How do spatial flows of resources drive ecosystem stability and productivity?

Theoretical insights from meta-ecosystem models

Isabelle Gounand and Benoît Pichon

Chaire MMB, Paris 25/04/2022

cross-ecosystem resource spatial flows

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- ubiquitous
- important for ecosystem functioning
- sensitive to perturbations

salmon carcasses

Helfied & Naiman
2002 Oecologia

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terrestrial arthropods

~300
$g.m^{-2}.yr^{-1}$

Inoue et al. 2013 Ecol. Fresh. Fish

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Deacy et al 2017 PNAS

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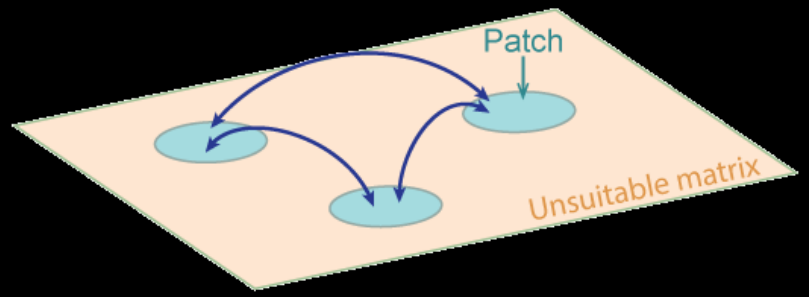
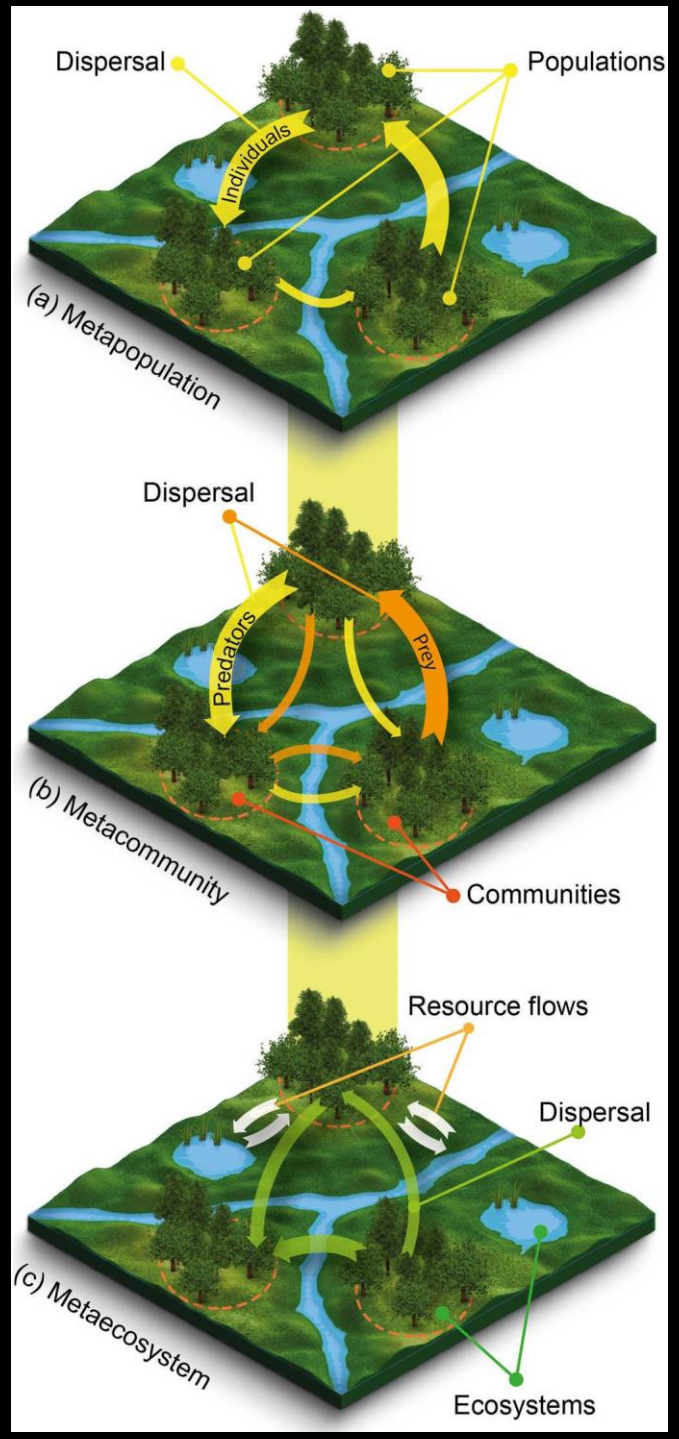
From meta-populations to meta-ecosystems

- Postulates :
  - hierarchy et heterogeneity in spatial structure.
  - connectivity
  - local ecological processes





Schiesari et al. 2019, *Perspectives in Ecology and Conservation*

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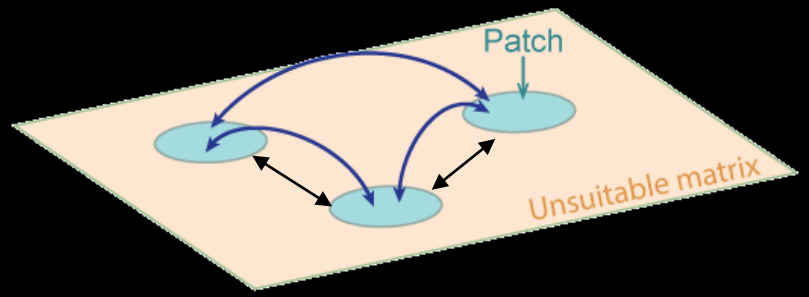
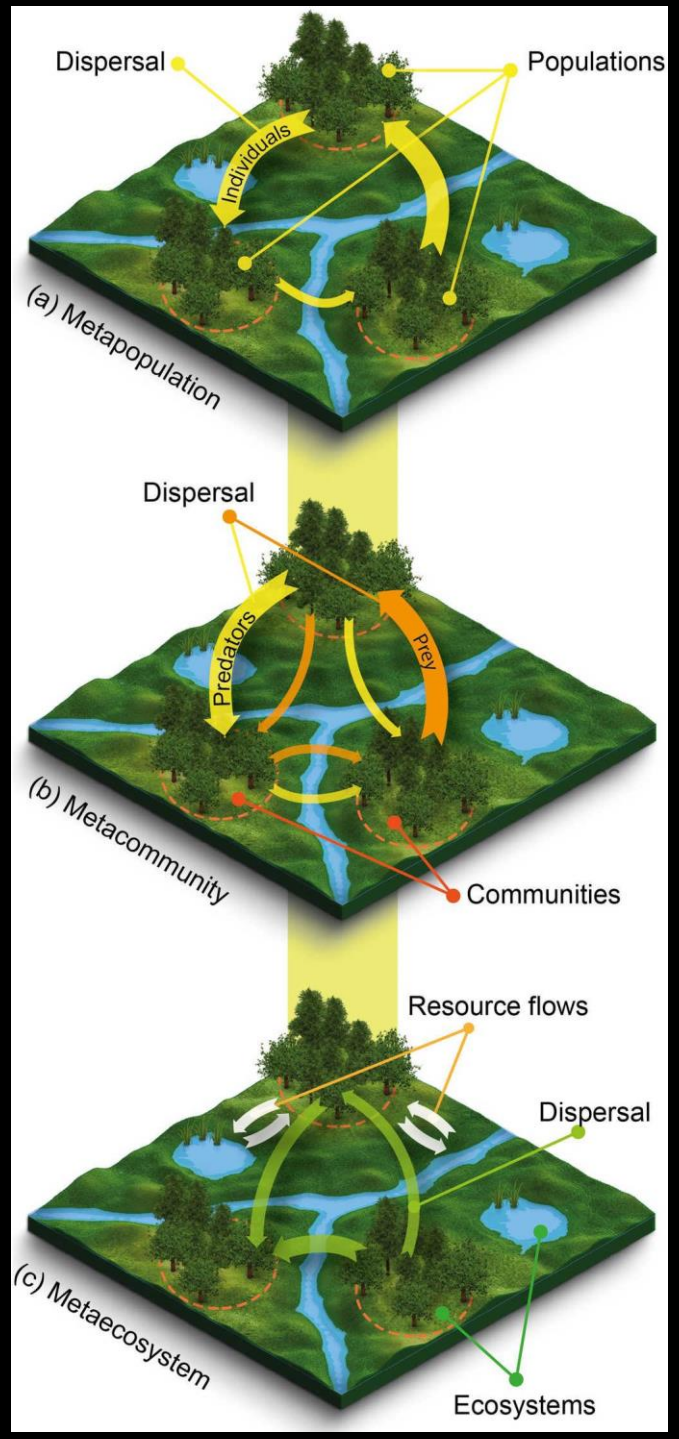


- Meta-ecosystems: adding resource flows & recycling



Schiesari et al. 2019, *Perspectives in Ecology and Conservation*

OUTLINE

1) How do spatial flow affect ecosystem structure and stability in simple meta-ecosystem models? (*Isabelle Gounand)*

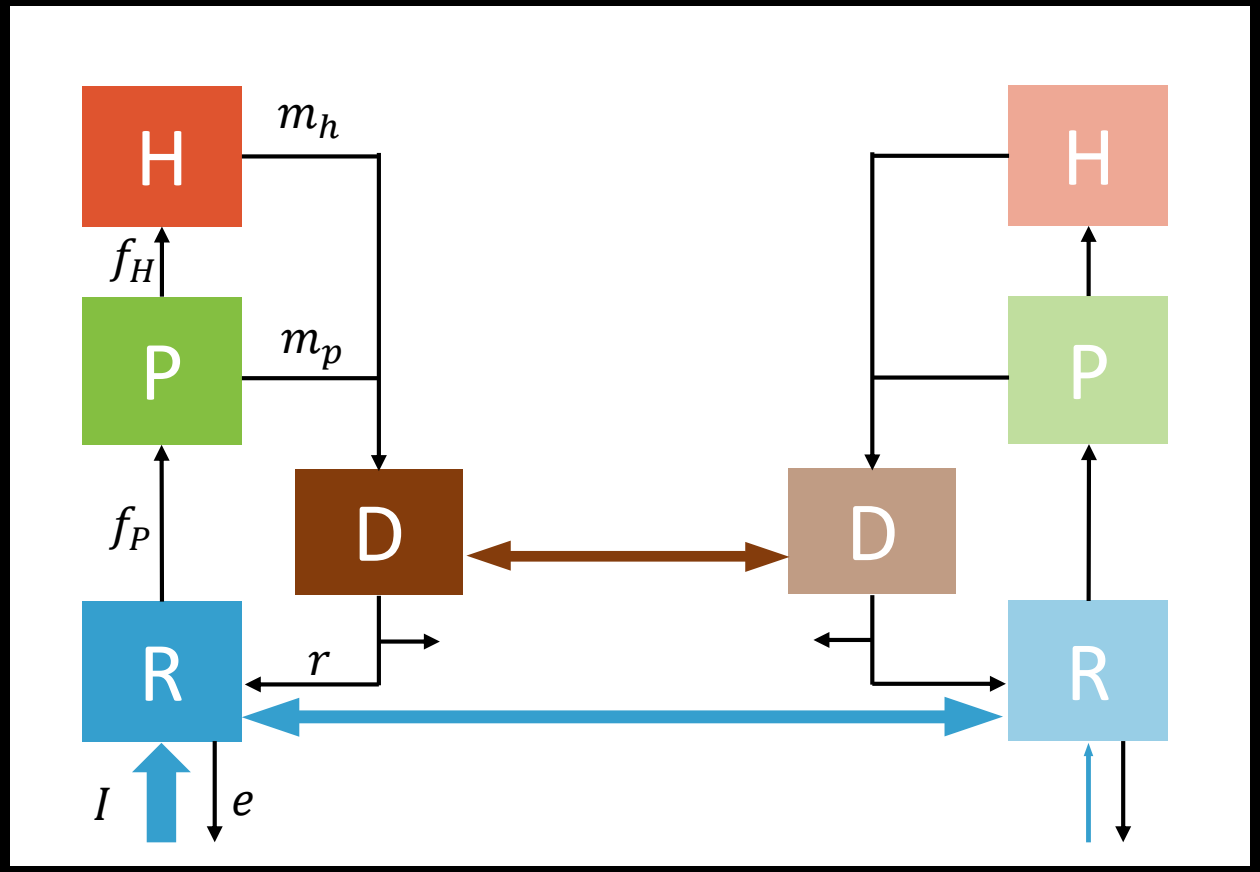
   ⇒ *Empirical observations on resource spatial flows*

2) How does spatial flow stoichiometry constrains ecosystem productivity in a heterogeneous meta-ecosystem model *(Benoît Pichon)*

   => Perspective: Meta-ecosystem at the landscape extent

How do spatial flow affect ecosystem **structure** and stability?

Source-sink dynamics ?



$$\frac{dR_x}{dt} = I_x - eR_x - f_{Px}(R_x, P_x) + r(1 - e_D)D_x + \Delta_{R_x}$$

$$\frac{dP_x}{dt} = f_{Px}(R_x, P_x) - m_p P_x - f_{Hx}(P_x, H_x)$$

$$\frac{dH_x}{dt} = f_{Hx}(P_x, H_x) - m_h H_x$$

$$\frac{dD_x}{dt} = m_p P_x + m_h H_x - rD_x + \Delta_{D_x}$$

Diffusion

$$\Delta_{R_1} = d_R(R_2 - R_1)$$

Gravel et al et al. 2010, *Ecology*

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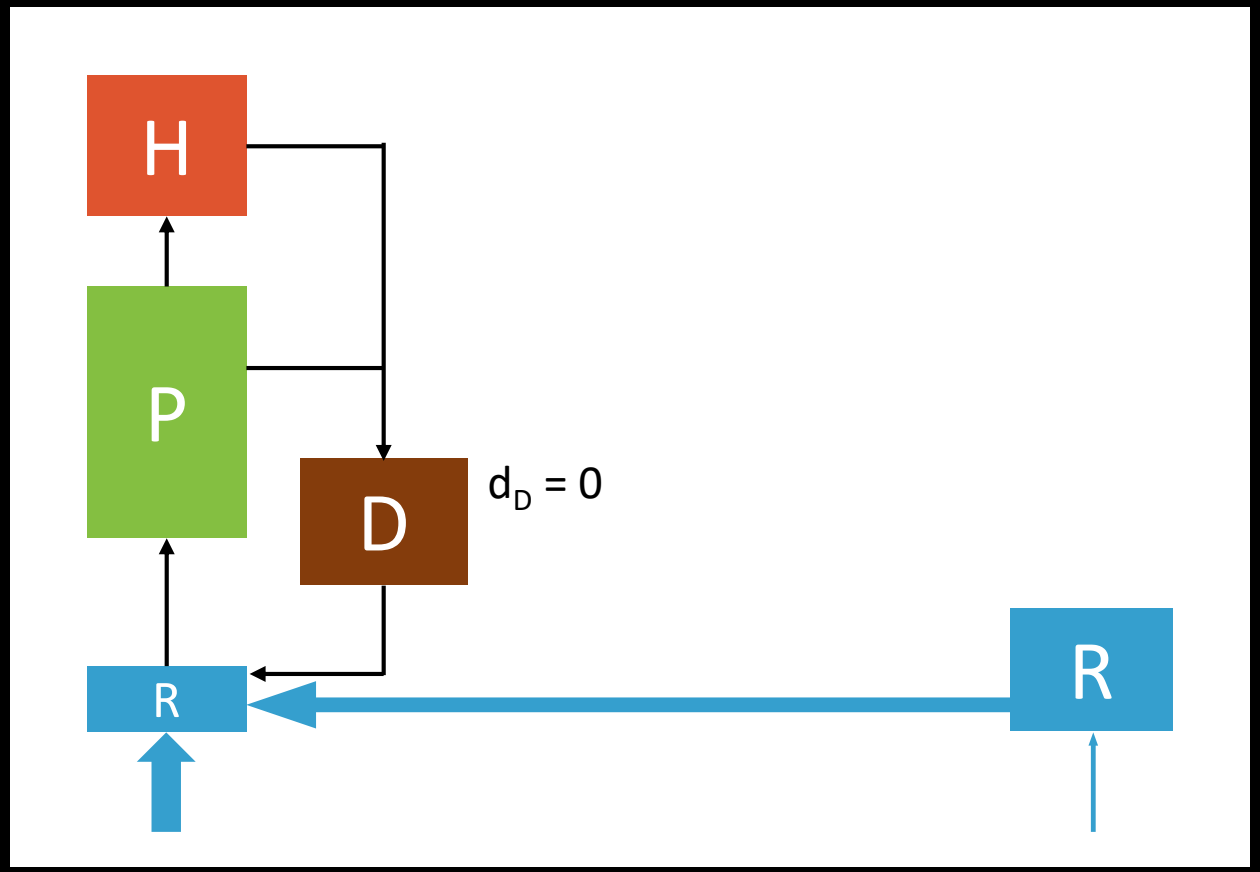

Gravel et al et al. 2010, *Ecology*

Resource flows to the most productive ecosystem

How do spatial flow affect ecosystem **structure** and stability?

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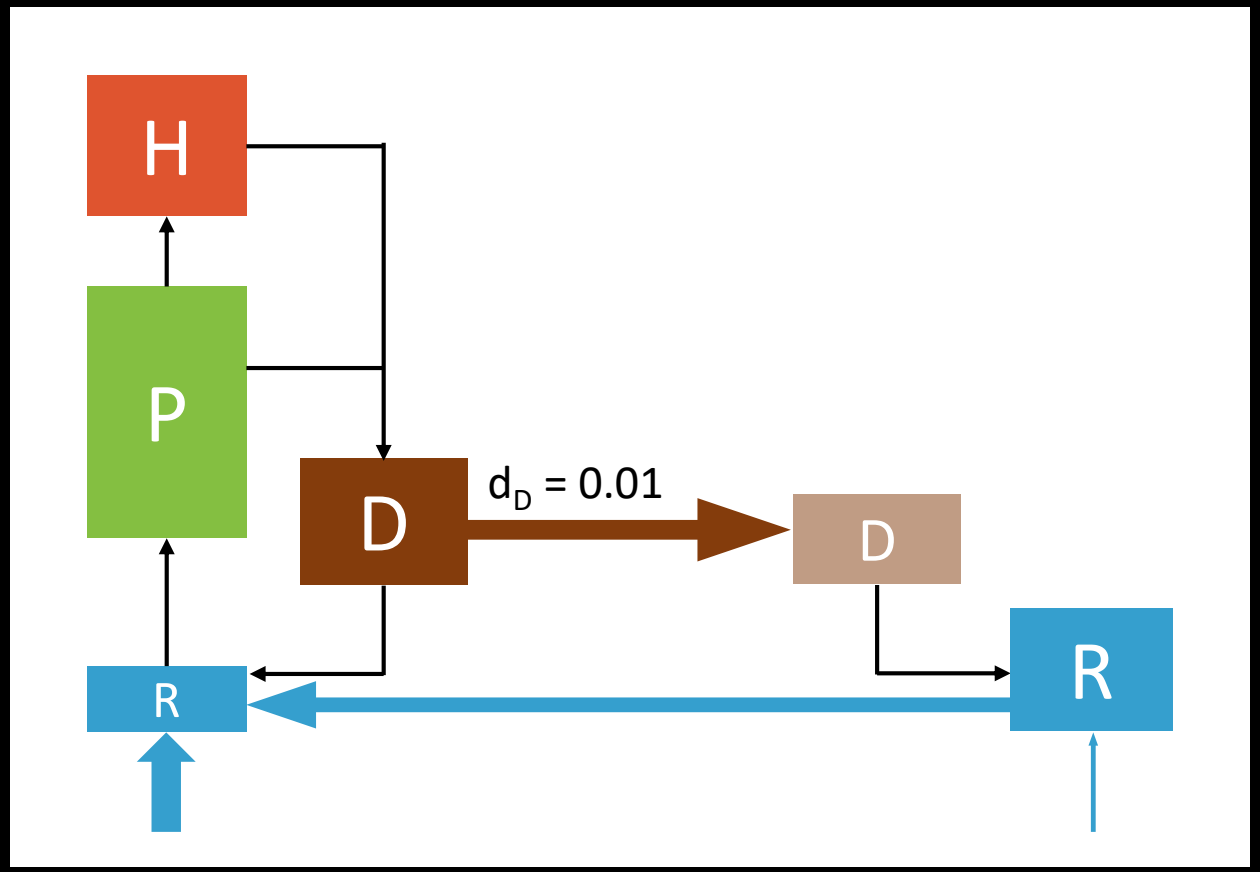
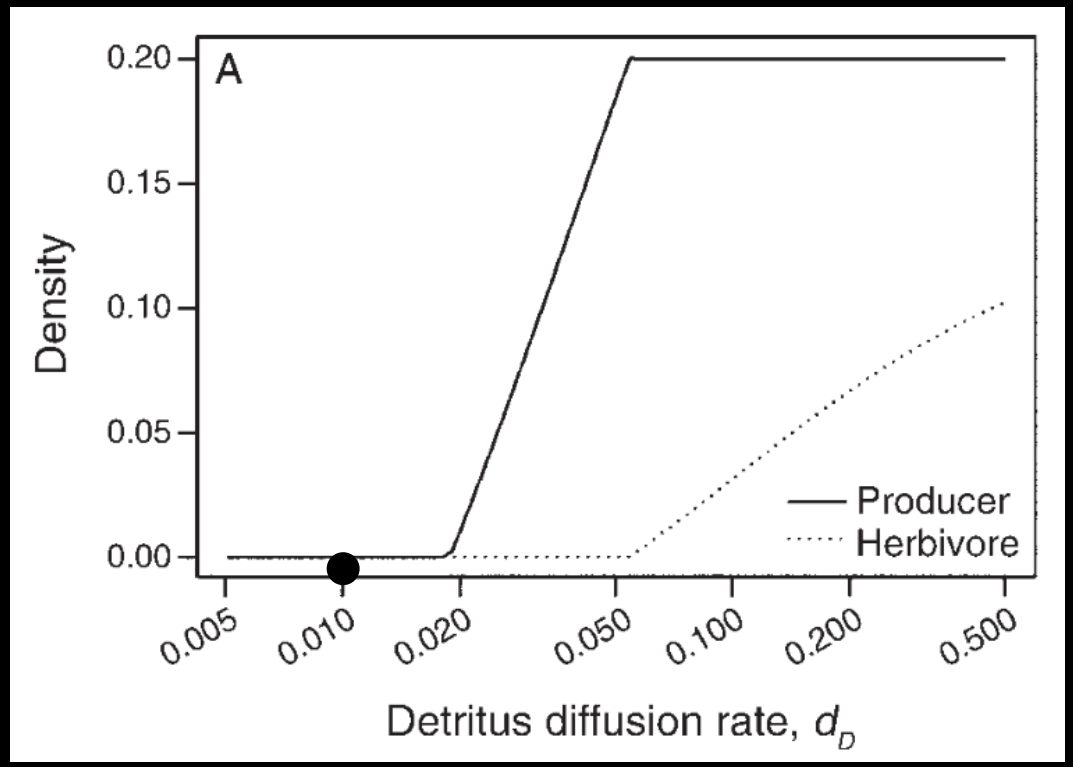


sink patch



Gravel et al et al. 2010, *Ecology*

Detritus flows to the less productive ecosystem

How do spatial flow affect ecosystem **structure** and stability?

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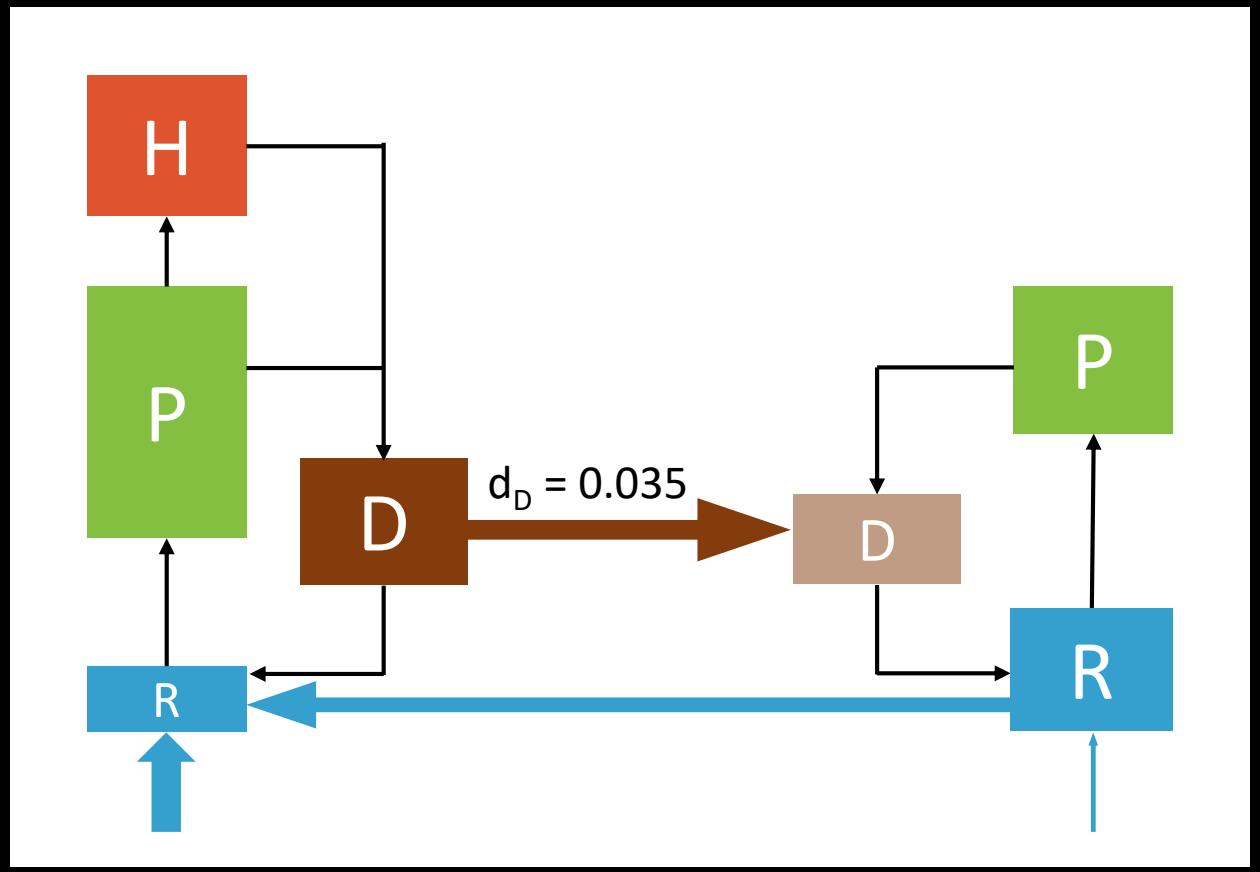

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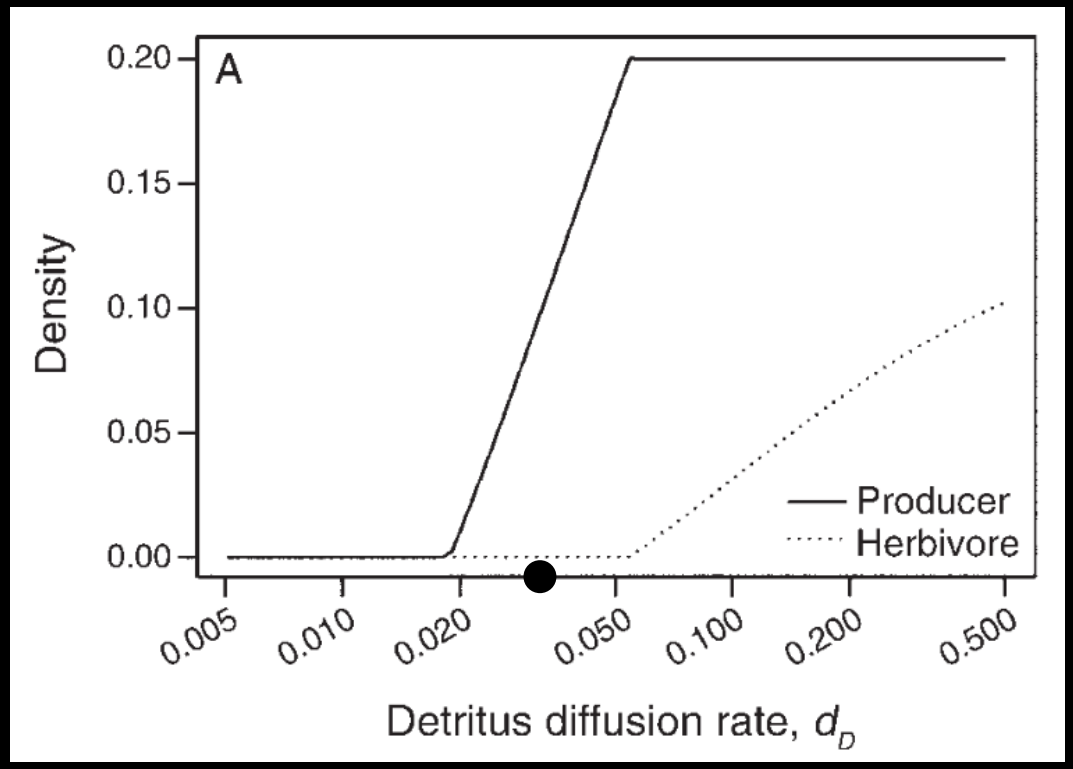

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Detritus flows can increase persistence in poor ecosystems

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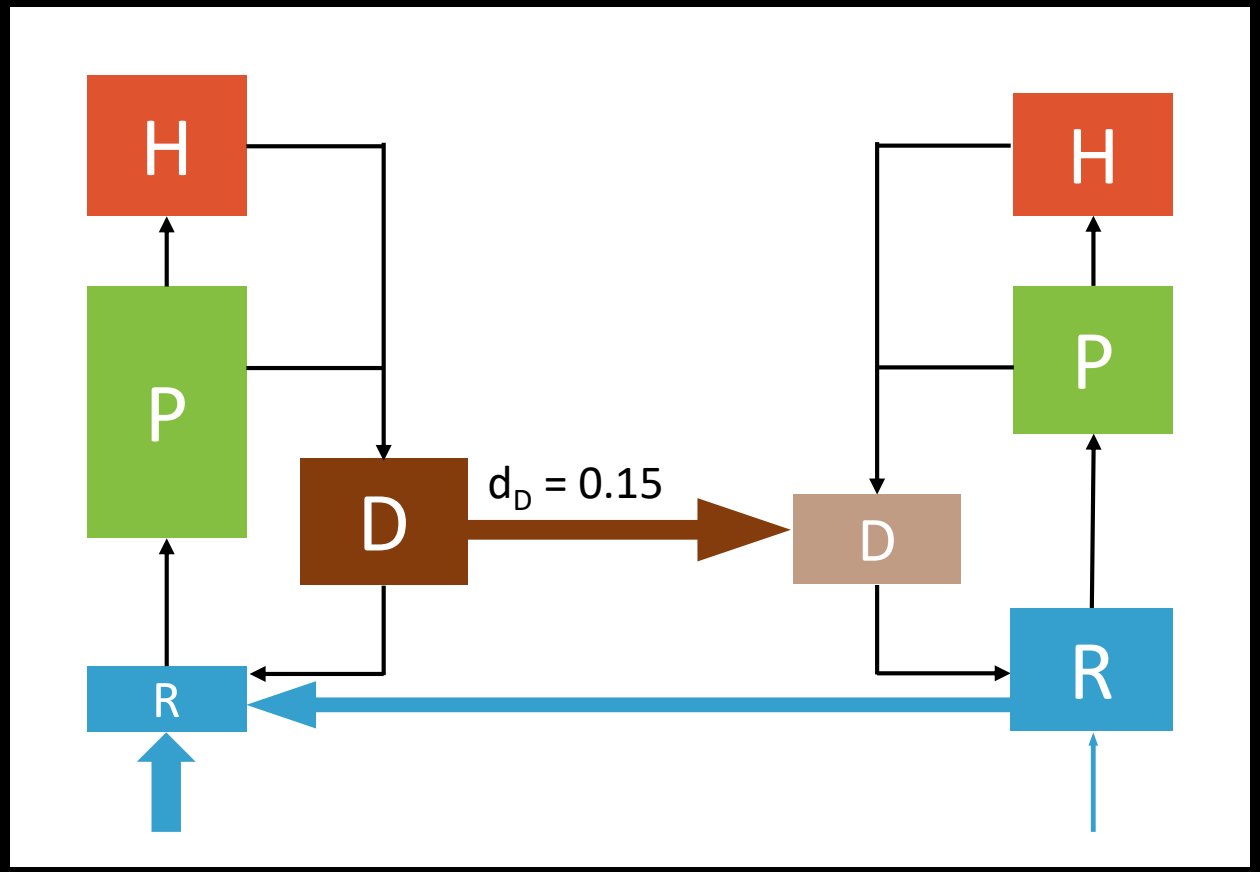

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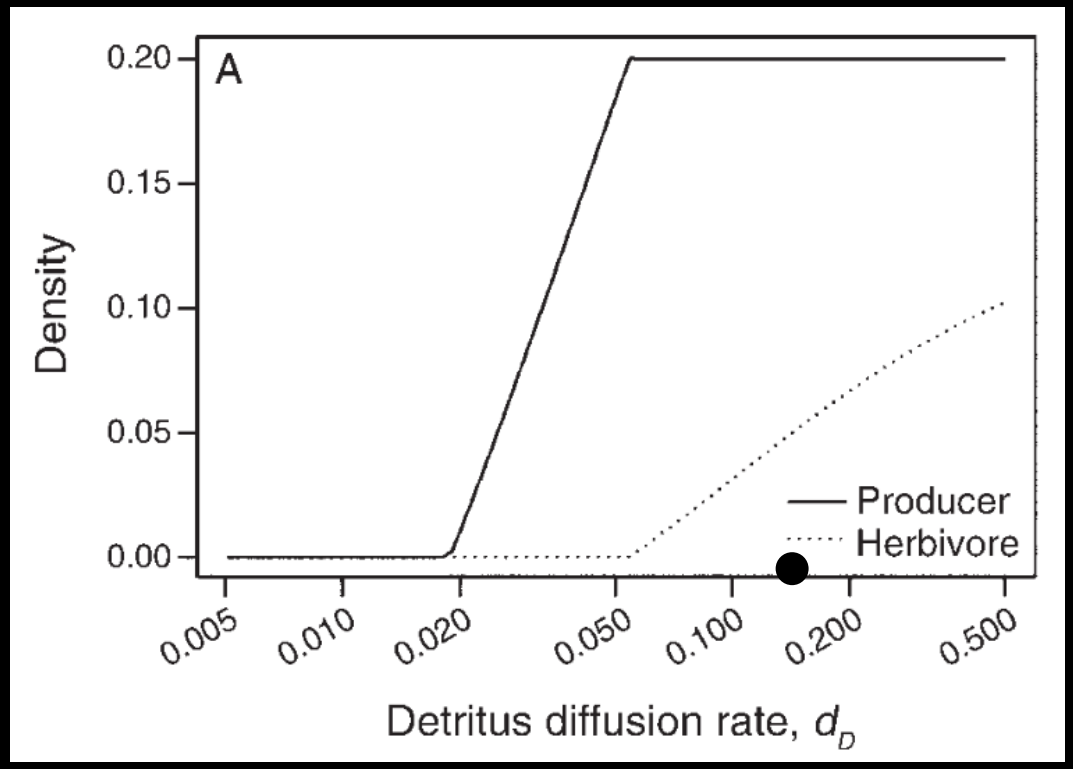

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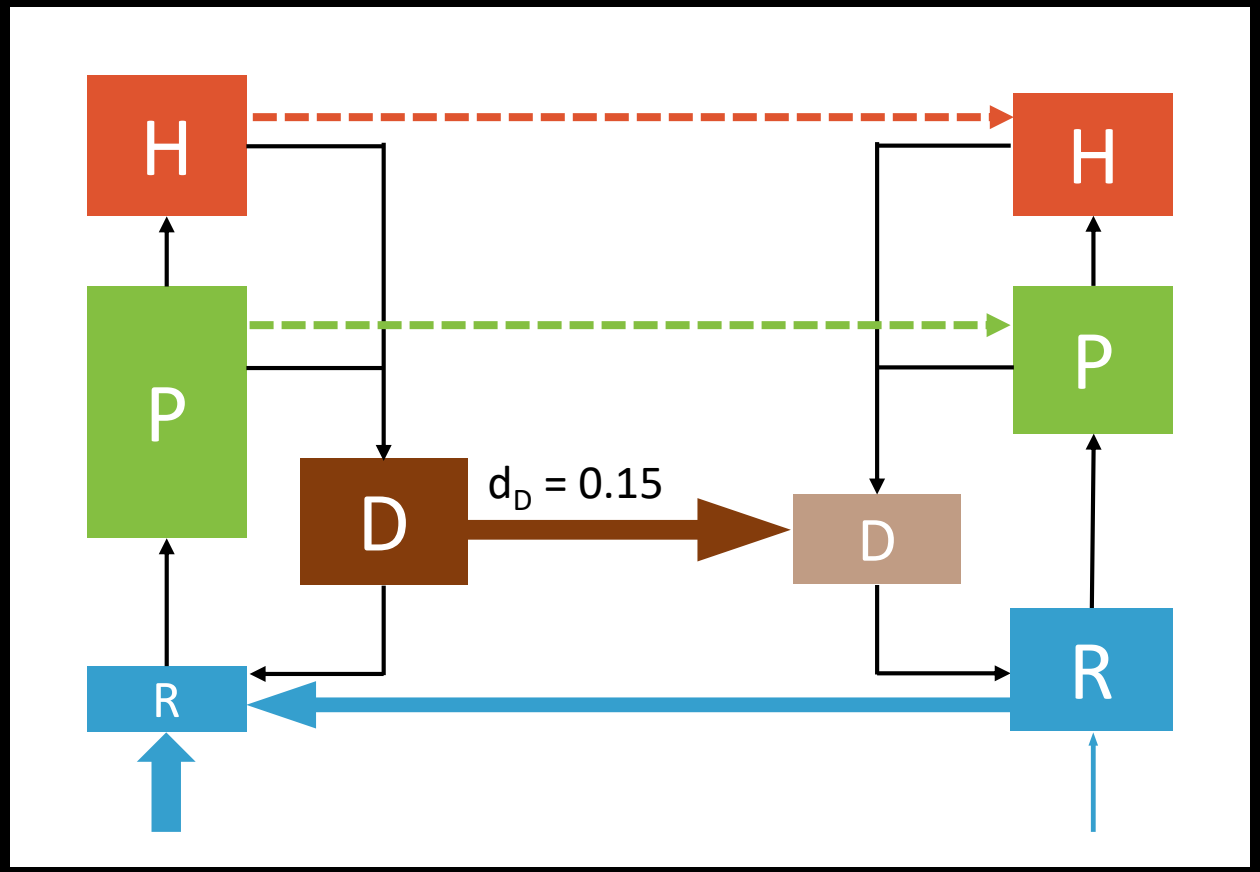

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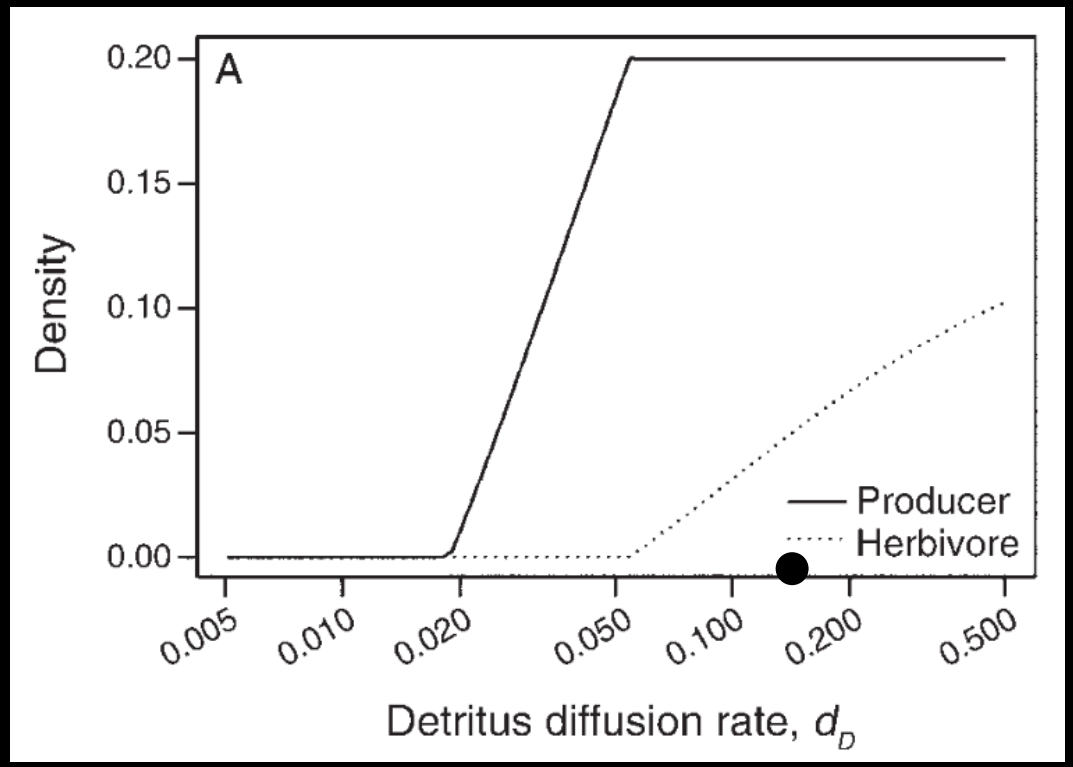
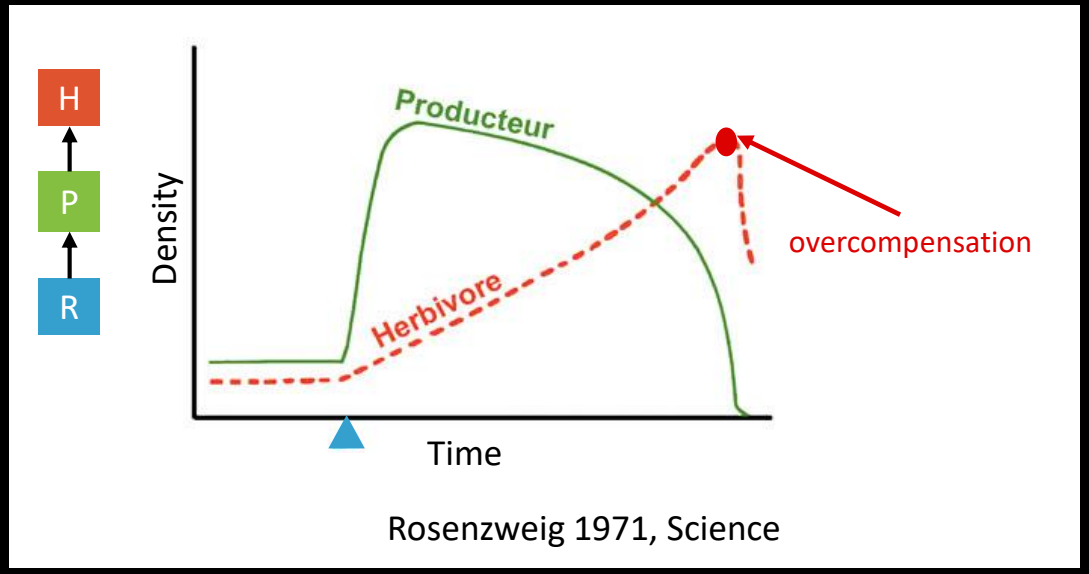


Gravel et al et al. 2010, *Ecology*

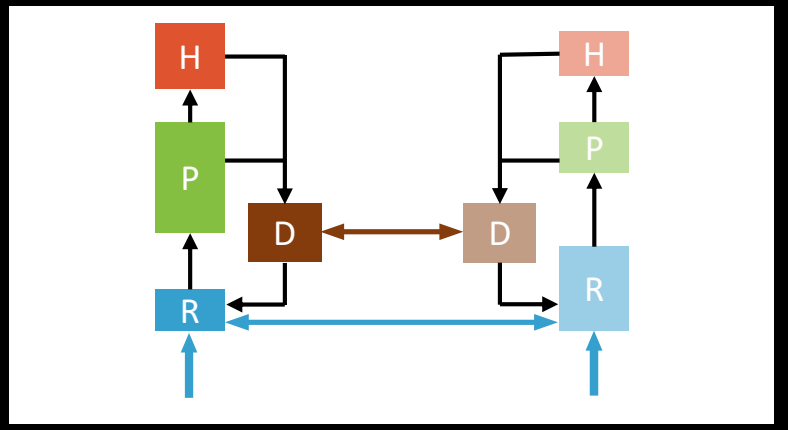
Plant and herbivore flow to the poorest ecosystem

How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems



Rosenzweig 1971, Science



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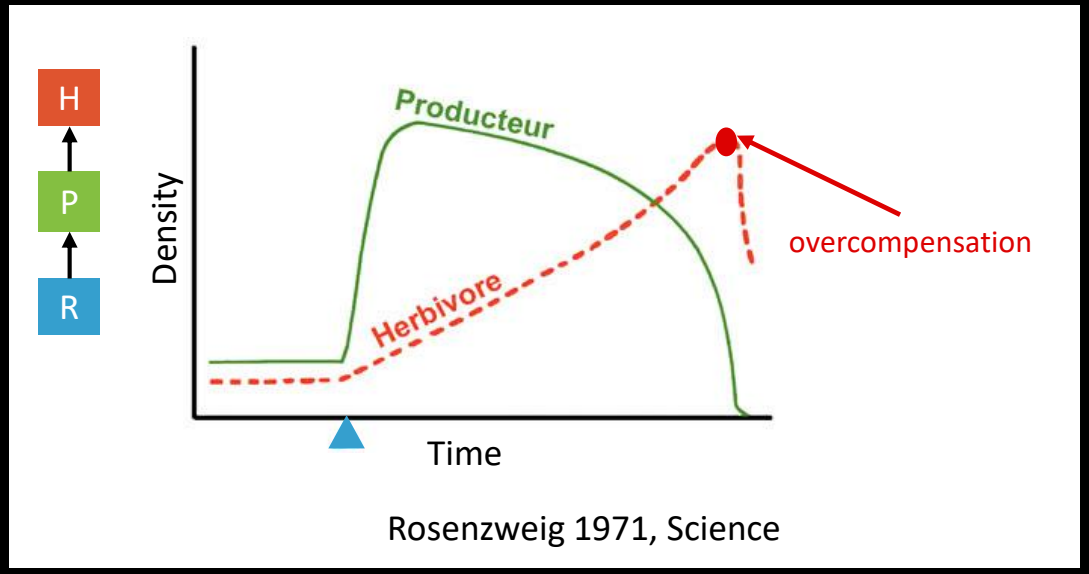

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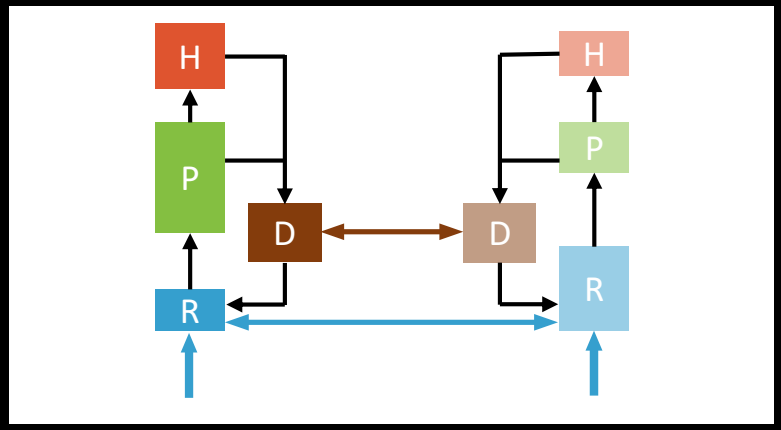
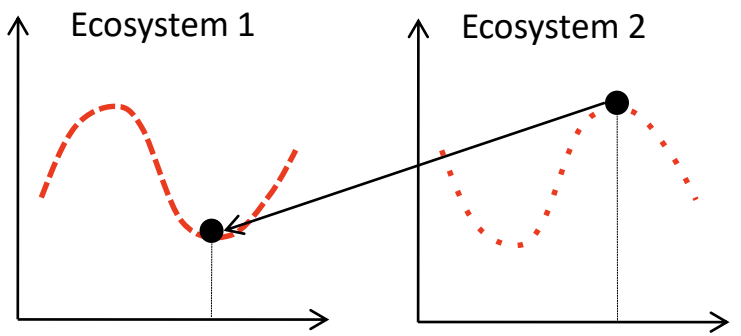


Spatial flows in meta-communities

Stabilizing / Destabilizing



(Jansen 1995, Briggs&Hoopes 2004)

- Does spatial flow dampen enrichment?

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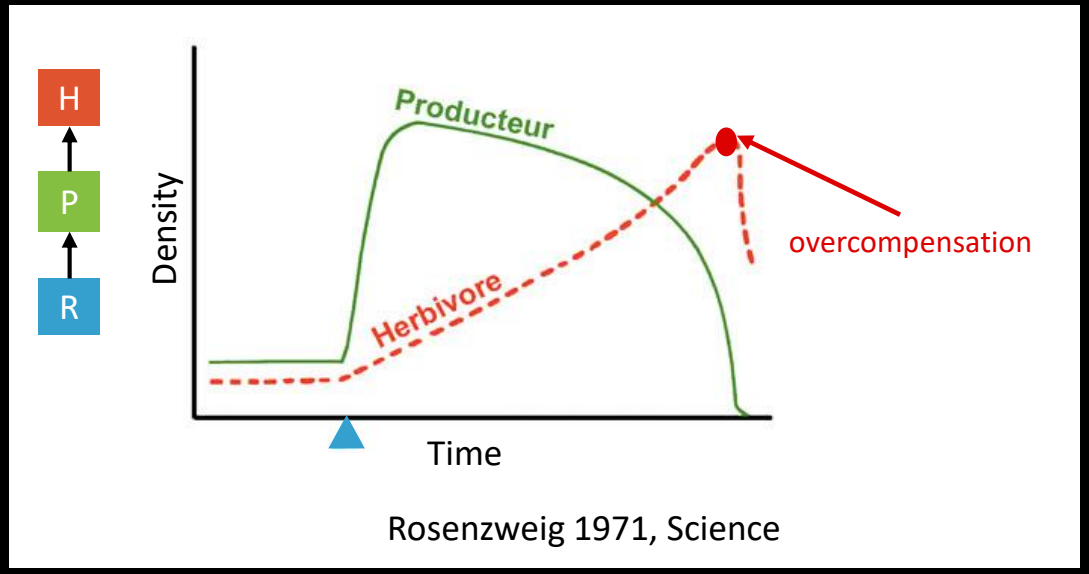

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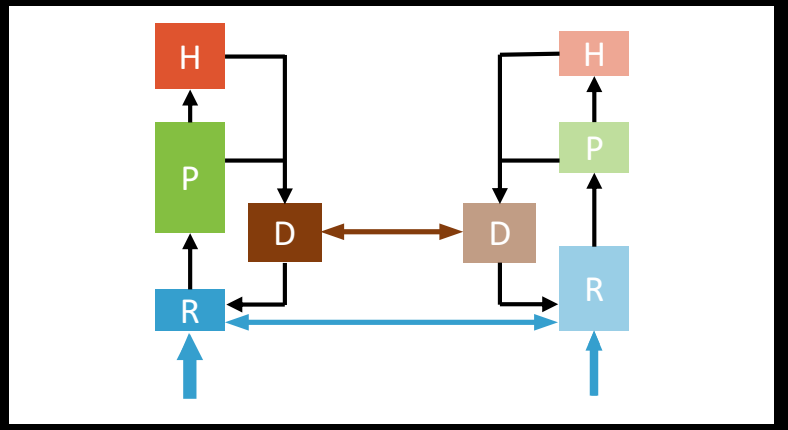
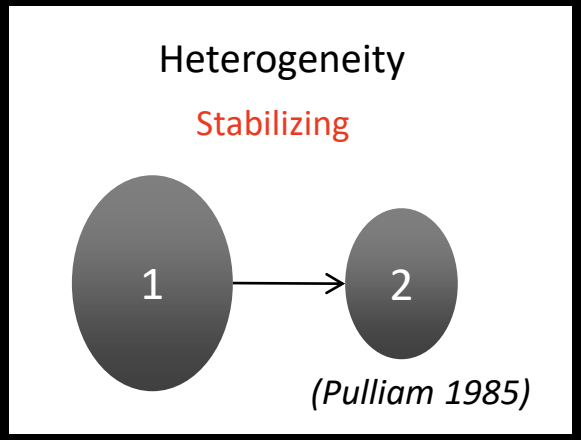


- Does spatial flow dampen enrichment?

- Does heterogeneity in enrichment matter?



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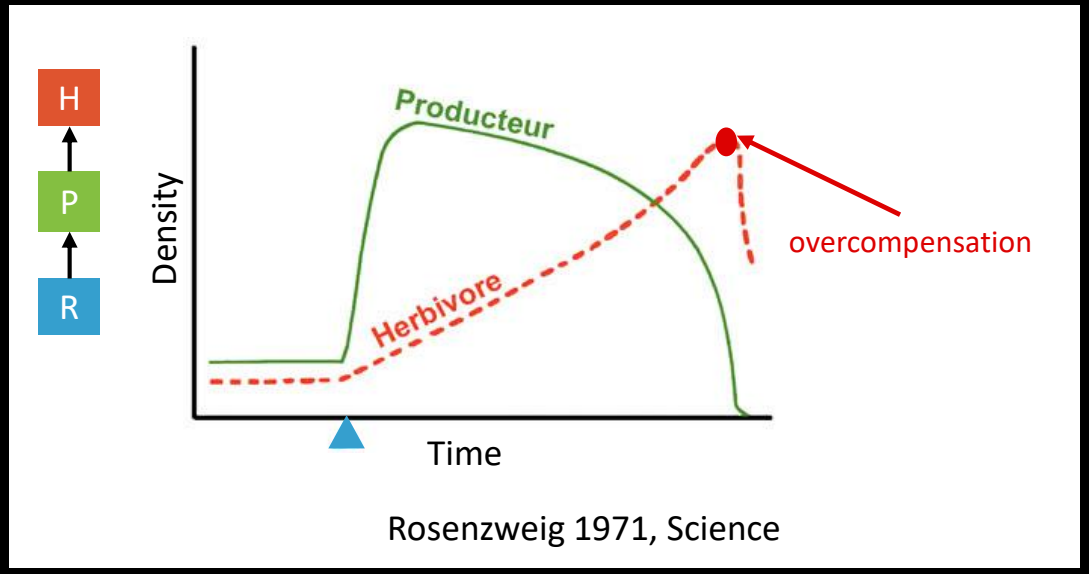

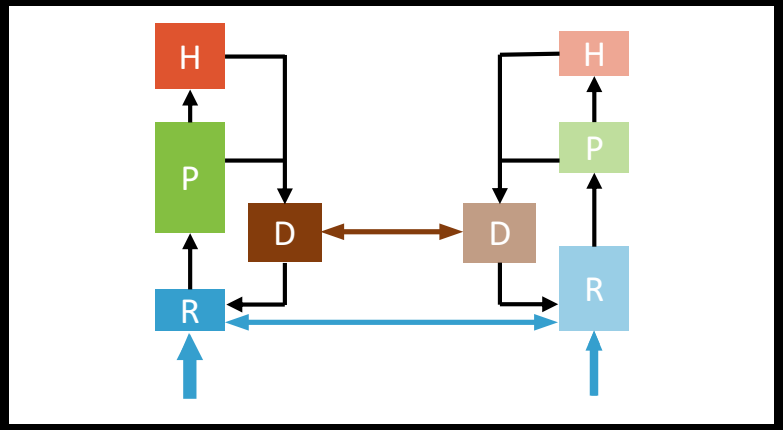

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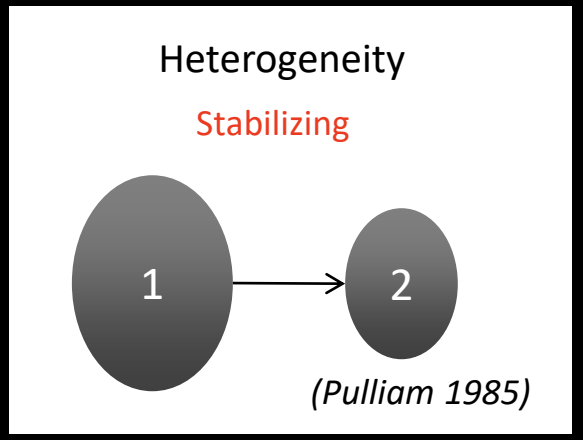

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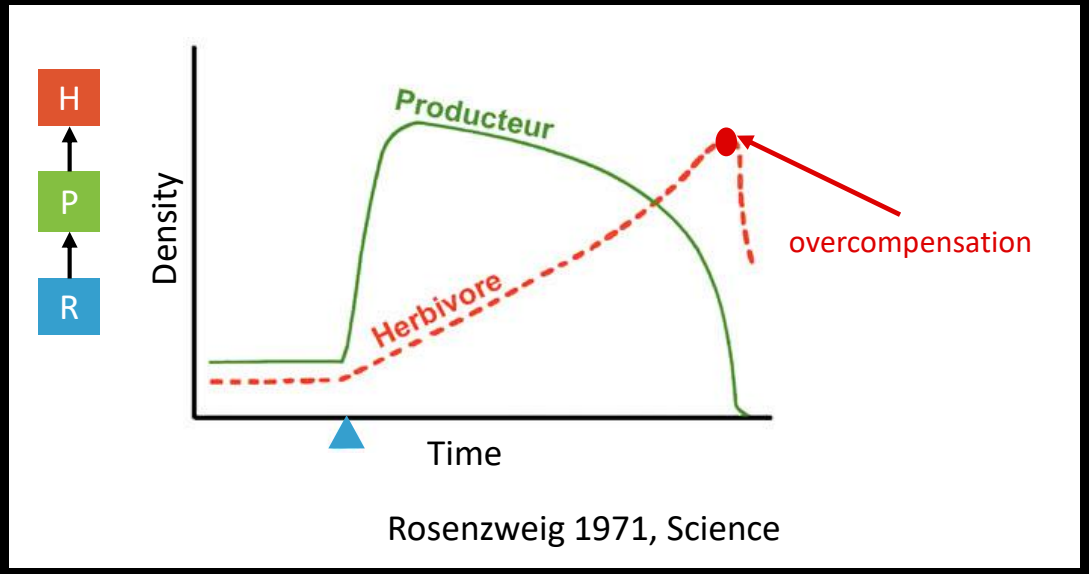

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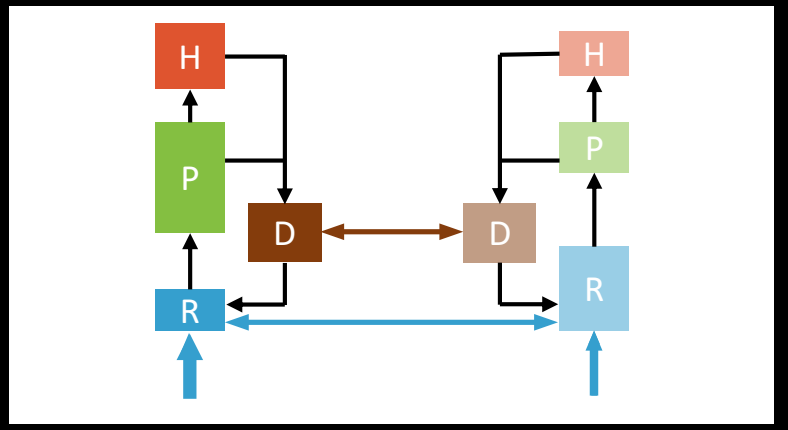

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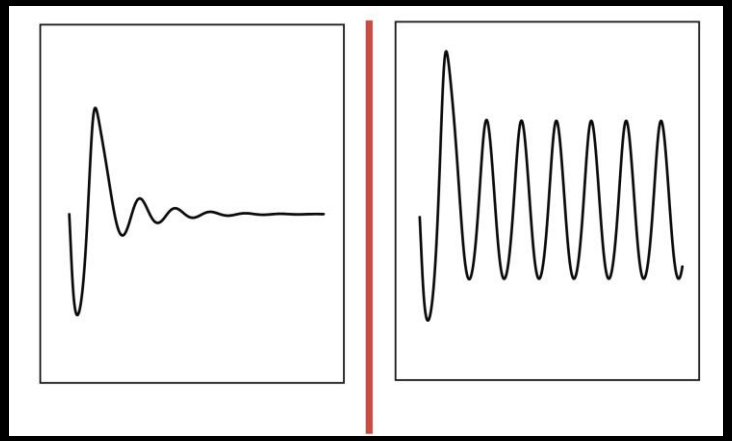
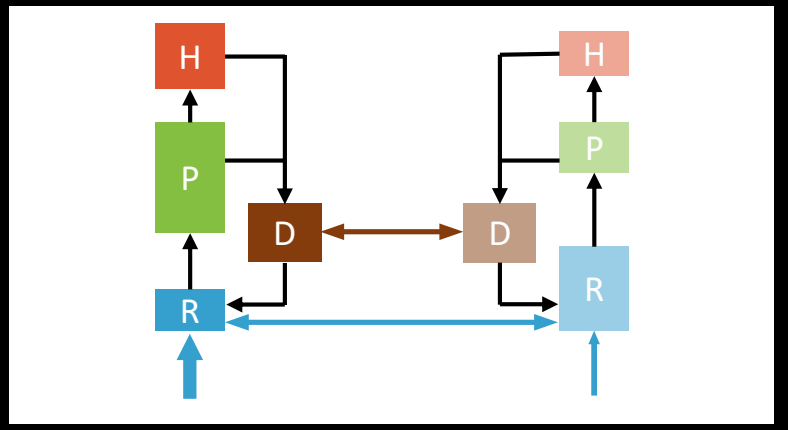
Gounand et al et al. 2014, *The American Naturalist*

How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

Local stability analysis





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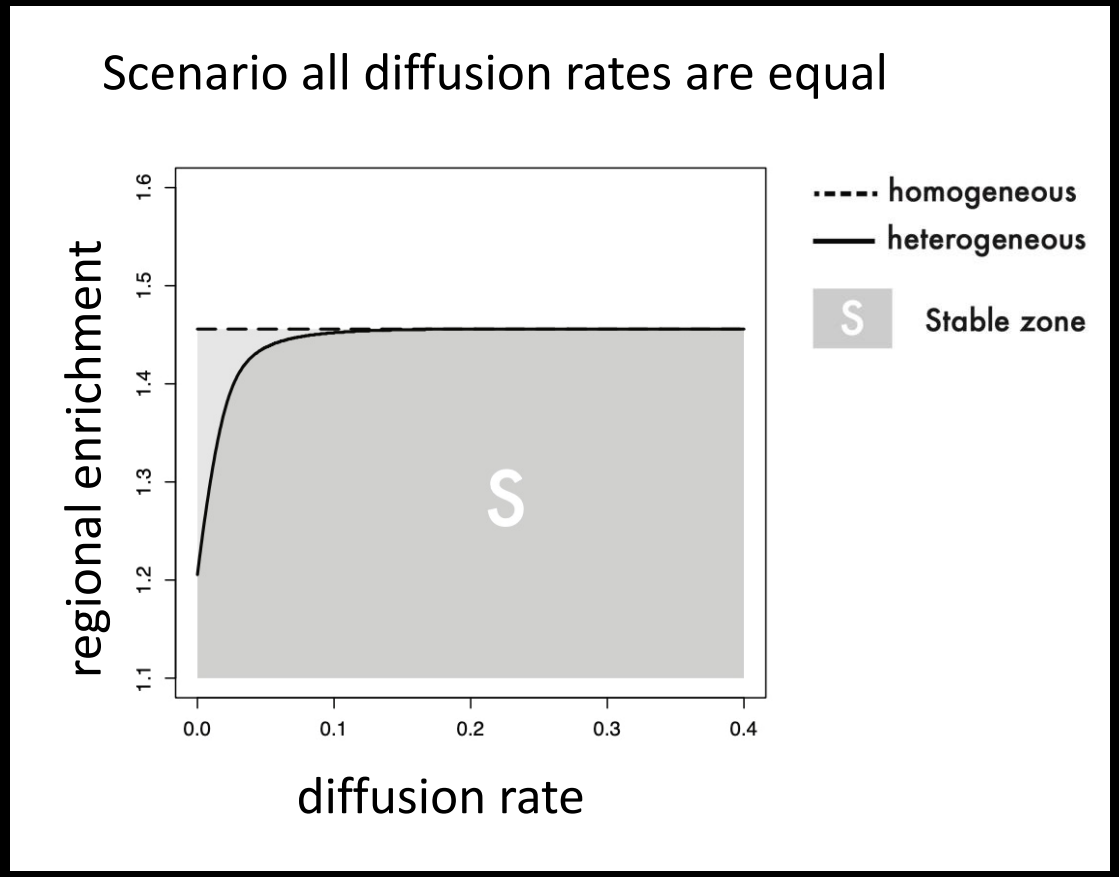
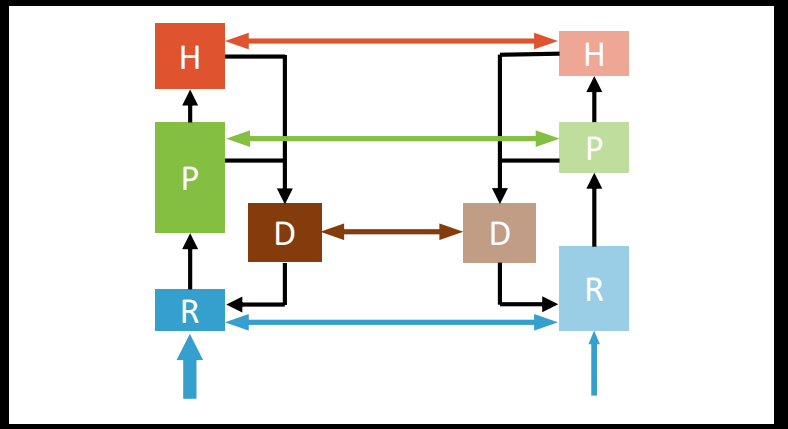
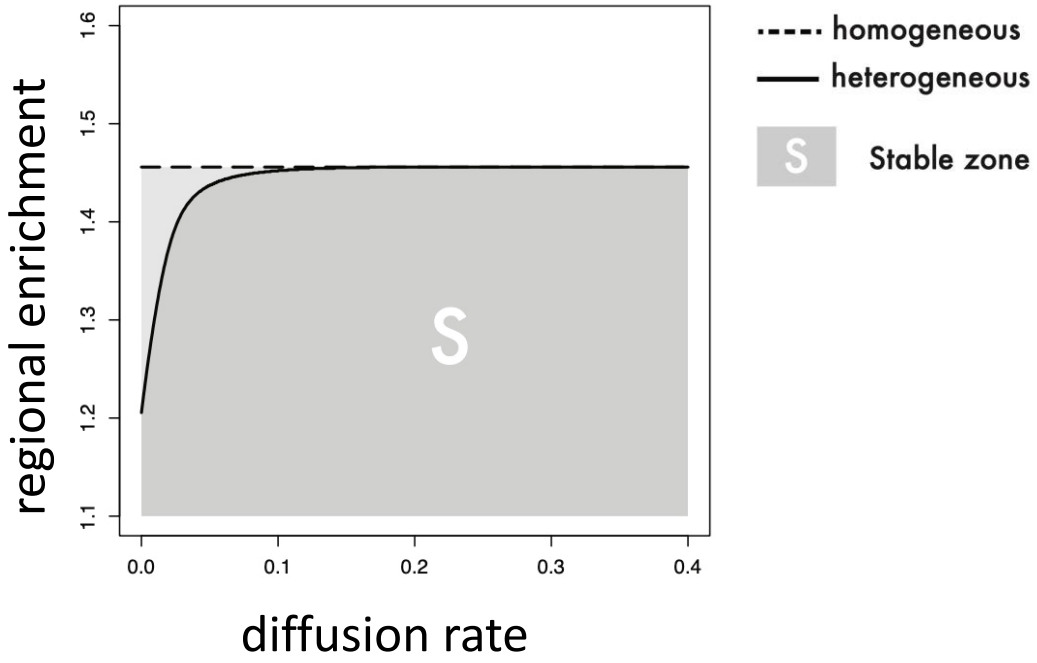




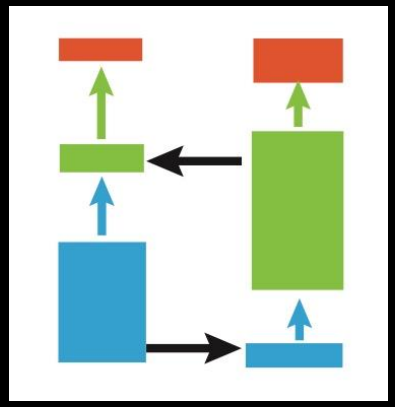
How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

Scenario all diffusion rates are equal



- No stabilisation via spatial flows (homogenous)



No fixed carrying capacity

How do spatial flow affect ecosystem structure and **stability**?

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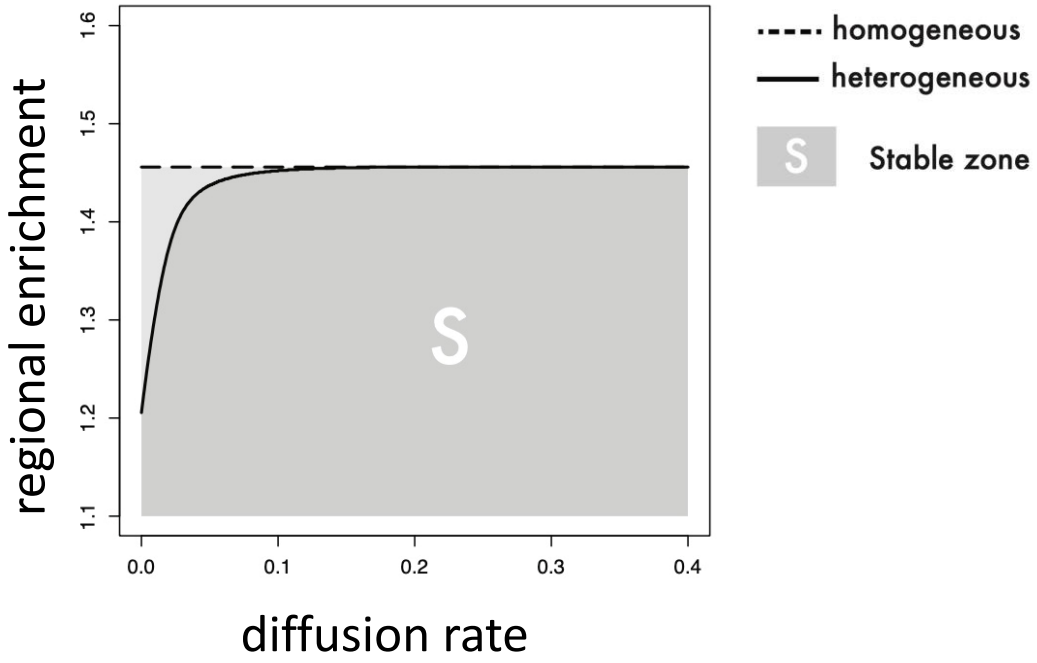

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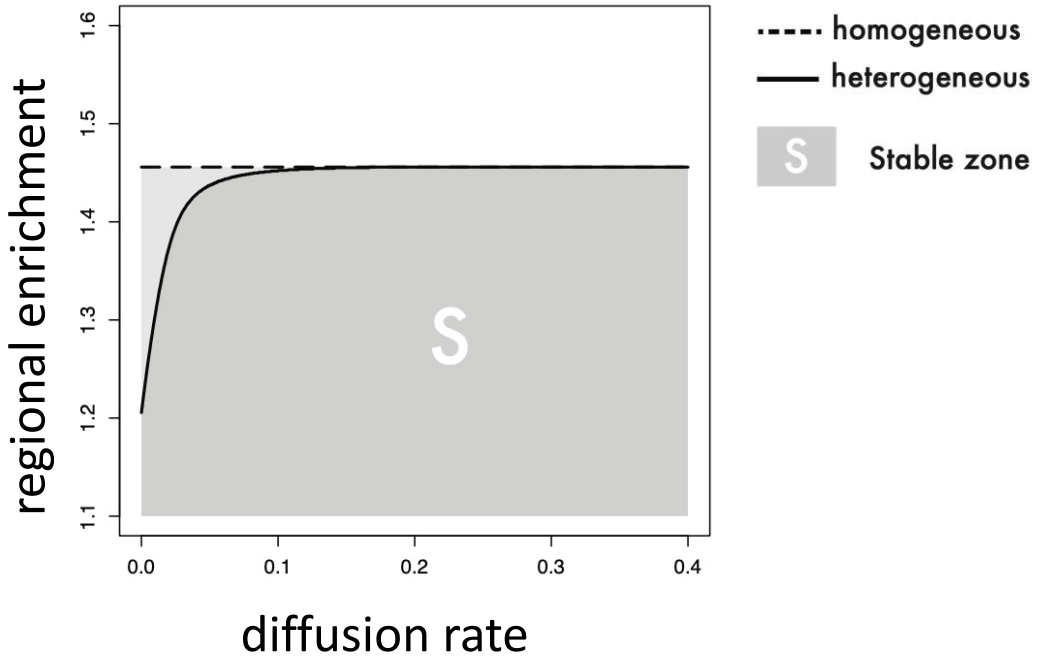

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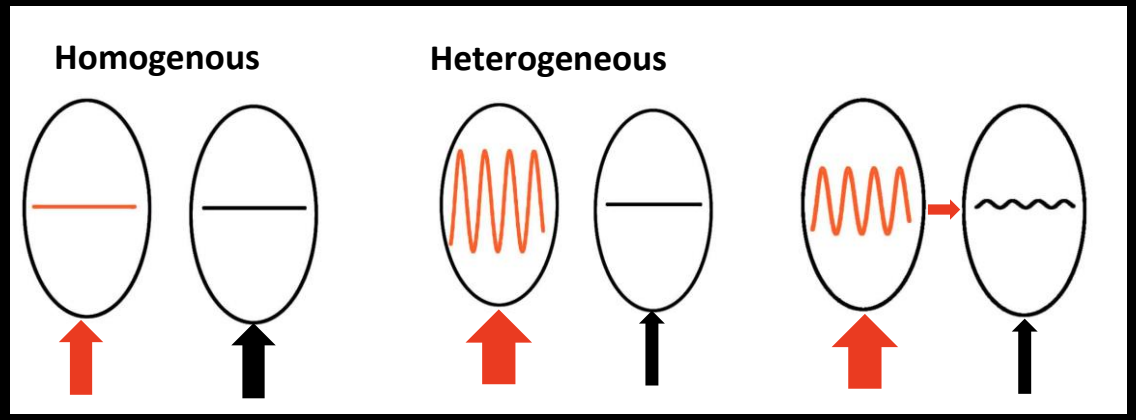

Source-sink matter transfer dampen unstability in heterogeneous case

How do spatial flow affect ecosystem structure and **stability**?

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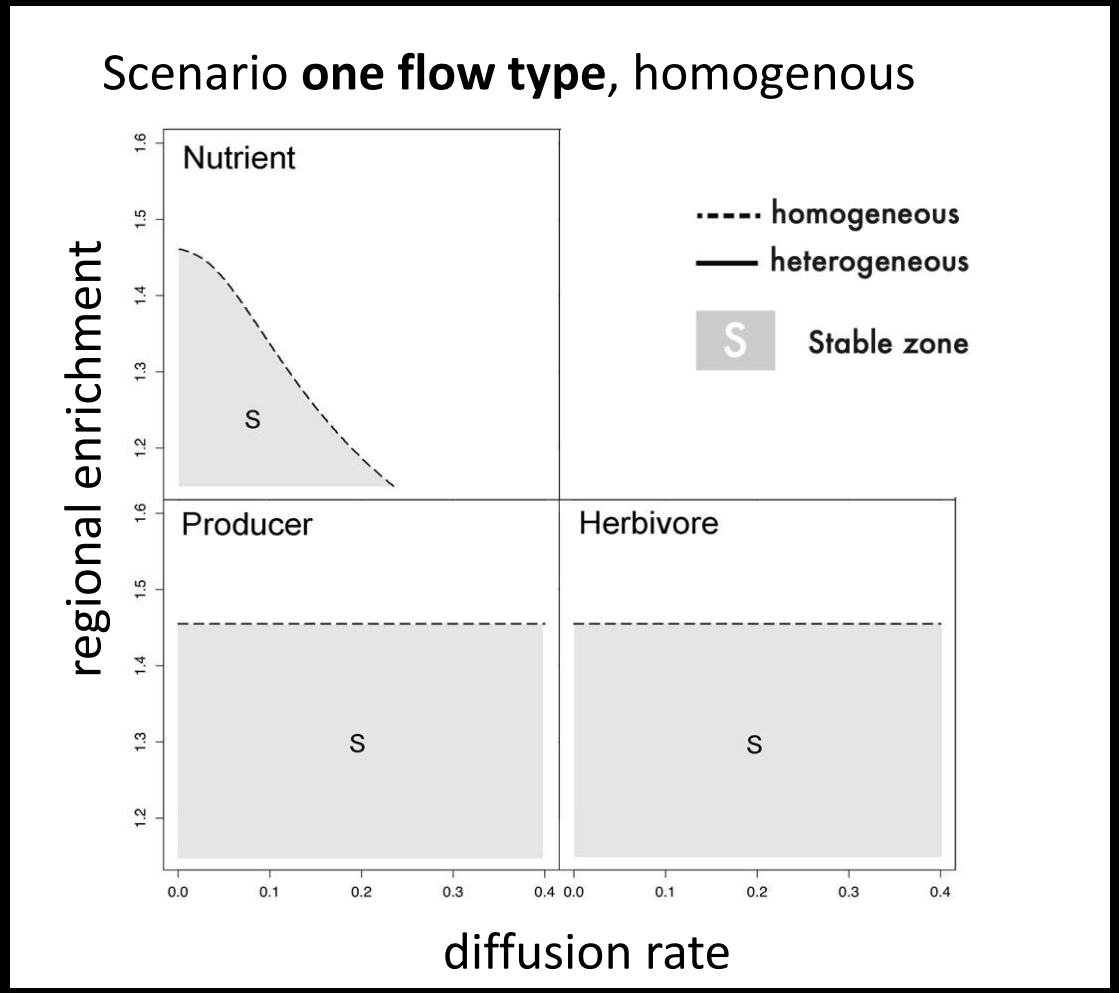

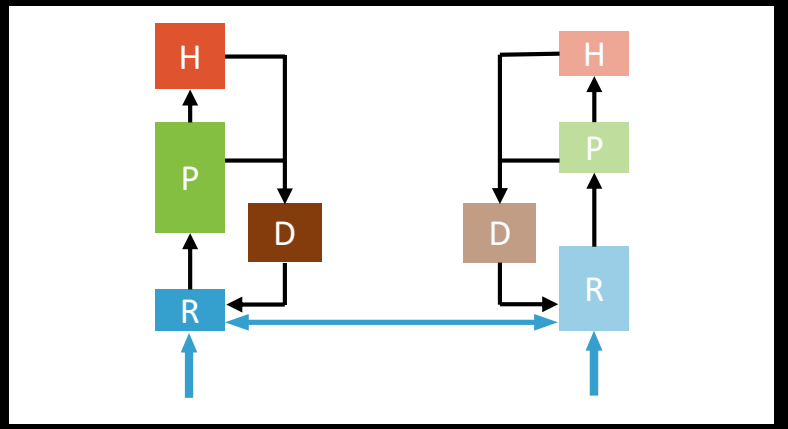

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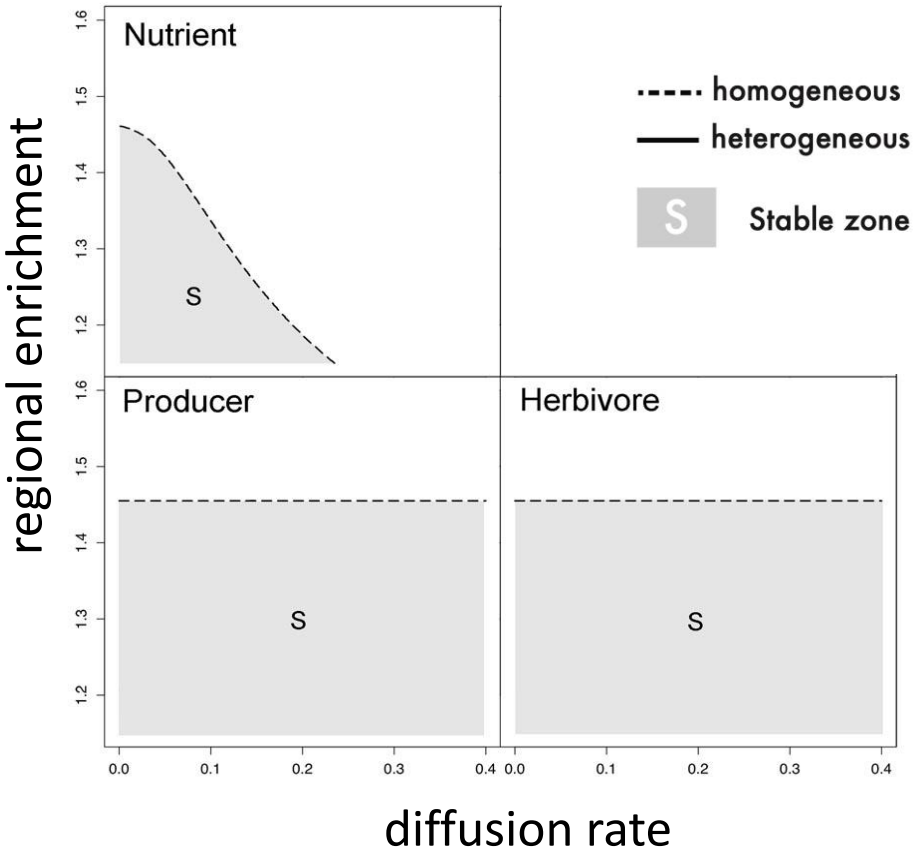
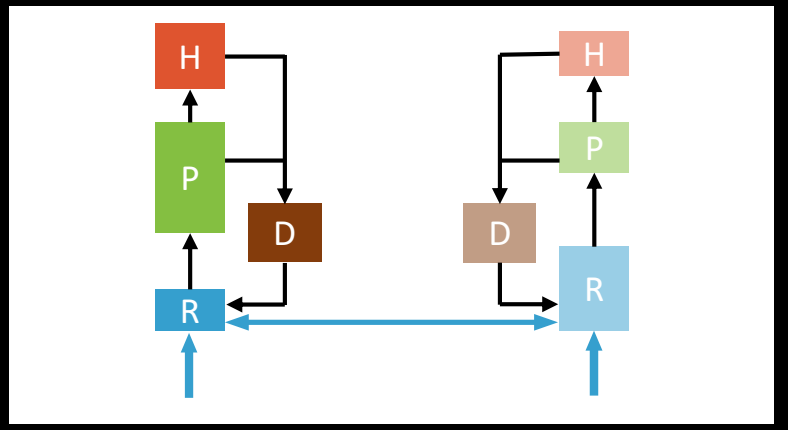
Scenario **one flow type**, homogenous





- Nutrient flows are destabilizing
- Producer and Herbivore flow are neutral

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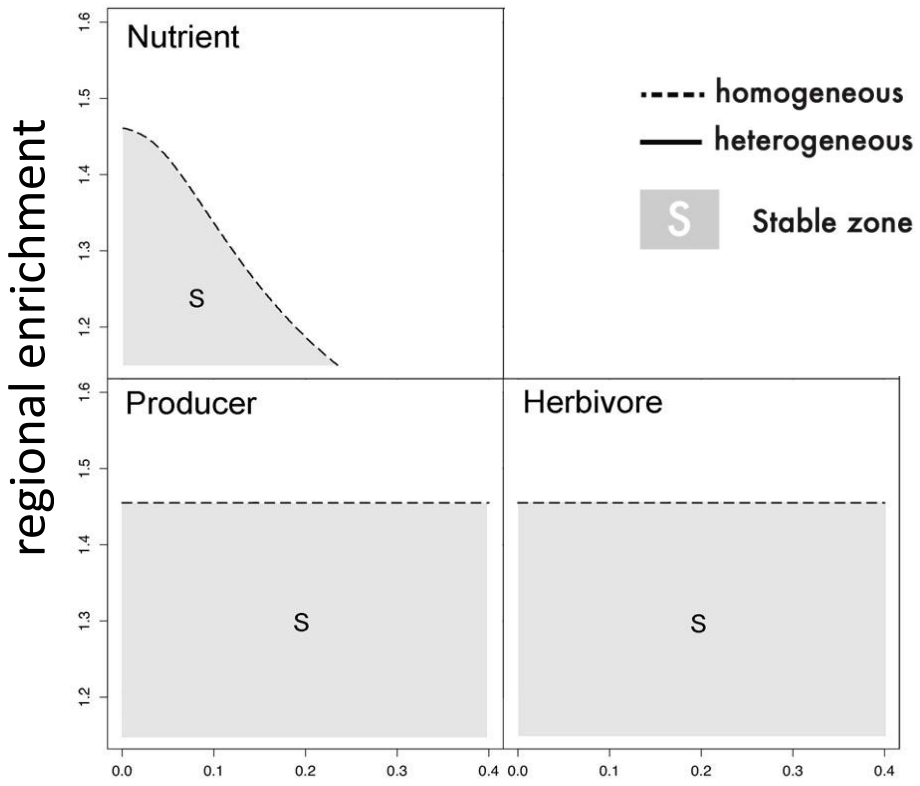

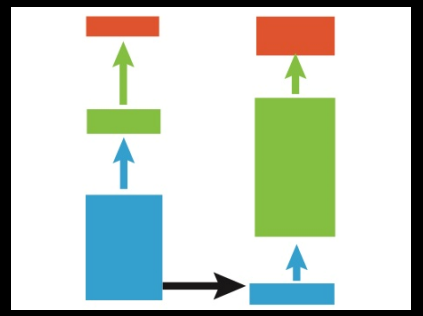

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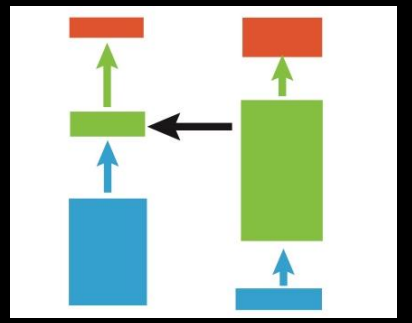

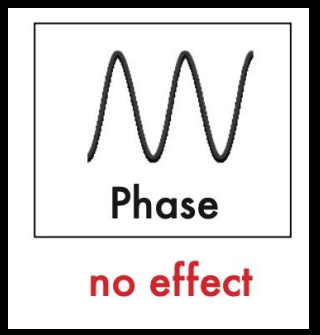

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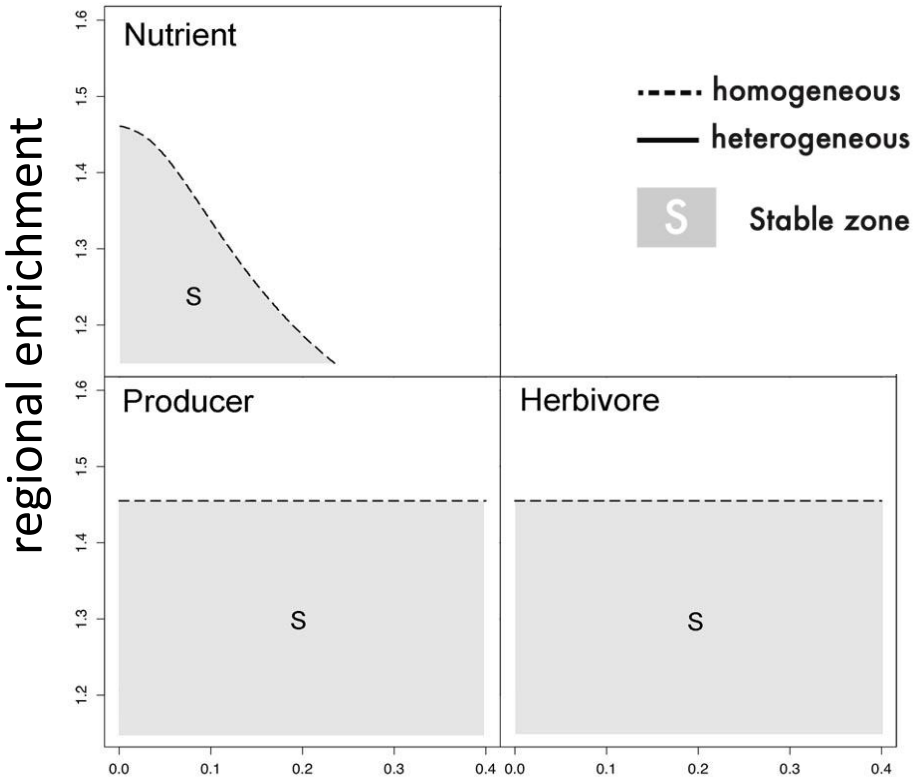
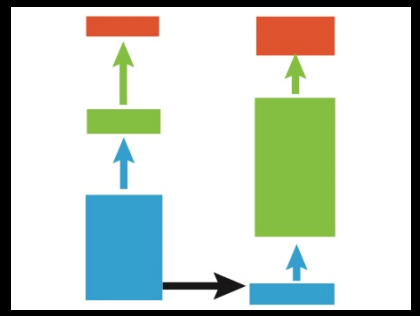
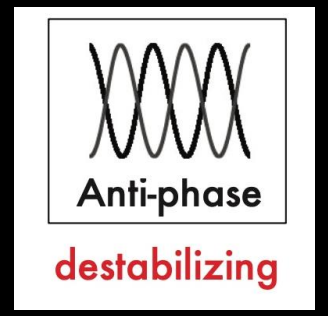
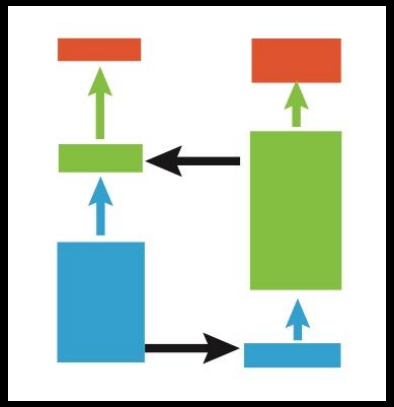




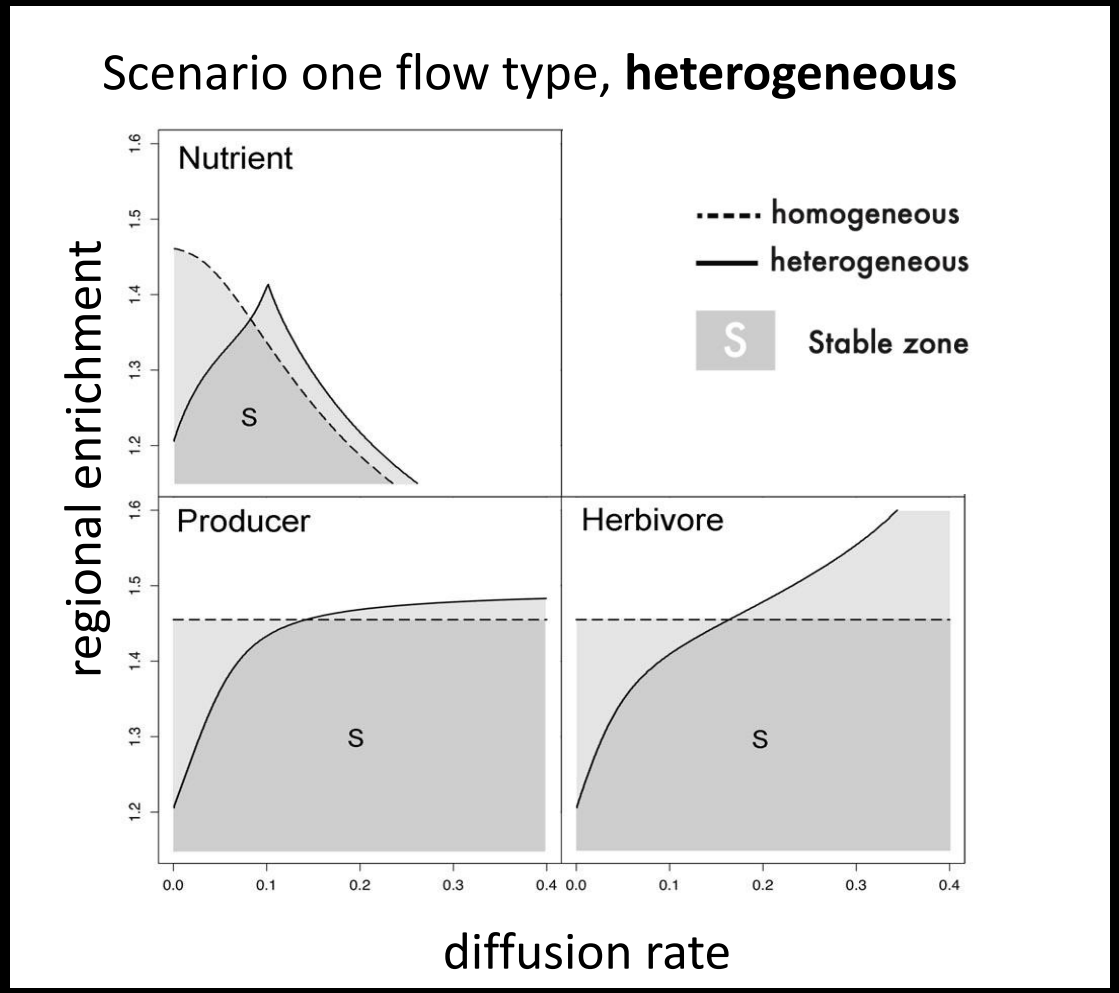


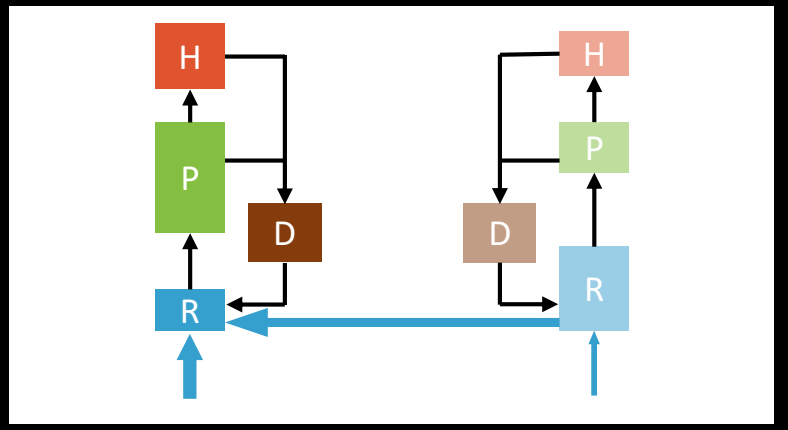
- Compensatory dynamics stabilize



How do spatial flow affect ecosystem structure and **stability**?

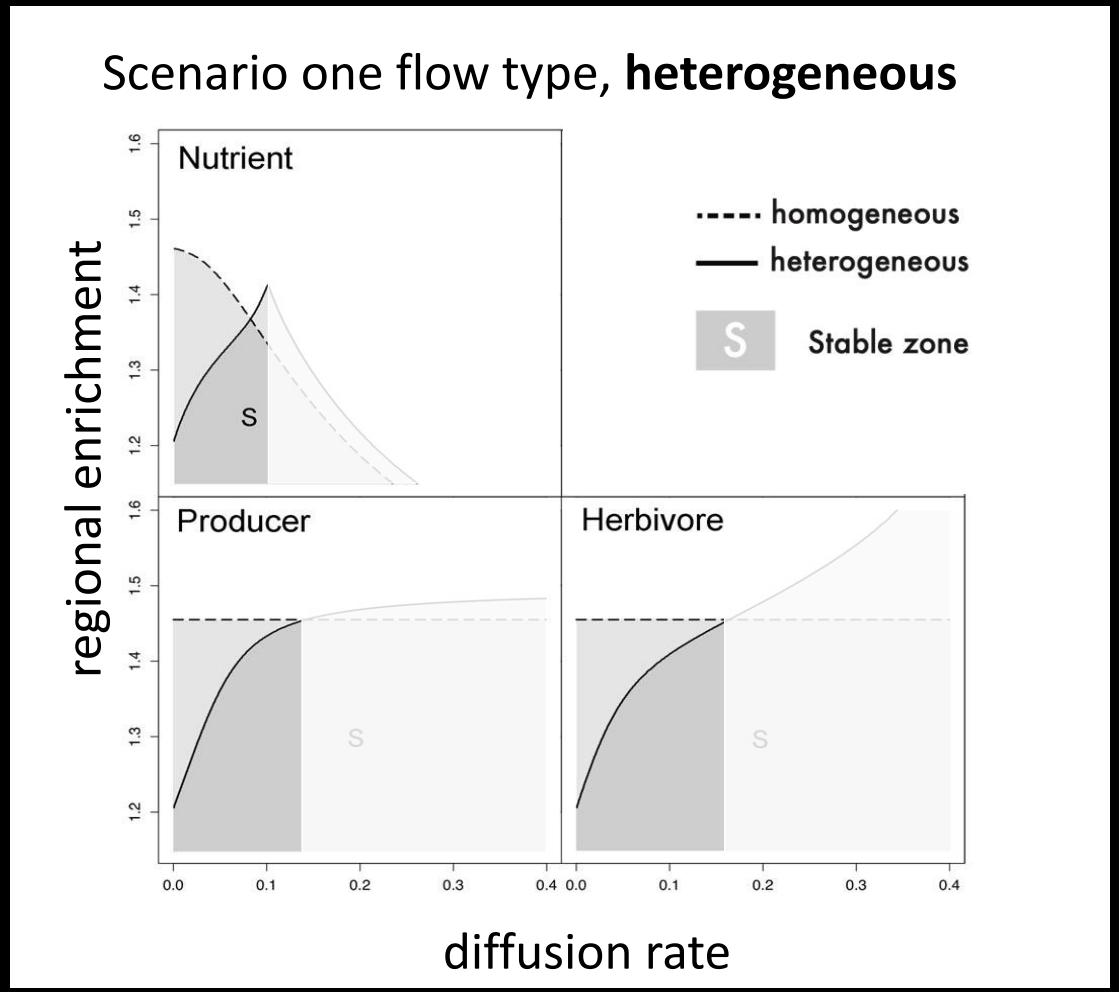
The paradox of enrichment in metaecosystems





How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

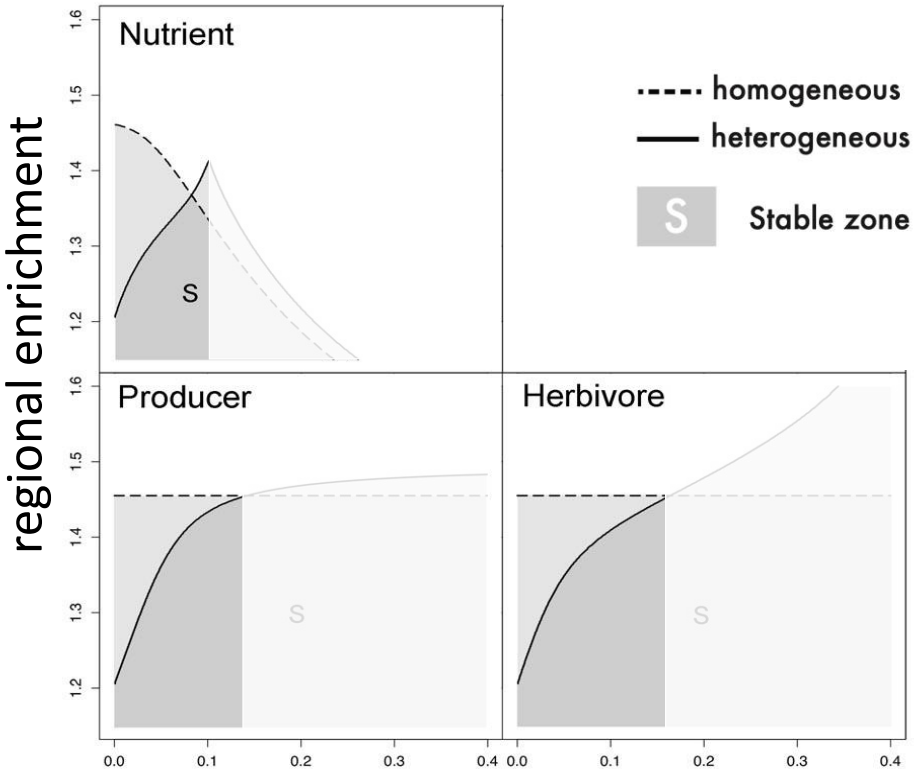


- At low diffusion, heterogeneity destabilizes

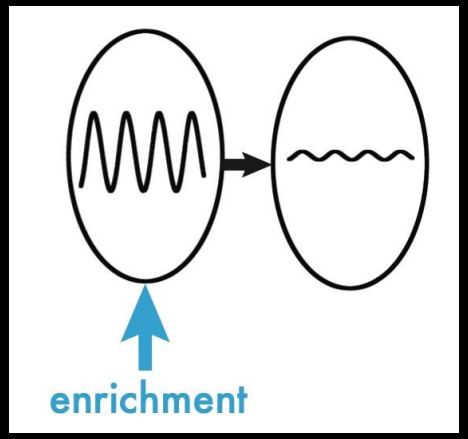
How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

Scenario one flow type, **heterogeneous**

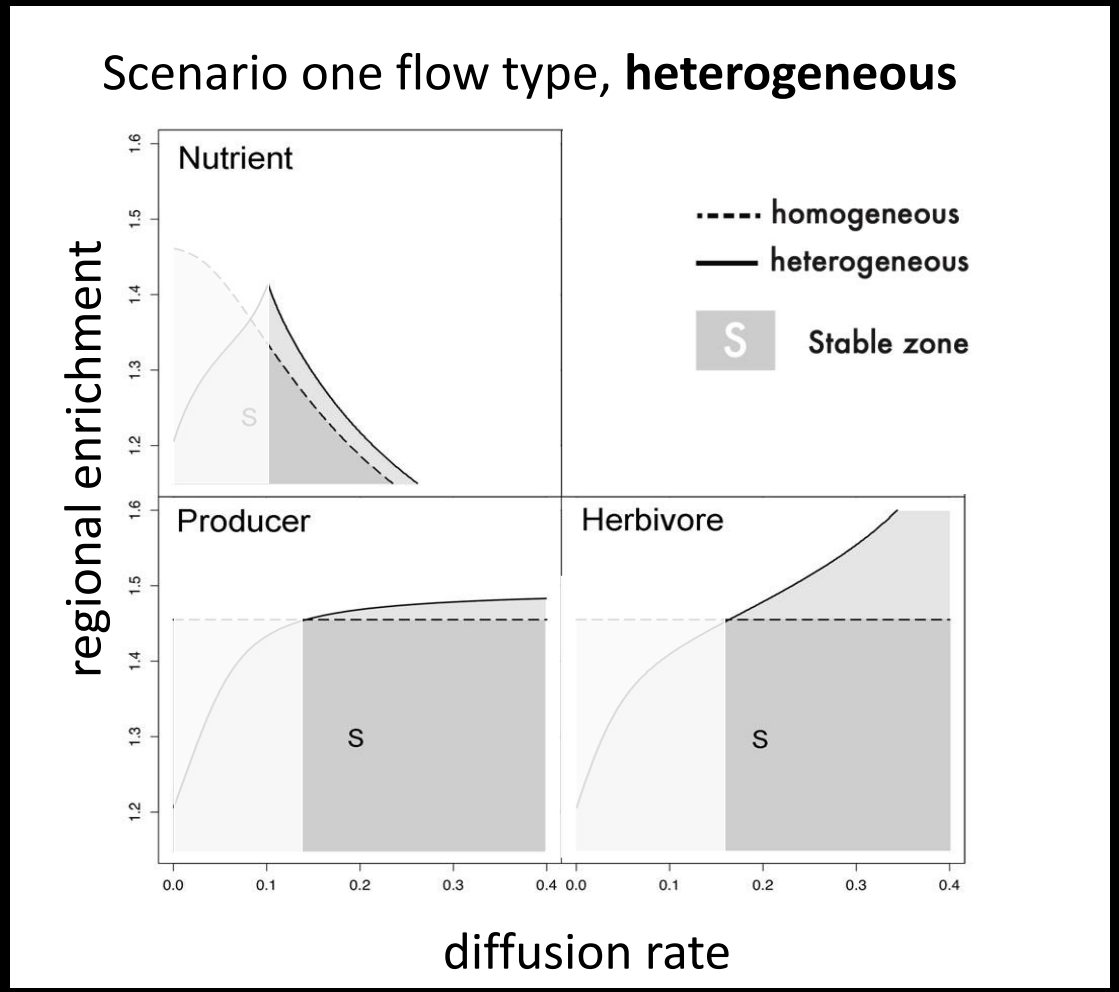


- At low diffusion, heterogeneity destabilizes



How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

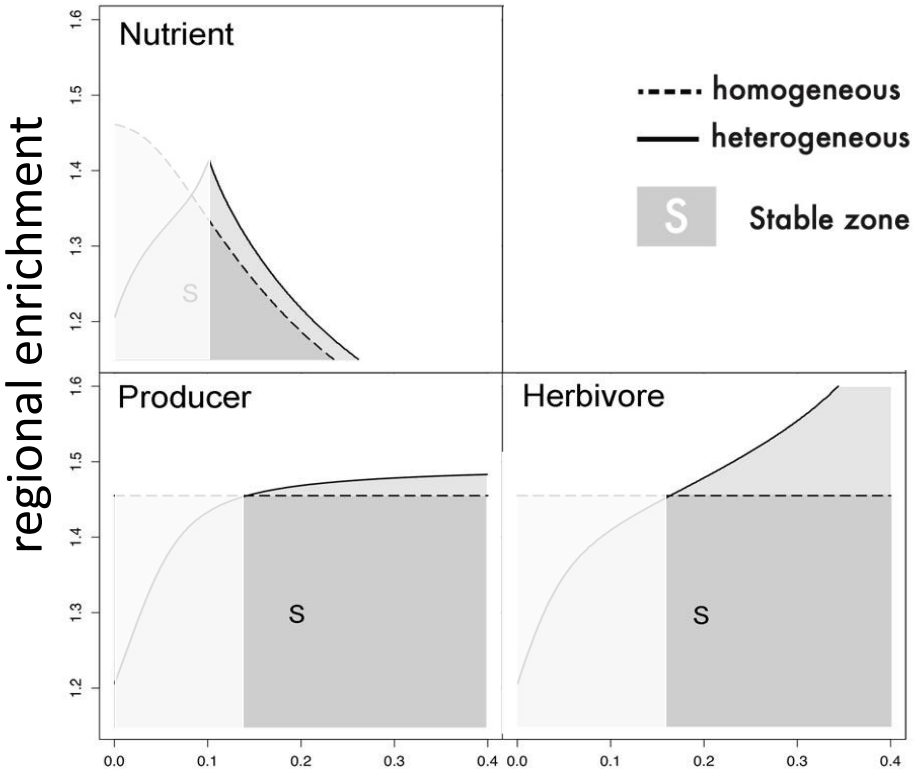


- At low diffusion, heterogeneity destabilizes
- At high diffusion, heterogeneity stabilizes

How do spatial flow affect ecosystem structure and **stability**?

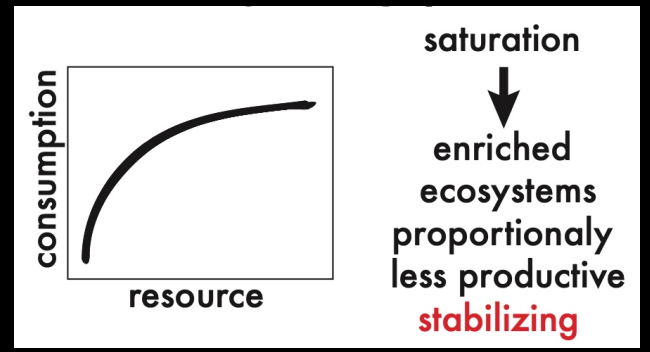
The paradox of enrichment in metaecosystems

Scenario one flow type, **heterogeneous**



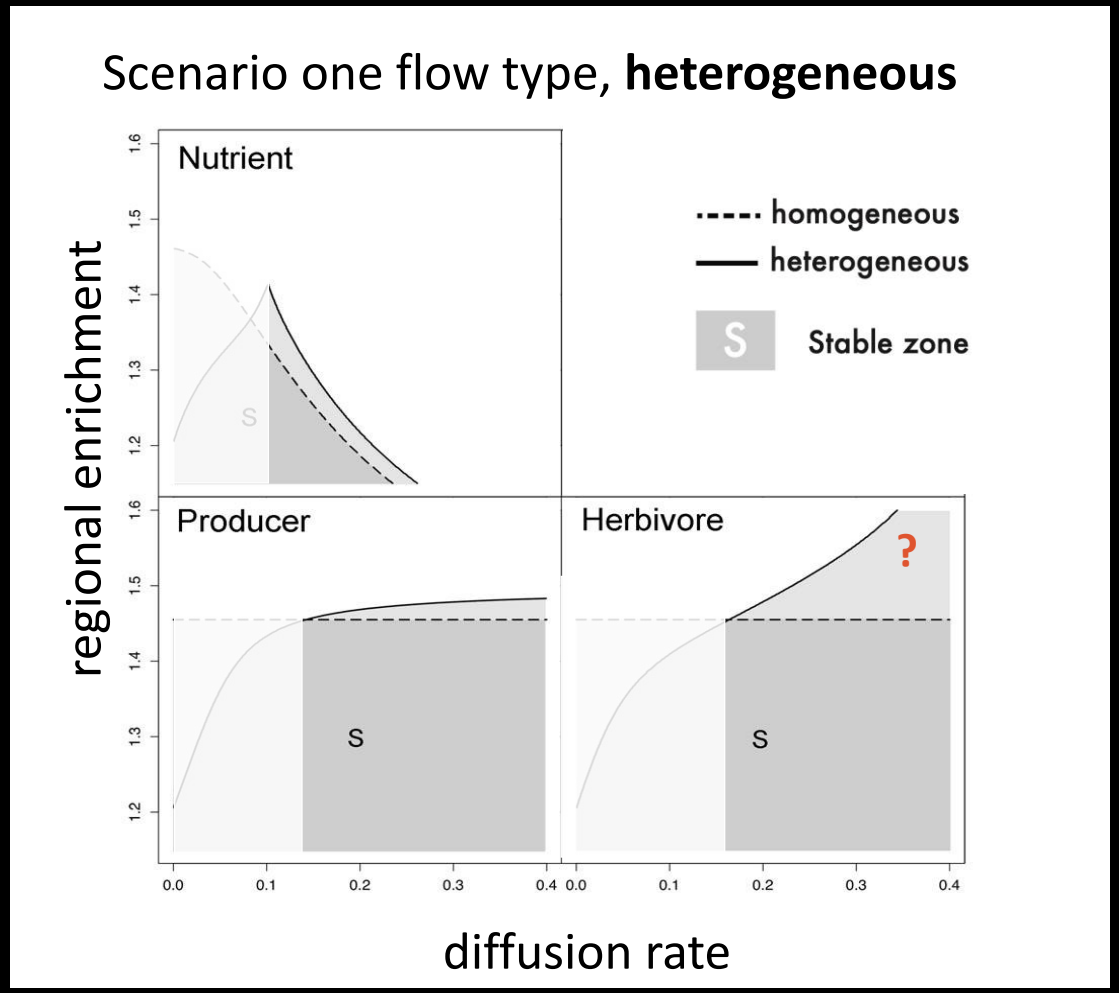
- At low diffusion, heterogeneity destabilizes
- Heterogeneity *per se* is stabilizing:

  primary production saturates at high resource levels



How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

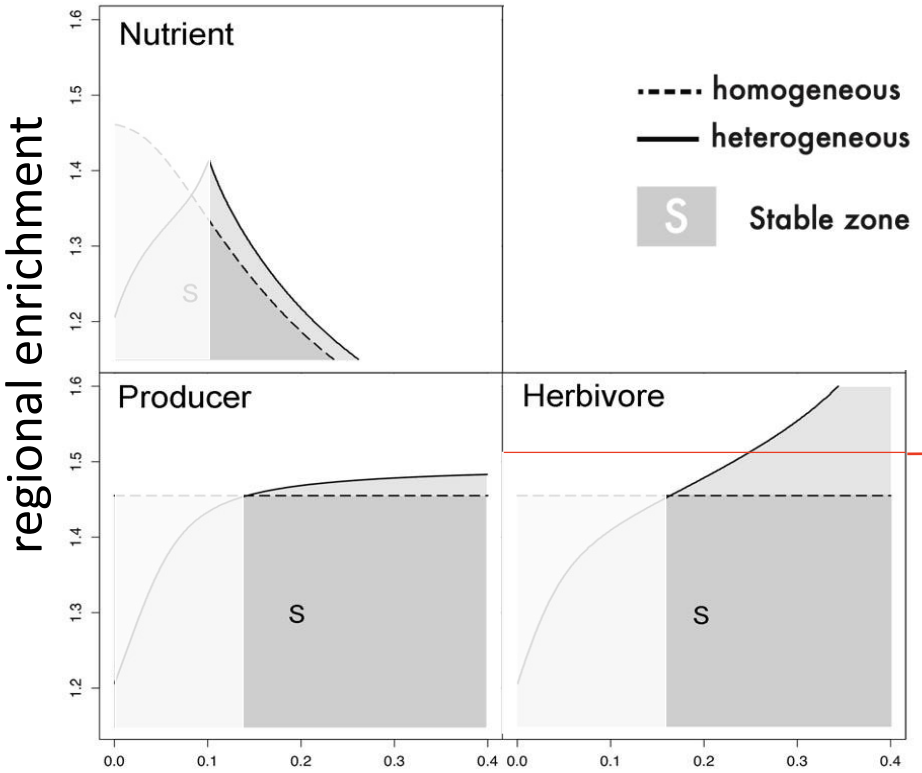


- At low diffusion, heterogeneity destabilizes
- Heterogeneity *per se* is stabilizing
- Herbivore diffusion is stabilizing

How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems

Scenario one flow type, **heterogeneous**



- At low diffusion, heterogeneity destabilizes
- Heterogeneity *per se* is stabilizing
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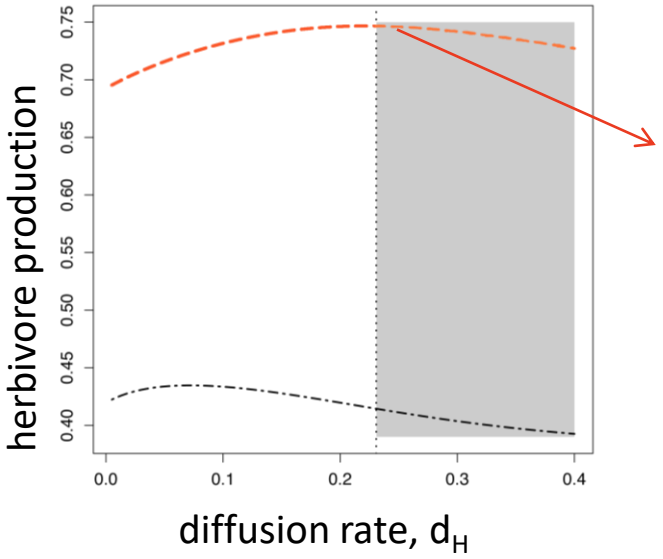
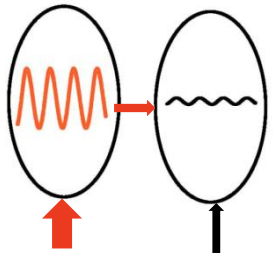


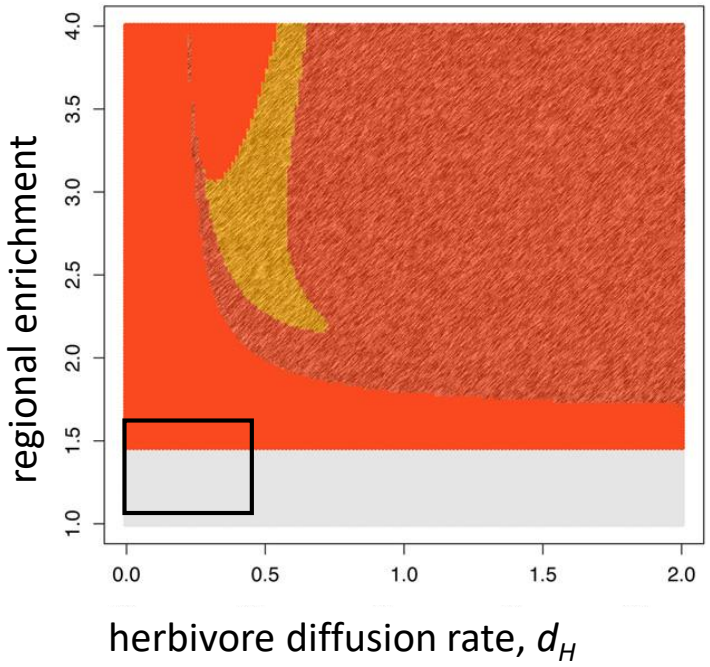
decreases the risks of overconsumption in the rich ecosystem



How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems, herbivore effects

Scenario **herbivore diffusion only**
homogenous enrichment

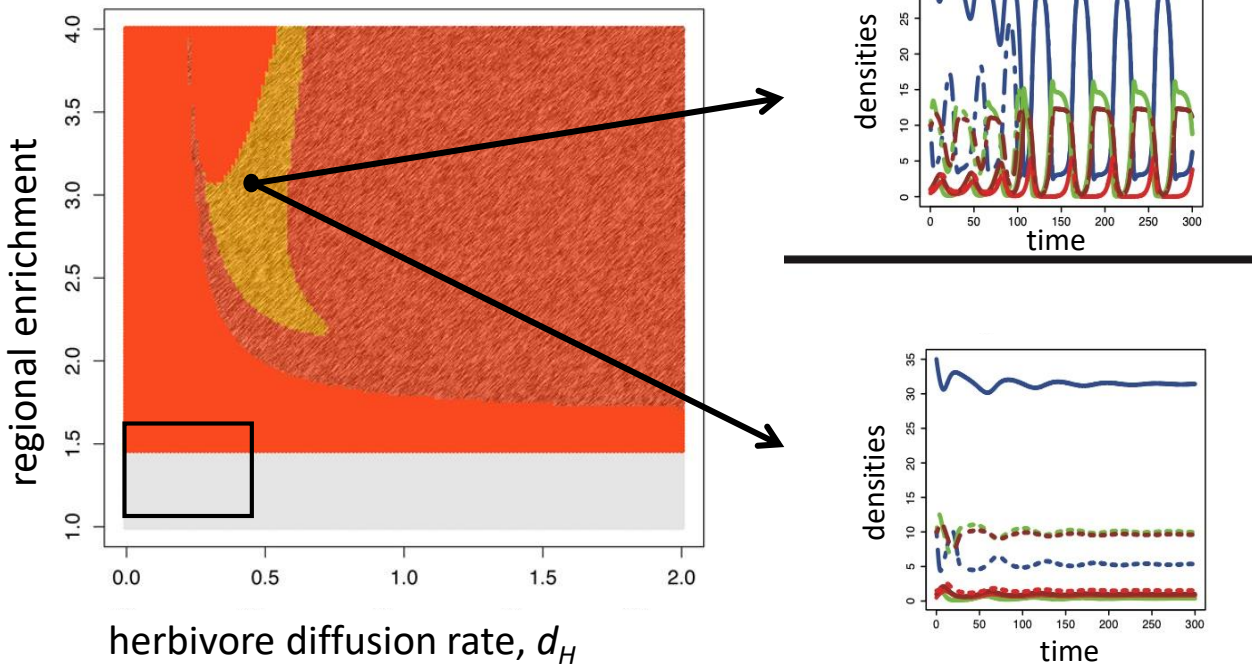


Stable
Oscillating
Multi. Eq, one stable
Multi. Eq, both oscillating

How do spatial flow affect ecosystem structure and **stability**?

The paradox of enrichment in metaecosystems, herbivore effects

Scenario **herbivore diffusion only**
homogenous enrichment

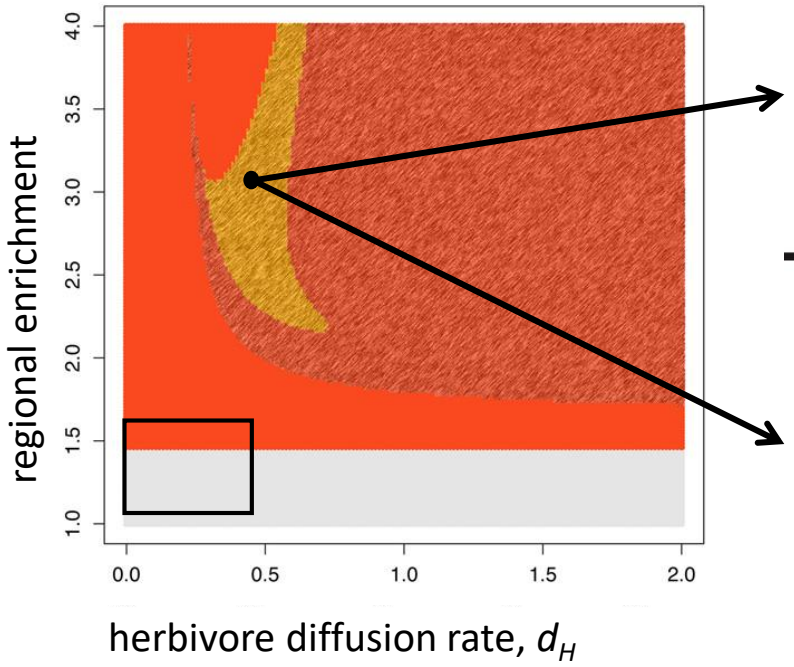


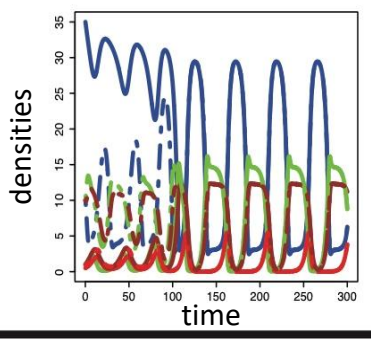
Herbivore diffusion can induce alternative stable states

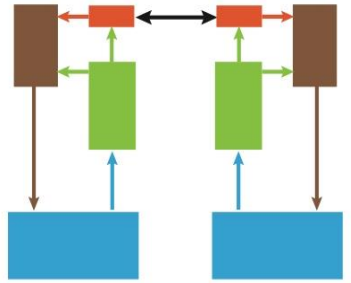
How do spatial flow affect ecosystem structure and **stability**?

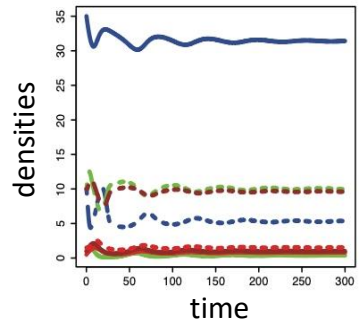
The paradox of enrichment in metaecosystems, herbivore effects

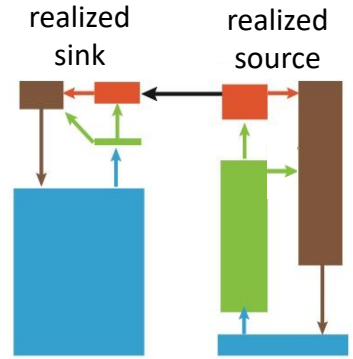
Scenario **herbivore diffusion only homogenous** enrichment











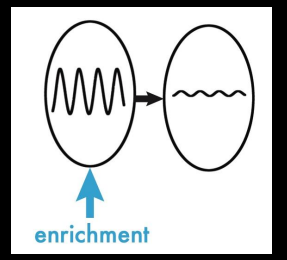
Herbivore diffusion can induce alternative stable states

Source-sink structure emerge from top-down regulation

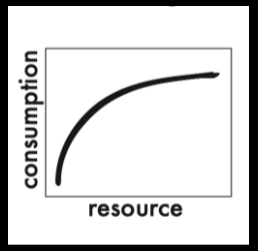
How do spatial flow affect ecosystem structure and **stability**?

Take Home messages

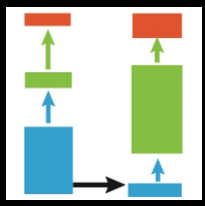
1. With wide connectivity, **spatial flows dampen local enrichment** by resource transfers but there is no additionnal stabilizing effect



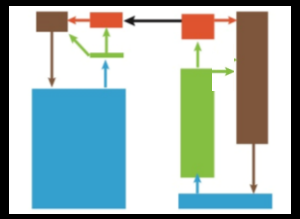
2. **Heterogeneity can be stabilizing** when connectivity is partial



3. **Nutrient flows are destabilizing** while biotic flows are neutral or stabilizing

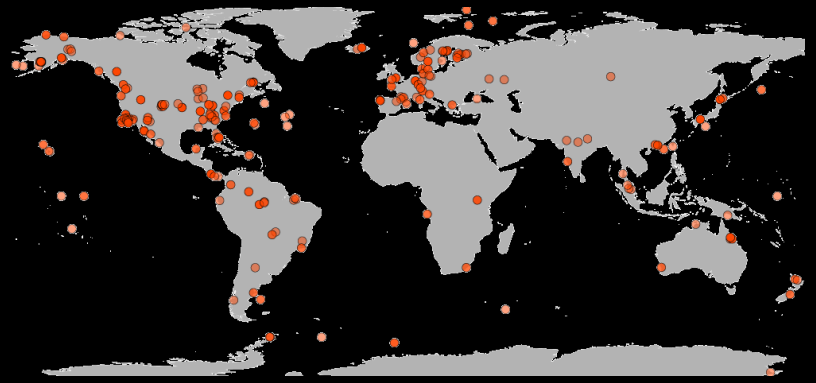


4. **Intermediate diffusion of herbivores can stabilize high regional enrichment**



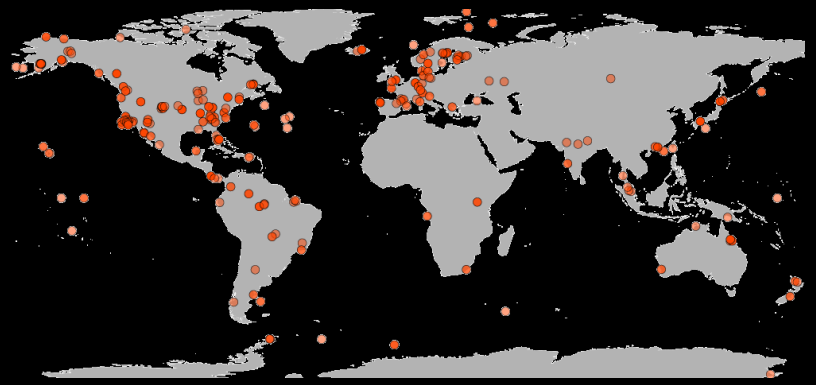
What about empirical observations ?

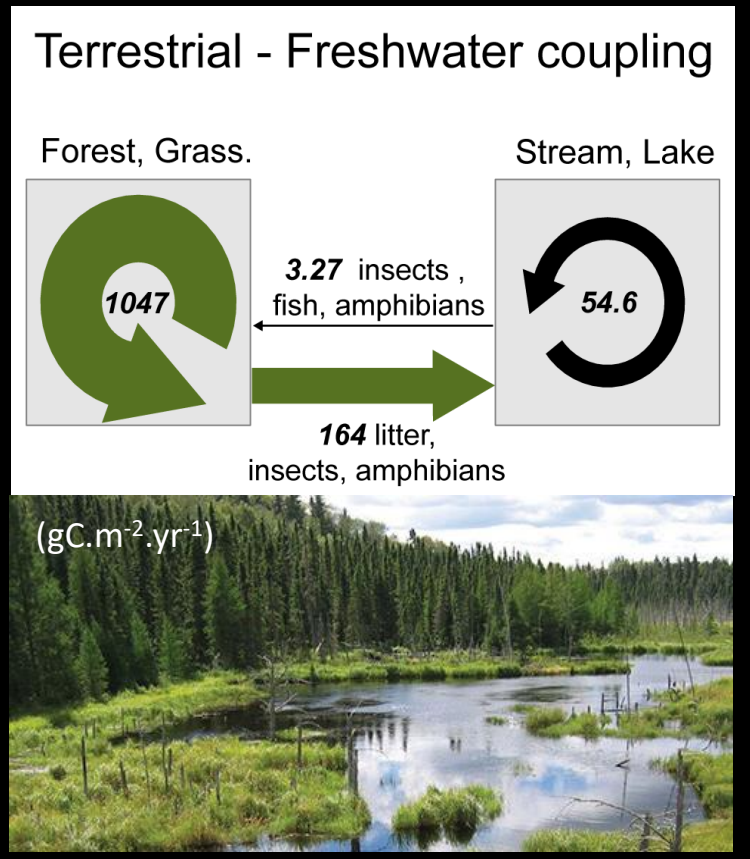
Data synthesis on C spatial flows (n=518)

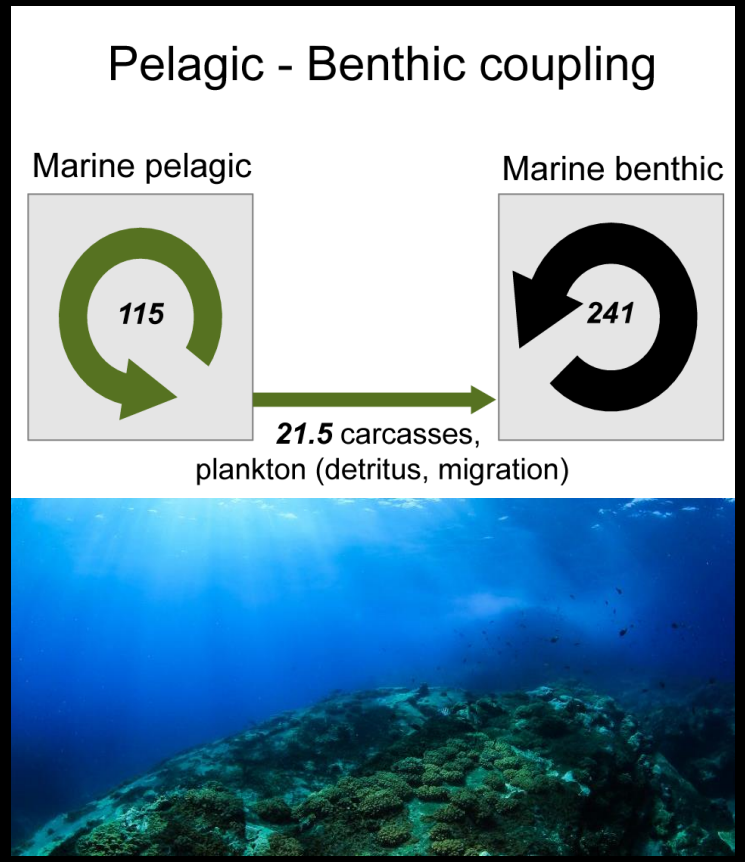


What about empirical observations ?

Data synthesis on C spatial flows (n=518)



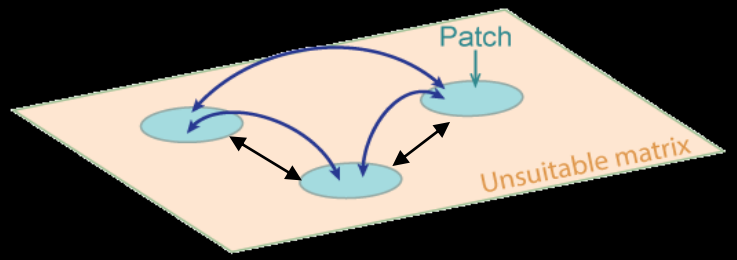




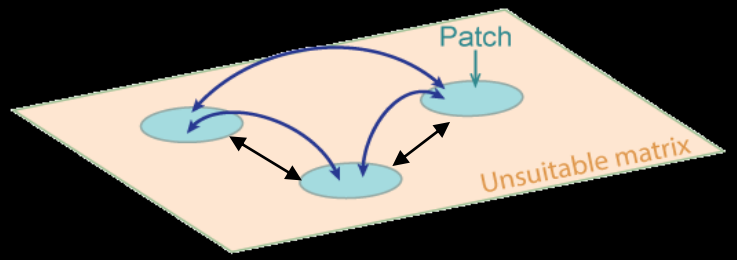
Gounand et al. 2018, *Nat. Comm.*

Resource spatial flow couple very different habitat types

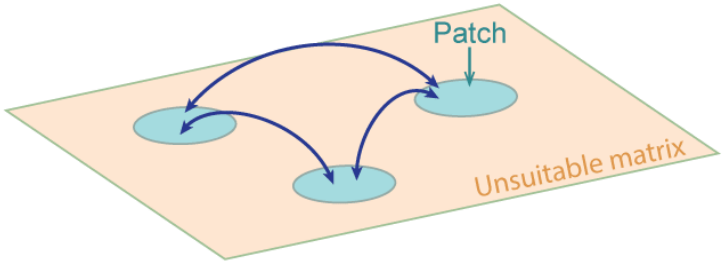
What about empirical observations ?



What about empirical observations ?

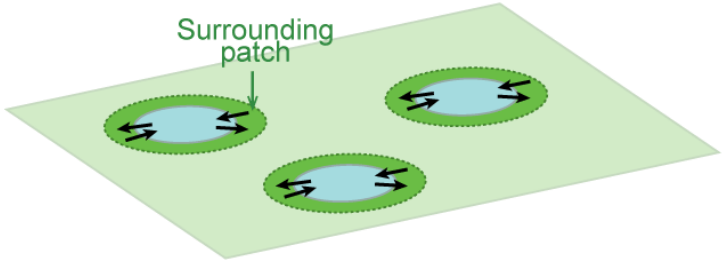


Dispersal-based meta-ecosystem



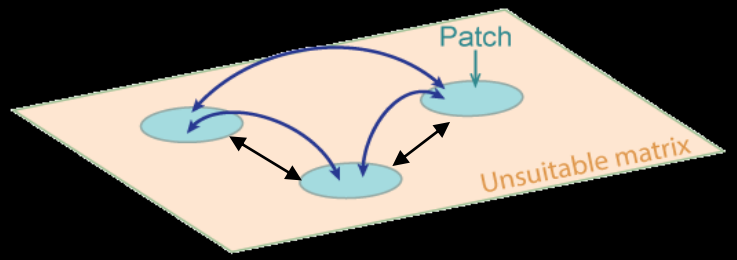
...

Resource-flow based meta-ecosystem

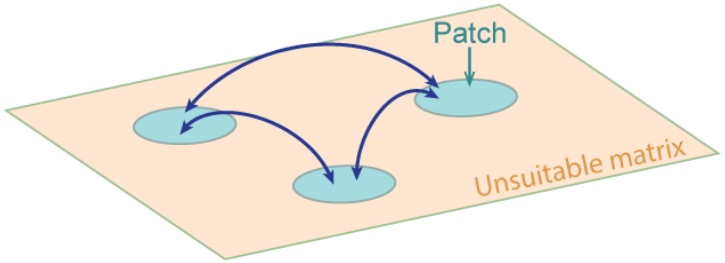


Gounand et al. 2018, *Trends in Ecology & Evolution*

What about empirical observations ?



Dispersal-based meta-ecosystem



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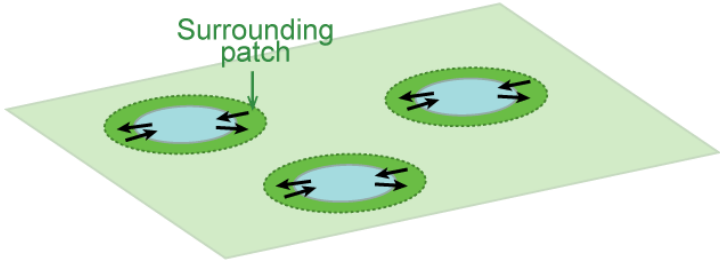
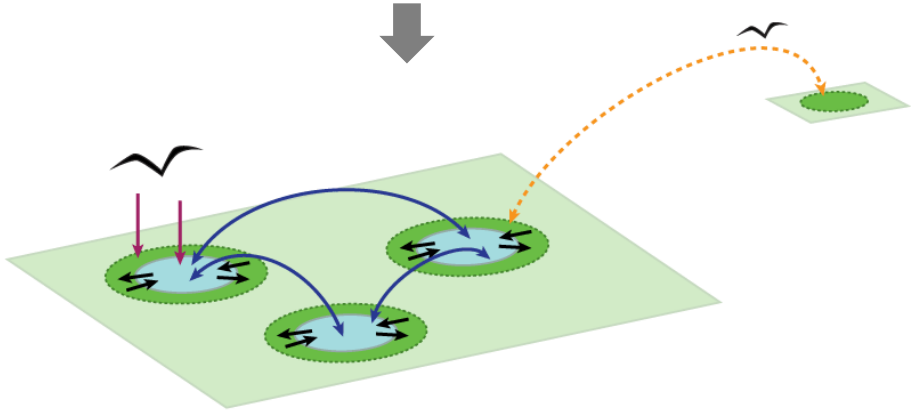
Resource-flow based meta-ecosystem



spatial integration

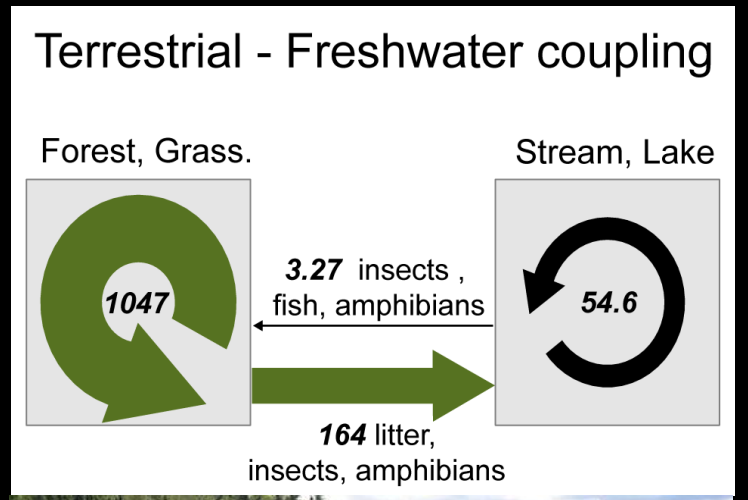


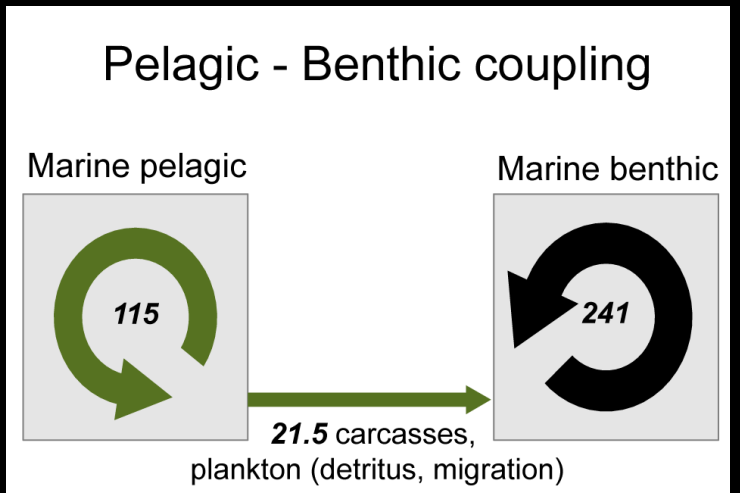
Flows occur at different spatial scales

Gounand et al. 2018, *Trends in Ecology & Evolution*

What about empirical observations ?

What about
nutrient spatial flows?





What about empirical observations ?

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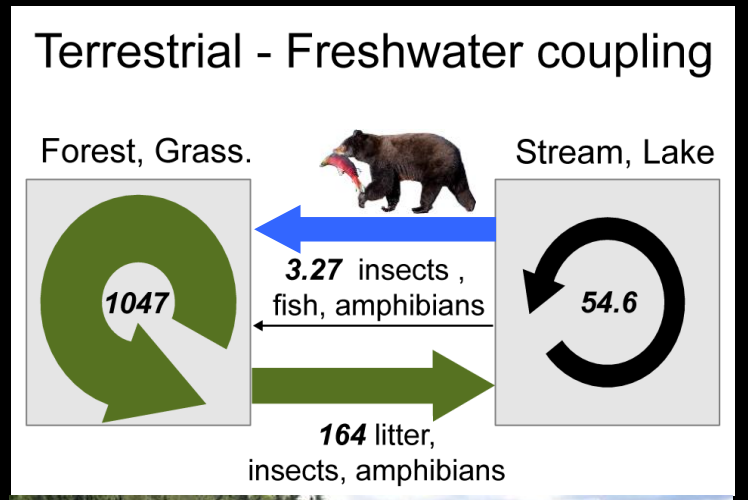

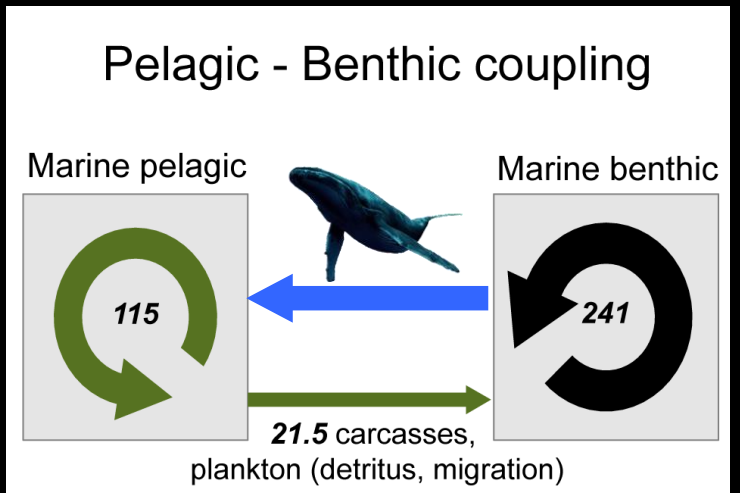

What about empirical observations ?

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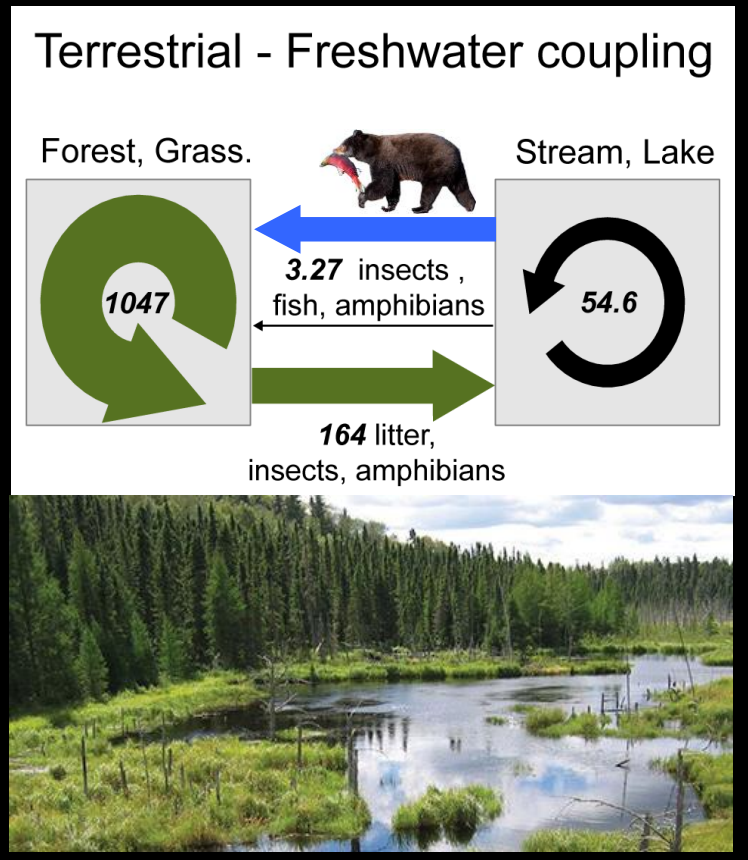
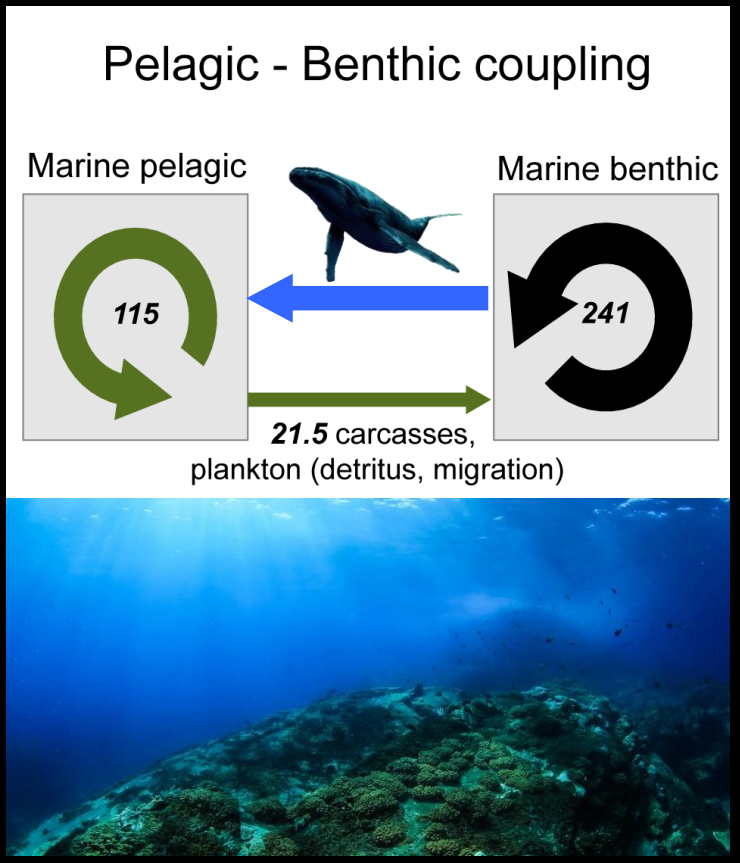
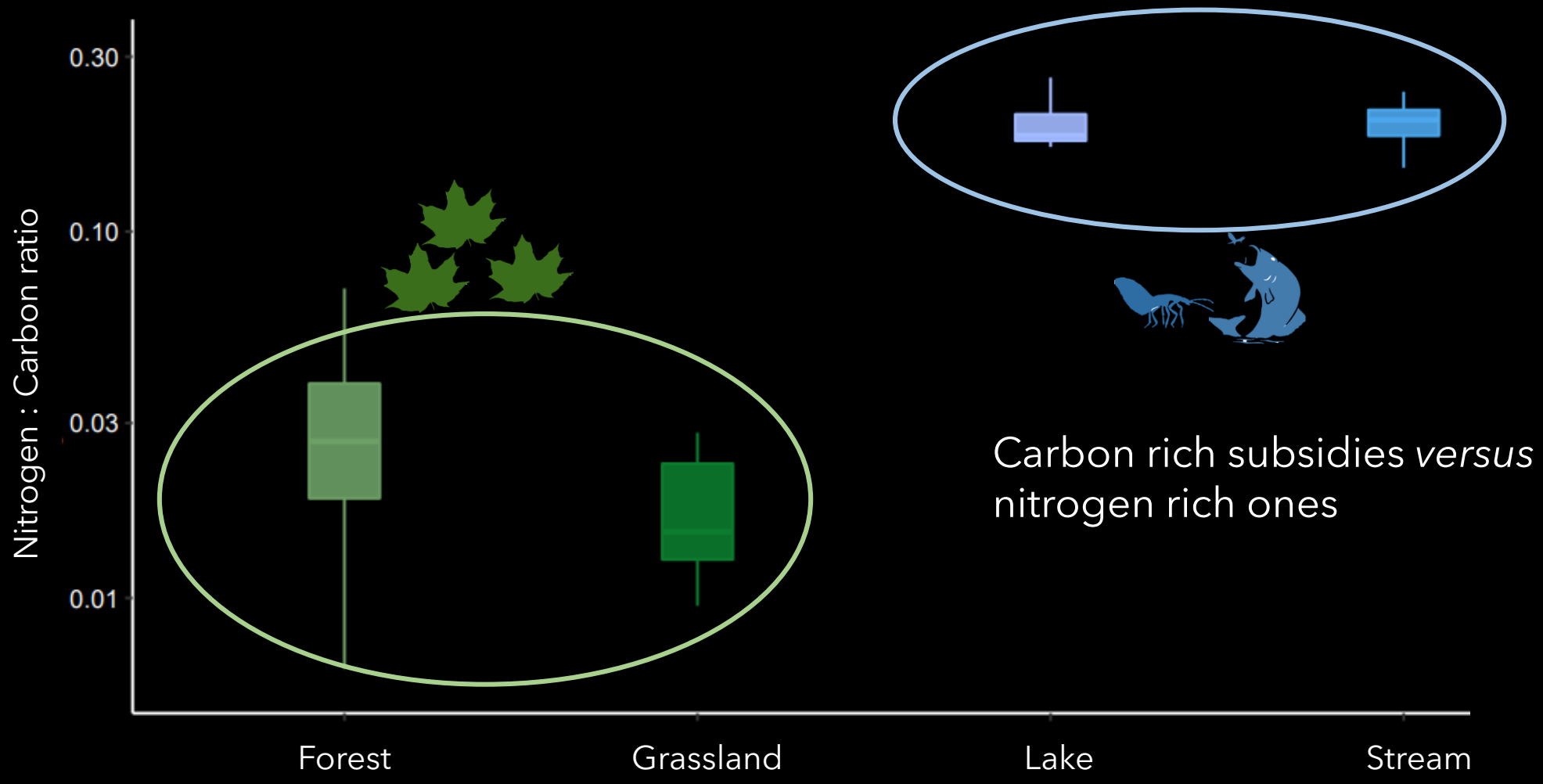




Simple meta-ecosystem experiments shows that quality / stoichiometry of resource flows is a crucial driver of spatial flow effects

Gounand et al. 2016, *Oikos;* Harvey et al. 2017 *ProcB*, Harvey et al. 2020 *Oikos*

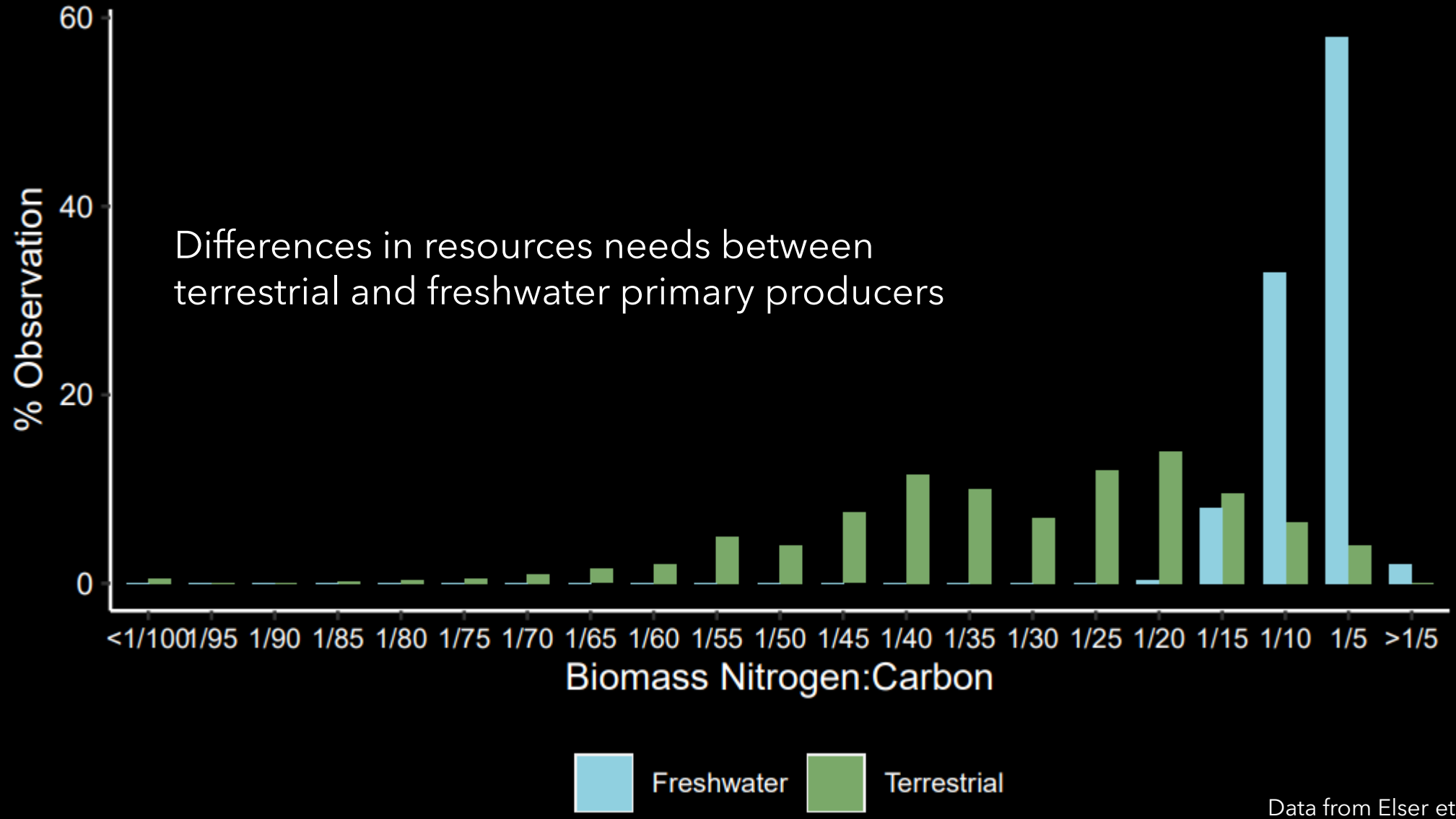
Coupling between ecosystems : asymmetry in **quality**



Carbon rich subsidies *versus* nitrogen rich ones

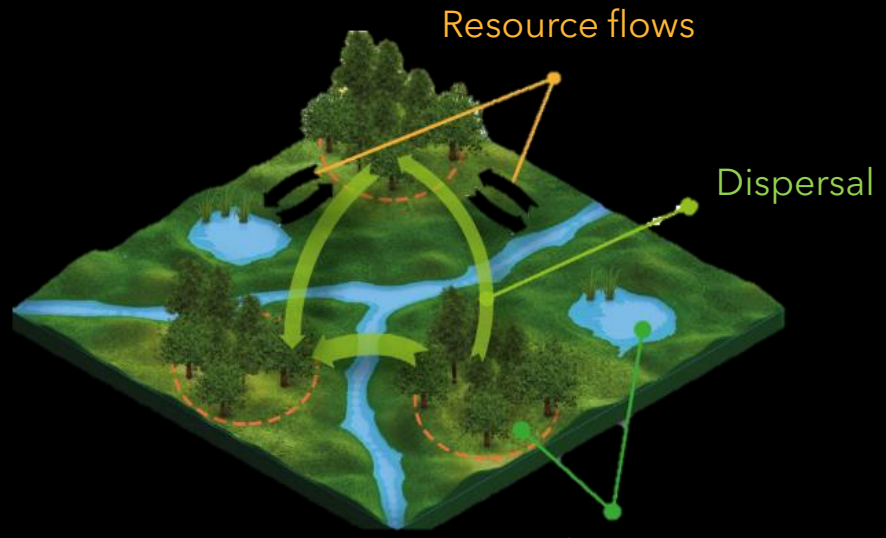
Gounand et al., unpublished data

Coupling between ecosystems : asymmetry in **stoichiometry of assemblages**



Data from Elser et al., 2000

The need of a **stoichiometric** understanding of ecosystems flows

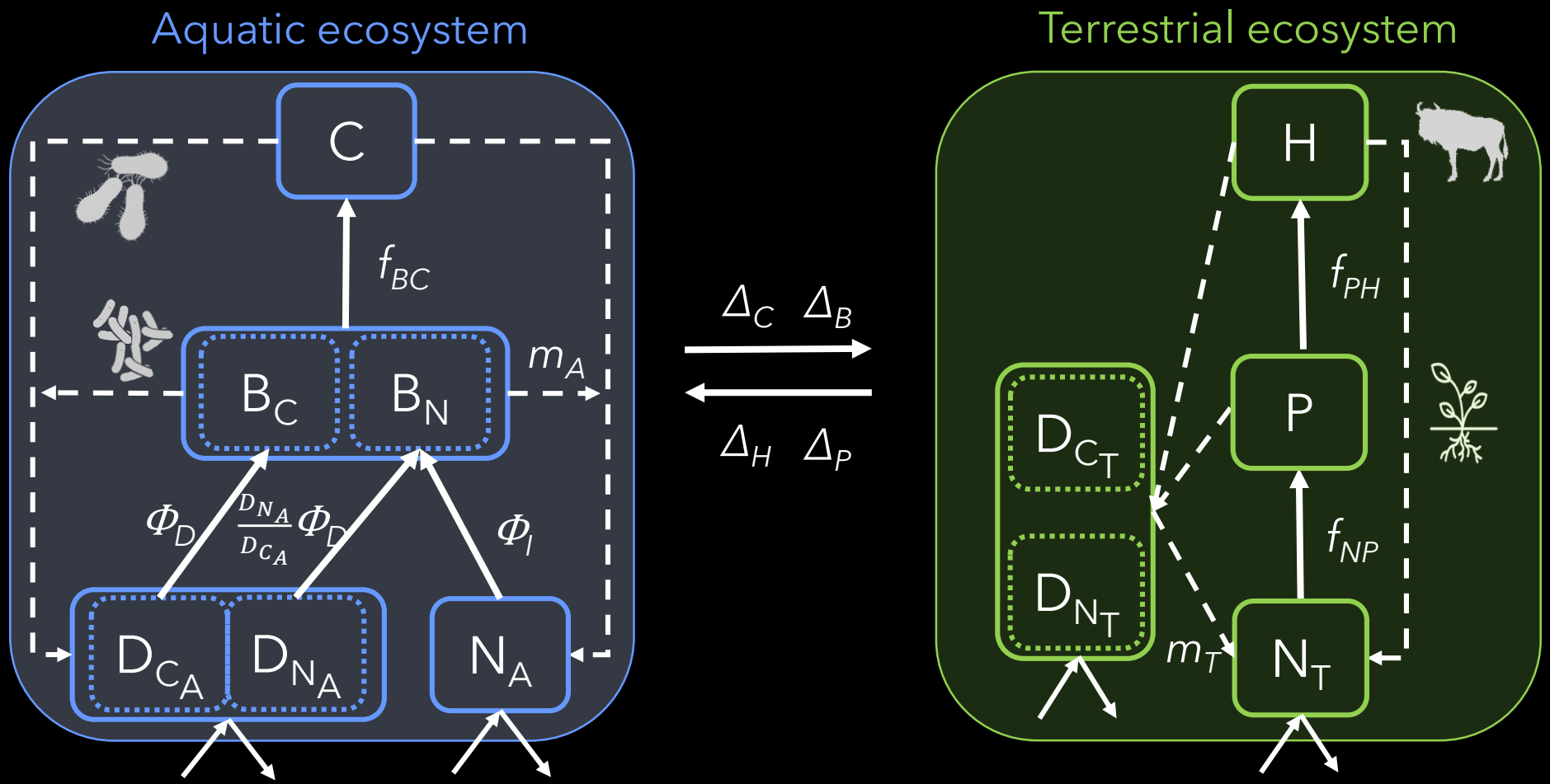


1 How does stoichiometry impacts ecosystems responses to subsidies flow ?

---

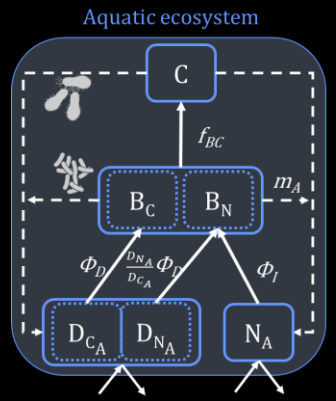
2 Can subsidies flows relax local limitations and lead to higher production at the meta-ecosystem scale ?

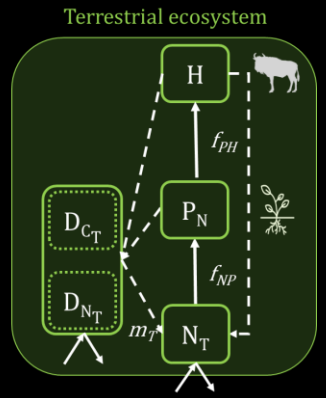
Stoichiometric metaecosystem model



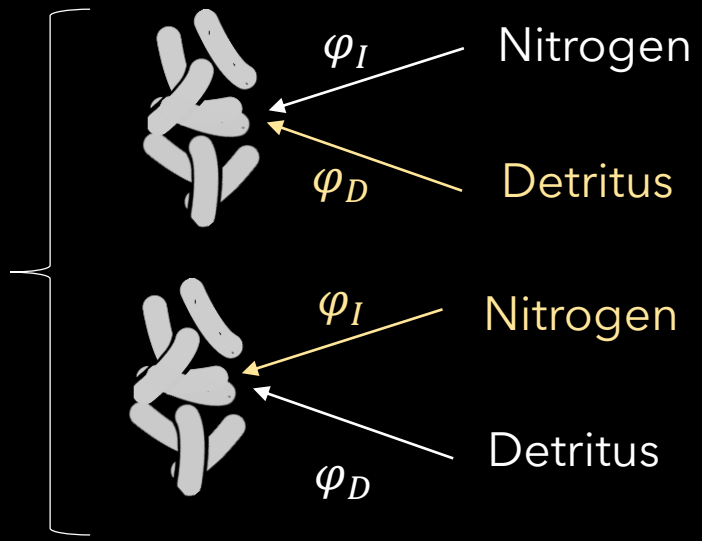
Methods

Local dynamics and regional coupling





Stoichiometry of organism is fixed (stoichiometric homeostasis; N:C ratio constant)



$$\min\left[\left(r_B - \frac{D_N}{D_C}\right) e_B f_{BD}, f_{BN}\right]$$

Decomposers are either C- or N-limited

$$\begin{cases} \varphi_D = e_B f_{BD} D_C \\ \varphi_I = \left(r_B - \frac{D_N}{D_C}\right) e_B f_{BD} D_C \end{cases}$$

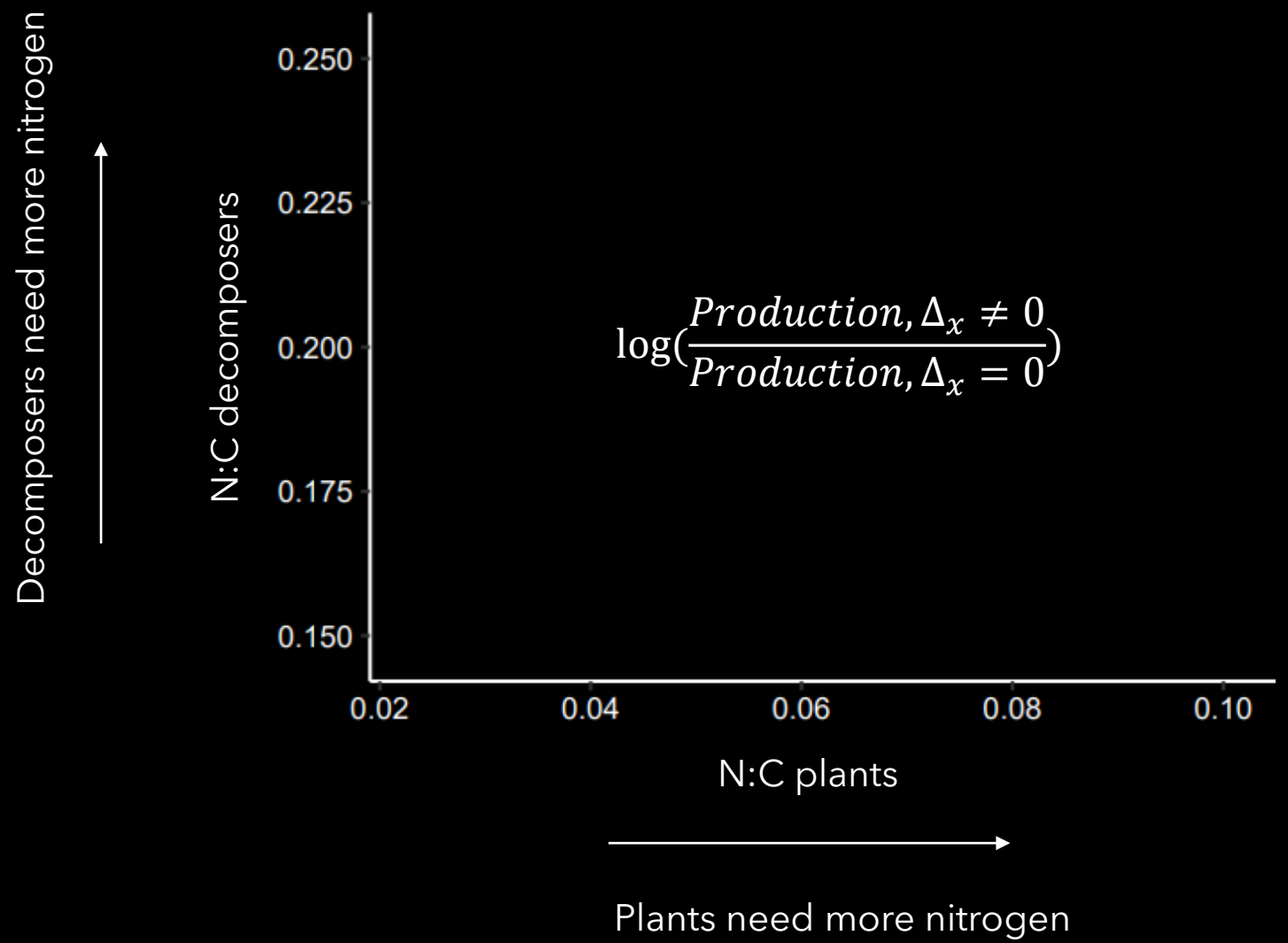
$$\begin{cases} \varphi_D = \left(r_B - \frac{D_N}{D_C}\right)^{-1} f_{BN} N \\ \varphi_I = f_{BN} N \end{cases}$$

Local dynamics

$\Delta_C, \Delta_B, \Delta_H, \Delta_P$ Ecosystems connected by passive spatial flows of detritus and nitrogen

Regional coupling

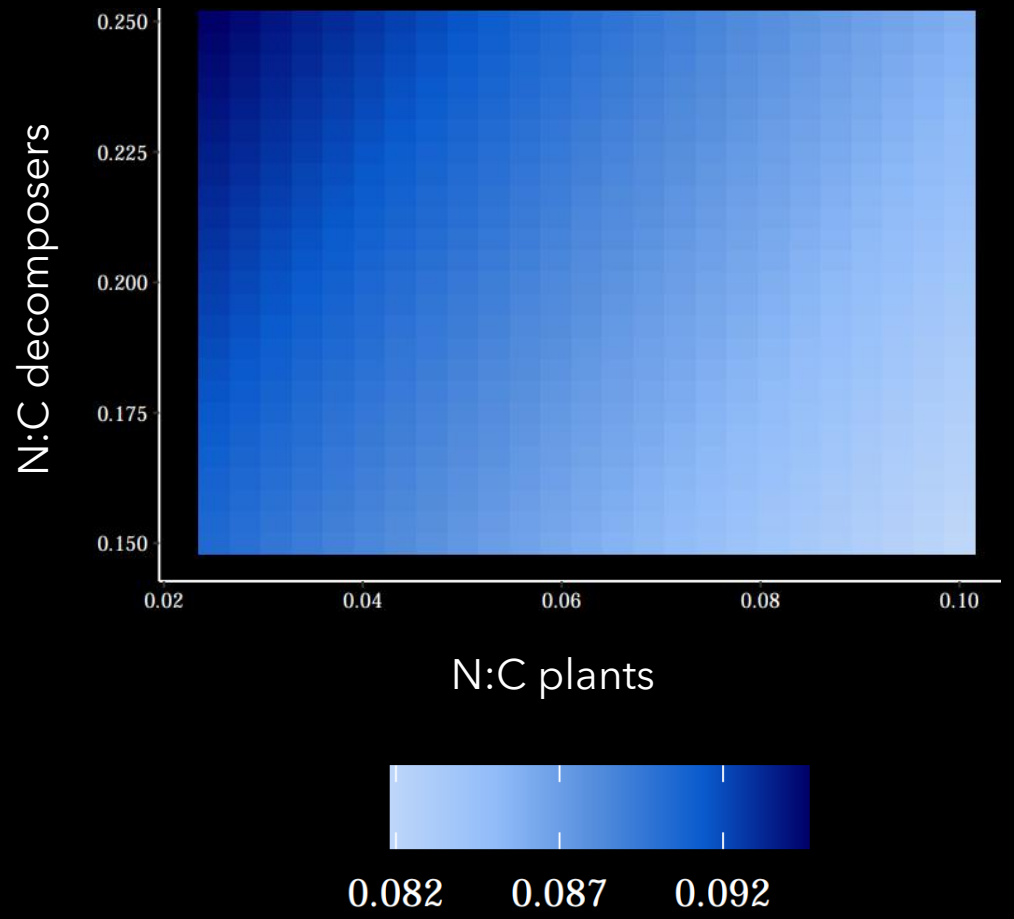
Effect of subsidies flow on the meta-ecosystem primary production



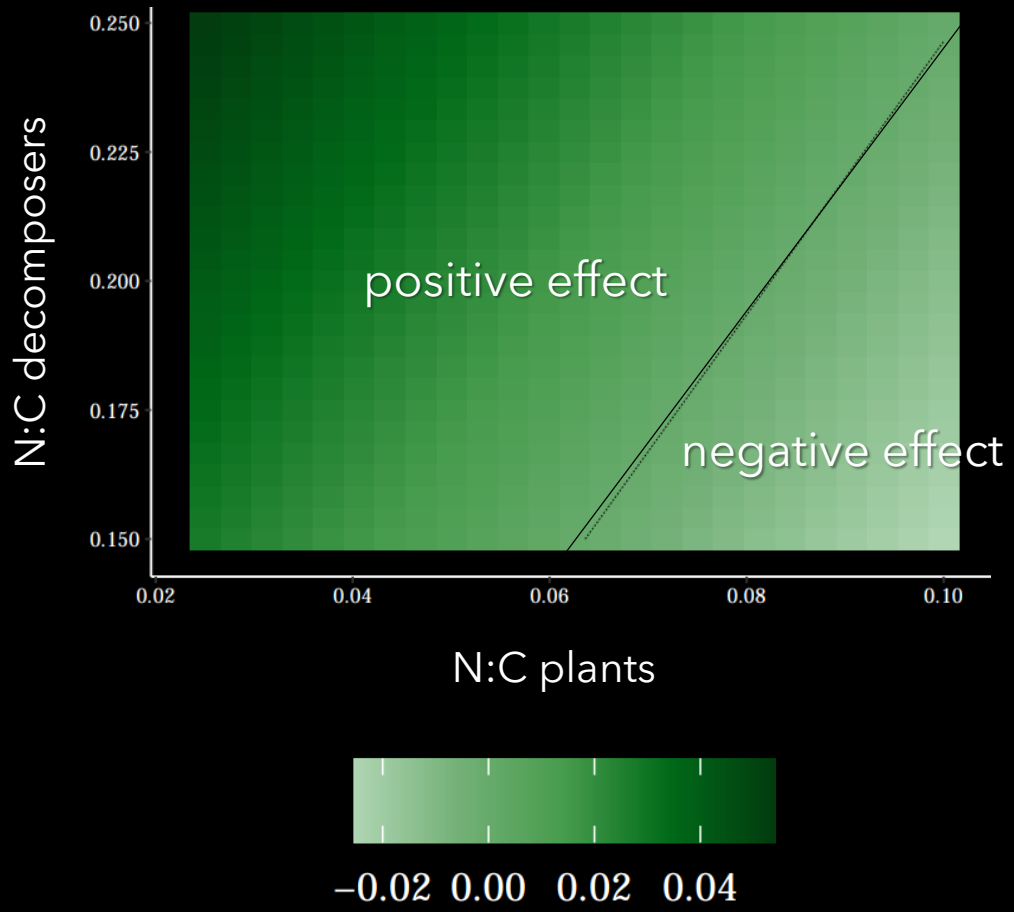
Effect of subsidies flow on the meta-ecosystem **primary production**

C-limited decomposers

Aquatic ecosystem

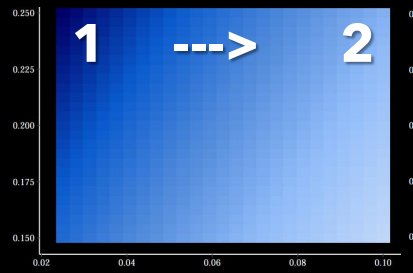


Terrestrial ecosystem

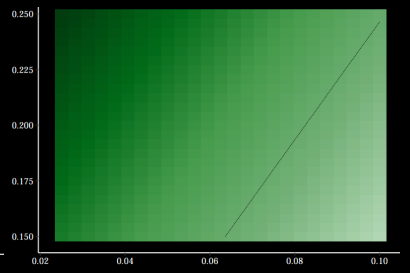


Effect of subsidies flow on the meta-ecosystem primary production : **effect of r_P**

Aquatic ecosystem

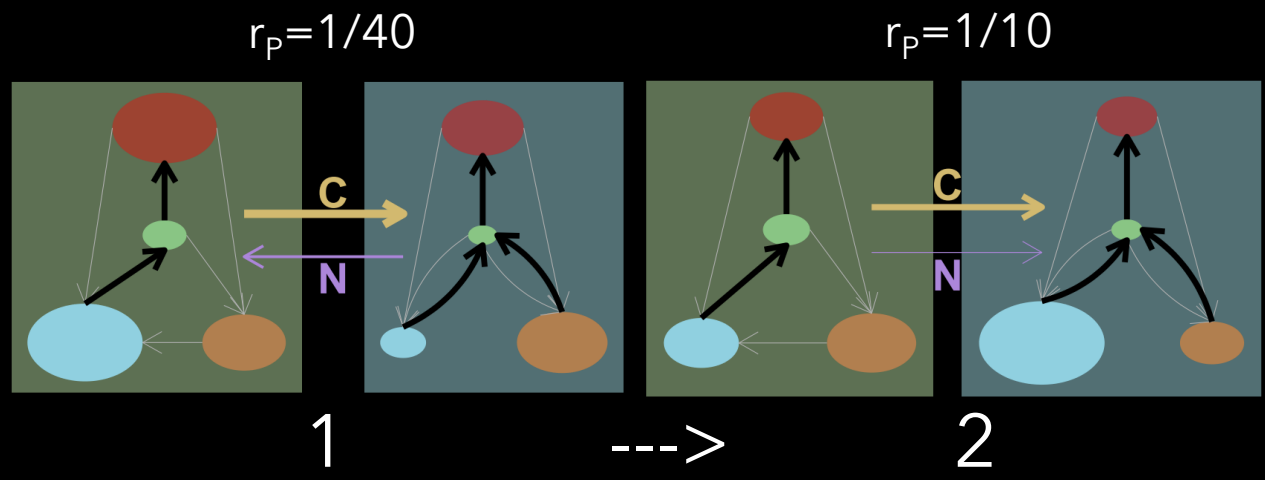


Terrestrial ecosystem



What happens ?

C-limited decomposers

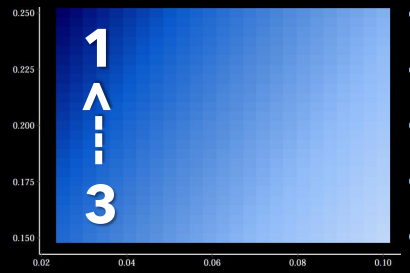


When plants need more nitrogen (increasing r_P) :

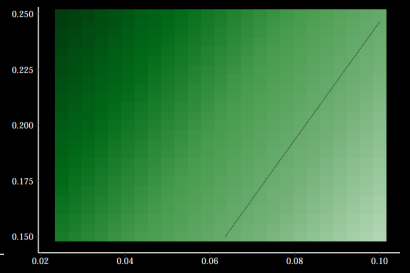
- Benefits of spatial flows decrease
- Plants deplete the nitrogen in terrestrial ecosystem
- Herbivores decreases in density
- Less detritus transported to the aquatic ecosystem

Effect of subsidies flow on the meta-ecosystem primary production : **effect of r_B**

Aquatic ecosystem

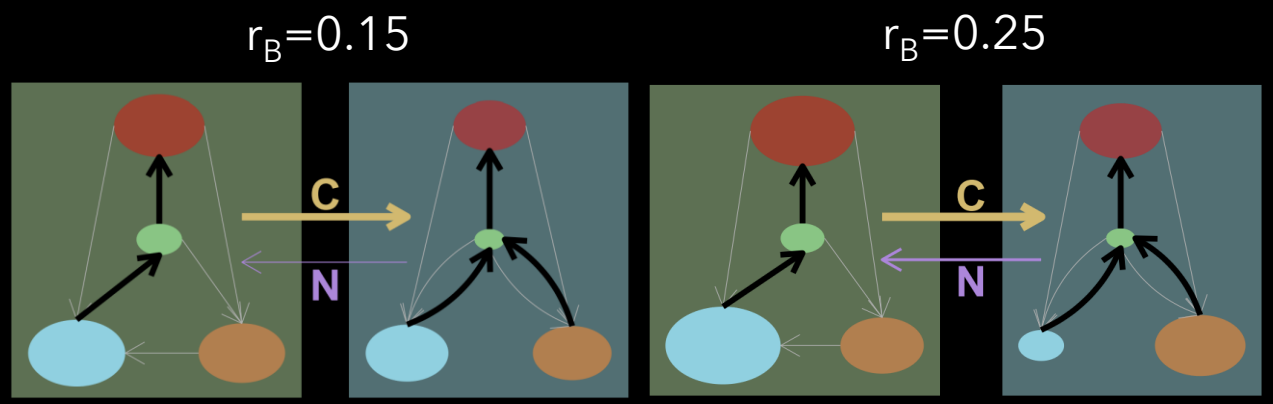


Terrestrial ecosystem



What happens ?

C-limited decomposers



When decomposers need more nitrogen (increasing r_B) :

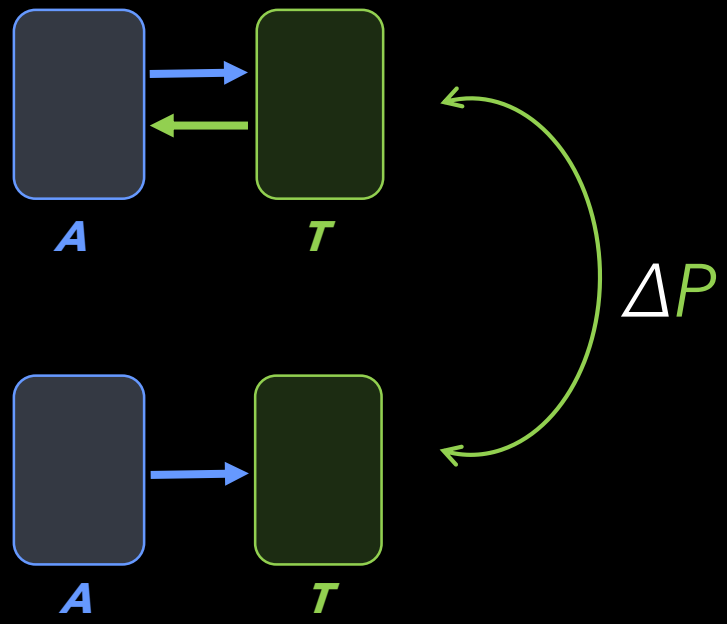
- Increases the quantity of nitrogen transfered to the terrestrial ecosystem
- More nitrogen for plants
- Herbivores increase in density which feedback positively on aquatic ecosystem

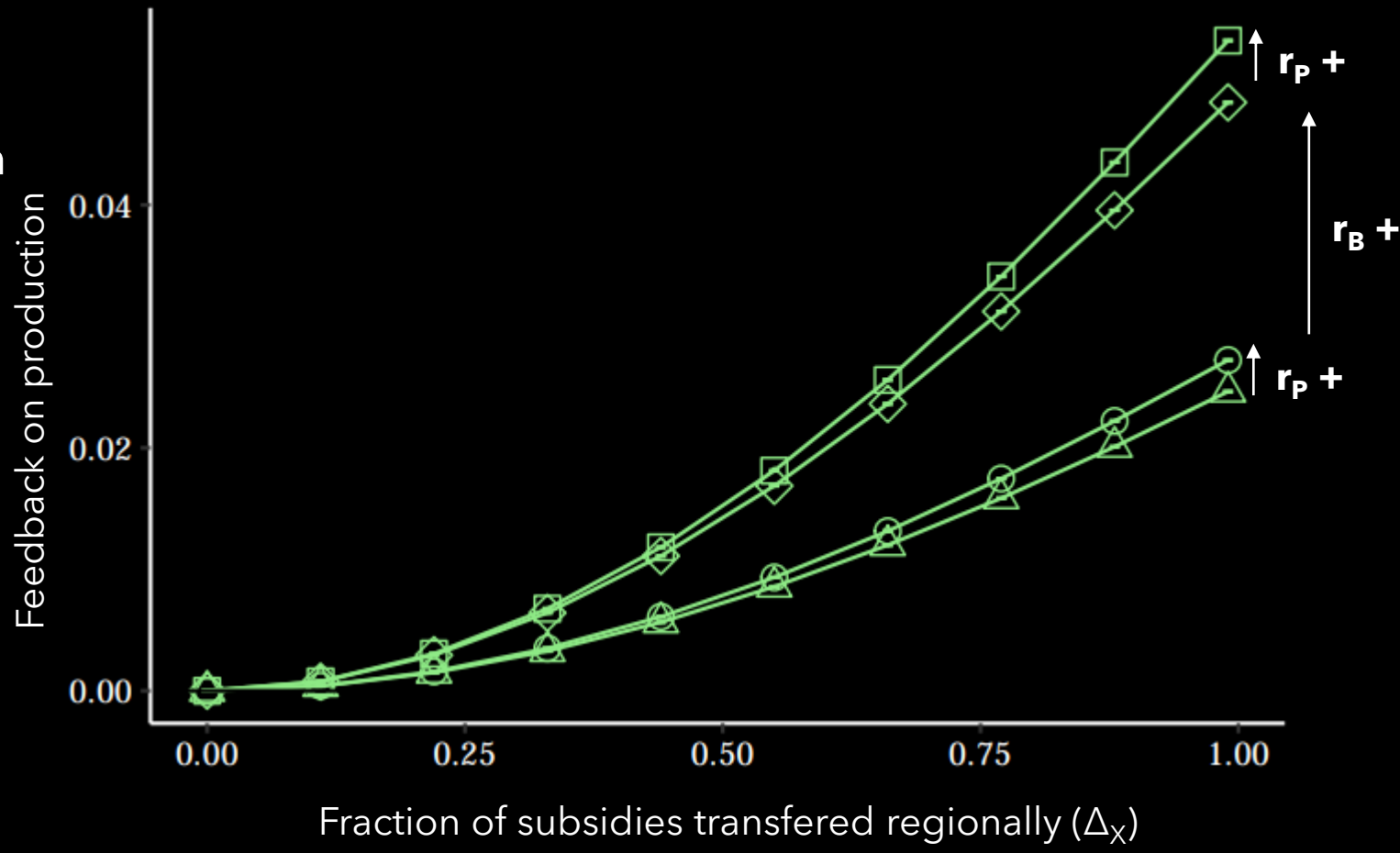
Positive feedback at the meta-ecosystem scale

C-limited decomposers

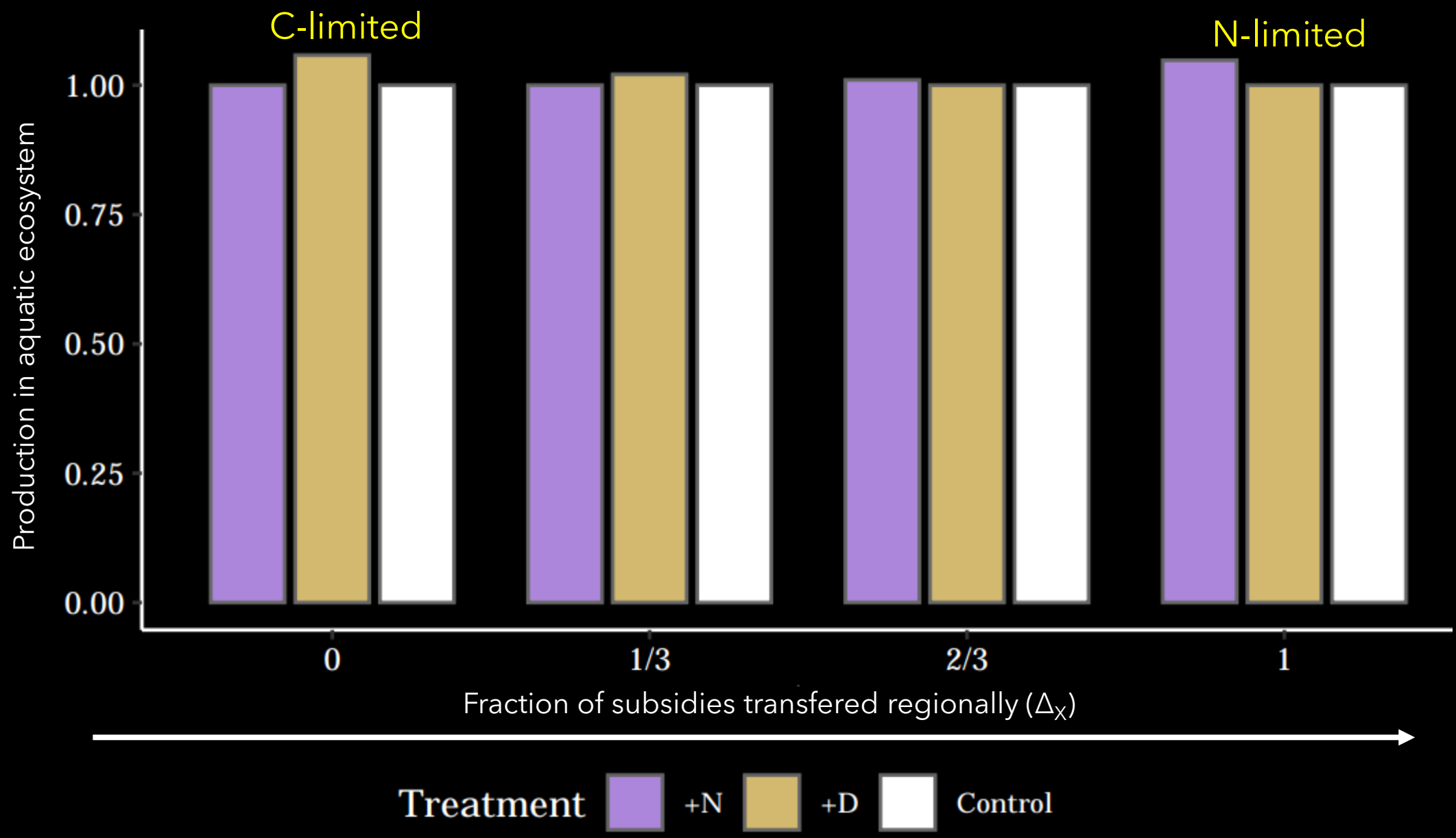
Quantifying the Feedback

e.g., on terrestrial ecosystem production





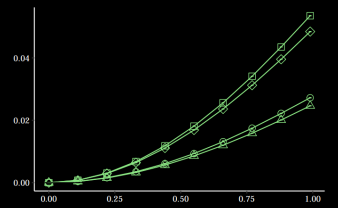
SUBSIDIES FLOW CAN SWITCH THE LOCAL LIMITATION OF DECOMPOSERS



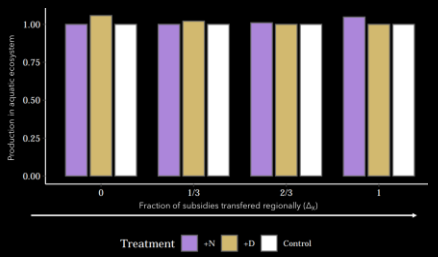
CONCLUSION

- Importance of **stoichiometry** of subsidies for the response of local ecosystems

- Detritus-induced **positive feedbacks** at the landscape extent



- Subsidies flow can **relaxe local limitation** and contribute to higher production at the meta-ecosystem

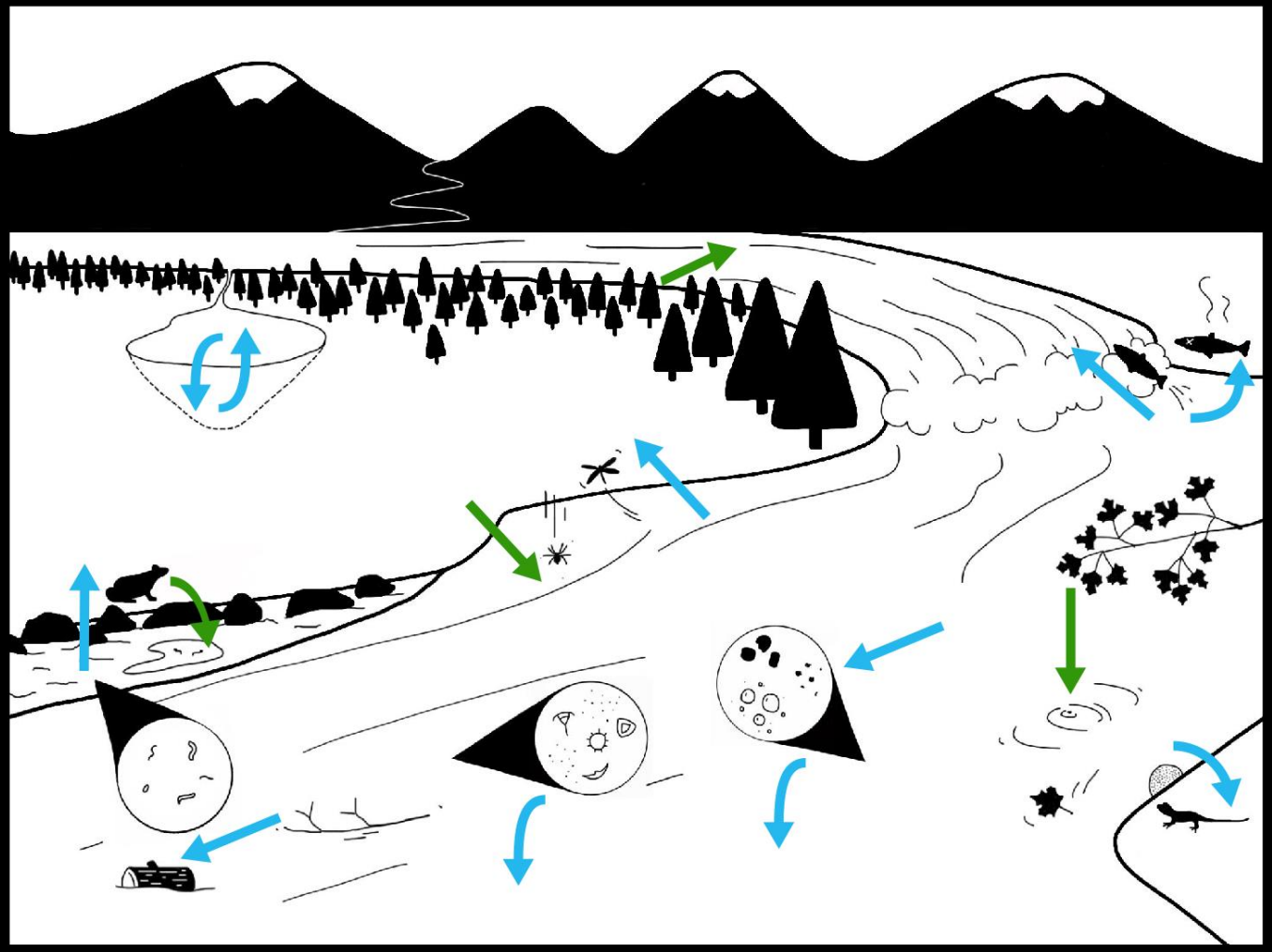


- **Spatial complementarity** at the landscape extent depends on the local limitation

→ **Cross-ecosystem efficiency hypothesis (Harvey et al., 2021)**

Perspectives

How to integrate spatial complexity ?



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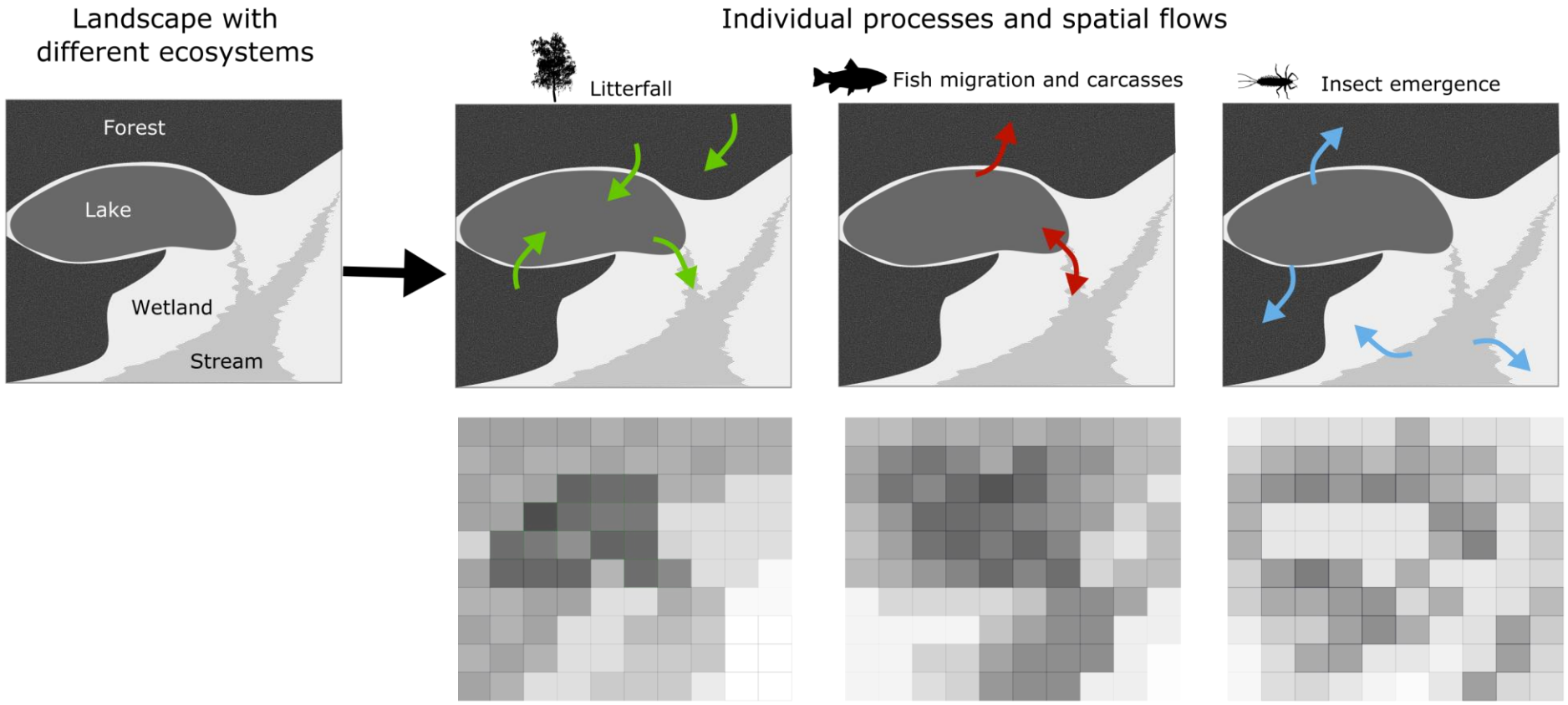
Harvey*, Marleau* et al. 2021 *Authorea*

Perspectives

How to integrate spatial complexity ?



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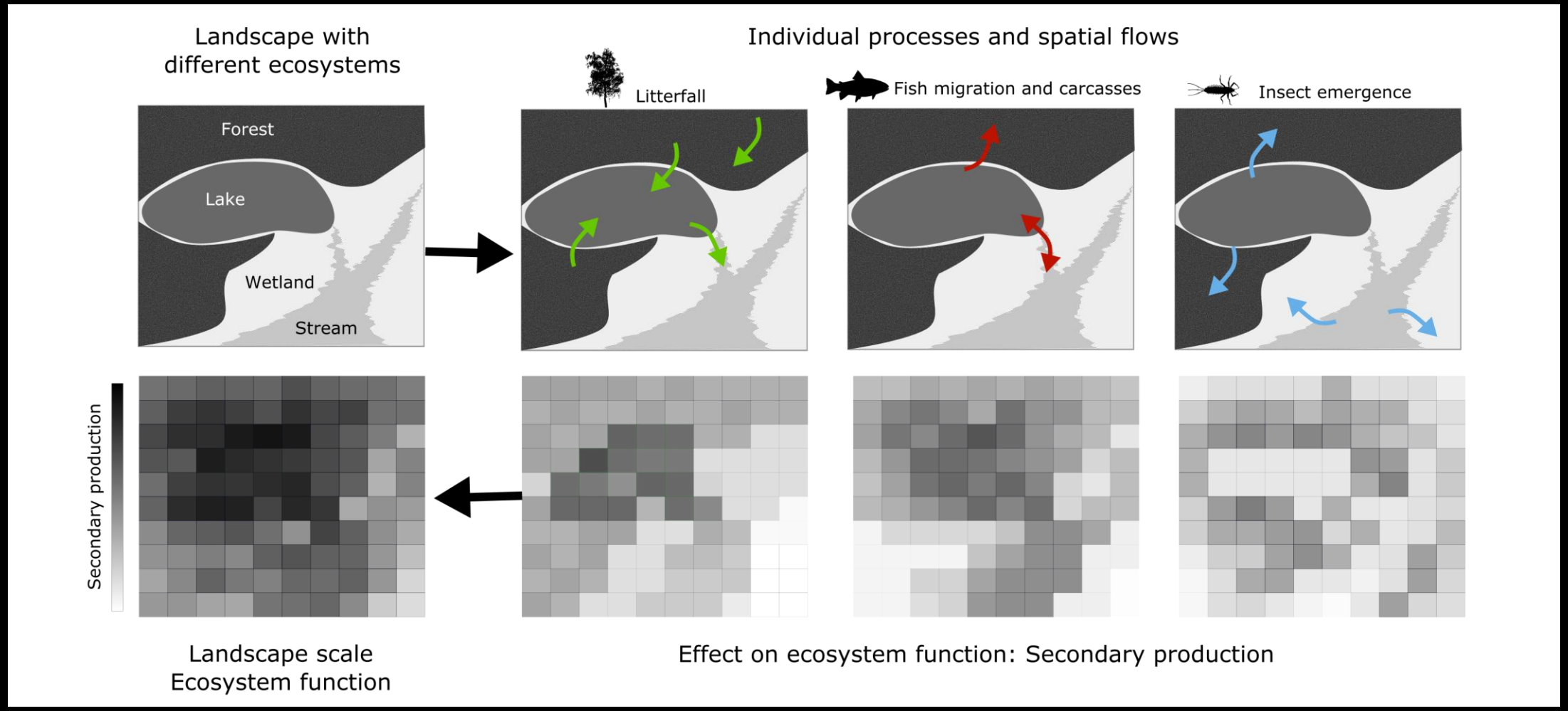
Perspectives

How to integrate spatial complexity ?



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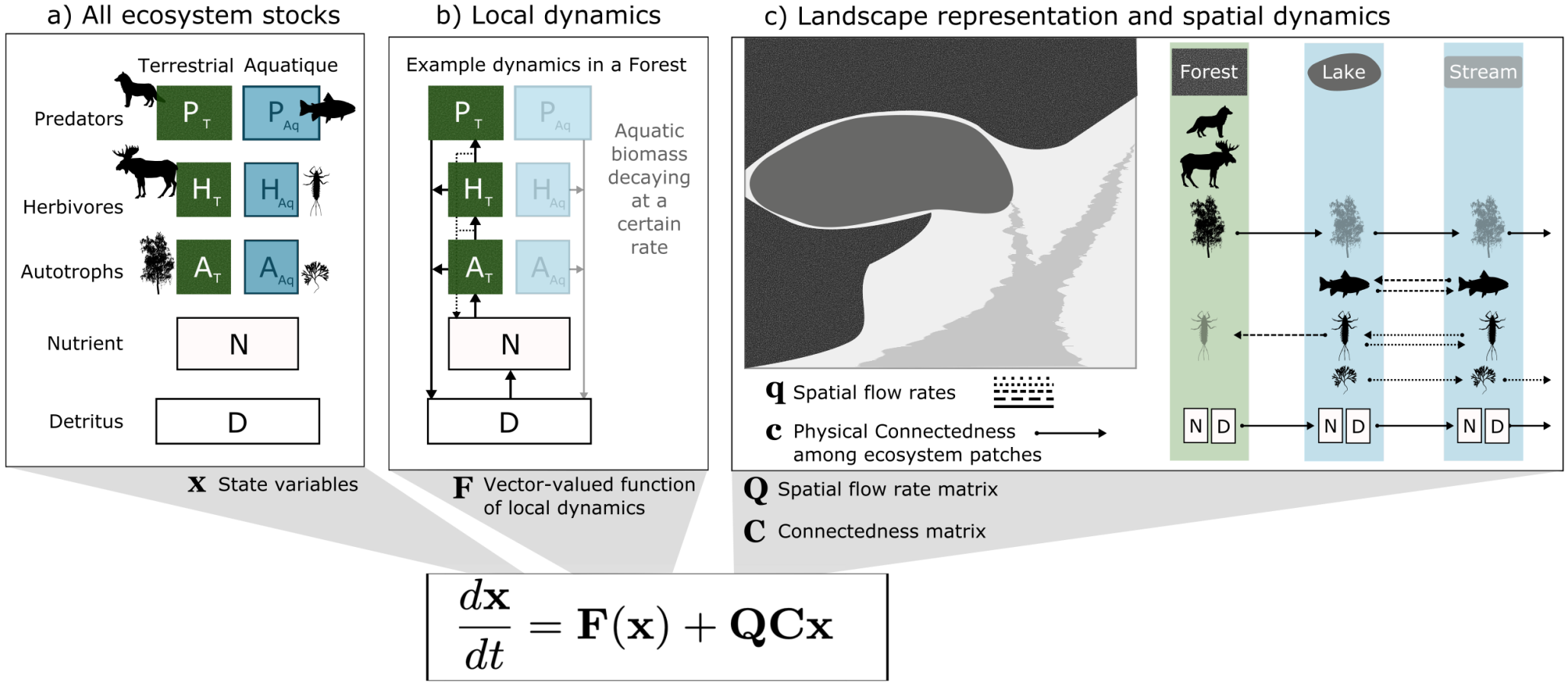
Perspectives: a meta-ecosystem model at landscape extent



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Perspectives: a meta-ecosystem model at landscape extent

$$\mathbf{Q}' = \begin{pmatrix} q_1 & 0 & \dots & 0 \\ 0 & q_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & q_m \end{pmatrix} \quad \mathbf{I}_{(n,n)} = \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 \end{pmatrix} \quad \mathbf{Q} = \mathbf{Q}' \otimes \mathbf{I}_{(n,n)} = \begin{pmatrix} q_1\mathbf{I}_{(n,n)} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & q_2\mathbf{I}_{(n,n)} & \dots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & q_m\mathbf{I}_{(n,n)} \end{pmatrix}$$

$\mathbf{F(x)} = [f_{1,1}(\mathbf{x}_1),\ f_{2,1}(\mathbf{x}_2),\ \dots,\ f_{i,1}(\mathbf{x}_i),\ \dots,\ f_{n,1}(\mathbf{x}_n), f_{1,2}(\mathbf{x}_1),$
$\dots,\ f_{n,2}(\mathbf{x}_n), \dots, f_{i,k}(\mathbf{x}_i), \dots, f_{n,m}(\mathbf{x}_n)]^{\mathrm{T}}$

where $\mathbf{x}_i = (x_{i,1}, \dots, x_{i,k}, \dots, x_{i,m})$ describe the local flows

m, the number of ecosystem compartments
n, the number of ecosystem patches

$$\mathbf{C}_k = \begin{pmatrix} c_{11k} & \dots & c_{1nk} \\ \vdots & \ddots & \vdots \\ c_{n1k} & \dots & c_{nnk} \end{pmatrix}$$

$$\mathbf{C} = \bigoplus_{k=1}^{m} (\mathbf{C}_k)^T = \begin{pmatrix} (\mathbf{C}_1)^T & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & (\mathbf{C}_2)^T & \dots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & (\mathbf{C}_m)^T \end{pmatrix}$$

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}) + \mathbf{QCx}$$

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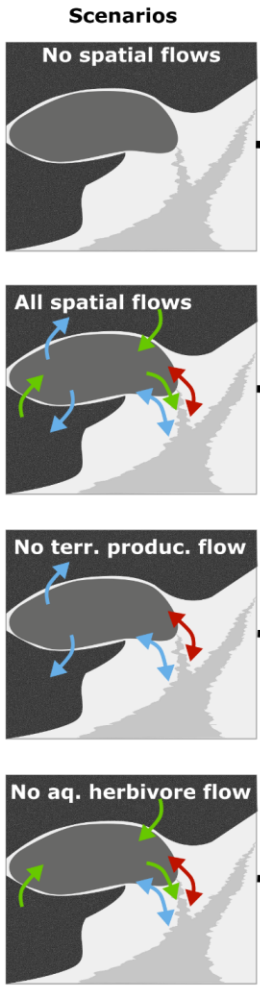
Perspectives: a meta-ecosystem model at landscape extent



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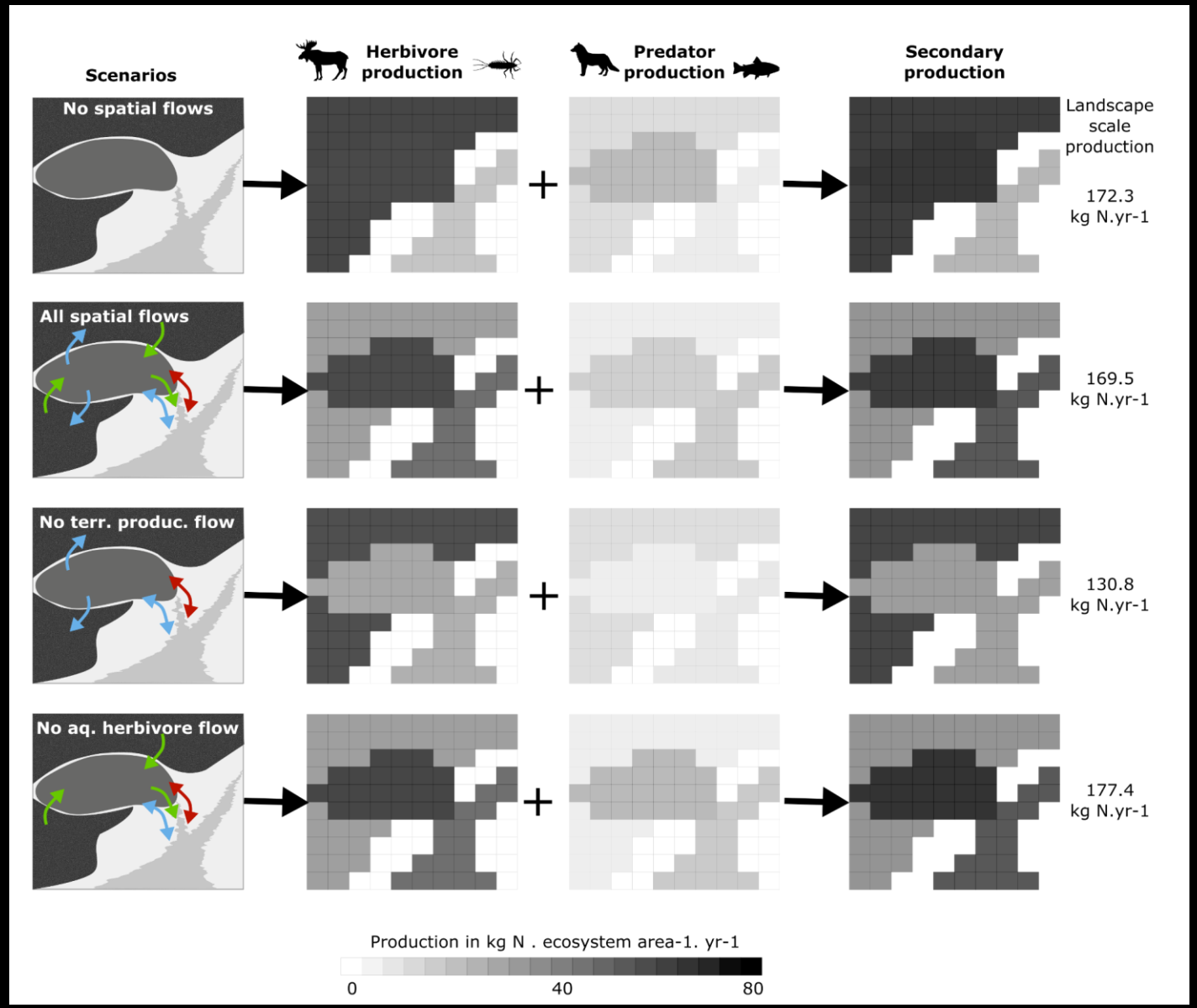
Perspectives: a meta-ecosystem model at landscape extent



Resource spatial flow reallocate secondary production among habitats in the landscape and might increases total secondary production

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The paradox of enrichment in meta-ecosystems

Empirical / experimental work on meta-ecosystem

Stoichiometric meta-ecosystem model

Meta-ecosystem model at landscape extent

THANK YOU!

Dominique Gravel
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