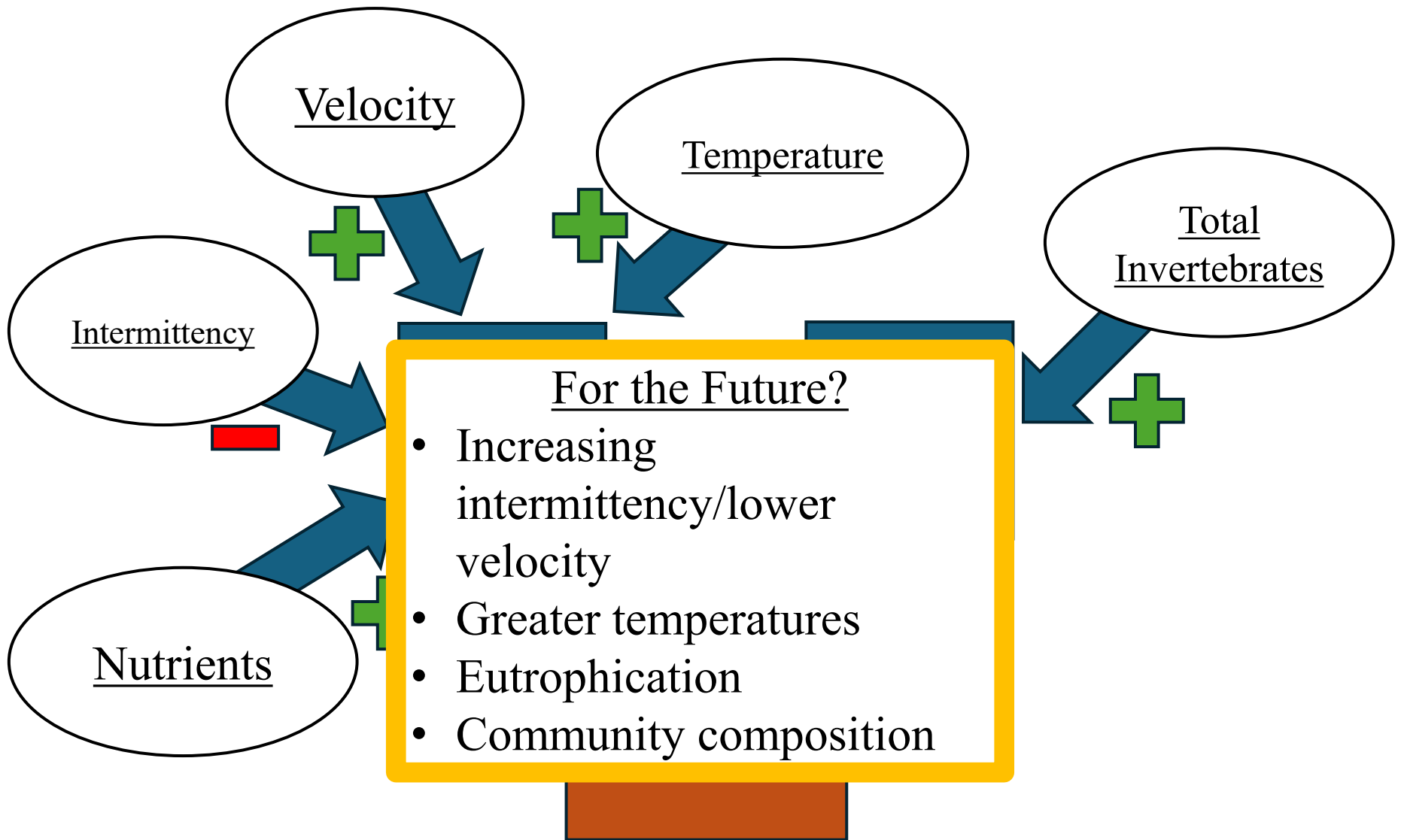
# Decomposition in the Future



# Decomposition in the Future

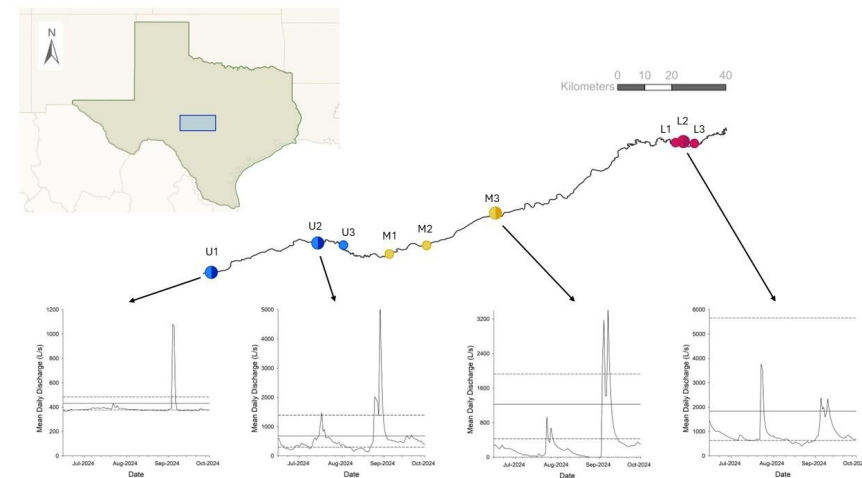
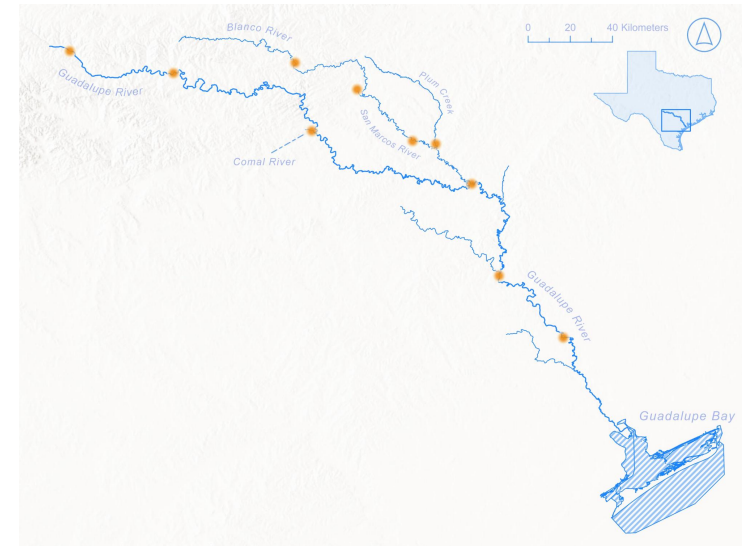


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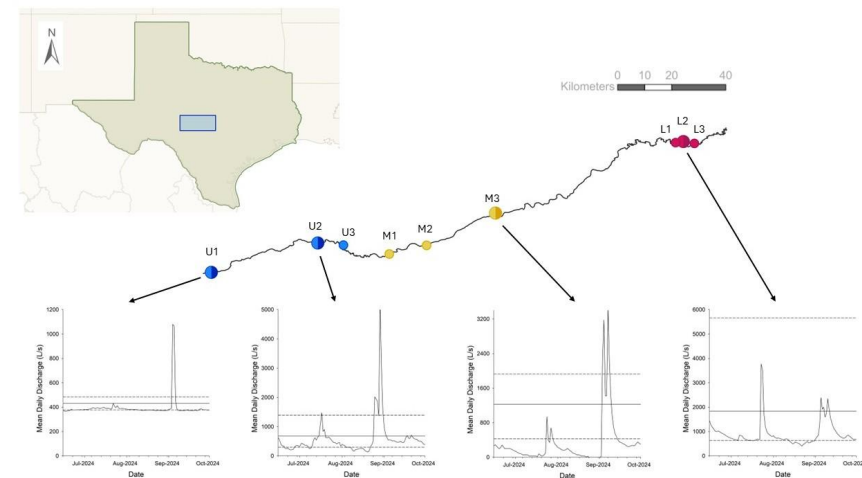
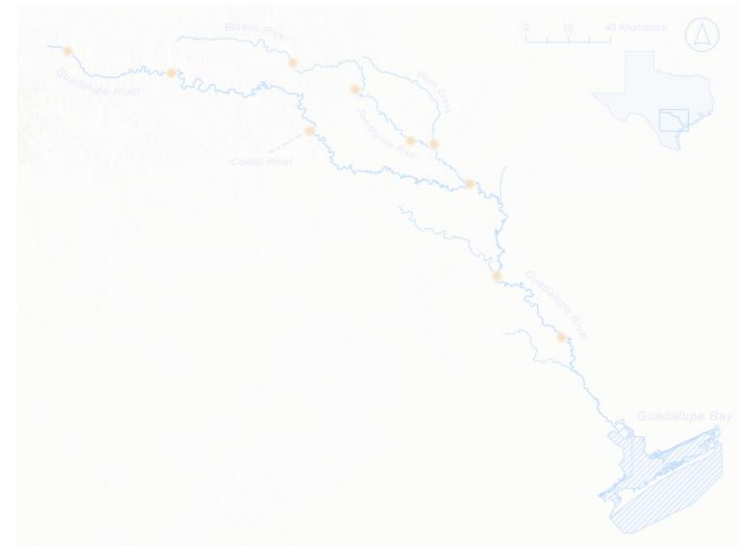
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- Seasonal dynamics of terrestrial leaf litter decomposition across a flow and environmental gradient within a single drainage basin
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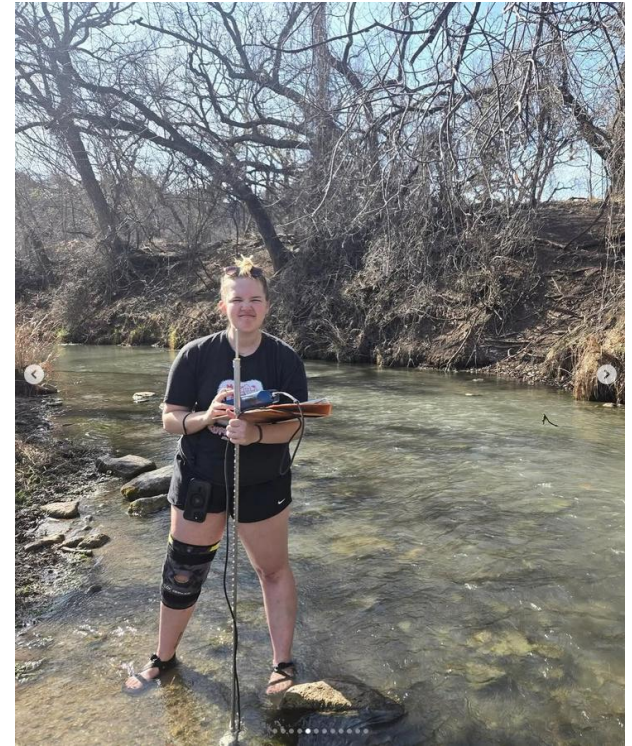
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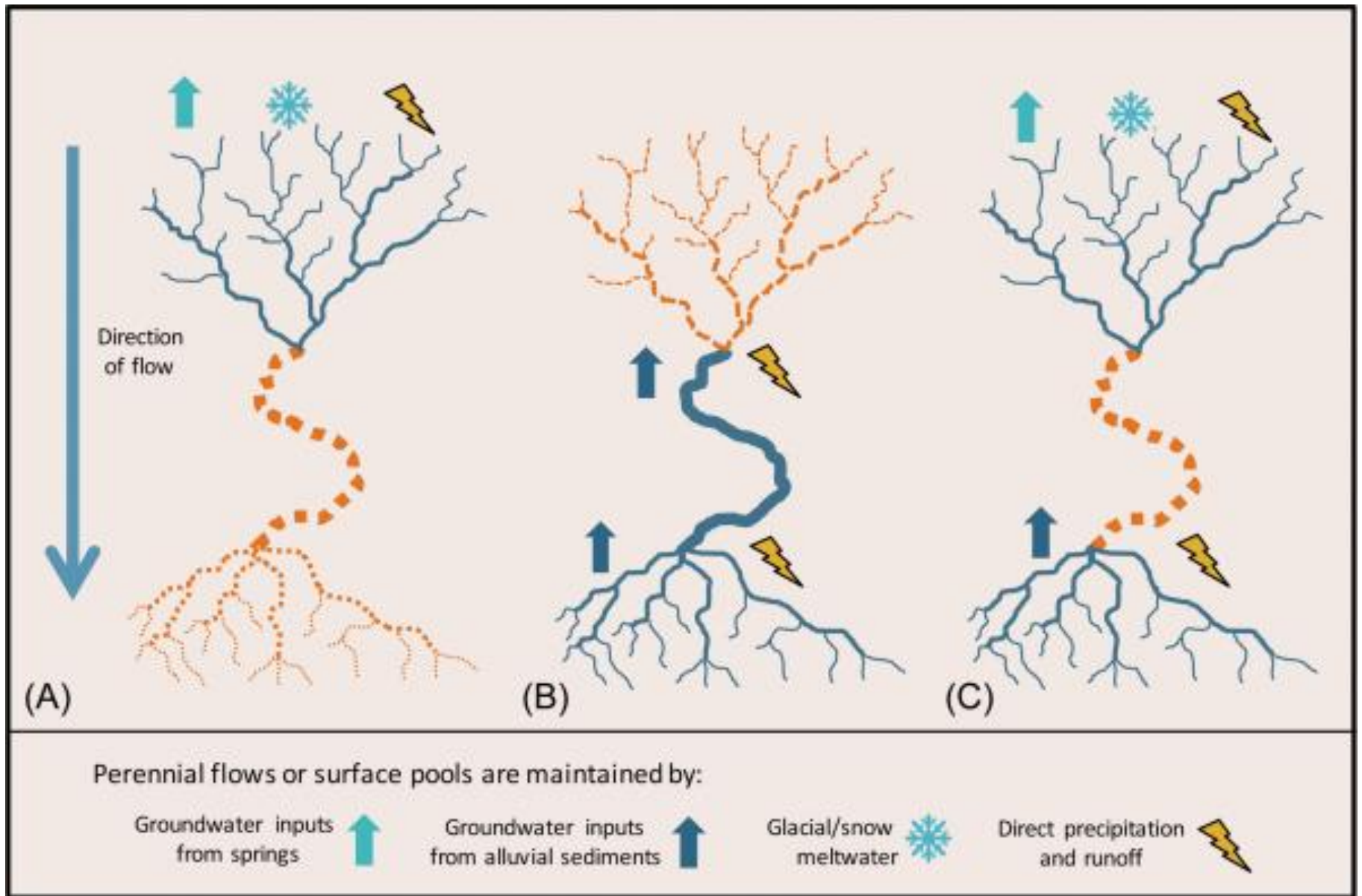
# Acknowledgements



Jered Davenport    Ailish Collins    Dr. Parvathi Nair



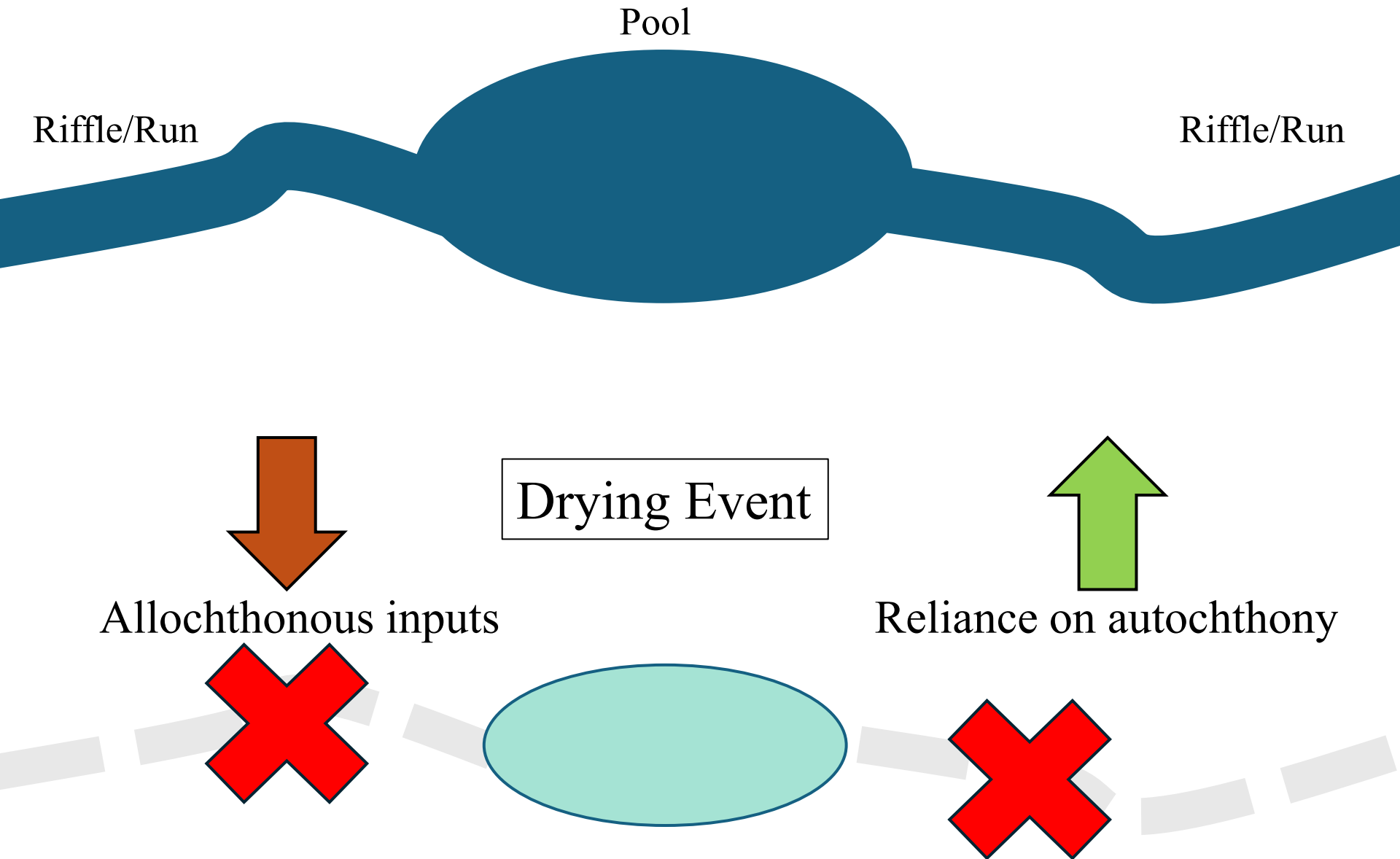
Hannah Mattes



Boulton et al. (2017)

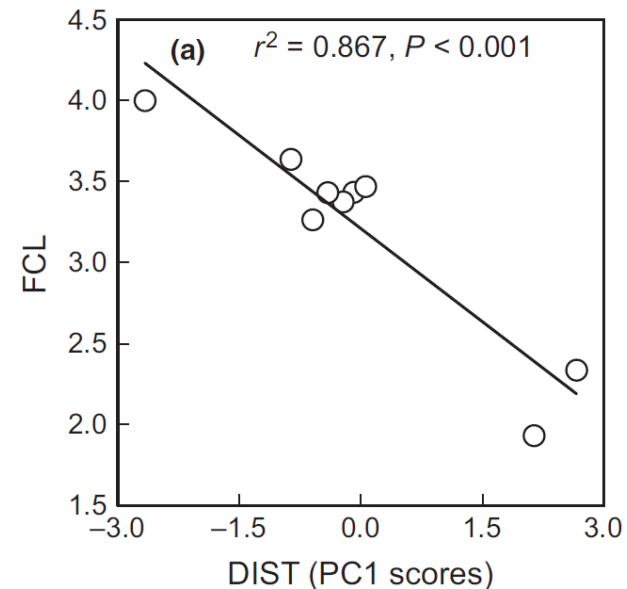
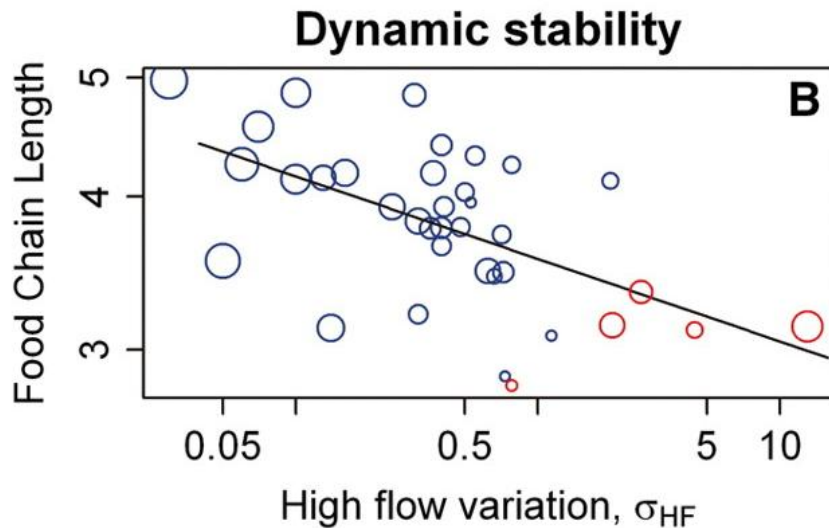
*In: Intermittent Rivers and Ephemeral Streams: Ecology and Management*

# Disconnection and Allochthony



# Intermittency and Food Webs

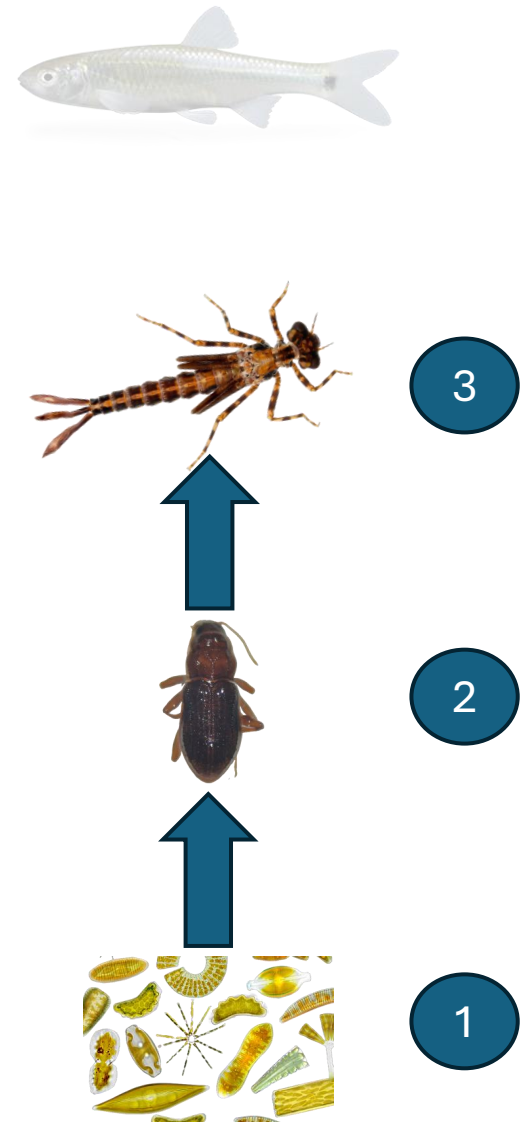
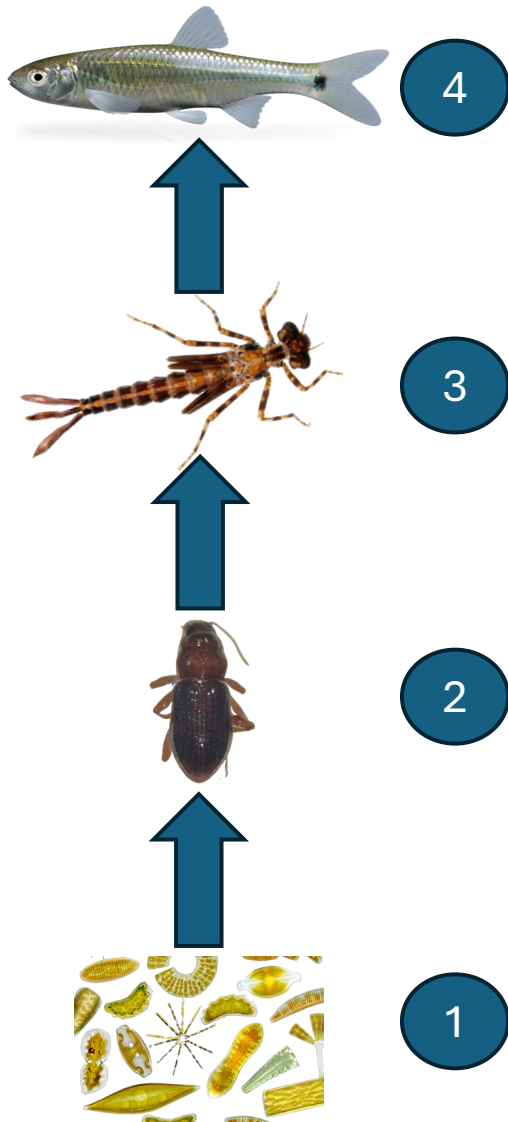
- Food chain length and trophic position of consumers sensitive to disturbance
  - Shorter food chains and lower estimated trophic position of upper trophic level consumers



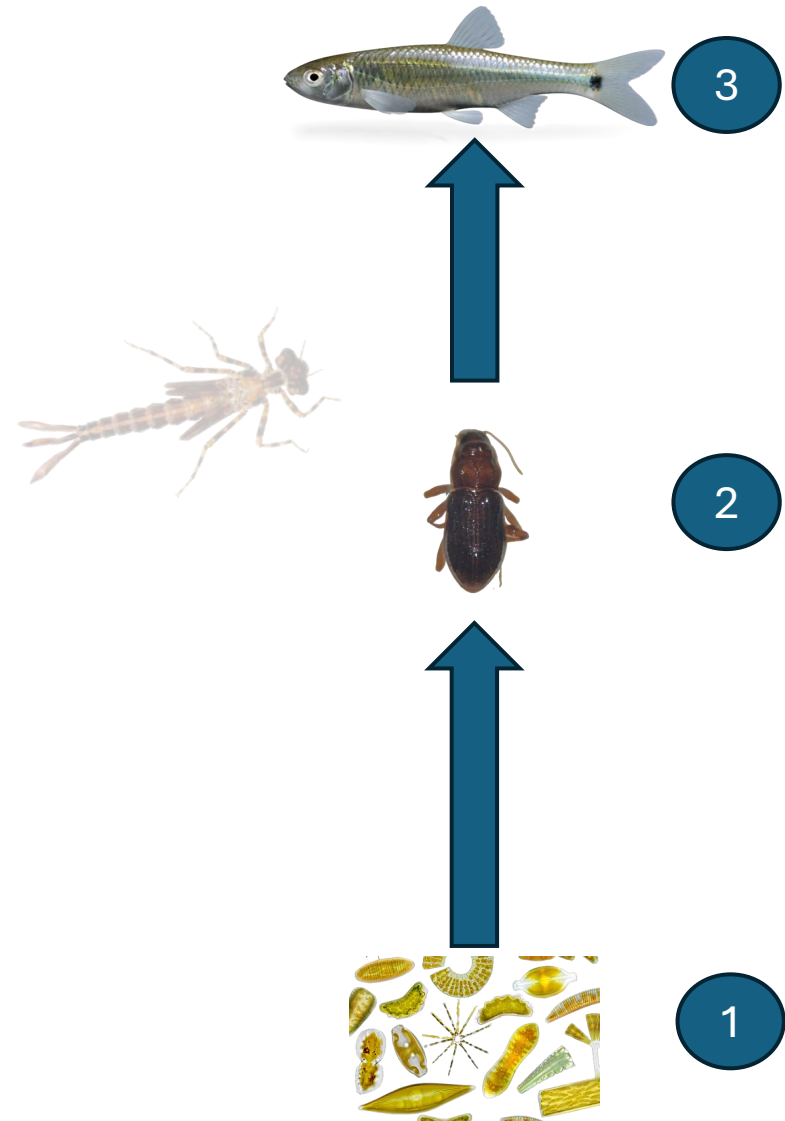
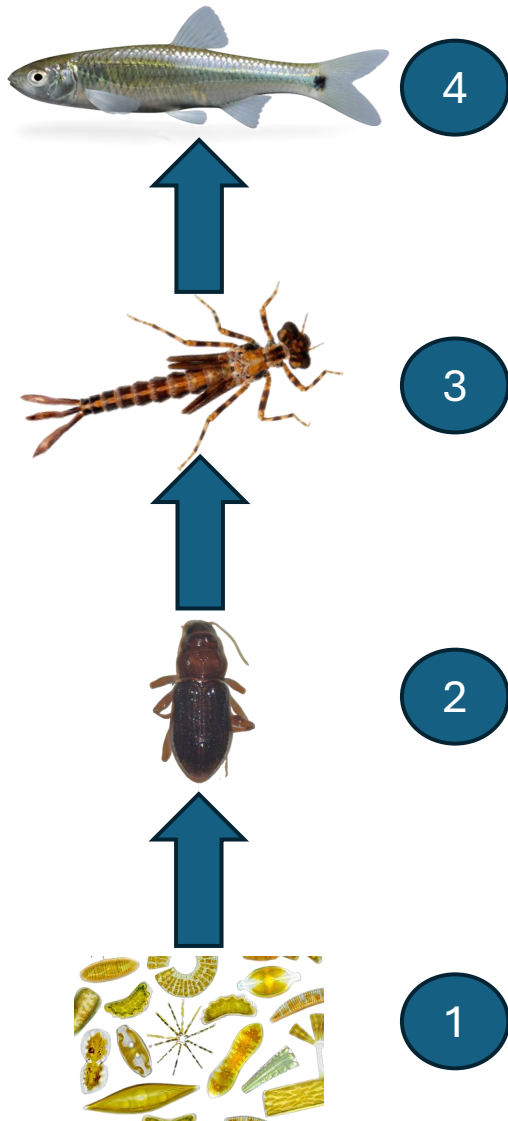
Sabo et al. (2010). *Science*.

Ruhí et al. (2016). *Freshwater Biology*.

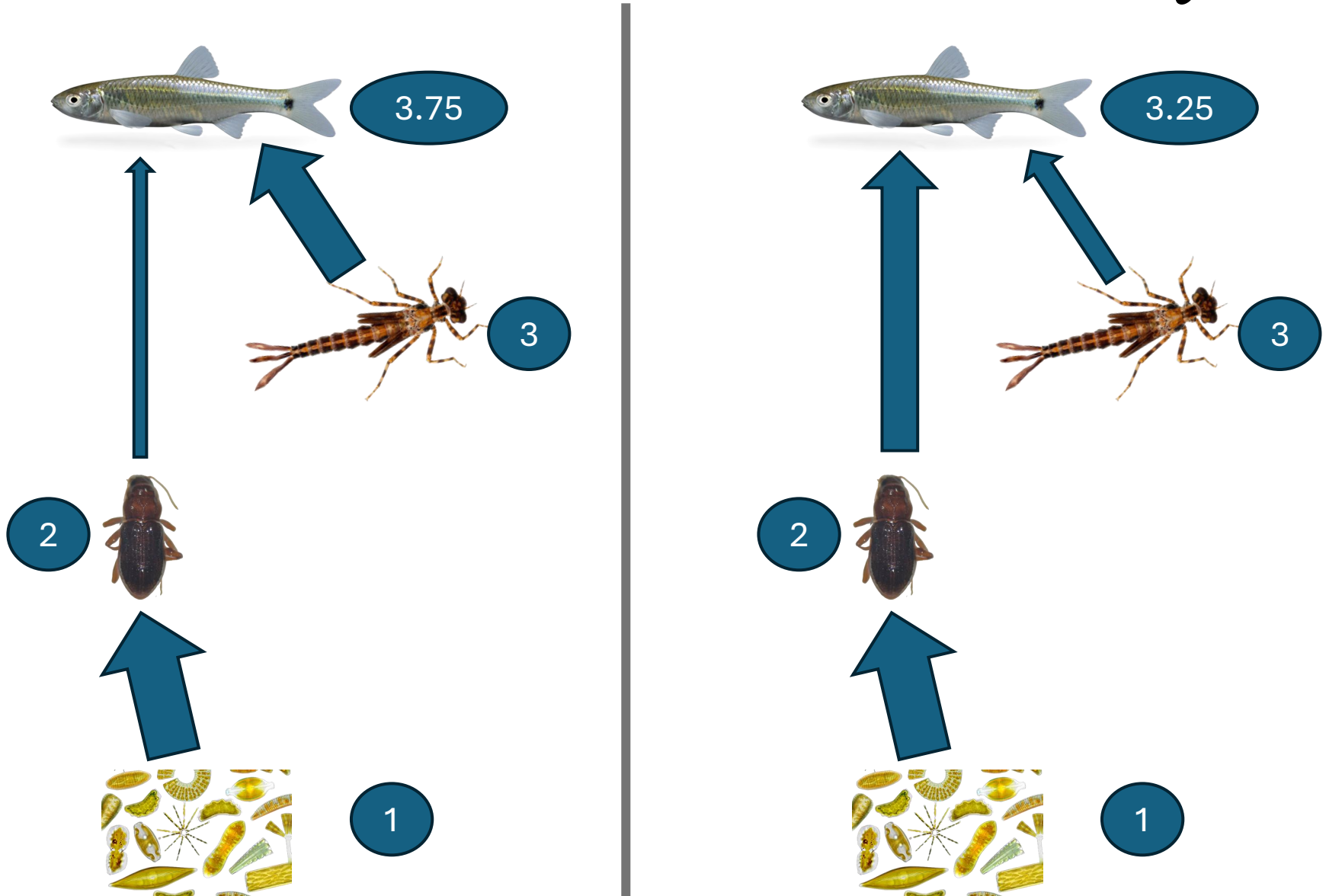
# Structural Mechanism - Deletion



# Structural Mechanism - Removal

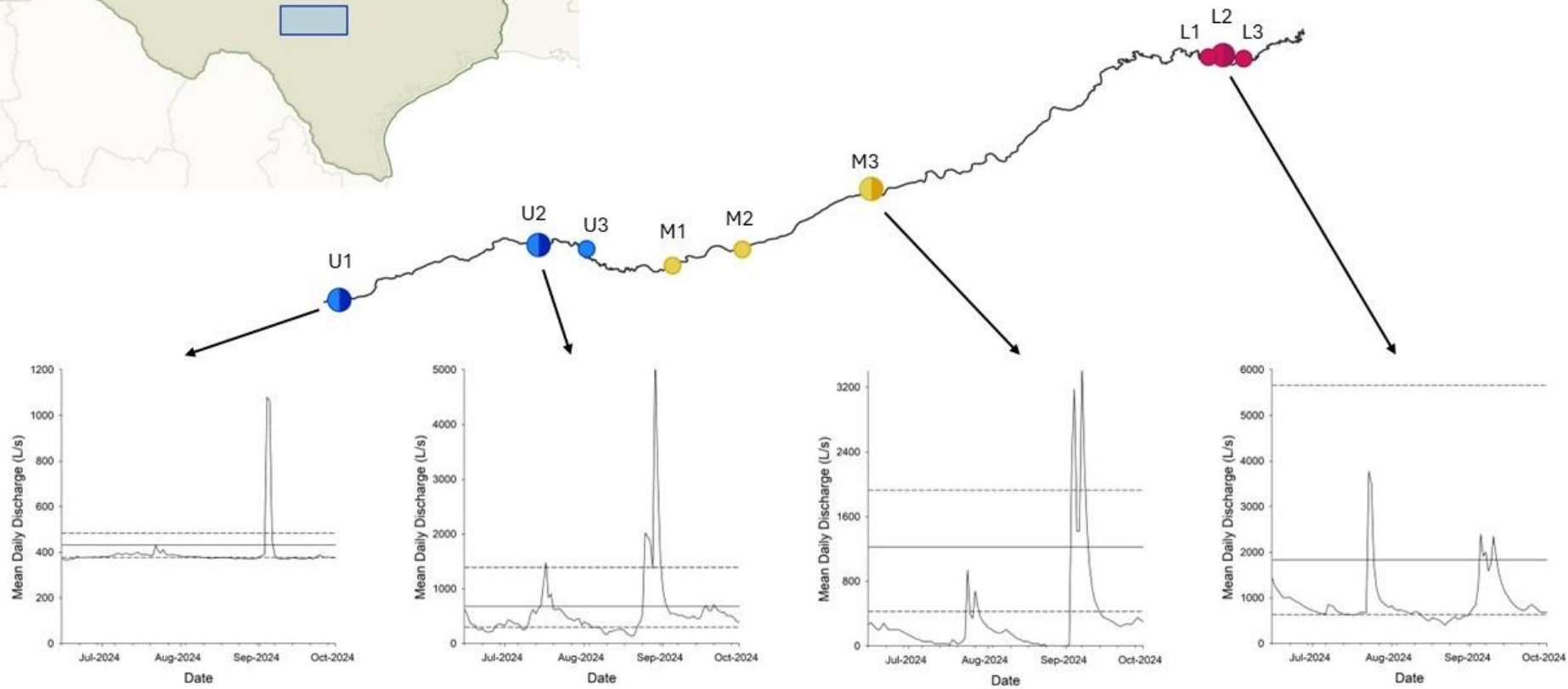
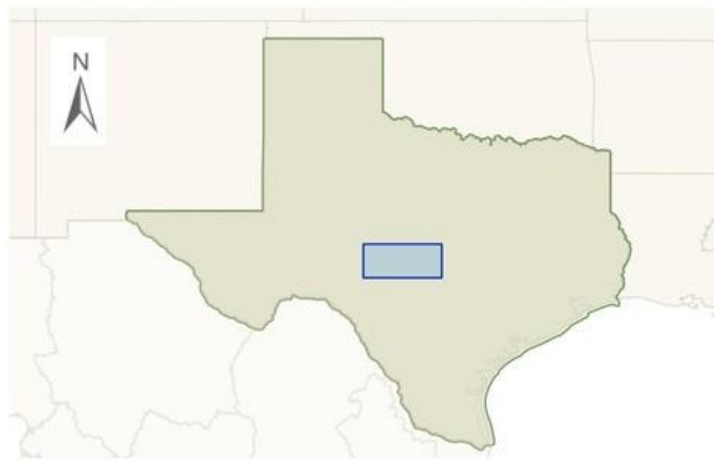


# Structural Mechanism - Omnivory



# Questions and Predictions

- Does trophic position of consumers change in response to differences in intermittency in a single river system?
  - Consumers will have lower estimated trophic position at study reaches with intermittent summer flows
- Does the relative importance of autochthonous resources increase in response to intermittency?
  - The proportion of autochthonous resources supporting consumers will be greater in reaches with intermittent flows



## San Saba River, central Texas

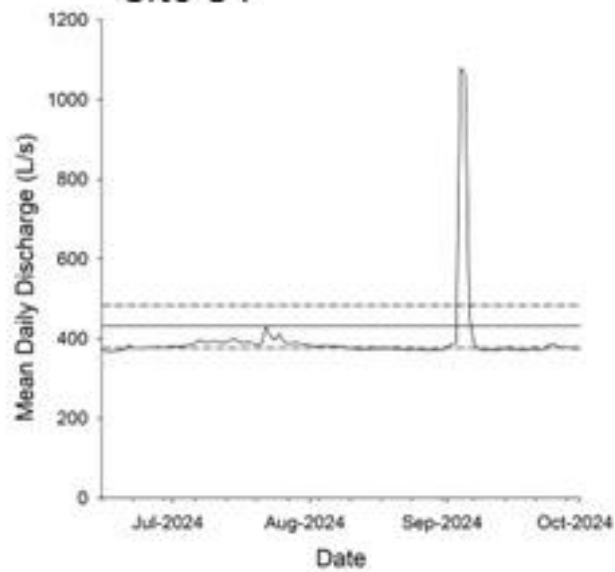
Longitudinal intermittency gradient  
Upper, Middle, and Lower segments

# Study Design and Methods

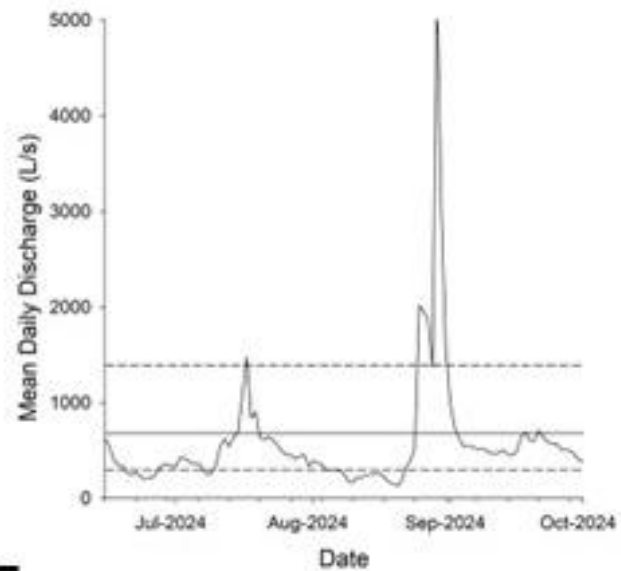
- Three segments
  - Upper = Hydrologically “stable” and no intermittency
  - Middle = Less stable, frequently intermittent and dries most years
  - Lower = More dynamic, only dries during extended/severe drought
- Three study reaches (~200 m) per site ( $n = 9$ )
- Collected fish, invertebrates, algae, and in-stream terrestrial leaf litter at
- Sampled two time periods:
  - Early season (June) and late summer (September)

**B**

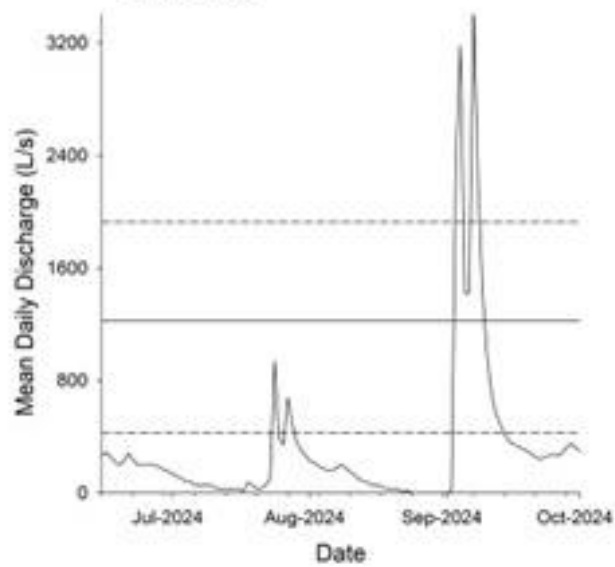
Site U1

**C**

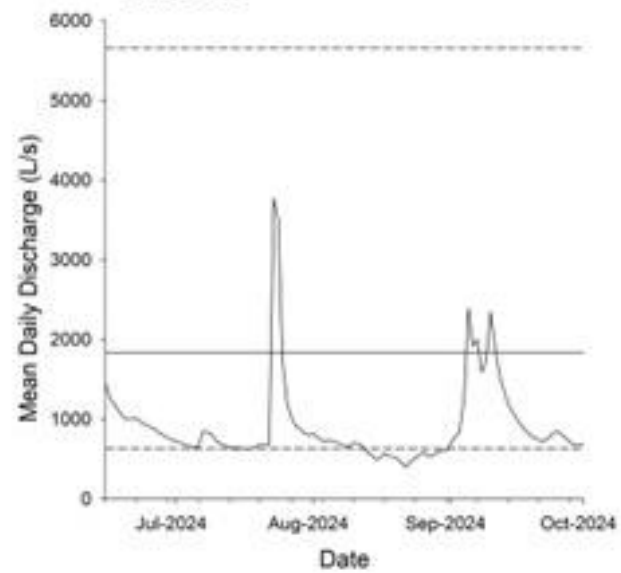
Site U2

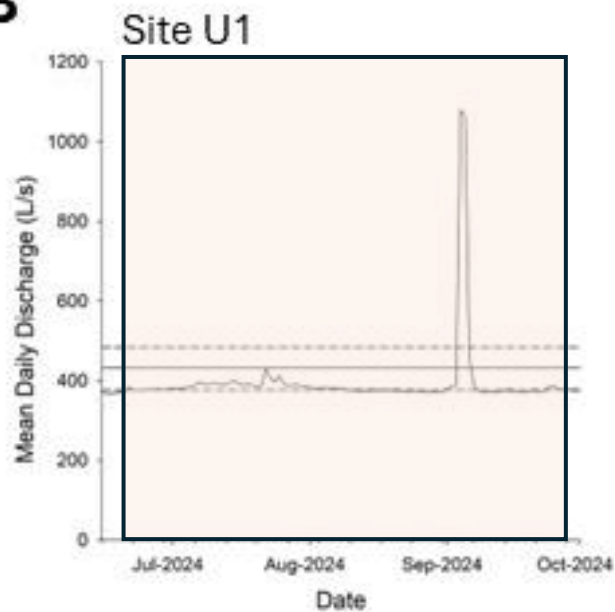
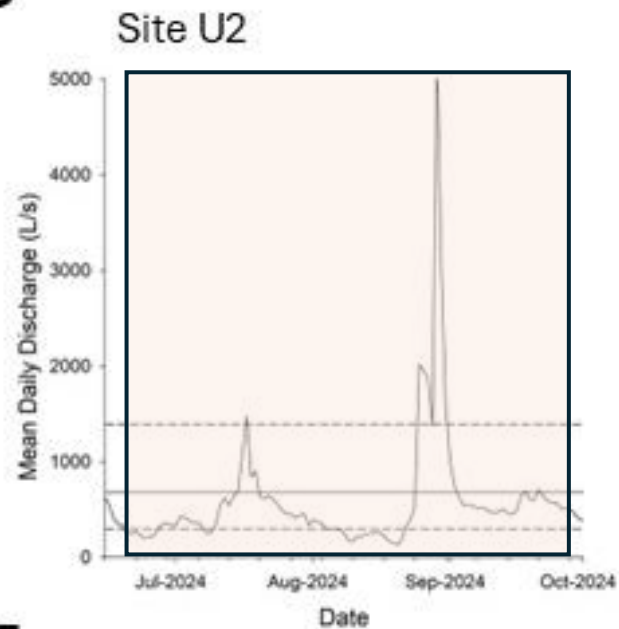
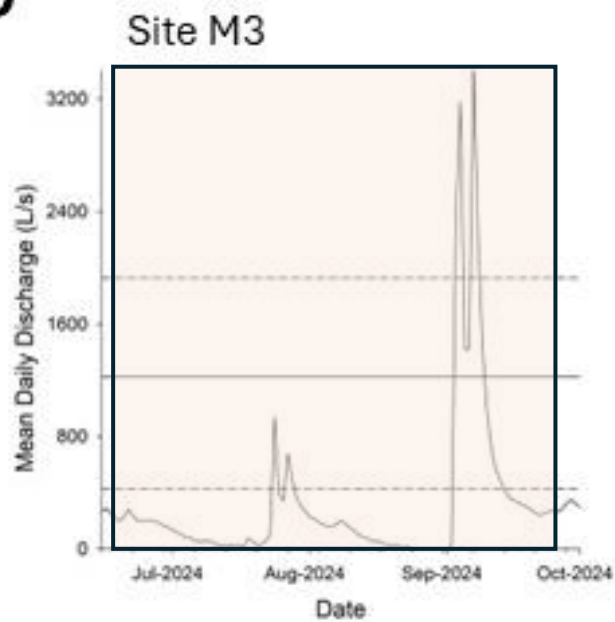
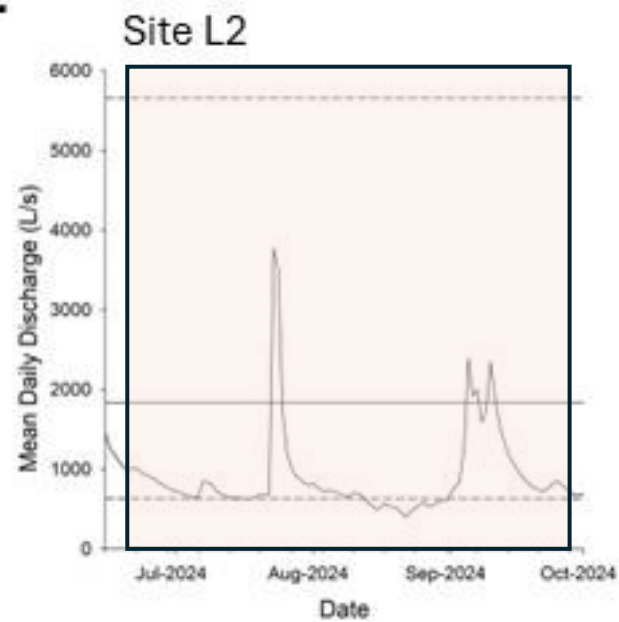
**D**

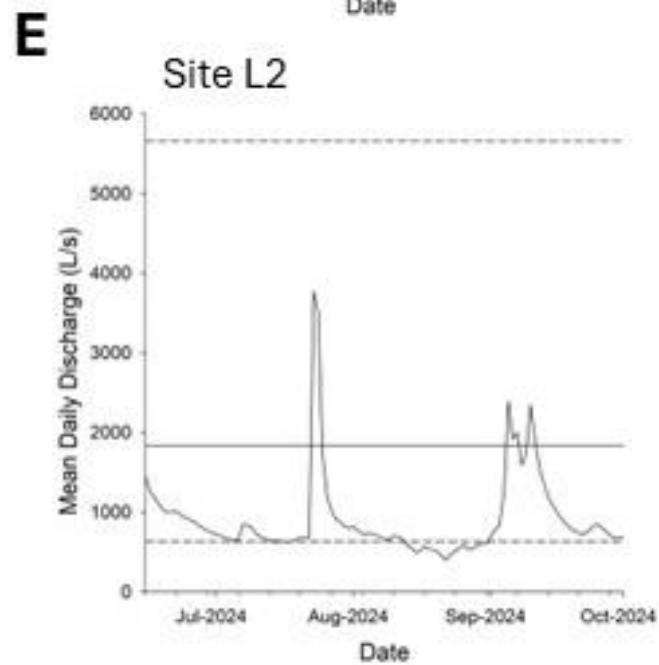
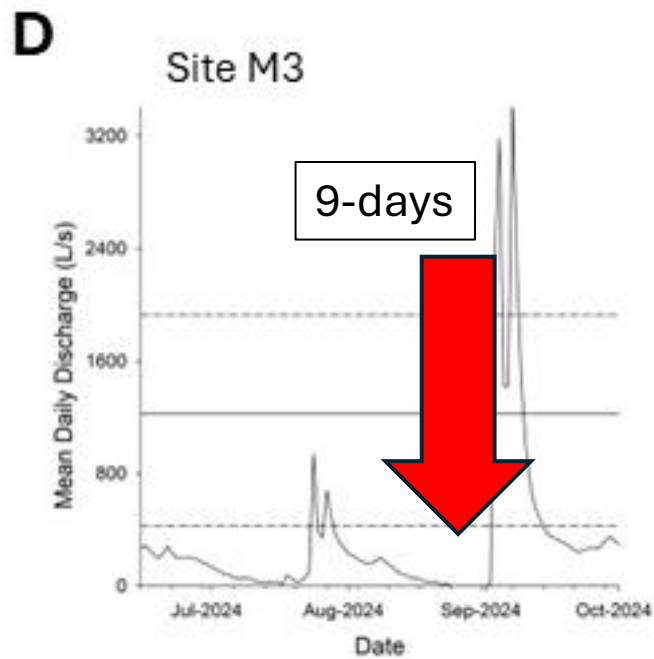
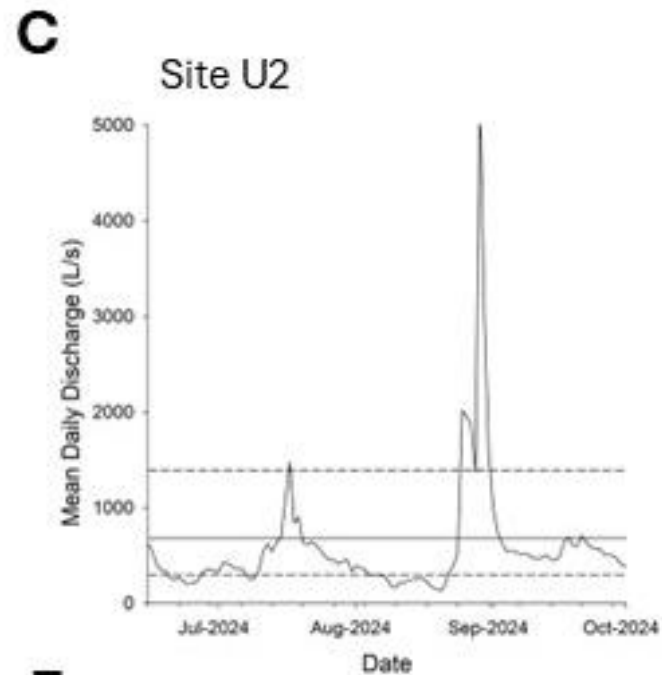
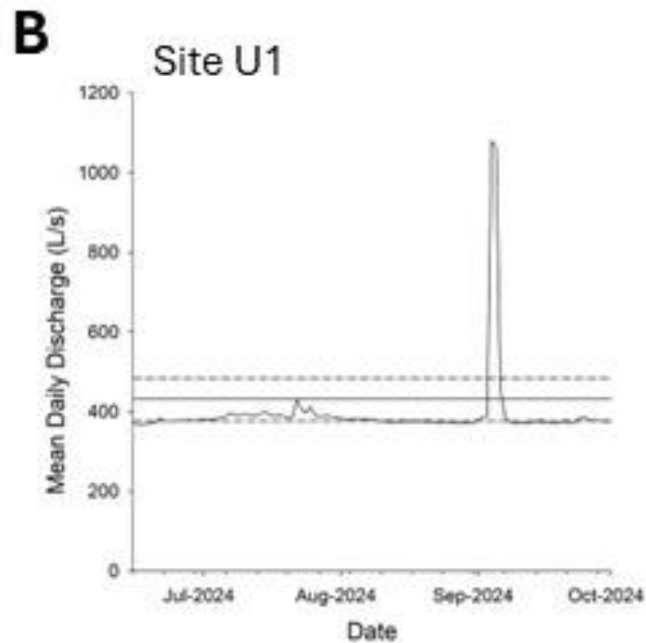
Site M3

**E**

Site L2



**B****C****D****E**



# Methods

- Assessed trophic position of defined “target” consumers
  - Cosmopolitan distribution in the drainage
  - Represent different potential trophic positions
    - Allows assessment of different structural mechanisms for TP
    - Examine potential shifts in diet in same taxon
- Performed analysis of TP and % autochthonous OM in diets of consumers with stable isotopes
  - “You are what you eat (plus or minus some amount).”
  - $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$
  - $\delta^{13}\text{C}$  = food sources (autochthonous *versus* allochthonous)
  - $\delta^{15}\text{N}$  = trophic position

# Target Groups

- *Hexacyllopus*

- Algivorous



- *Thraulodes* and *Tricorythodes*

- Collectors



- Chironominae

- Collector



- *Corbicula fluminea*

- Collector - filterer



- *Argia*

- Predator



- *Cyprinella venusta*

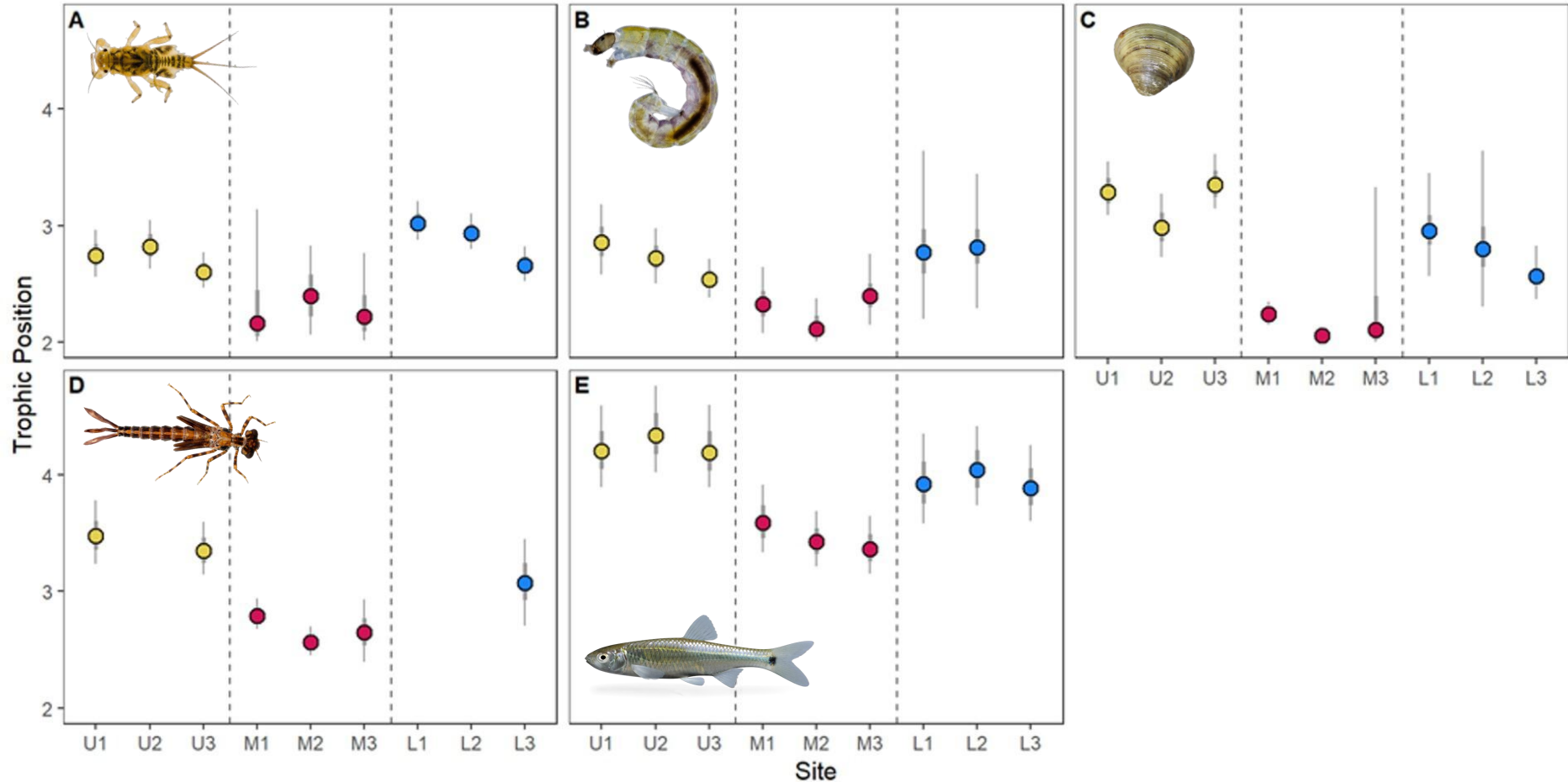
- Predator



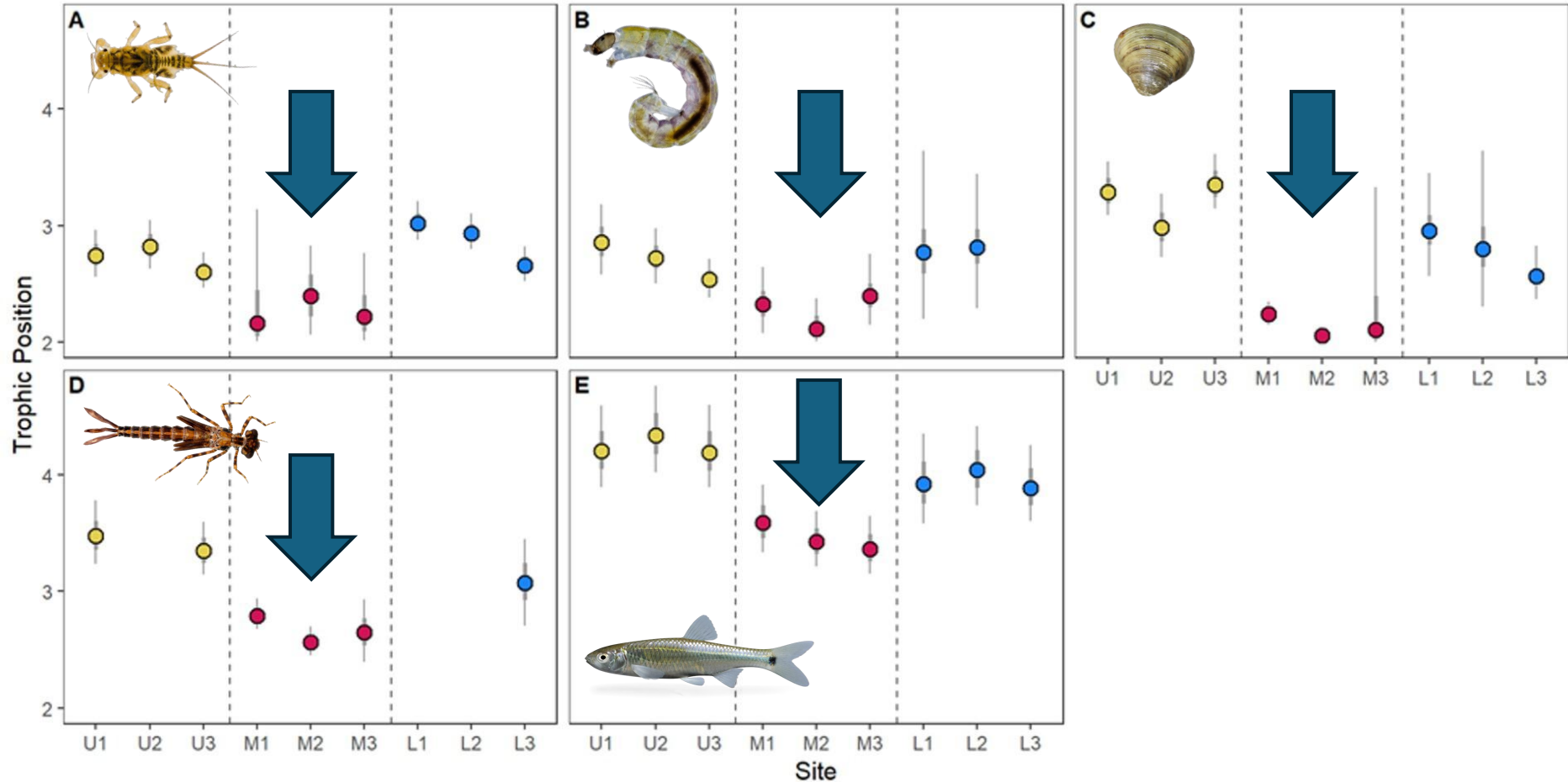
# Isotope Methods and Analysis

- Collected “target” consumers at each site
- Trophic position of each target consumer at each site was estimated with the *trps* package
  - Bayesian estimation of trophic position
    - Posterior probability distribution of estimated trophic position (95% credible interval)
    - Used site-specific baseline (TP = 2) at each site with *Hexacyllopus*
    - TEF = 3.14 ‰
    - $\delta^{15}\text{N}$
- Percent autochthonous OM in the diet of each target consumer at each site ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ )
  - Bayesian dietary mixing model (*MixSIAR* package)
  - Site-specific sources
  - Autochthonous (algal) source = *Hexacyllopus*
  - Allochthonous (terrestrial) source = in-stream leaf litter

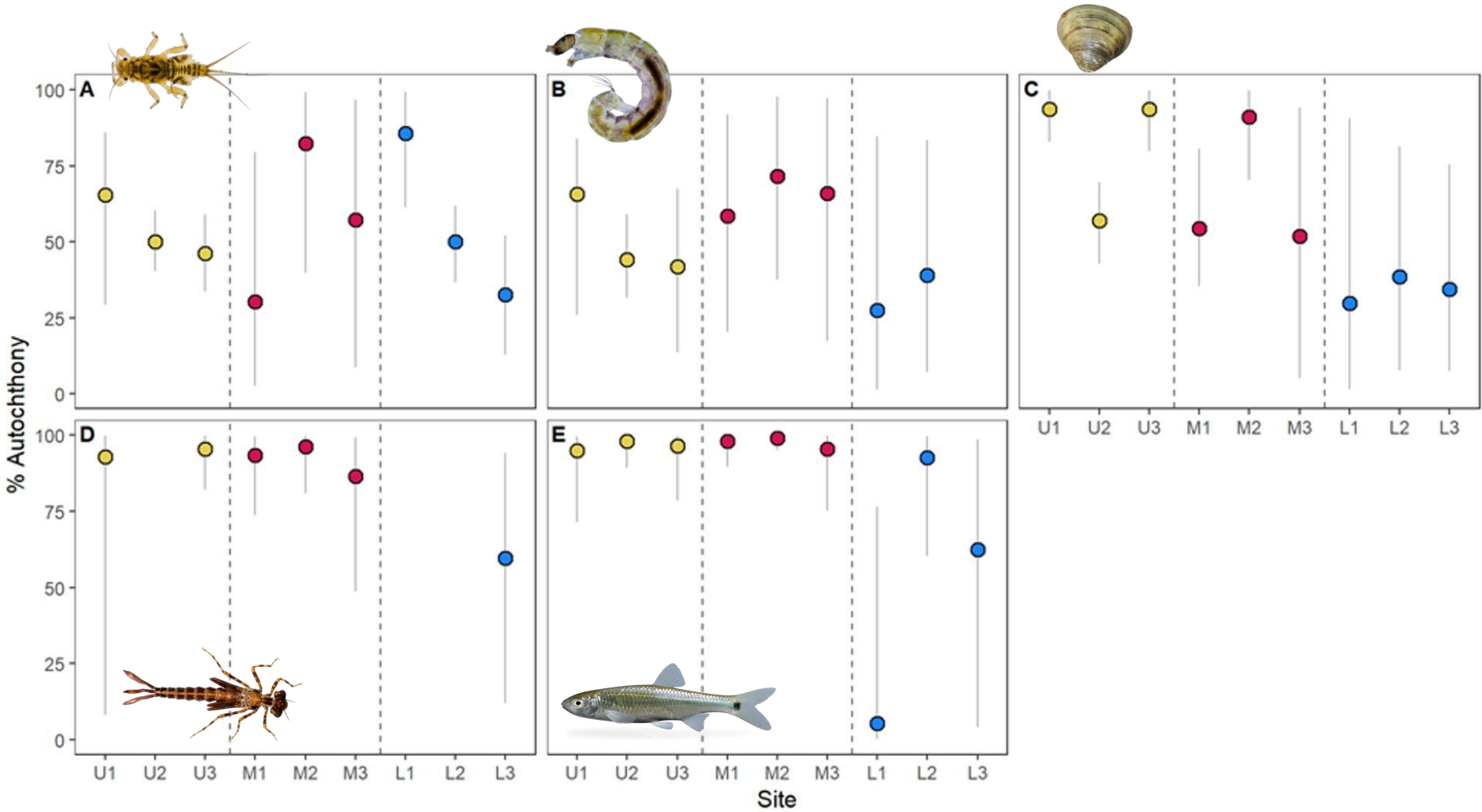
# Trophic Position of Target Consumers



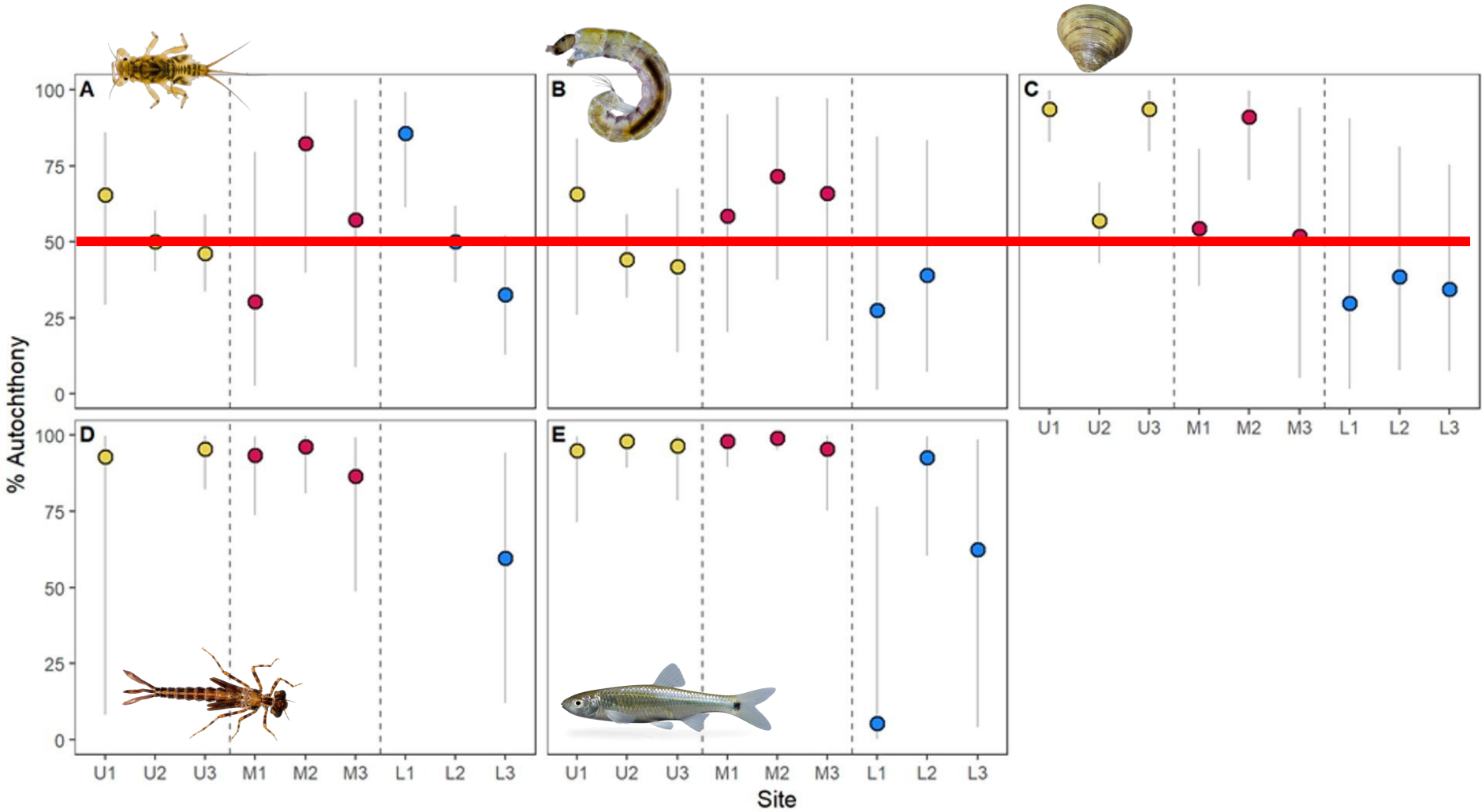
# Trophic Position of Target Consumers



# Percent Autochthony



# Percent Autochthony





# What Does It Mean?



- Trophic position of consumers lower in disconnected Middle Segment
  - ~ 0.5 trophic position across groups
  - Indicates combination of Removal and Omnivory
  - Deletion of highest consumers hard to capture
- Autochthonous dominance did not vary with intermittence
  - Collectors = mix of autochthonous and allochthonous
  - Predators = autochthonous OM
  - Lower reach = ??????



# Overall Conclusions



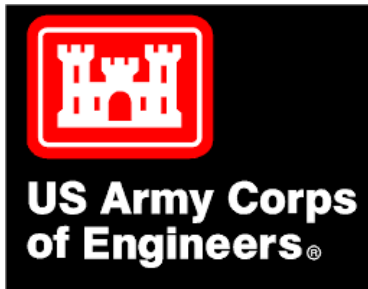
- Allochthonous resources important in semi-arid rivers
- Intermittency affects decomposition and trophic dynamics
- Microbial decomposition dominates detrital processing
  - Lack of shredders
- Invertebrates utilize leaf packs and affect mass loss
  - Importance of invertebrates varies with (1) temperature and (2) their density
  - Non-trophic reasons, but have an effect
    - Mechanisms?
- Lower-level invertebrates (collectors) represent a mix of autochthonous and allochthonous resources
- Predators appear to be highly dependent on green food chain
  - Assimilative efficiency greater or prey preference?

# Acknowledgements

## Students and Staff

Matthew Stehle, Kirby Marceau, Jasmine Rodriguez, Ashley Casarez, Jessica Kittridge, Ailish Collins, Jered Davenport, Hannah Mattes, Derreck Harris, Hannah Madler, Rachel Hill, Orion Mistry-Hovsepian, Incy Rojas-Pina, Hannah Bates, Spencer Sliter, Andrew San Miguel, Chloe Harrell, Al Wilson

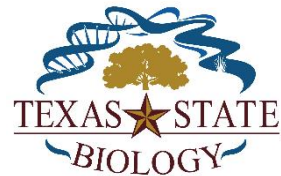
## Funding

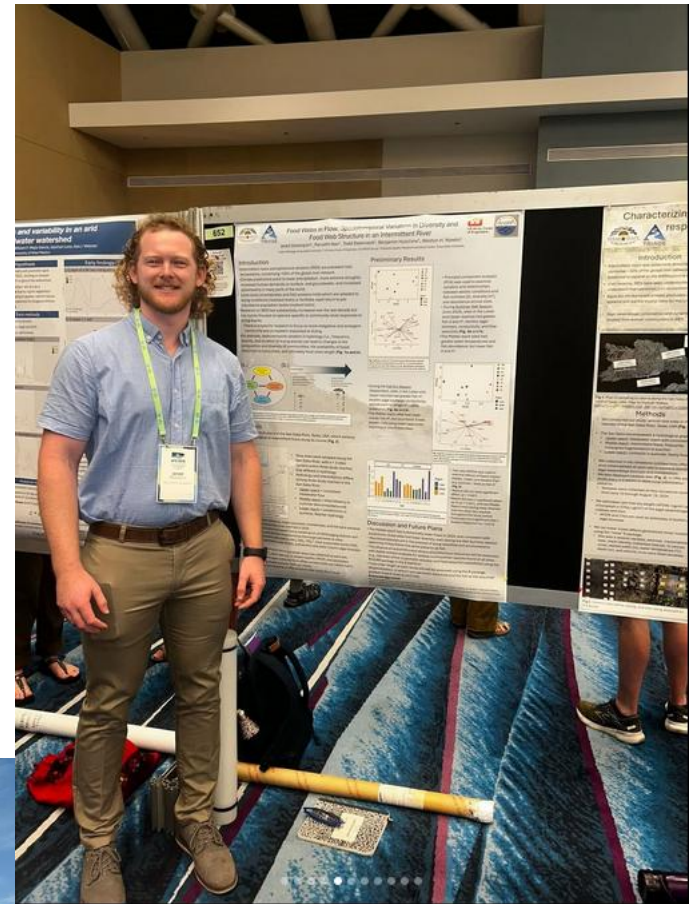


## Collaborators

Benjamin Schwartz, Astrid Schwalb, Josh Perkin, Tonya Ramey, Benjamin Hutchins, Matthew Chumchal, Paula Furey, Parvathi Nair

Todd Swannack, Aubrey Harris, Candice Piercy





# Invertebrates *versus* Microbes

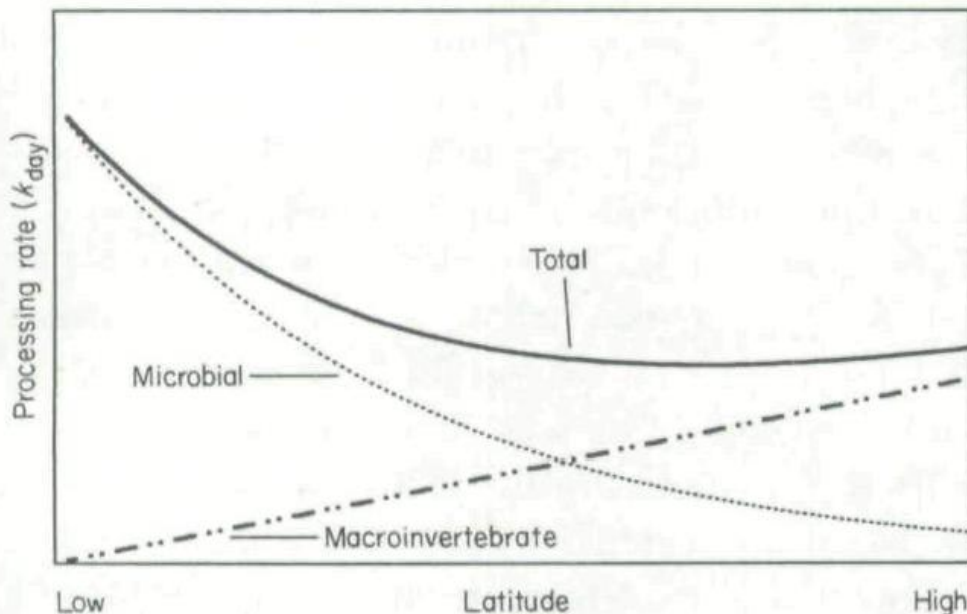


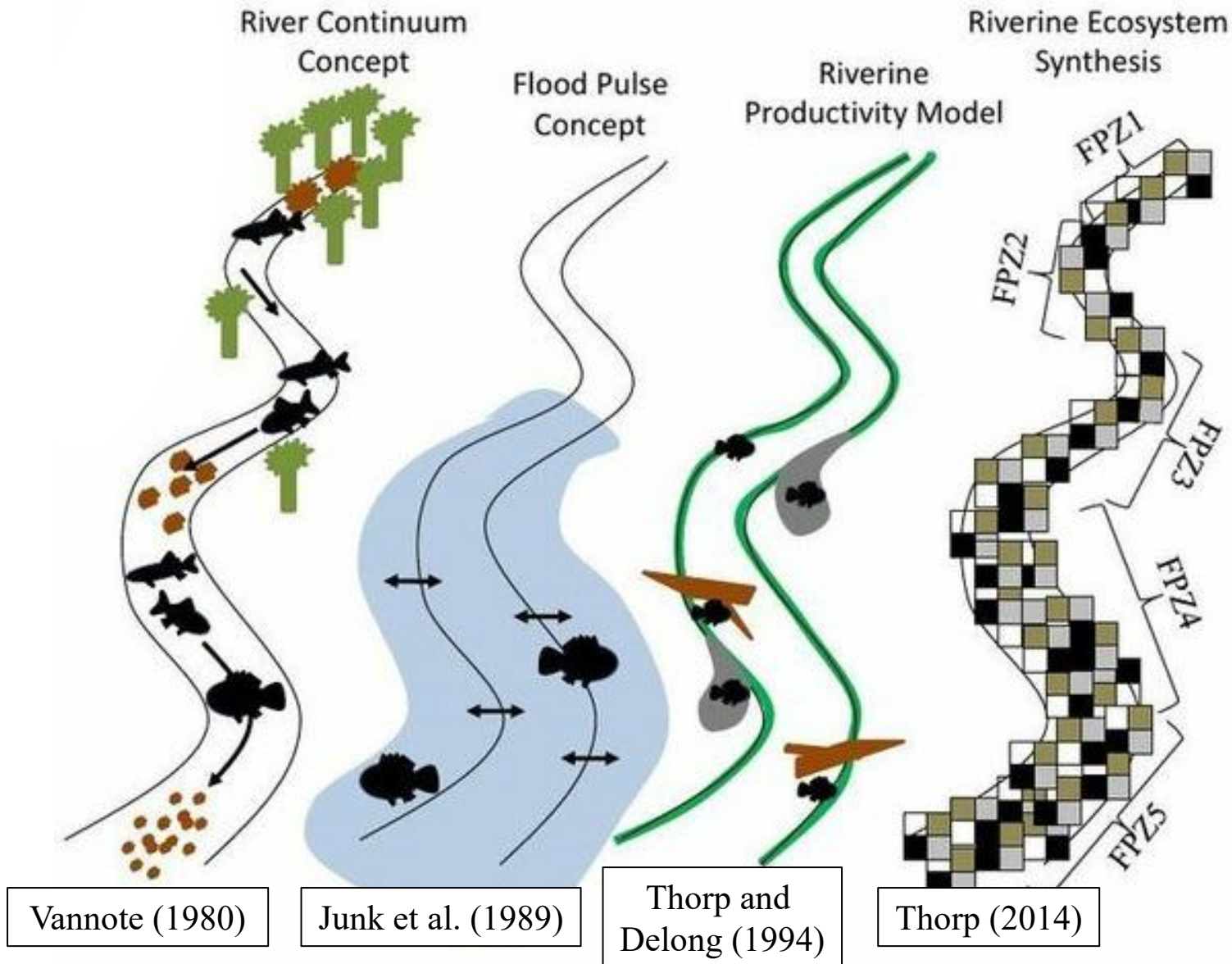
Fig. 5 Conceptual model of the relative contributions of microbial and invertebrate processing to total leaf litter breakdown rates on a per day basis.

Irons et al. (1994). *Freshwater Biology*

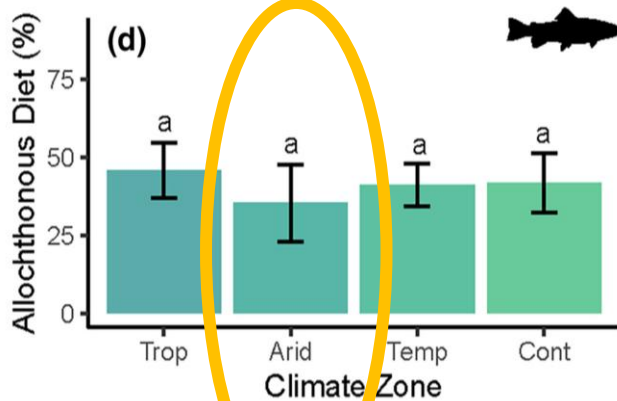
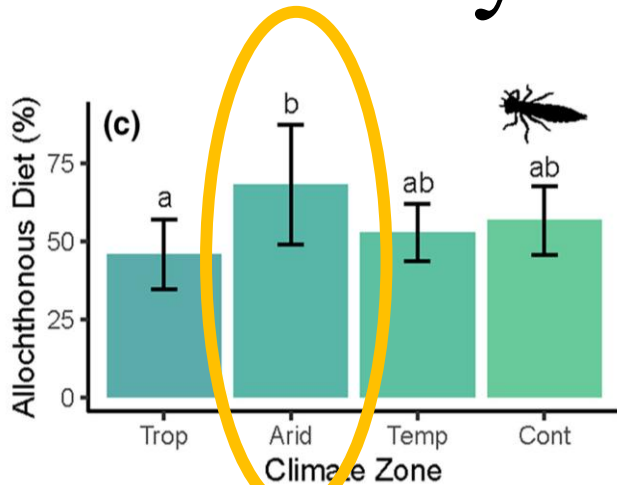
## Rationale

- Microbial metabolism more sensitive to temperature than invertebrates
- Lower densities of shredding insects
  - Biogeography and diversity of shredders highest in cold water systems

# Allochthony in Conceptual Models

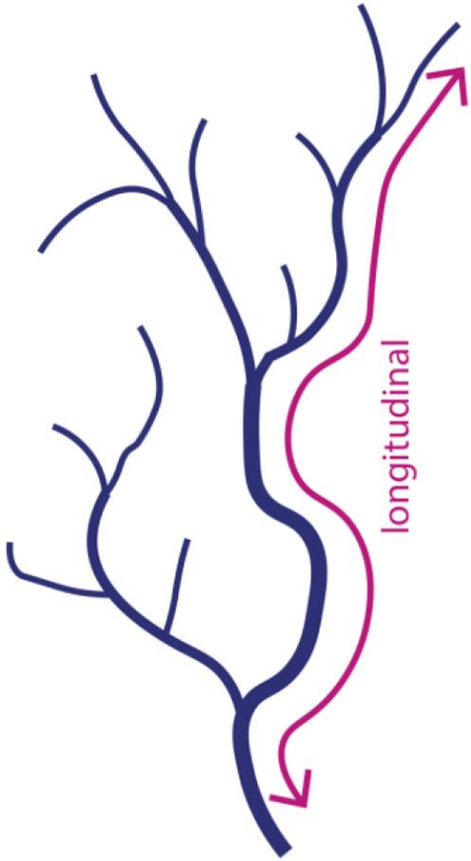


# Allochthony and Semi-Arid Rivers

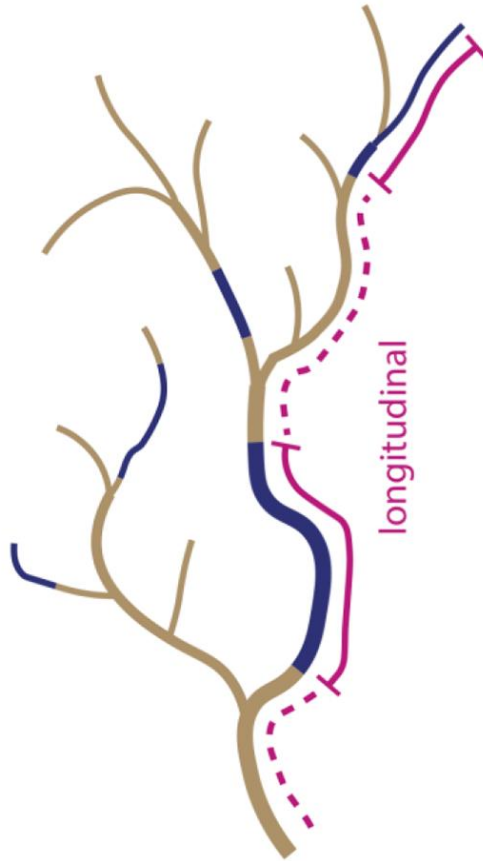


- Allen et al (2024), *Ecology Letters*
  - Not consistent with predictions
  - Context dependency
- Role of decreased seasonal variation?
  - Rivers = sub-humid (31° to 28° N latitude)
- Role of flow intermittency?
  - Spatiotemporal variation in

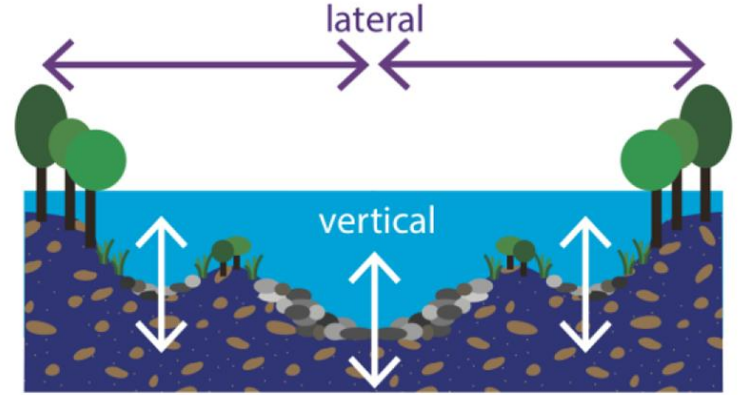
a) wetted river network, longitudinally connected



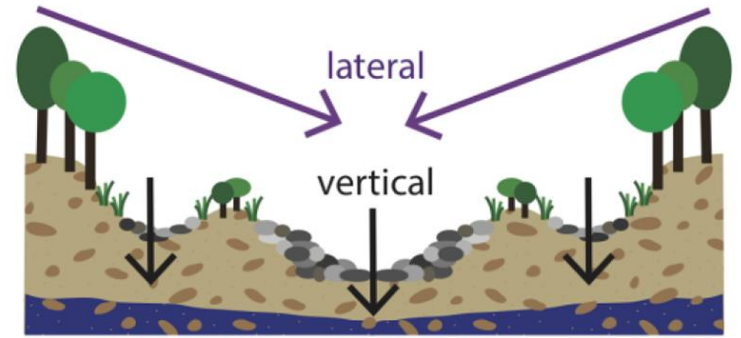
b) wet and dry river network, longitudinally disconnected

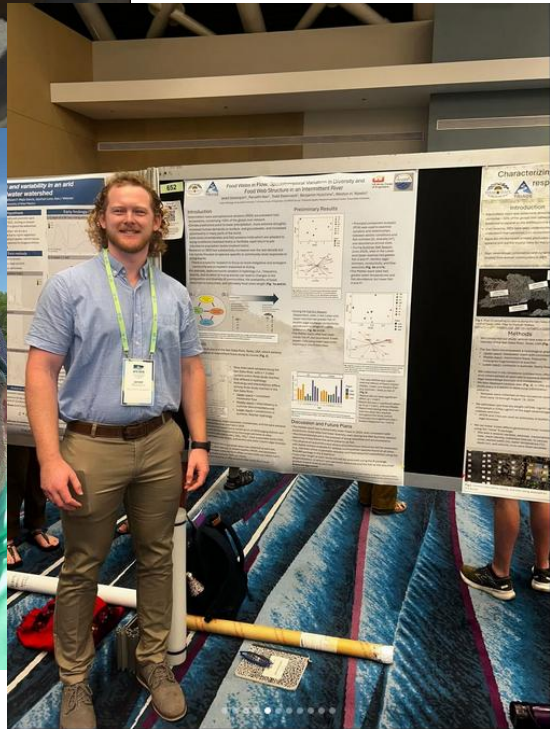
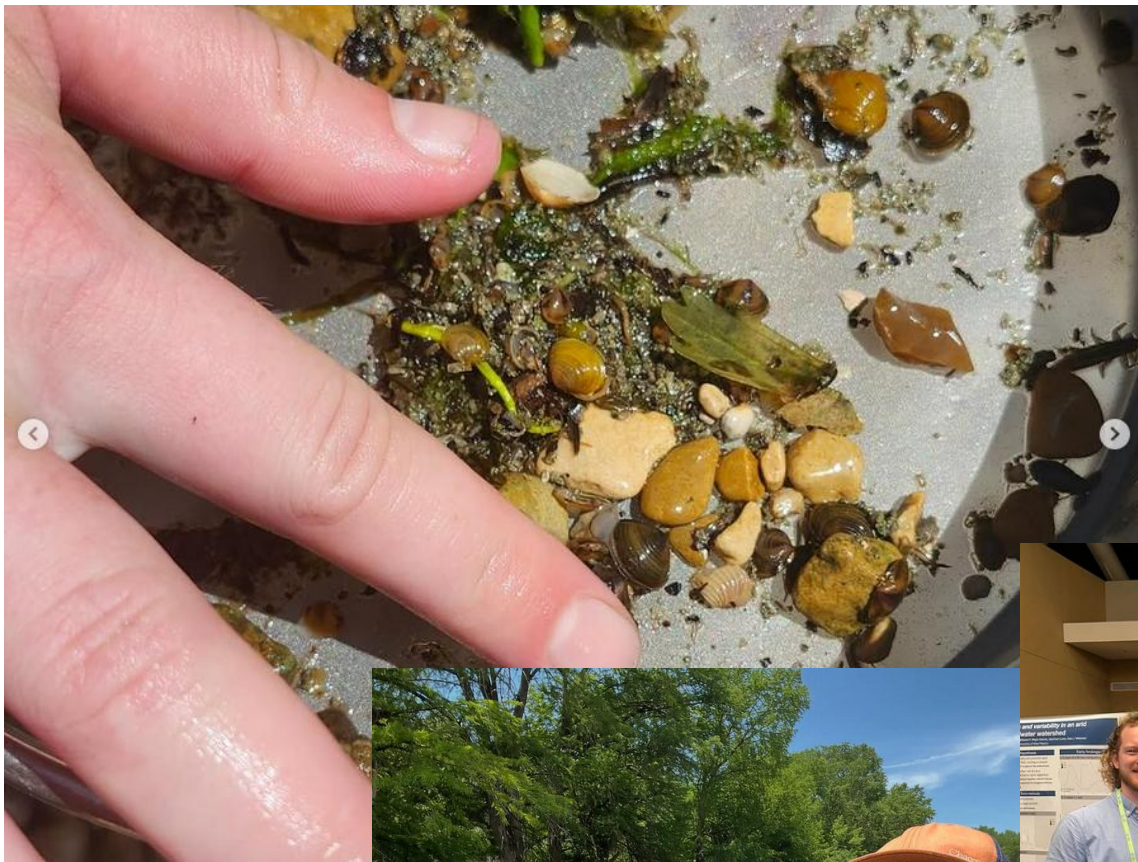


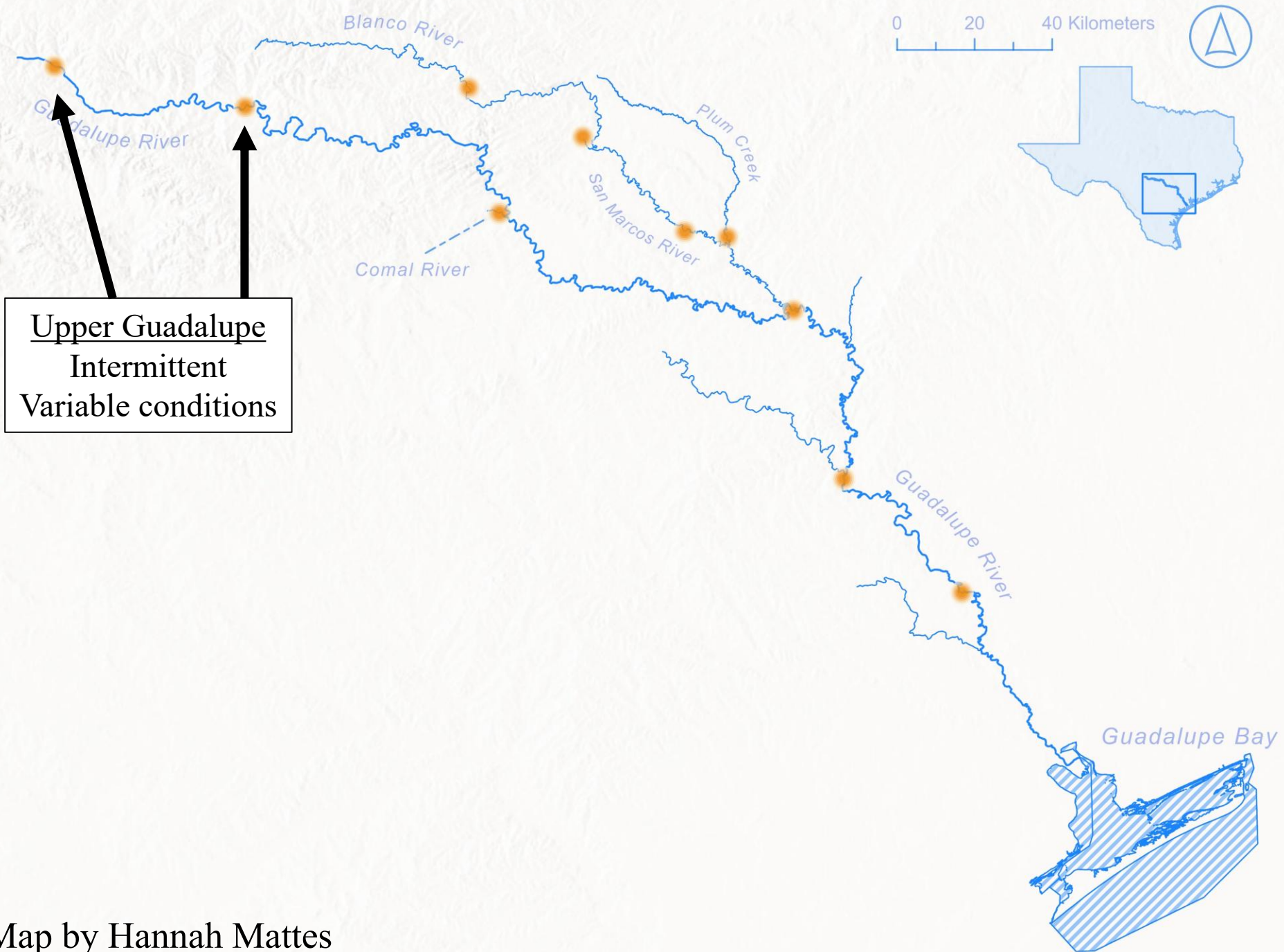
c) river cross-section at overbank flood stage, lateral and vertical continua bidirectional



d) river cross-section at dry channel stage, lateral and vertical continua unidirectional

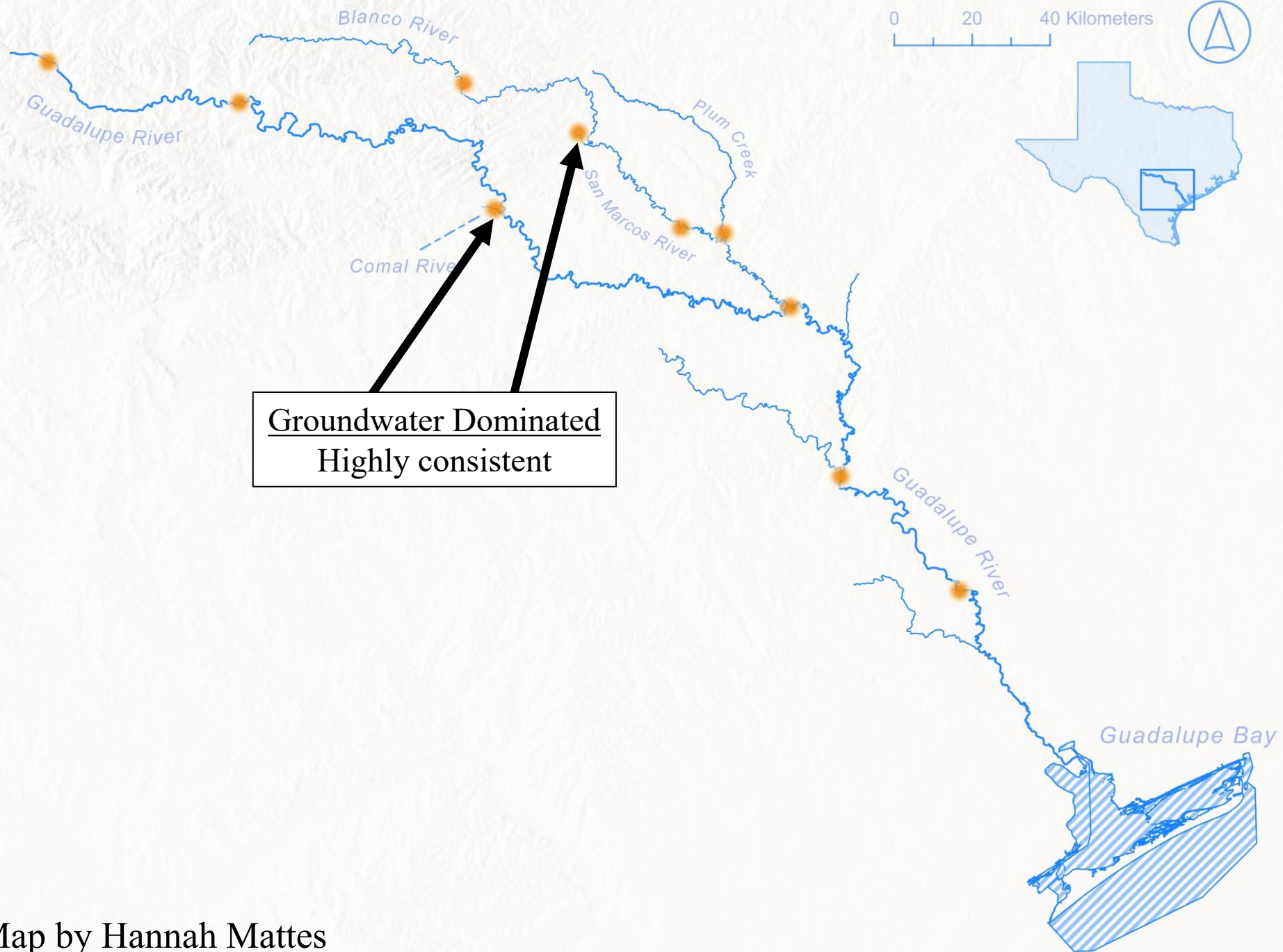






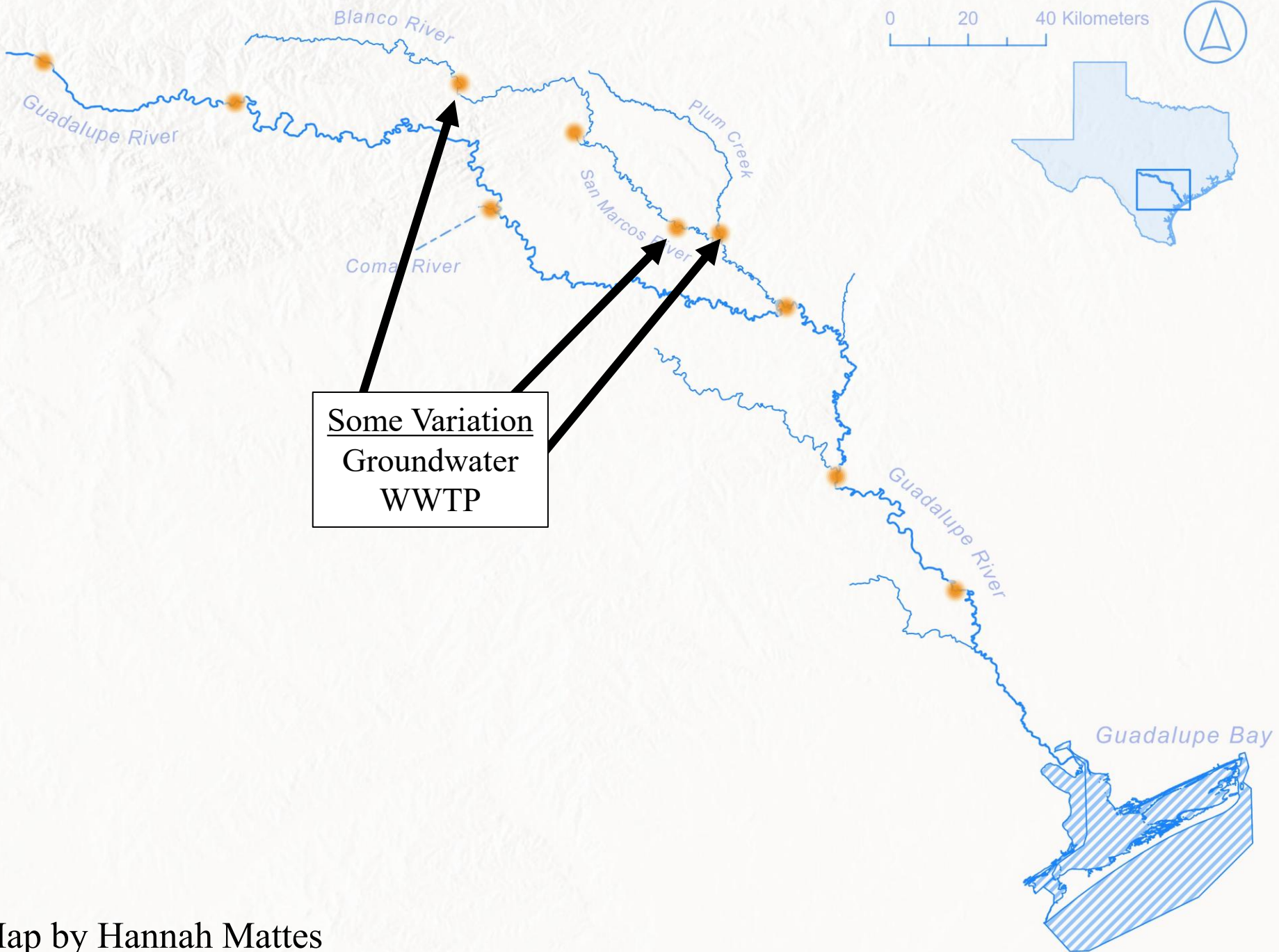
Upper Guadalupe  
Intermittent  
Variable conditions

Map by Hannah Mattes



Groundwater Dominated  
Highly consistent

Map by Hannah Mattes



Map by Hannah Mattes



Map by Hannah Mattes

# Factors Affecting Decomposition

