Linking bacterial diversity to ciliate abundance gives mechanistic framework for virus-to-bacteria ratios

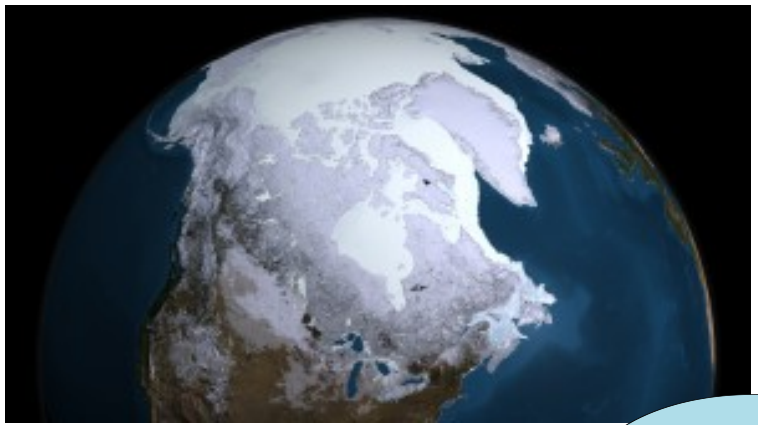
Selina Våge, Bernadette Pree, T. Frede Thingstad

ICES 6th Zooplankton Production Symposium
Bergen, Norway 9-13 May 2016

HJORT CENTRE
FOR MARINE ECOSYSTEM DYNAMICS

UNIVERSITAS BERGENSIS

Microbes at the basis of large-scale dynamics



CLIMATE

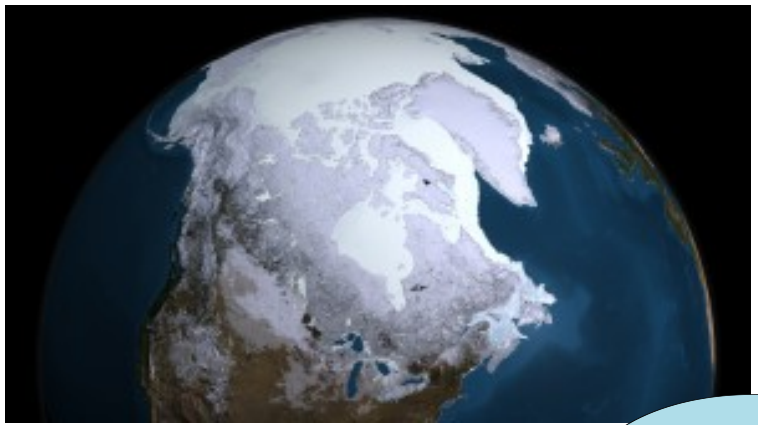
POLLUTION

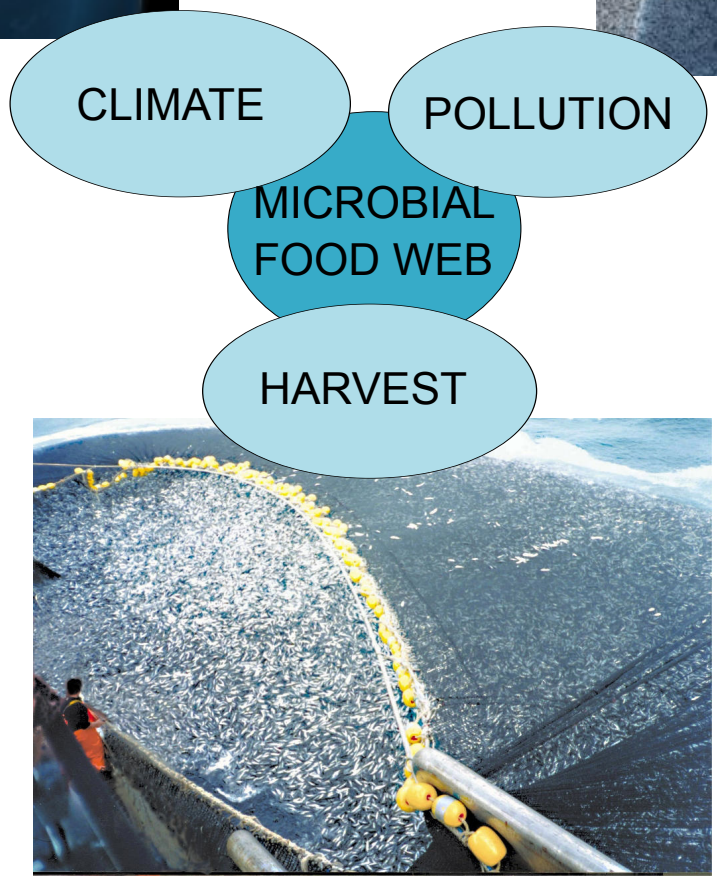
MICROBIAL FOOD WEB

HARVEST

selina.vage@uib.no

Microbes at the basis of large-scale dynamics

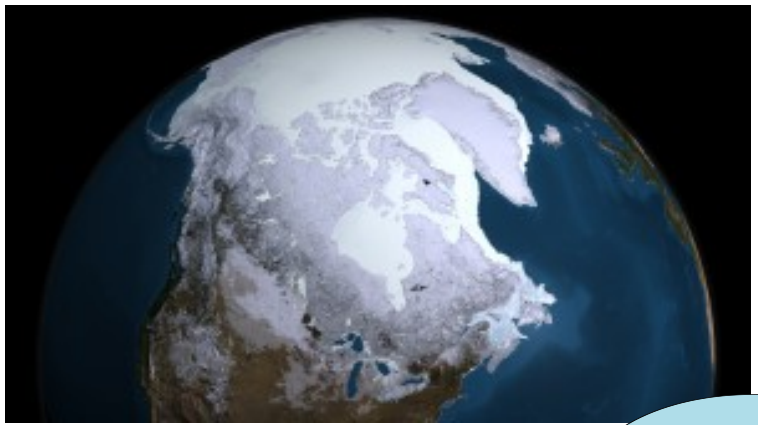


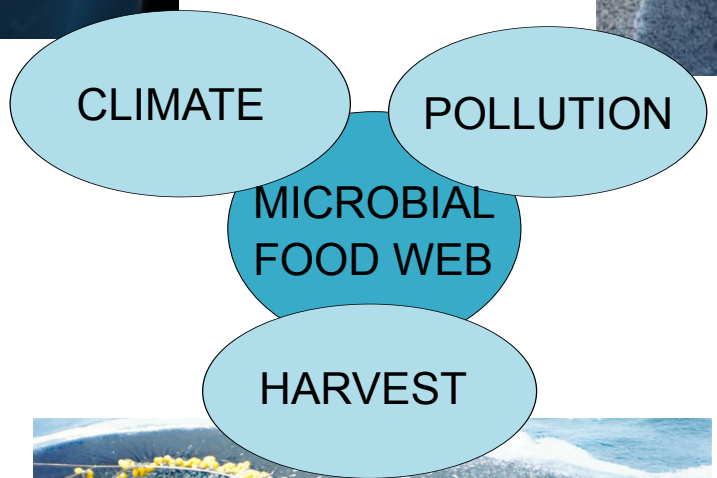


- Virus-to-bacteria ratios (VBR) measured as proxy for *'viral importance'* over 25 years

selina.vage@uib.no

Microbes at the basis of large-scale dynamics





- Virus-to-bacteria ratios (VBR) measured as proxy for *'viral importance'* over 25 years
- Mechanistic understanding still lacking

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities'

selina.vage@uib.no

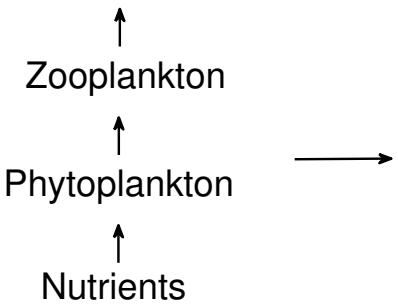
Lack of insight due to separating different scales?
A) 'Between communities'

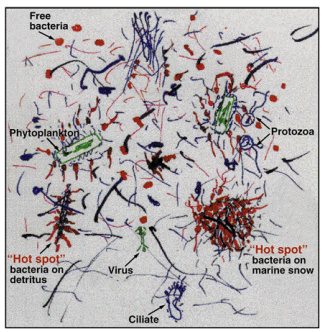
- **Microbial loop** concept in 1970s

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities'

- **Microbial loop** concept in 1970s $\Rightarrow$ Shift of emphasis from linear chain to complex foodweb



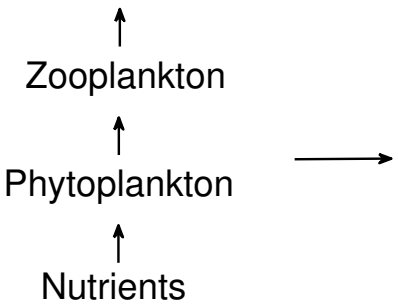


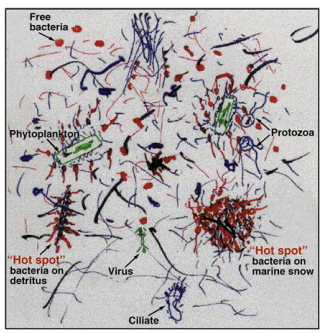
(Azam 1998, Science)

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities'

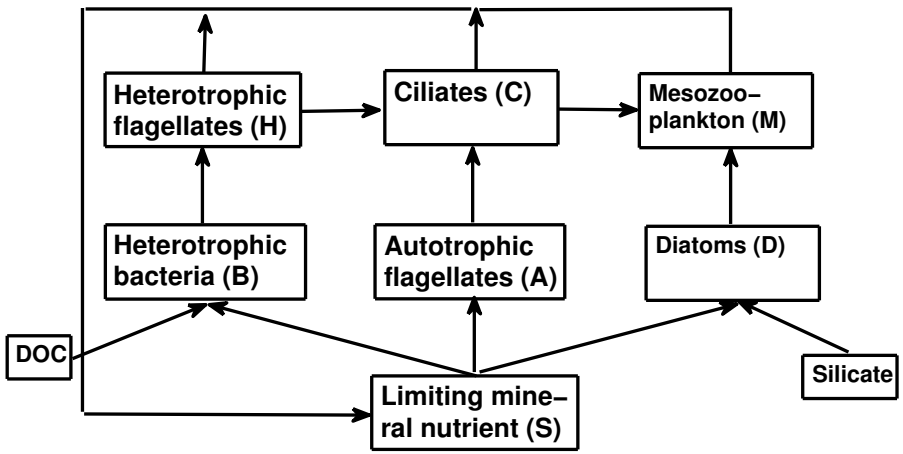
- **Microbial loop** concept in 1970s $\Rightarrow$ Shift of emphasis from linear chain to complex foodweb





(Azam 1998, Science)

$\Rightarrow$ Resolving 'plankton functional types' (PFT)

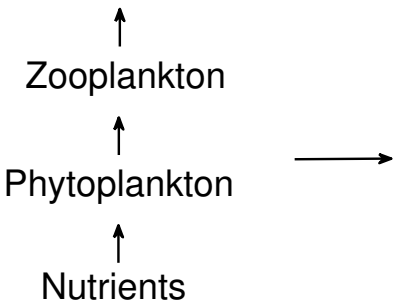


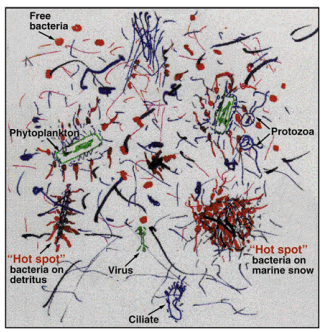
(Thingstad et al 2007, JMS)

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities'

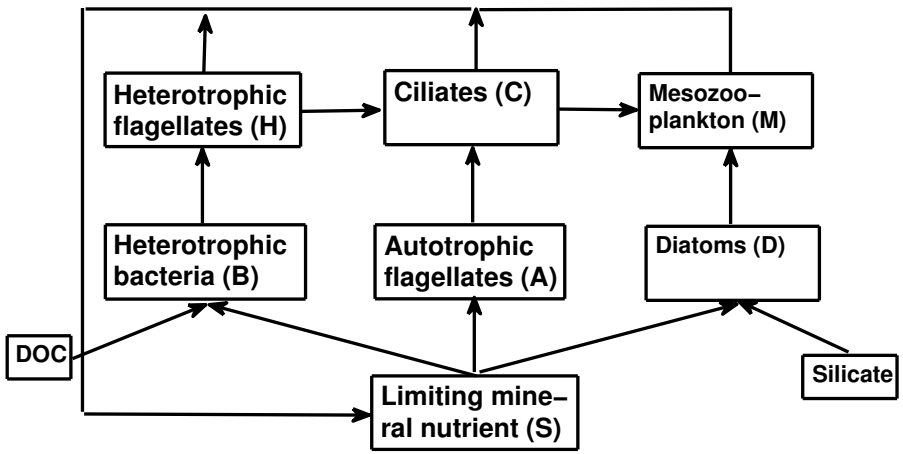
- **Microbial loop** concept in 1970s ⇒ Shift of emphasis from linear chain to complex foodweb





(Azam 1998, Science)

⇒ Resolving 'plankton functional types' (PFT)



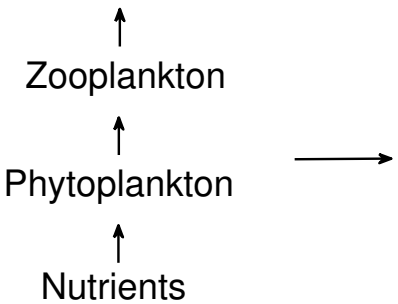
(Thingstad et al 2007, JMS)

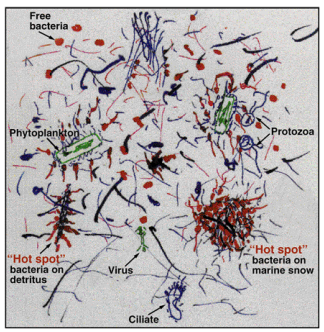
- Focus on **food web structure** at PFT resolution

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities'

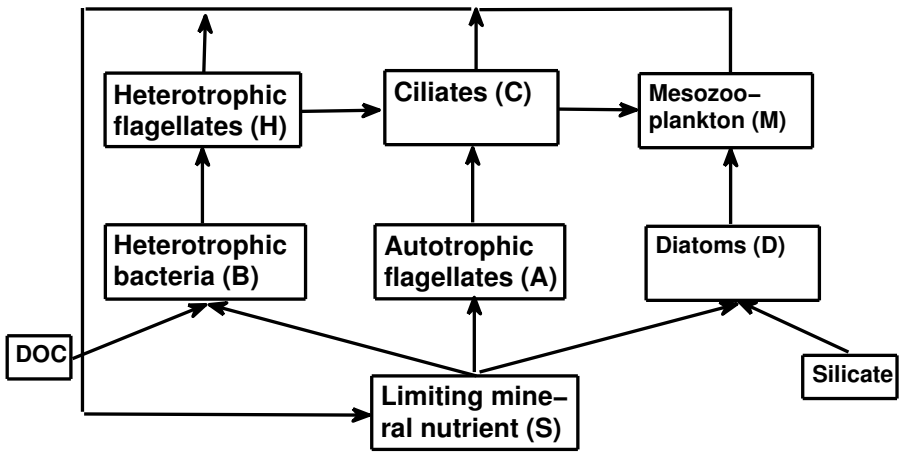
- **Microbial loop** concept in 1970s ⇒ Shift of emphasis from linear chain to complex foodweb





(Azam 1998, Science)

⇒ Resolving 'plankton functional types' (PFT)



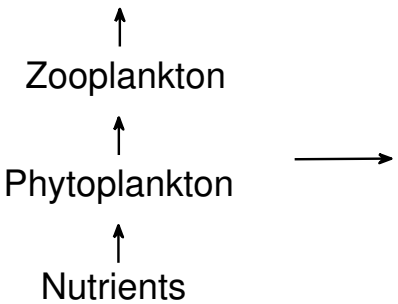
(Thingstad et al 2007, JMS)

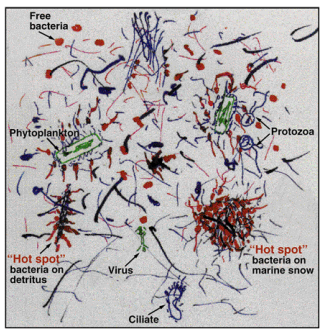
- Focus on **food web structure** at PFT resolution
- **Fits** dynamics from mesocosm experiments in **different environments** (Denmark, Svalbard) (Larsen et al 2015, L&O)

selina.vage@uib.no

Lack of insight due to separating different scales?
A) 'Between communities' **(External control)**

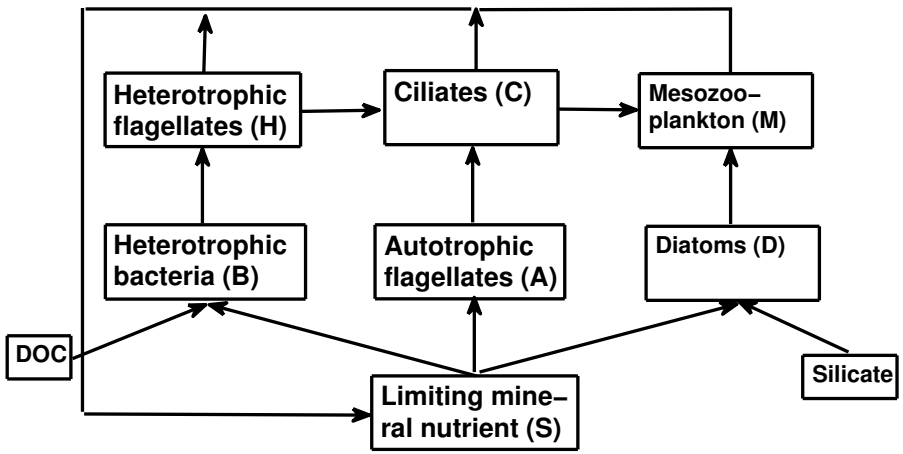
- **Microbial loop** concept in 1970s ⇒ Shift of emphasis from linear chain to complex foodweb





(Azam 1998, Science)

⇒ Resolving 'plankton functional types' (PFT)



(Thingstad et al 2007, JMS)

- Focus on **food web structure** at PFT resolution
- **Fits** dynamics from mesocosm experiments in **different environments** (Denmark, Svalbard) (Larsen et al 2015, L&O)

selina.vage@uib.no

Lack of insight due to separating different scales?
B) 'Within community'

selina.vage@uib.no

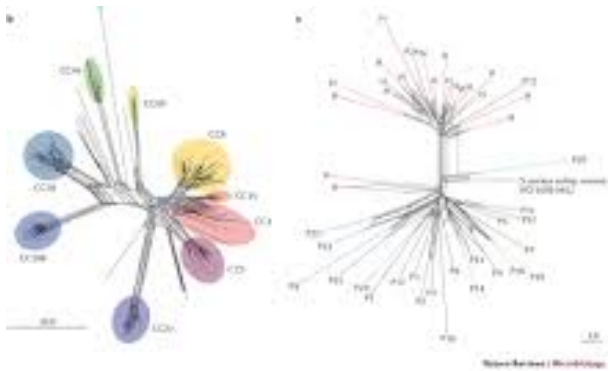
Lack of insight due to separating different scales?
B) 'Within community'

- **Molecular techniques** (DNA sequencing) from around 1990

selina.vage@uib.no

Lack of insight due to separating different scales?
B) 'Within community'

- **Molecular techniques** (DNA sequencing) from around 1990
  $\Rightarrow$ Focus on biodiversity

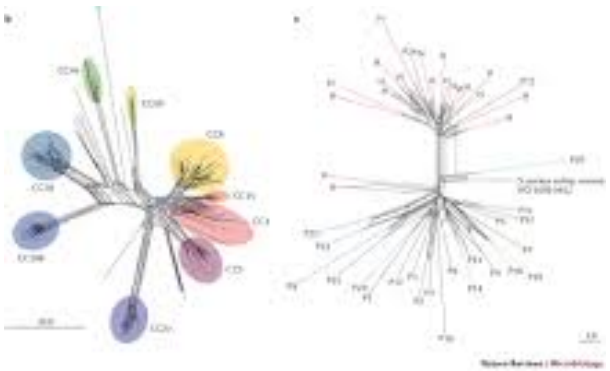


(Maiden et al 2013)

selina.vage@uib.no

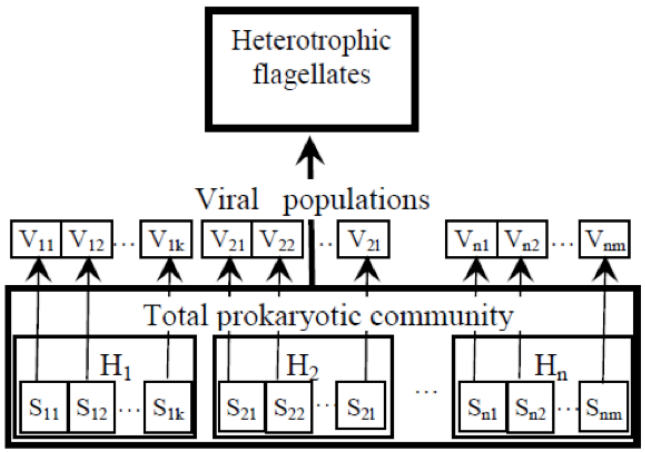
Lack of insight due to separating different scales?
B) 'Within community'

- **Molecular techniques** (DNA sequencing) from around 1990
  ⇒ Focus on biodiversity



(Maiden et al 2013)

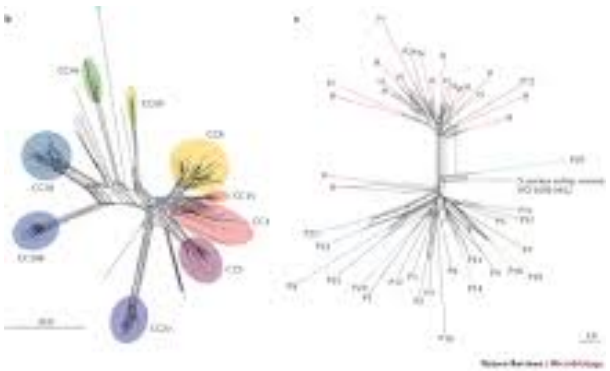
⇒ Resolving internal community structure



selina.vage@uib.no

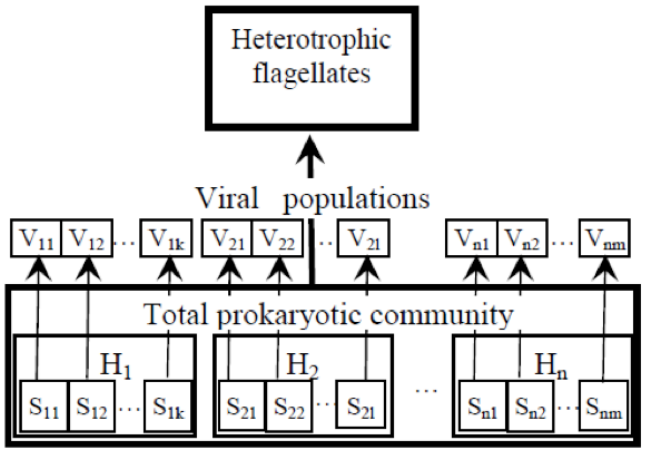
Lack of insight due to separating different scales?
B) 'Within community' **(Internal control)**

- **Molecular techniques** (DNA sequencing) from around 1990
  ⇒ Focus on biodiversity



(Maiden et al 2013)

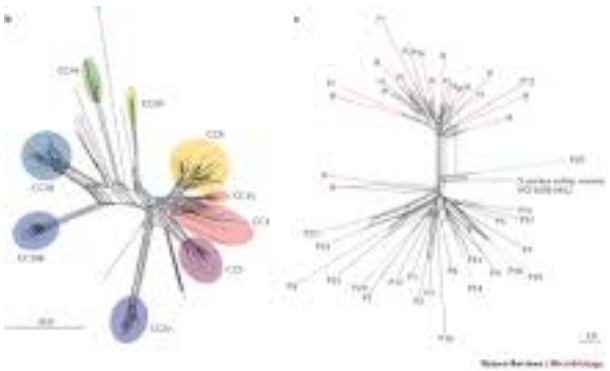
⇒ Resolving internal community structure



selina.vage@uib.no

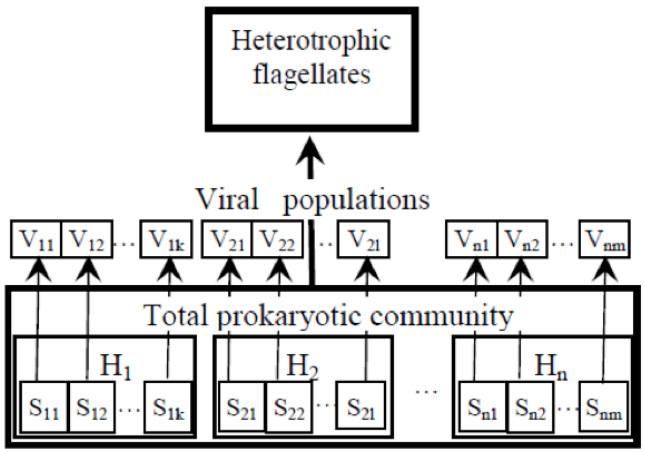
Lack of insight due to separating different scales?
B) 'Within community' **(Internal control)**

- **Molecular techniques** (DNA sequencing) from around 1990
  ⇒ Focus on biodiversity



(Maiden et al 2013)

⇒ Resolving internal community structure

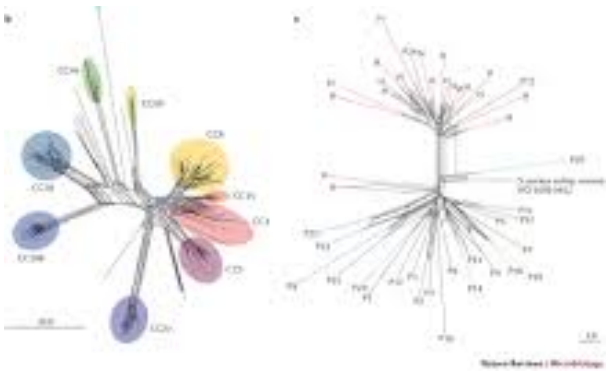


- **Strain-specific viruses regulate species diversity** in virus-host coevolution model (Thingstad et al 2014, PNAS)

selina.vage@uib.no

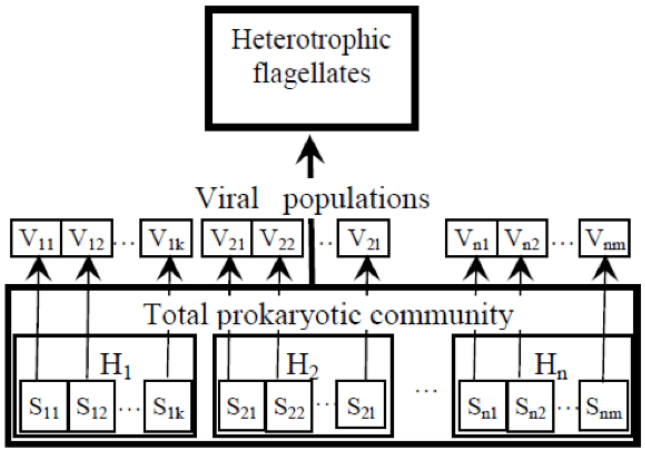
Lack of insight due to separating different scales?
B) 'Within community' **(Internal control)**

- **Molecular techniques** (DNA sequencing) from around 1990
  ⇒ Focus on biodiversity



(Maiden et al 2013)

⇒ Resolving internal community structure



- **Strain-specific viruses regulate species diversity** in virus-host coevolution model (Thingstad et al 2014, PNAS)
- Explains **high abundance** of **slow growing strains** (SAR11) by **costly defense** against viruses, rather than starvation, and reconciles **high abundance of SAR11 viruses** (Våge et al 2013, Nature)

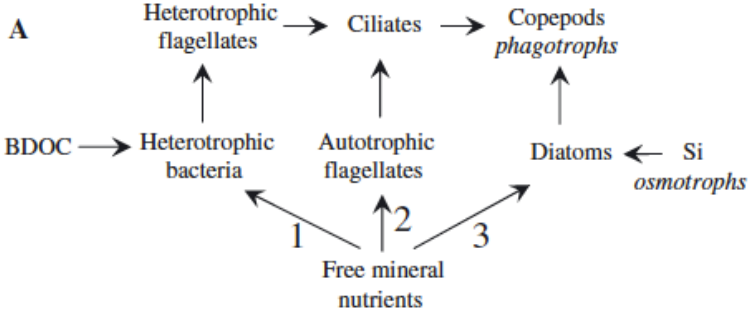
selina.vage@uib.no

Summary - Microbial food web control at different scales

selina.vage@uib.no

Summary - Microbial food web control at different scales

'Between-communities' pathways:



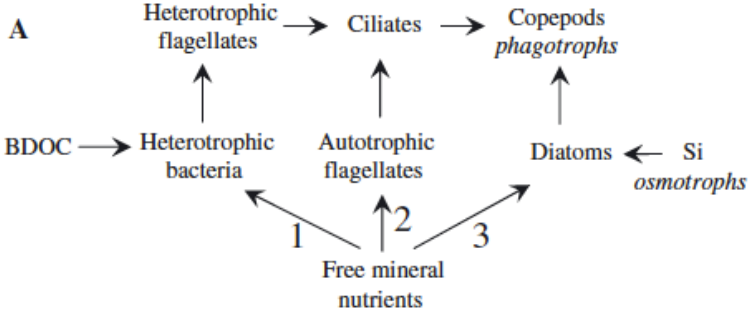
(Thingstad & Cuevas 2010, AME)

- Size-selective **grazing**
- Resource **competition between** plankton functional types (PFT) (linked to resource diversity)

selina.vage@uib.no

Summary - Microbial food web control at different scales

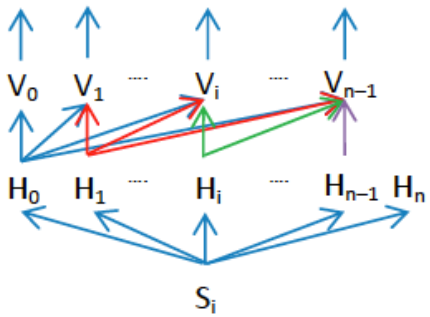
'Between-communities' pathways:



(Thingstad & Cuevas 2010, AME)

- Size-selective **grazing**
- Resource **competition between** plankton functional types (PFT) (linked to resource diversity)

'Within-community' structure:



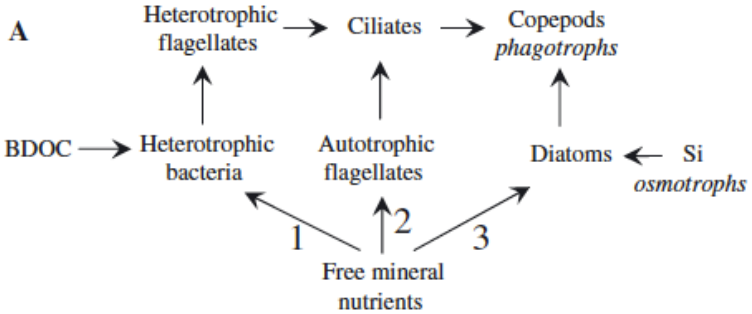
(Thingstad et al 2014, PNAS)

- Viral **infections**
- Resource **competition within** PFT (linked to resource diversity)

selina.vage@uib.no

Summary - Microbial food web control at different scales

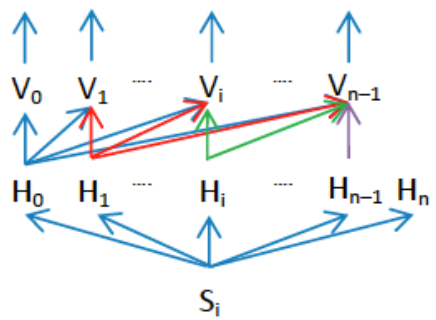
'Between-communities' pathways:



(Thingstad & Cuevas 2010, AME)

- Size-selective **grazing**
- Resource **competition between** plankton functional types (PFT) (linked to resource diversity)

'Within-community' structure:



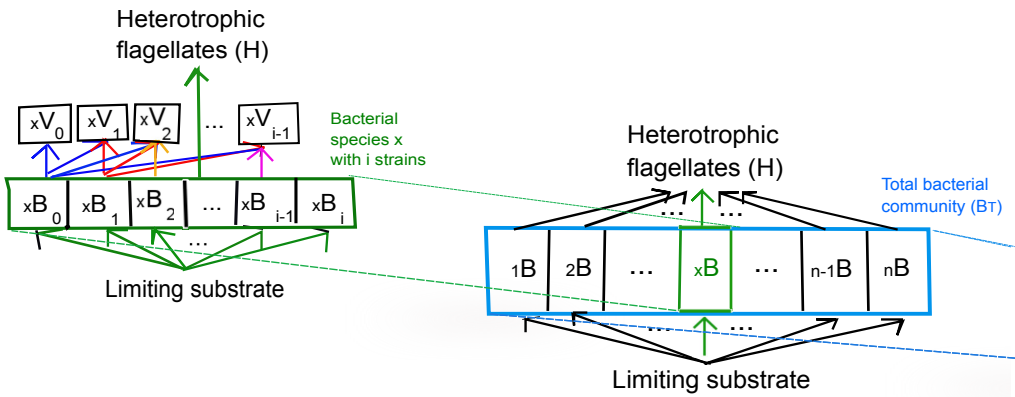
(Thingstad et al 2014, PNAS)

- Viral **infections**
- Resource **competition within** PFT (linked to resource diversity)

$\Rightarrow$ Unclear **how** trophic **interactions between** PFT **relate to** organism properties and **interactions within** PFT *(analogy to understanding 'macro-' from 'micro-economy')*

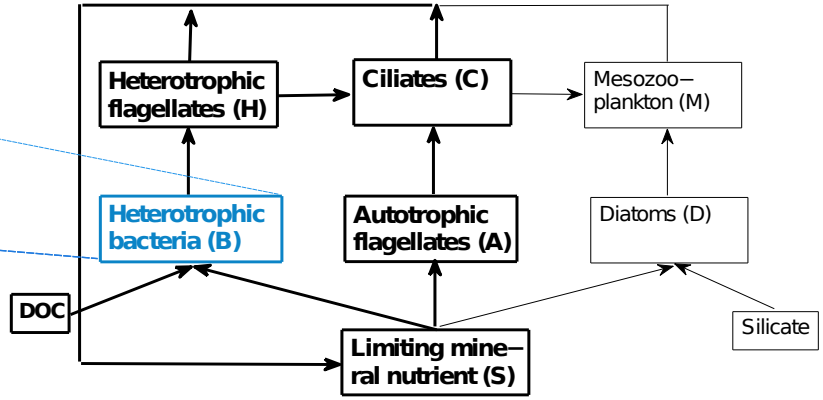
selina.vage@uib.no

Combining external & internal bacterial community control



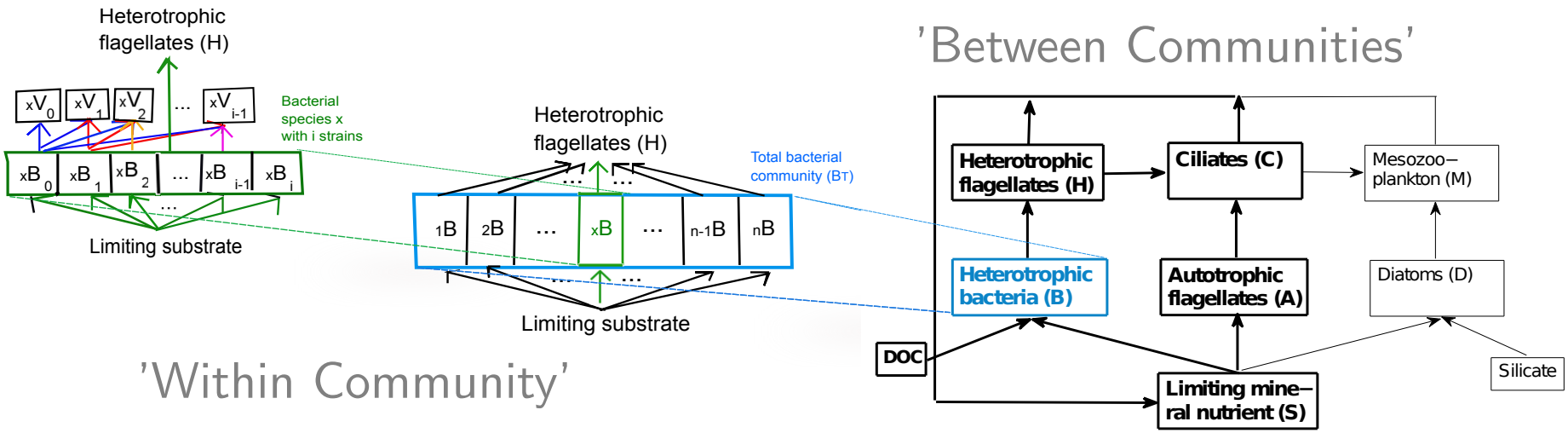
'Within Community'

'Between Communities'



selina.vage@uib.no

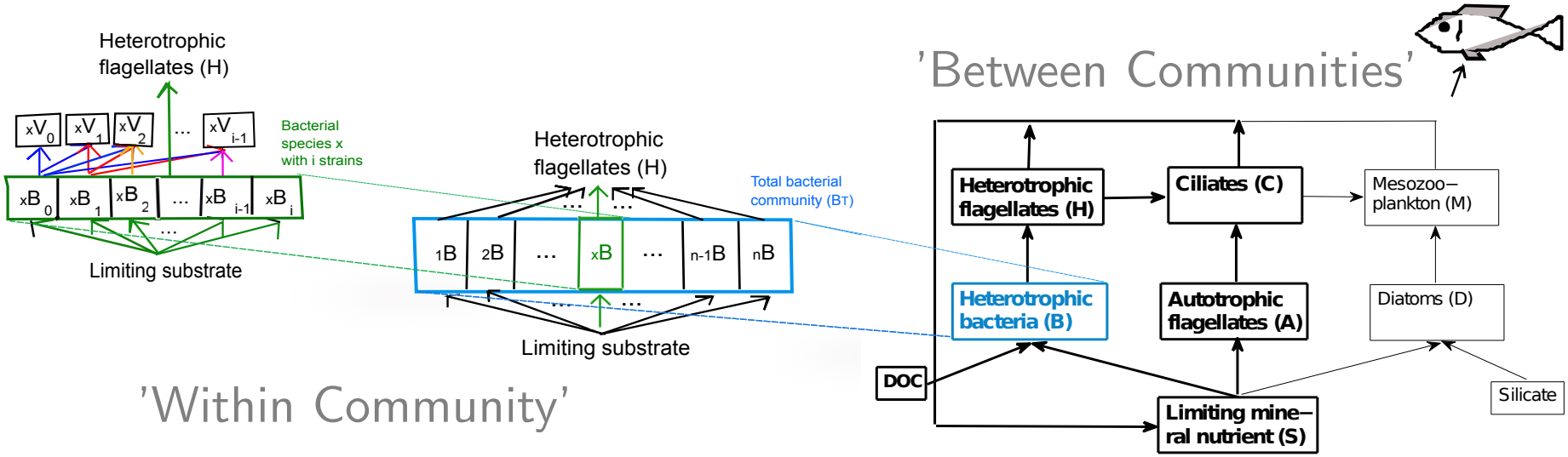
Combining external & internal bacterial community control



- Links coarse **PFTs** to detailed level of **species** and **strains**

selina.vage@uib.no

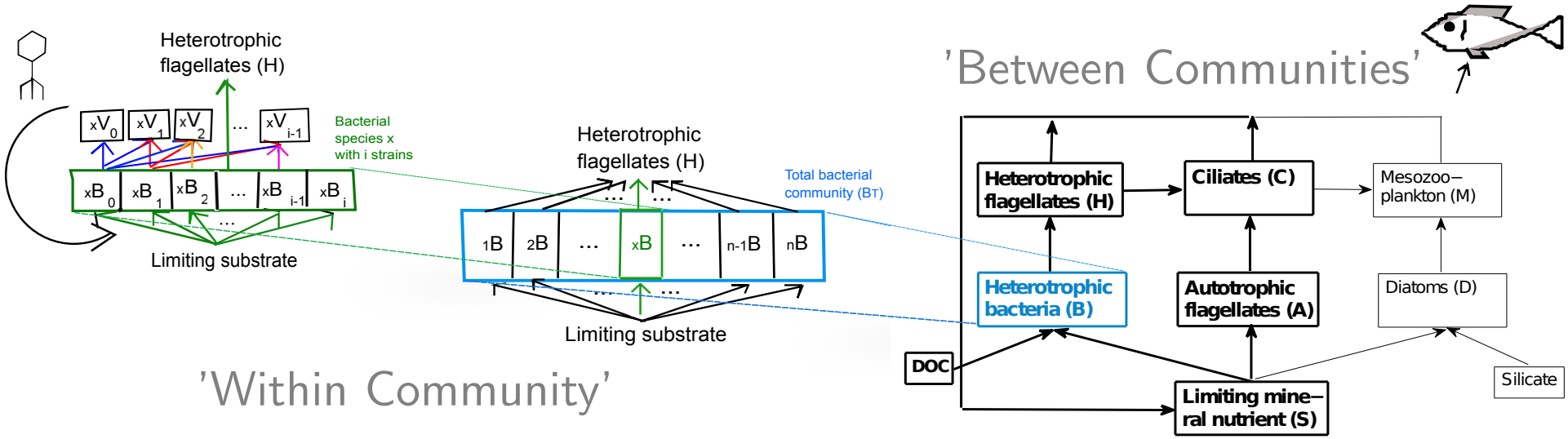
Combining external & internal bacterial community control



- Links coarse **PFTs** to detailed level of **species** and **strains**
- **Transport** of bacterial production **'up'** to particulate matter *(sequestration/higher trophic levels)* **vs 'down'** to dissolved matter *(remineralization/decreased efficiency)*

selina.vage@uib.no

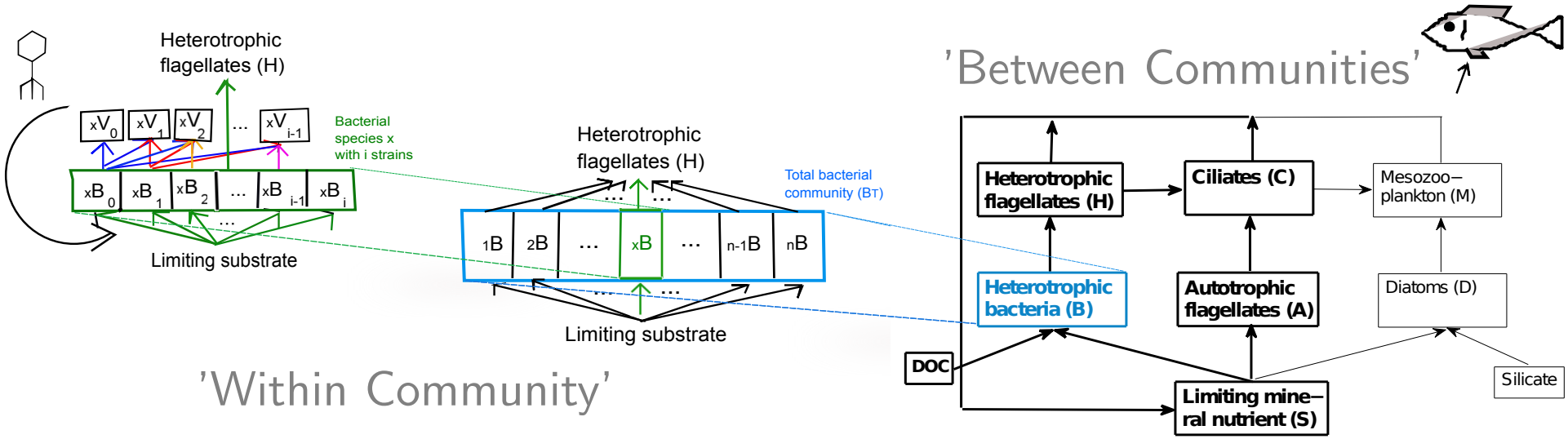
Combining external & internal bacterial community control



- Links coarse **PFTs** to detailed level of **species** and **strains**
- **Transport** of bacterial production **'up'** to particulate matter *(sequestration/higher trophic levels)* **vs 'down'** to dissolved matter *(remineralization/decreased efficiency)*

selina.vage@uib.no

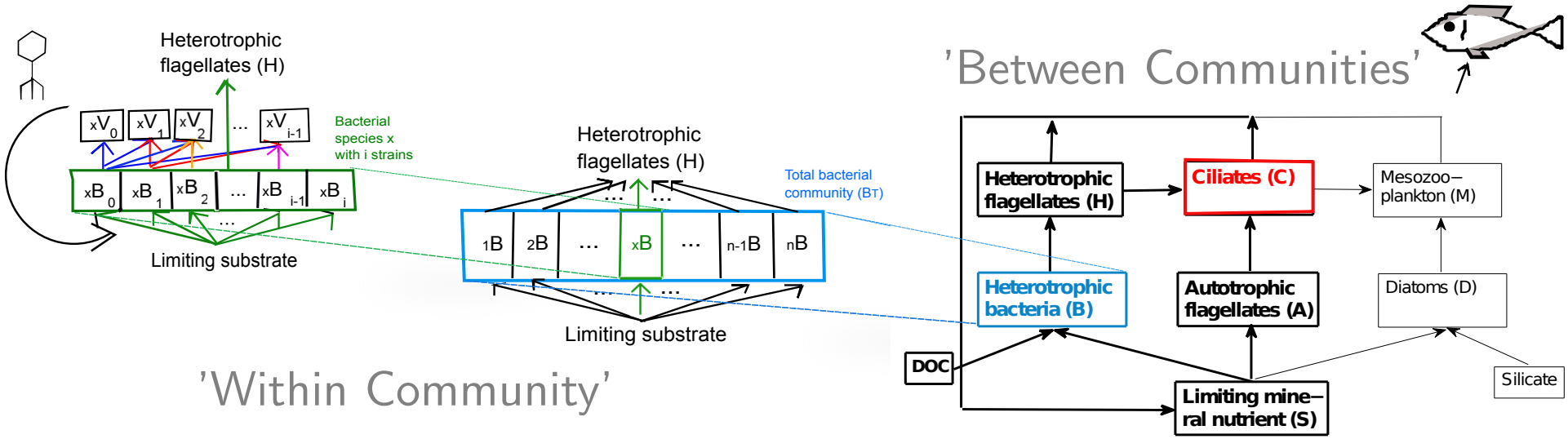
Combining external & internal bacterial community control



- Links coarse **PFTs** to detailed level of **species** and **strains**
- **Transport** of bacterial production **'up'** to particulate matter *(sequestration/higher trophic levels)* **vs 'down'** to dissolved matter *(remineralization/decreased efficiency)*
- **Links genetic information** (competiton vs defense specialist) to **biodiversity** (within PFT), **food web structure** and **biogeochemical cycling**

selina.vage@uib.no

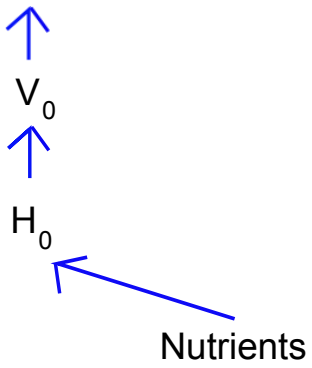
Combining external & internal bacterial community control

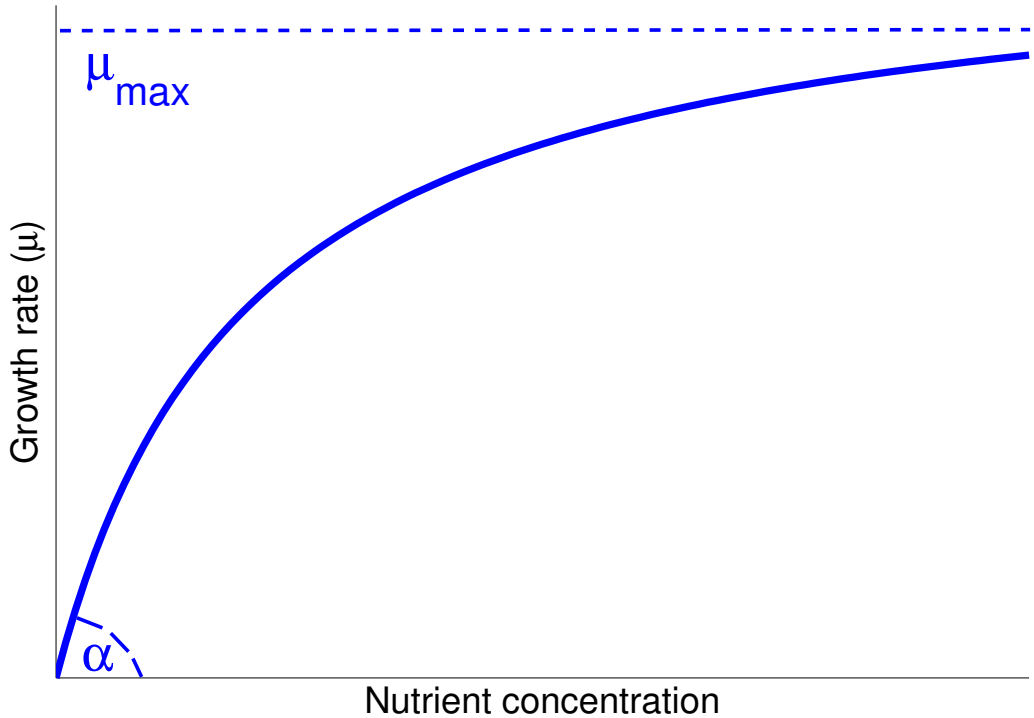


- Links coarse **PFTs** to detailed level of **species** and **strains**
- **Transport** of bacterial production **'up'** to particulate matter *(sequestration/higher trophic levels)* **vs 'down'** to dissolved matter *(remineralization/decreased efficiency)*
- **Links genetic information** (competiton vs defense specialist) to **biodiversity** (within PFT), **food web structure** and **biogeochemical cycling**
- $\mathbf{C} \propto \mathbf{B}_T$ and $\mathbf{C} \propto \mathbf{S}$

selina.vage@uib.no

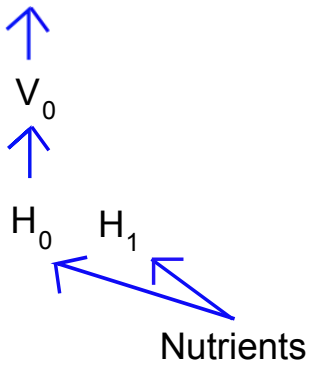
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

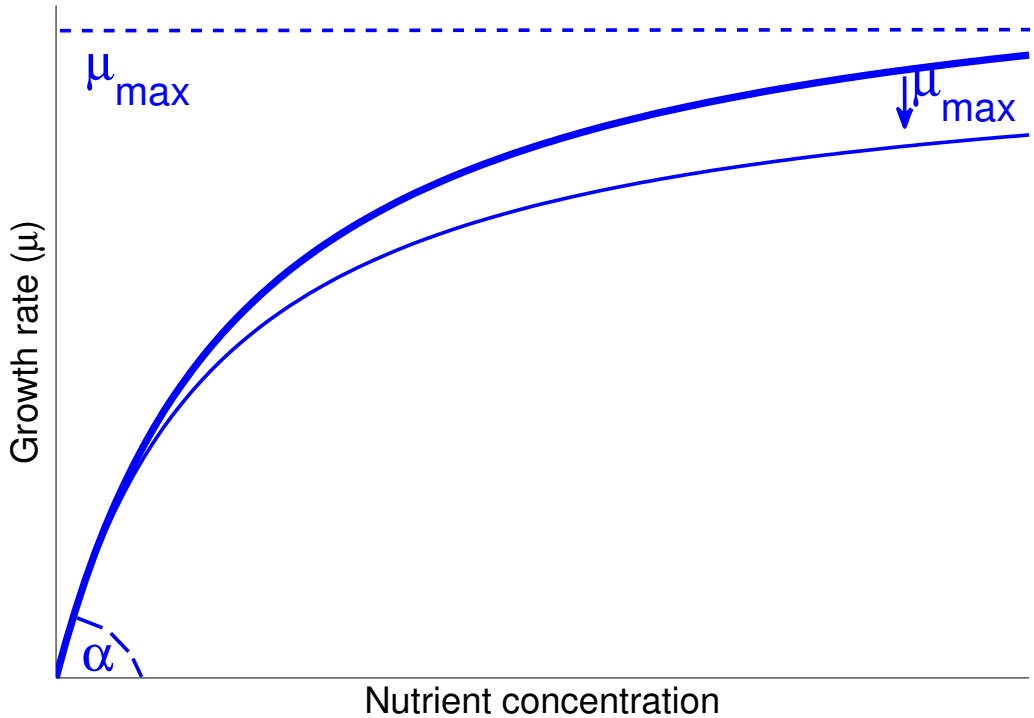




selina.vage@uib.no

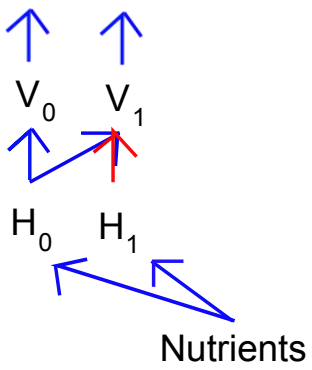
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

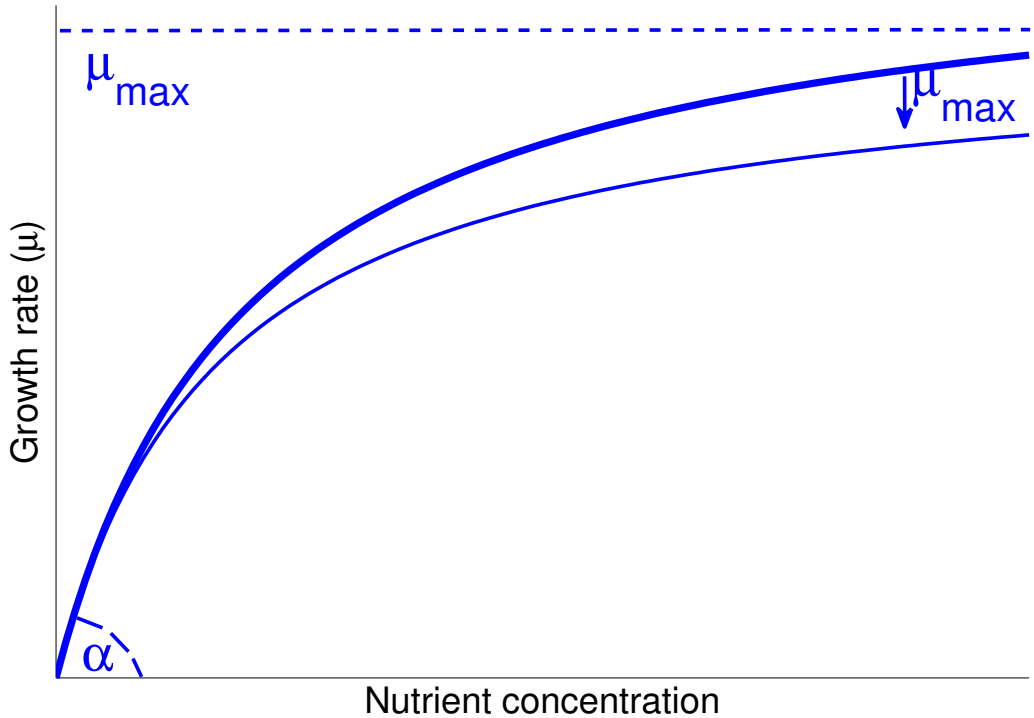




selina.vage@uib.no

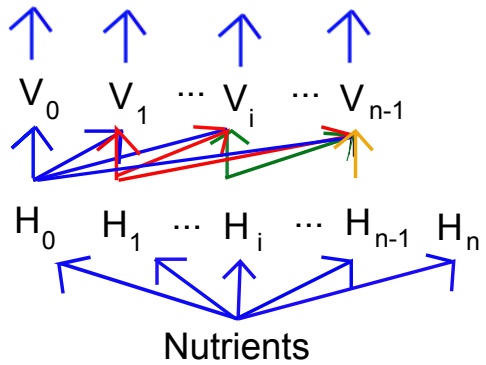
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

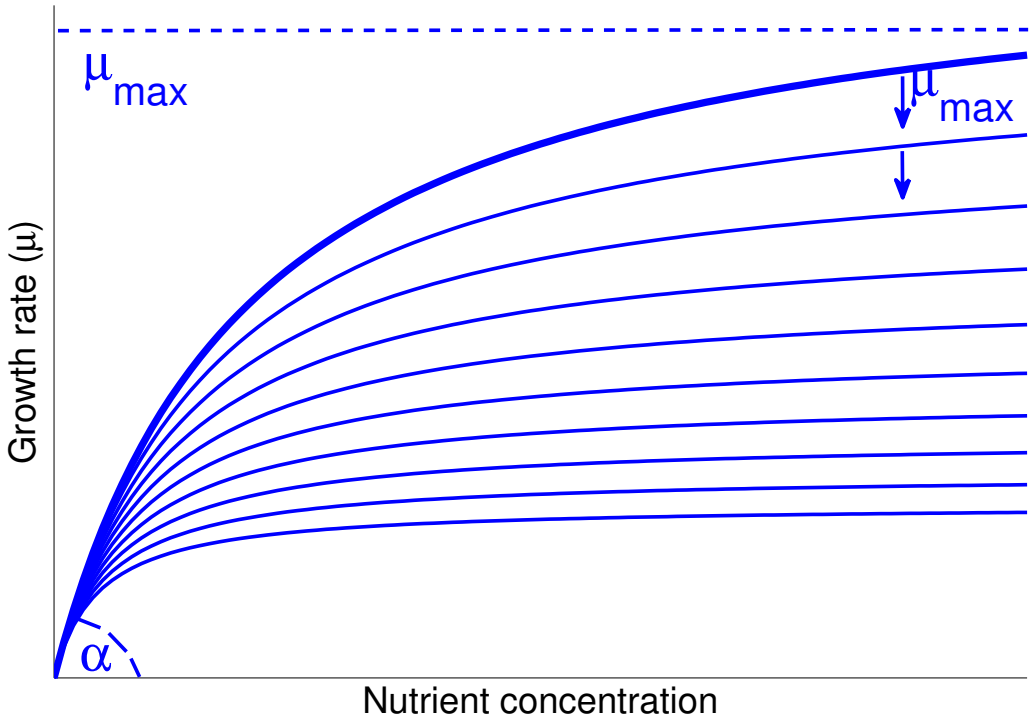




selina.vage@uib.no

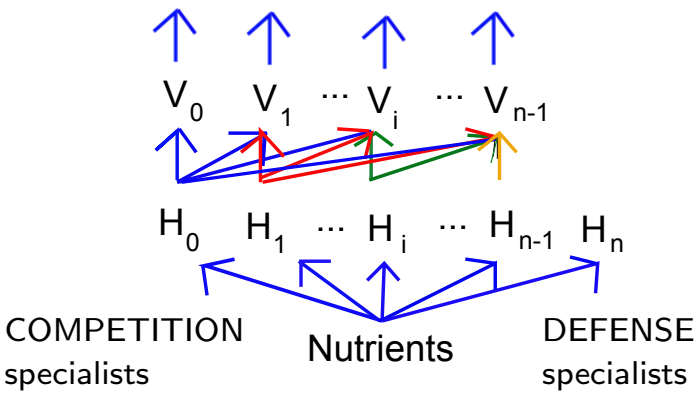
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

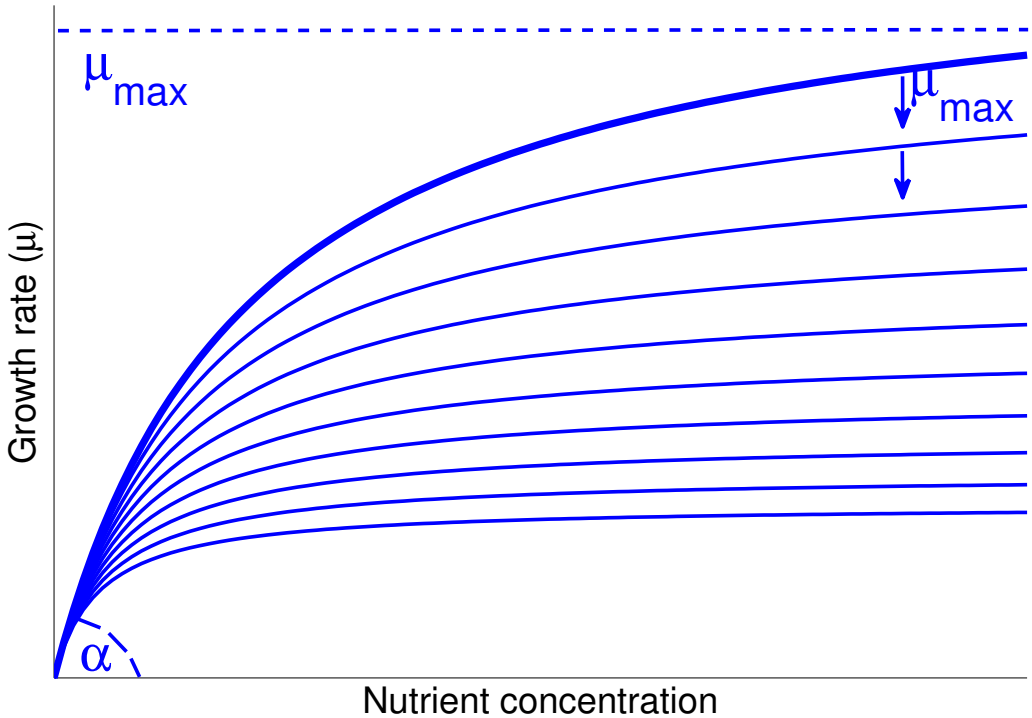




selina.vage@uib.no

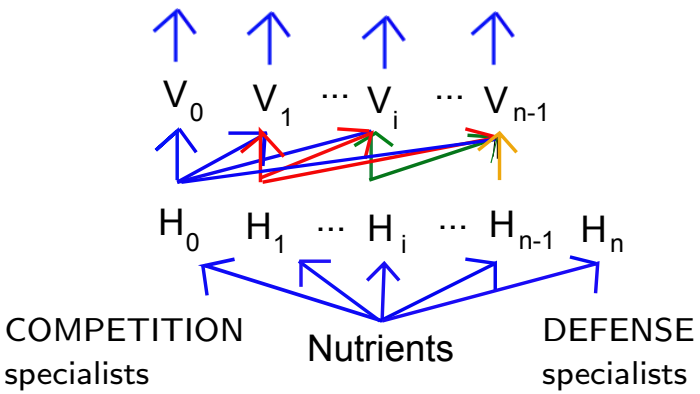
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

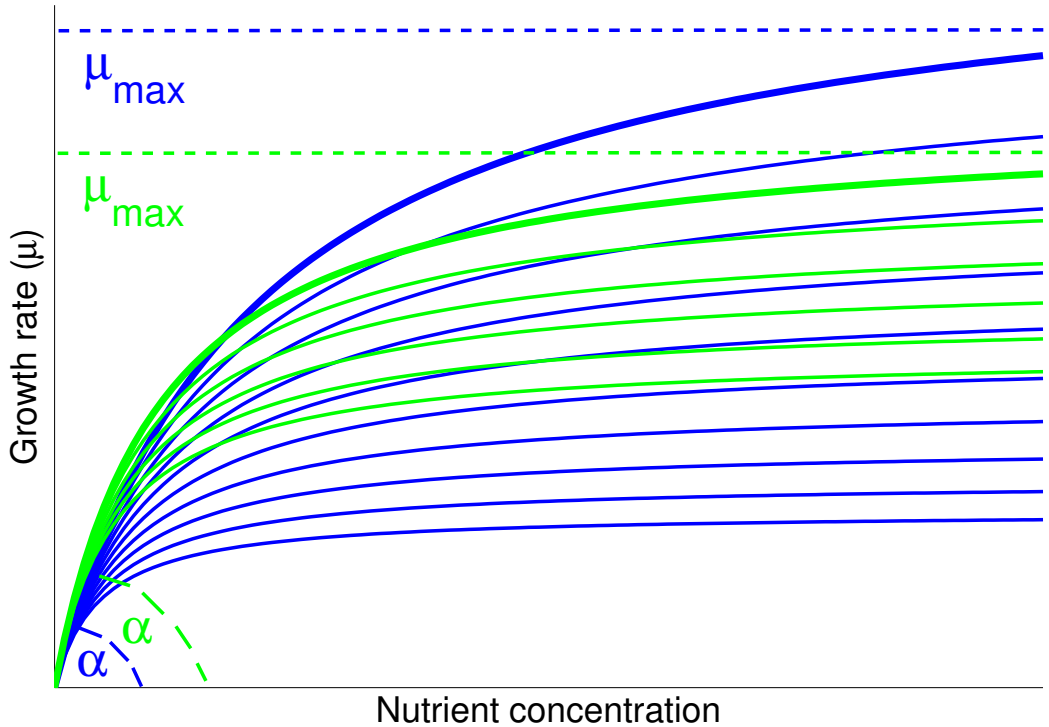




selina.vage@uib.no

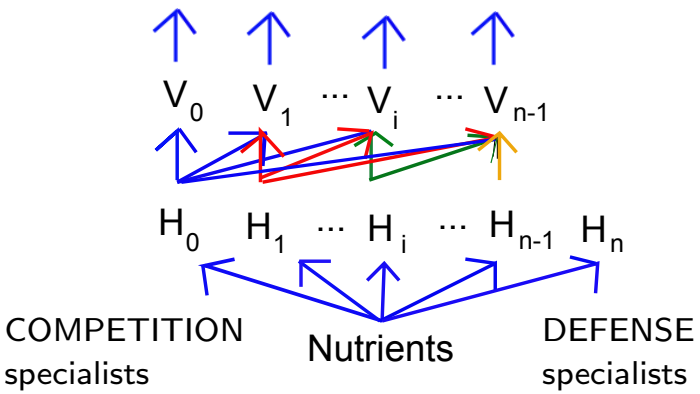
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

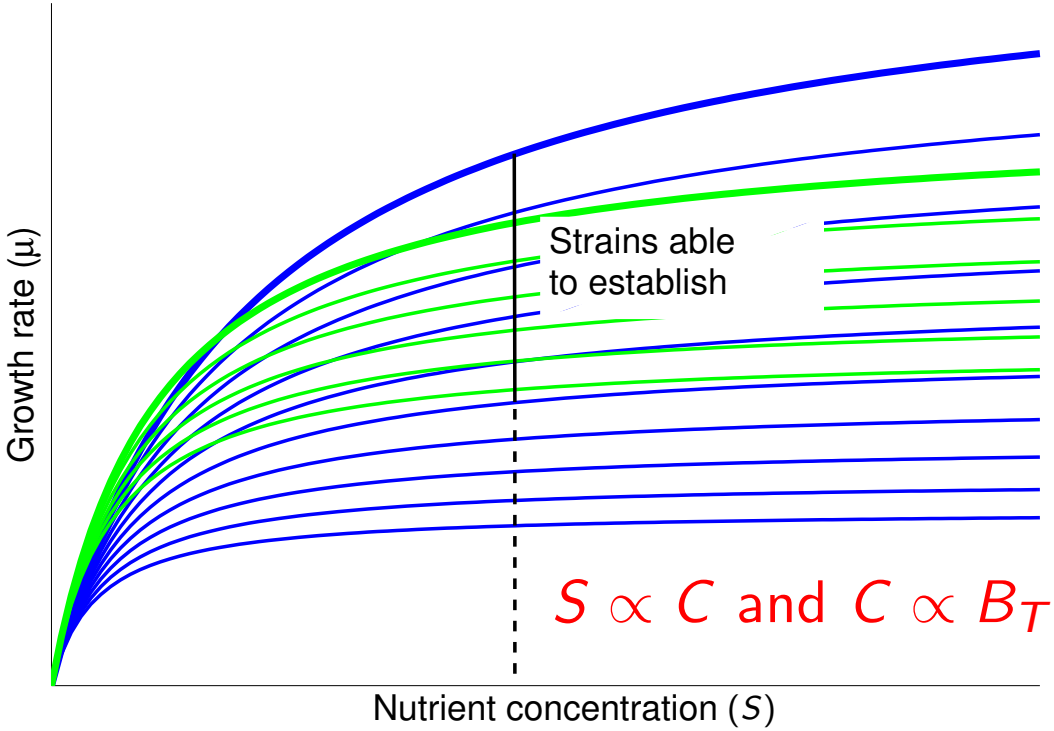




selina.vage@uib.no

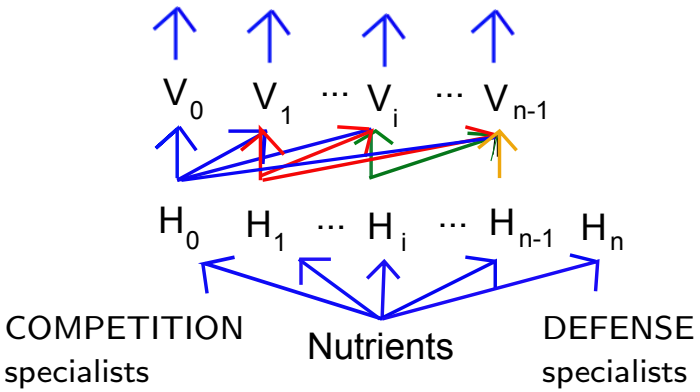
Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses

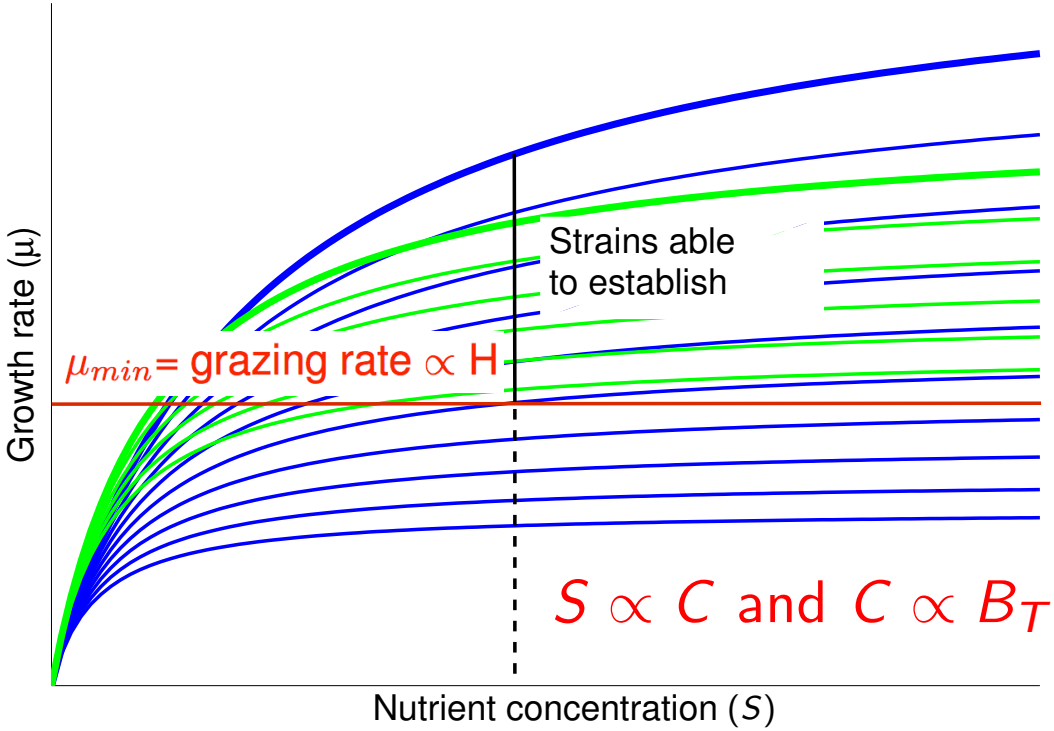


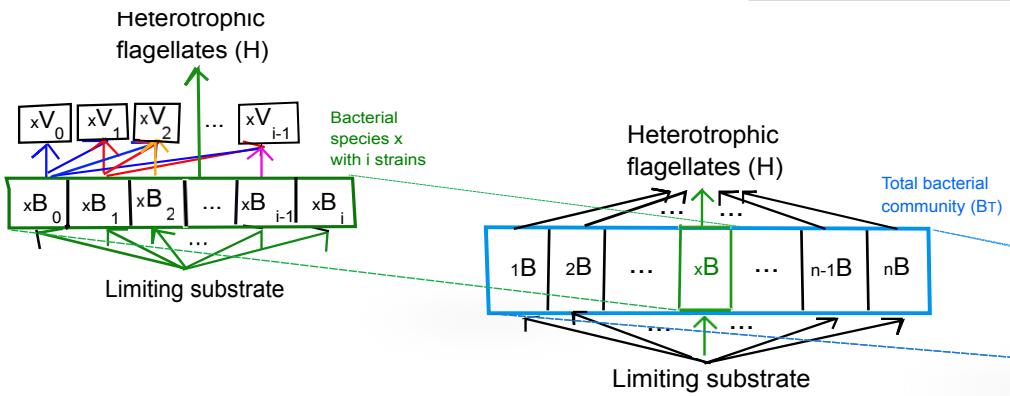


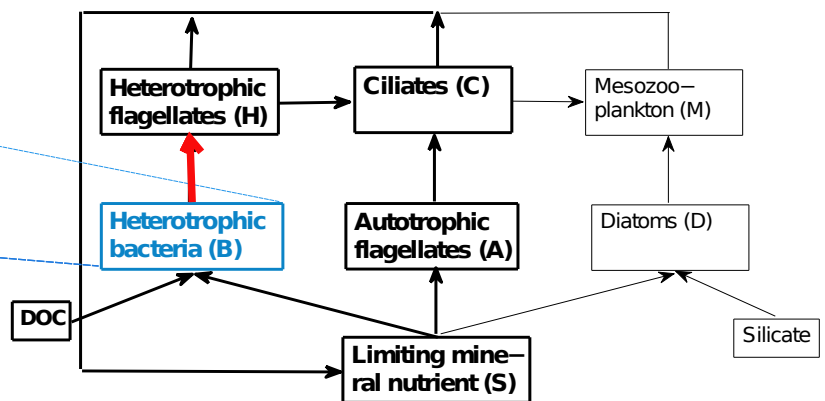
selina.vage@uib.no

Internal control: Cost of resistance (COR) lowers growth rates in evolutionary arms race between hosts and viruses



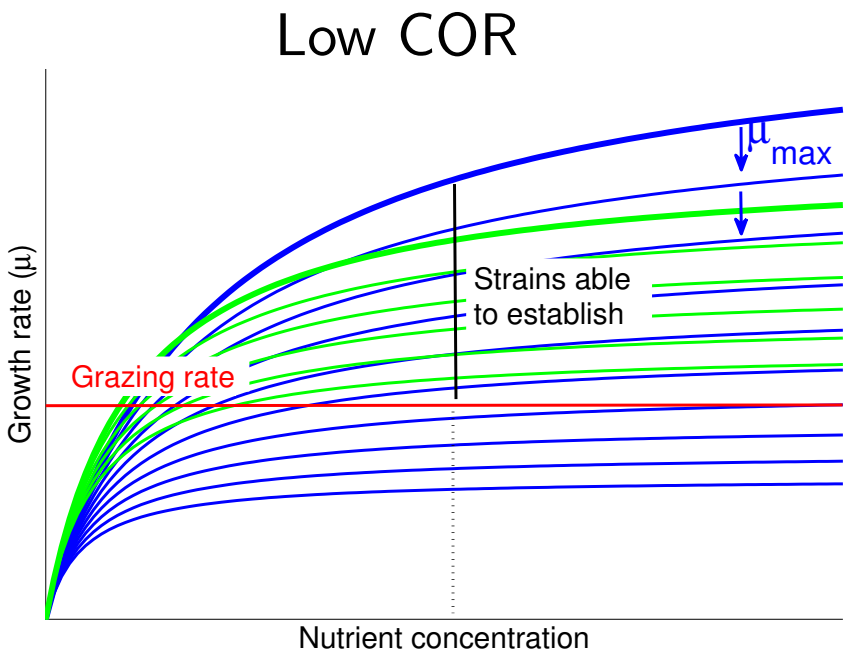






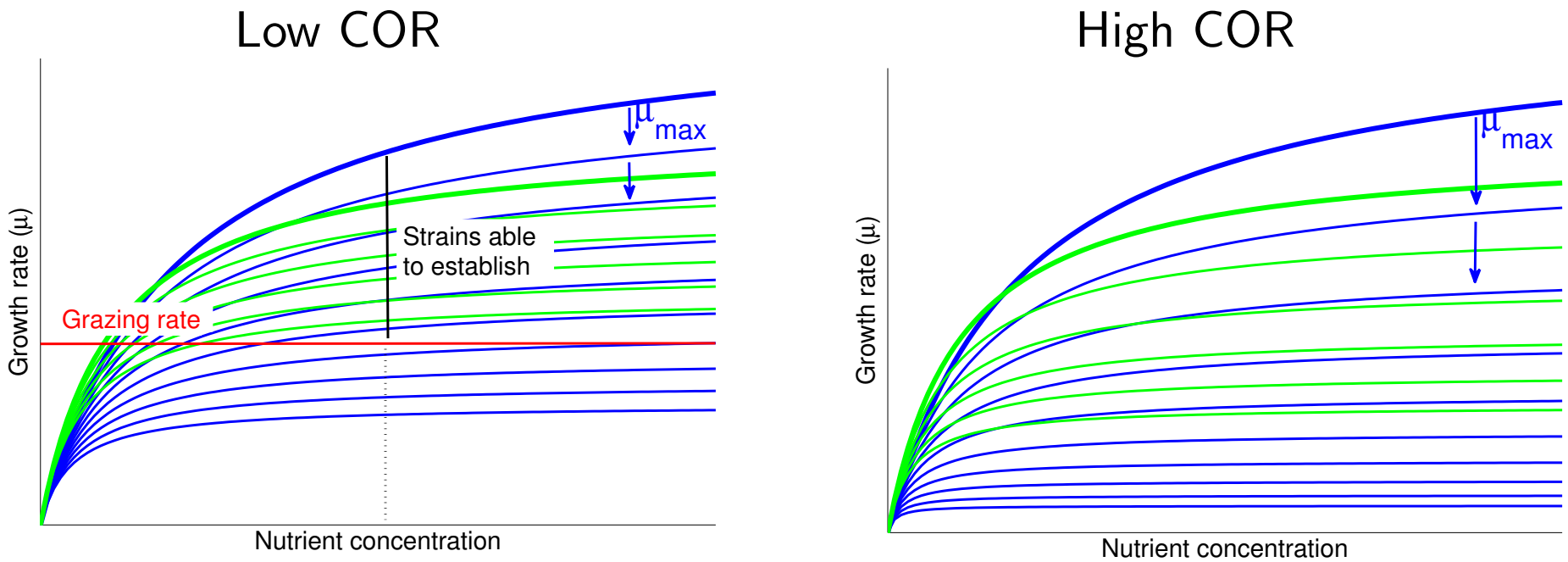
selina.vage@uib.no

Internal control: Central role of cost of resistance (COR)



selina.vage@uib.no

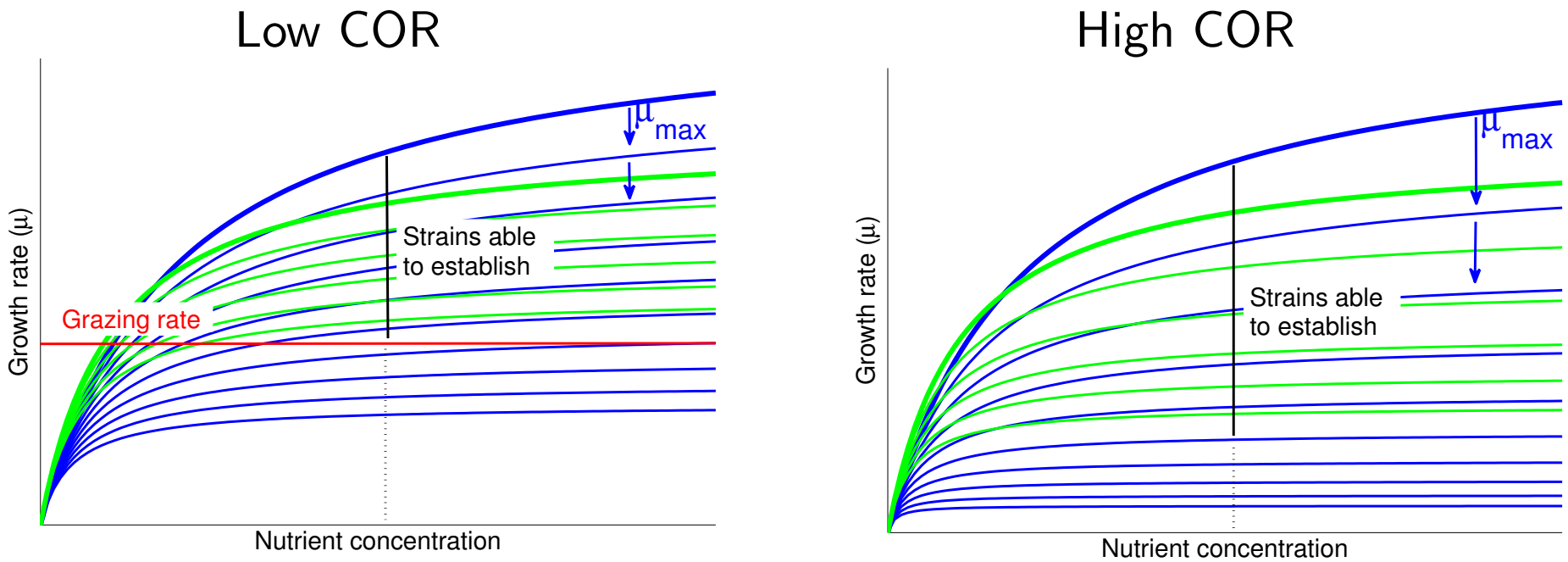
Internal control: Central role of cost of resistance (COR)



- **Increasing COR** increases spacing between growth curves

selina.vage@uib.no

Internal control: Central role of cost of resistance (COR)

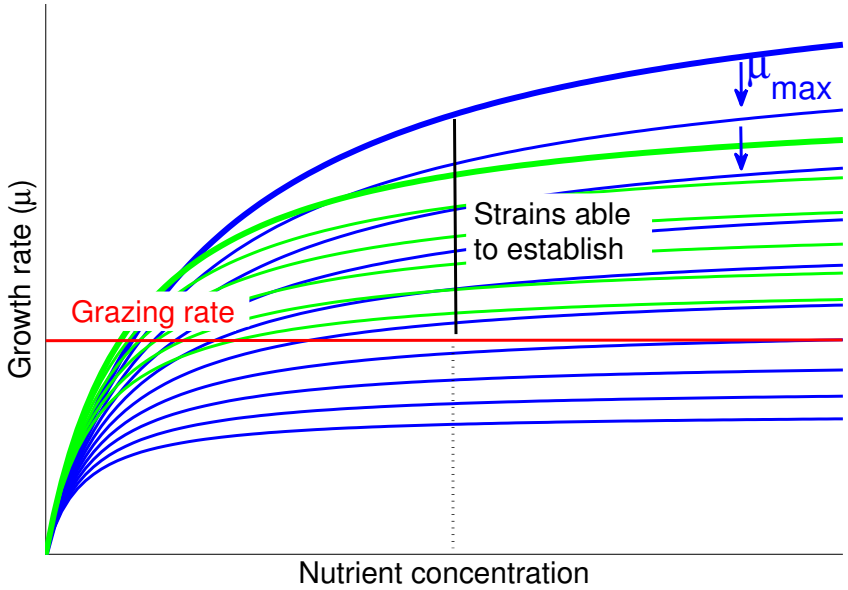


- **Increasing COR** increases spacing between growth curves
- **Lowers minimum growth rate** (from summing up strains until correct community size $B_T \propto C$ reached) and hence **abundance of grazers**

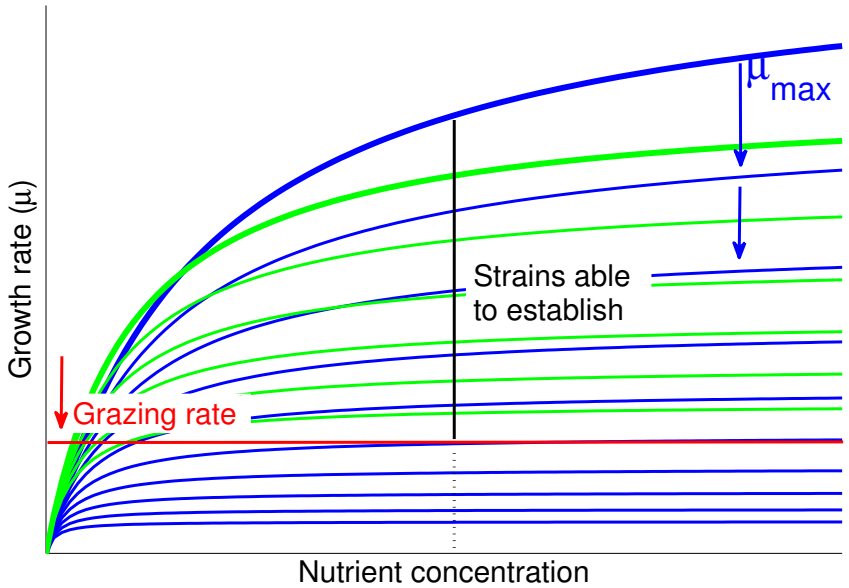
selina.vage@uib.no

Internal control: Central role of cost of resistance (COR)

Low COR



High COR

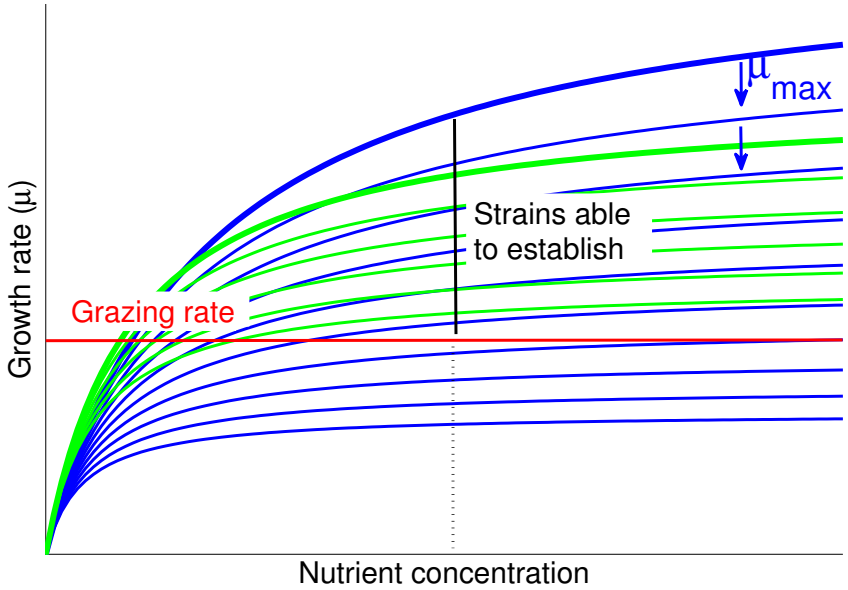


- **Increasing COR** increases spacing between growth curves
- **Lowers minimum growth rate** (from summing up strains until correct community size $B_T \propto C$ reached) and hence **abundance of grazers**

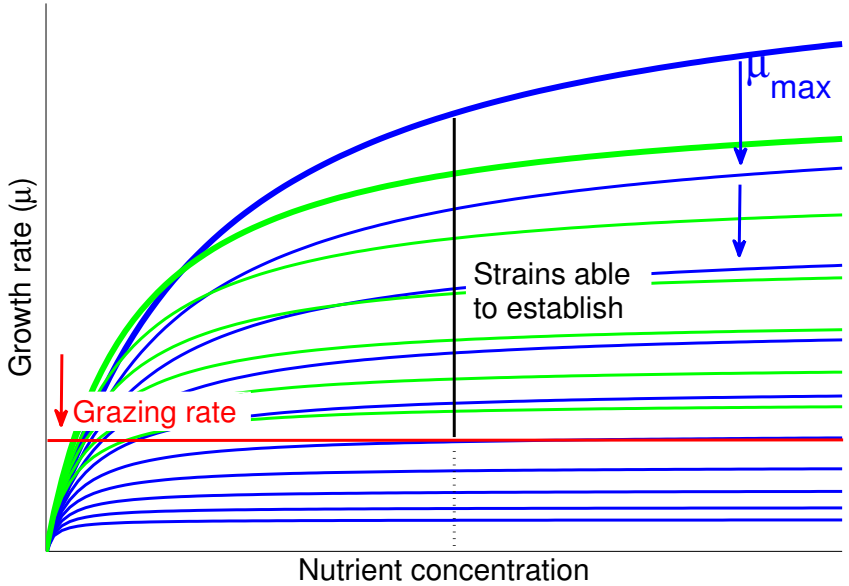
selina.vage@uib.no

Internal control: Central role of cost of resistance (COR)

Low COR



High COR



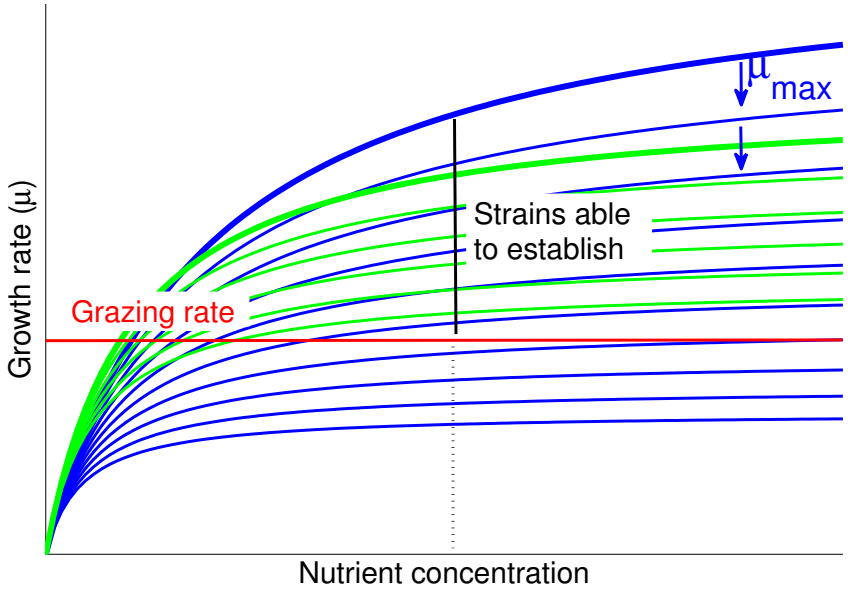
- **Increasing COR** increases spacing between growth curves
- **Lowers minimum growth rate** (from summing up strains until correct community size $B_T \propto C$ reached) and hence **abundance of grazers**

$\Rightarrow$ **High COR favors viruses** over grazers,

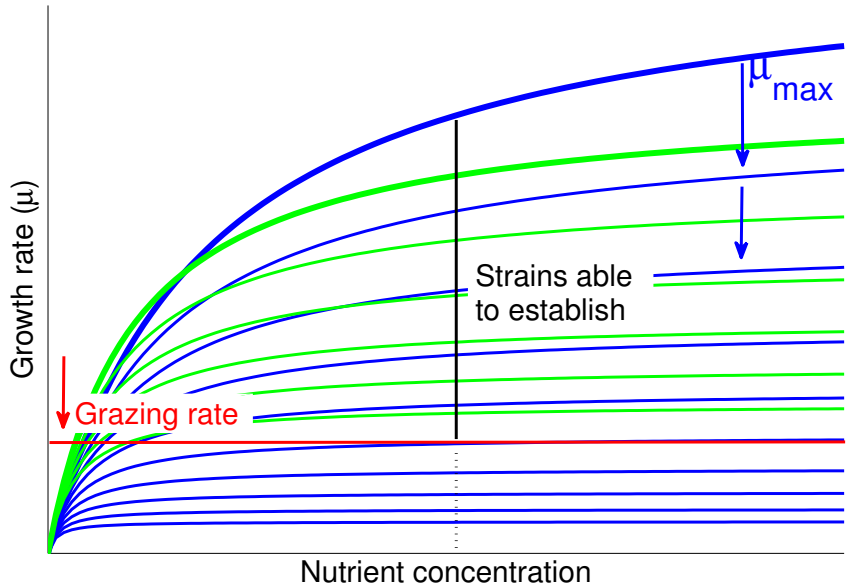
selina.vage@uib.no

Internal control: Central role of cost of resistance (COR)

Low COR



High COR

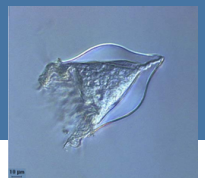


- **Increasing COR** increases spacing between growth curves
- **Lowers minimum growth rate** (from summing up strains until correct community size $B_T \propto C$ reached) and hence **abundance of grazers**

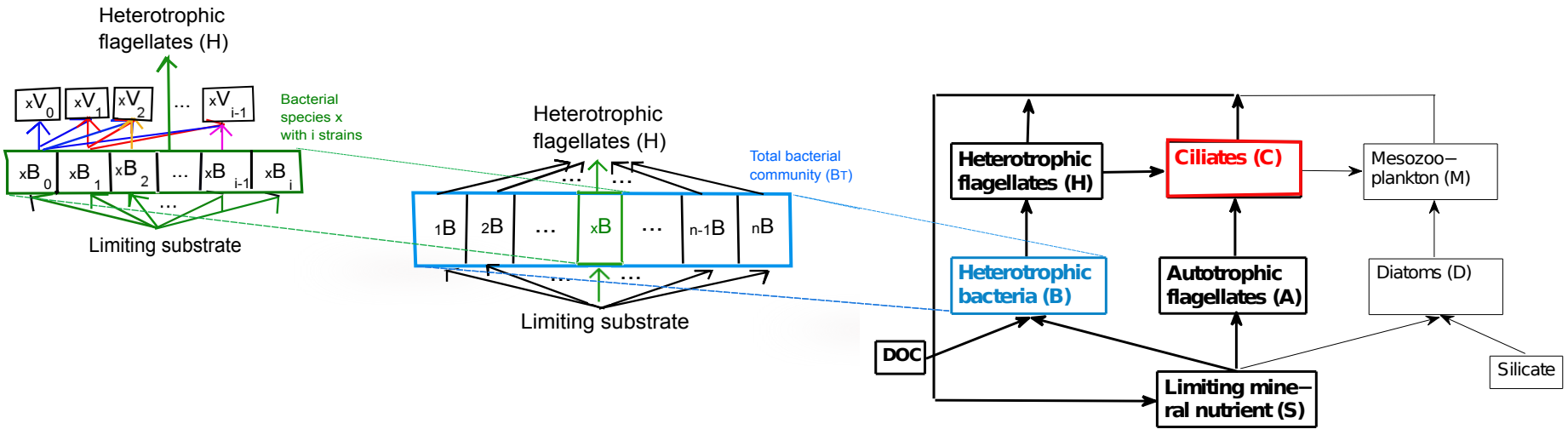
$\Rightarrow$ **High COR favors viruses** over grazers, **increasing fraction** of bacterial production **shunted 'down'** to viral loop (vs transfer to higher trophic levels - i.e. high COR reduces transfer efficiency)

selina.vage@uib.no

External control: Central role of ciliates

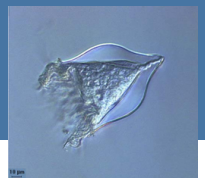


(Photo J. Rose)



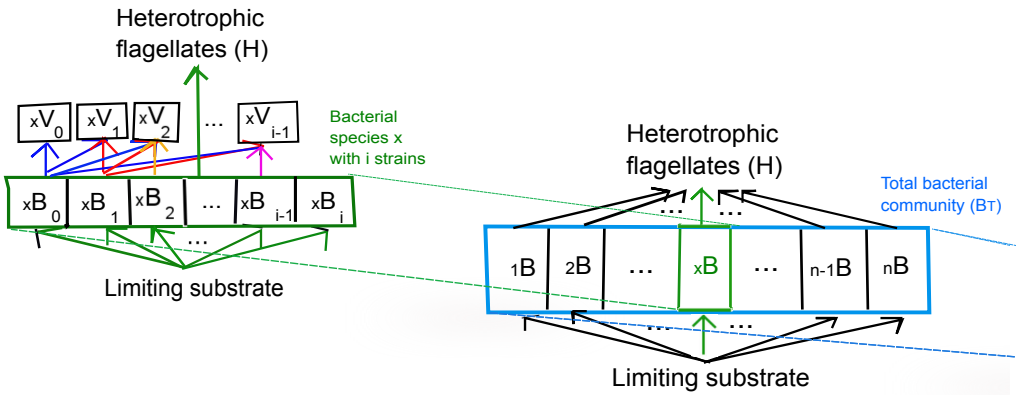
selina.vage@uib.no

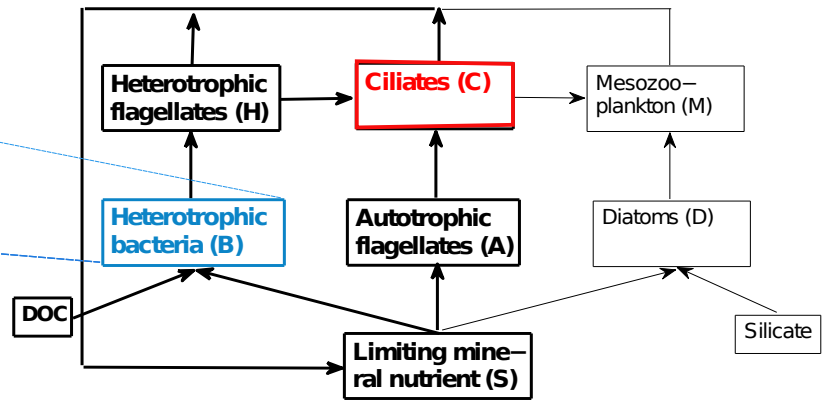
External control: Central role of ciliates



(Photo J. Rose)

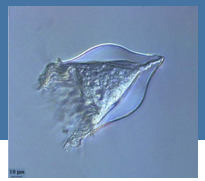
- **Ciliates** exert **top-down** and **bottom-up** control on bacteria





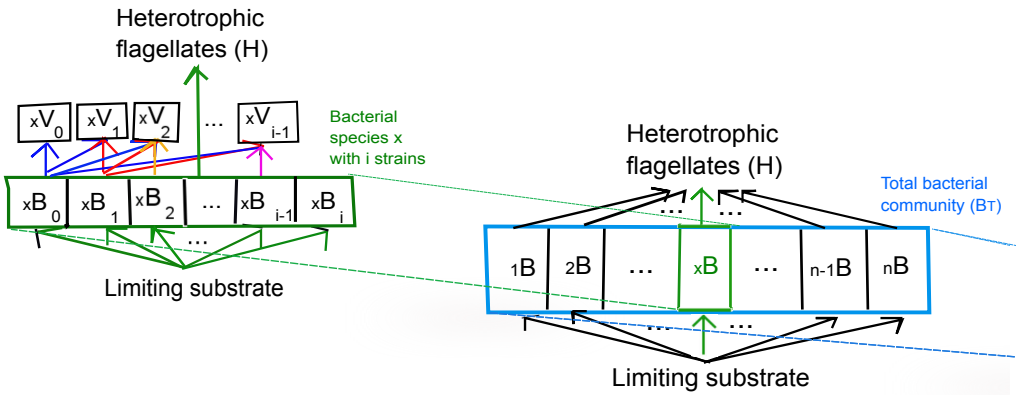
selina.vage@uib.no

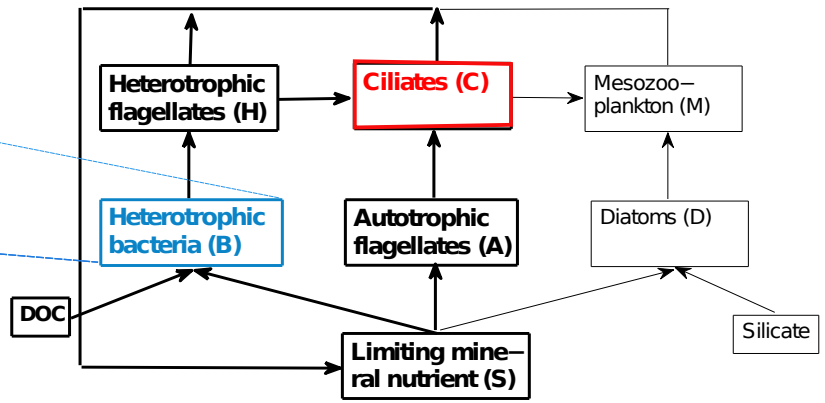
External control: Central role of ciliates

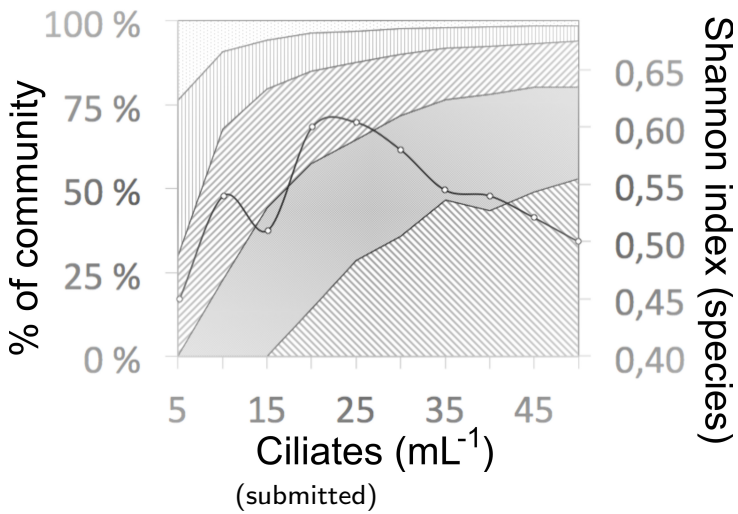


(Photo J. Rose)

- **Ciliates** exert **top-down** and **bottom-up** control on bacteria



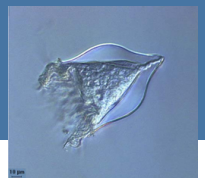




(submitted)

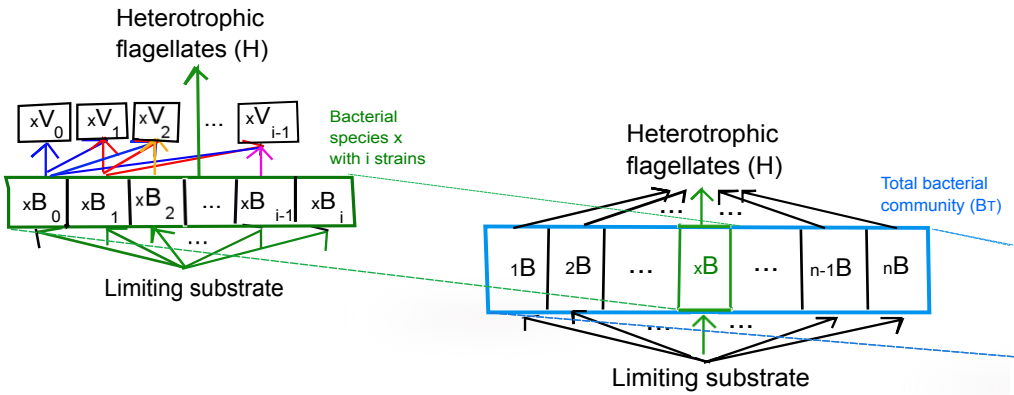
selina.vage@uib.no

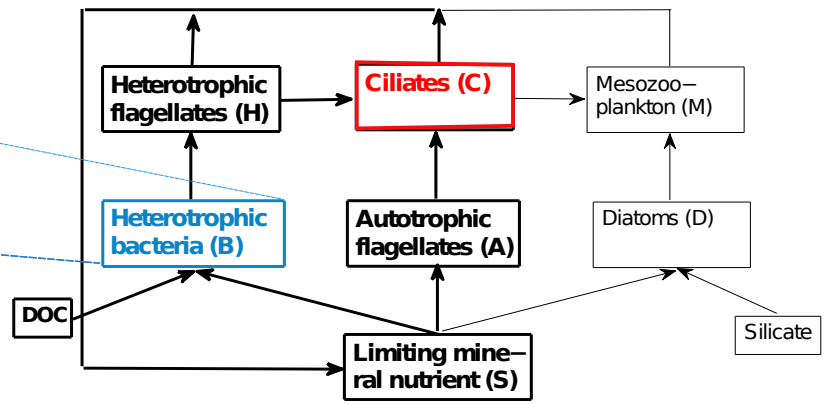
External control: Central role of ciliates

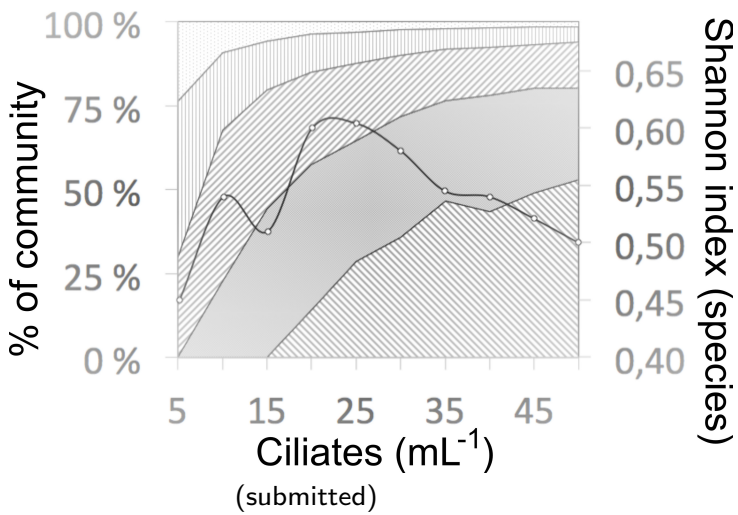


(Photo J. Rose)

- **Ciliates** exert **top-down** and **bottom-up** control on bacteria







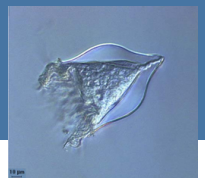
(submitted)

- **Intermediate** ciliate **abundance** gives **highest** bacterial **diversity** *(analogy to 'Intermediate Disturbance Theory')*

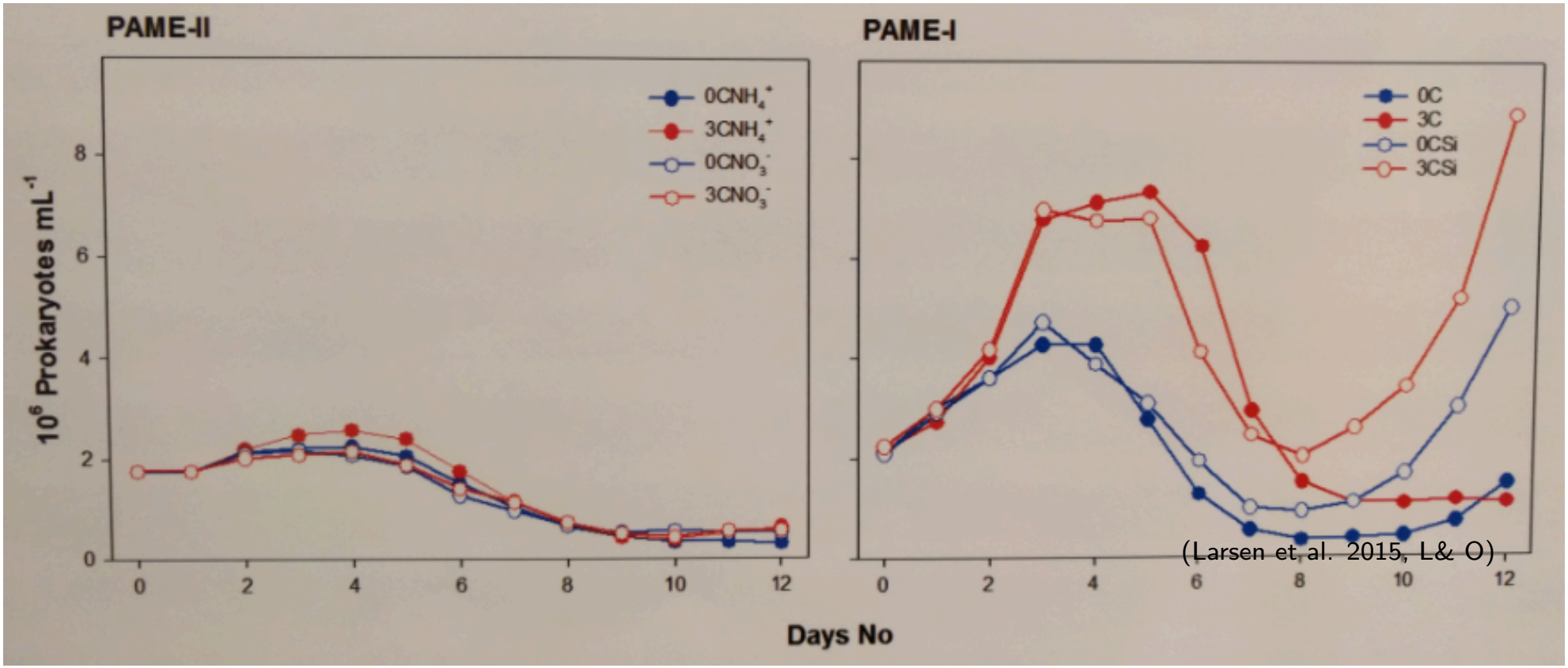
(Reynolds et al 1993, Hydrobiologia)

selina.vage@uib.no

External control: Central role of ciliates



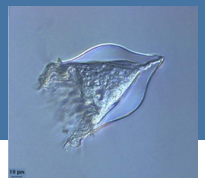
(Photo J. Rose)



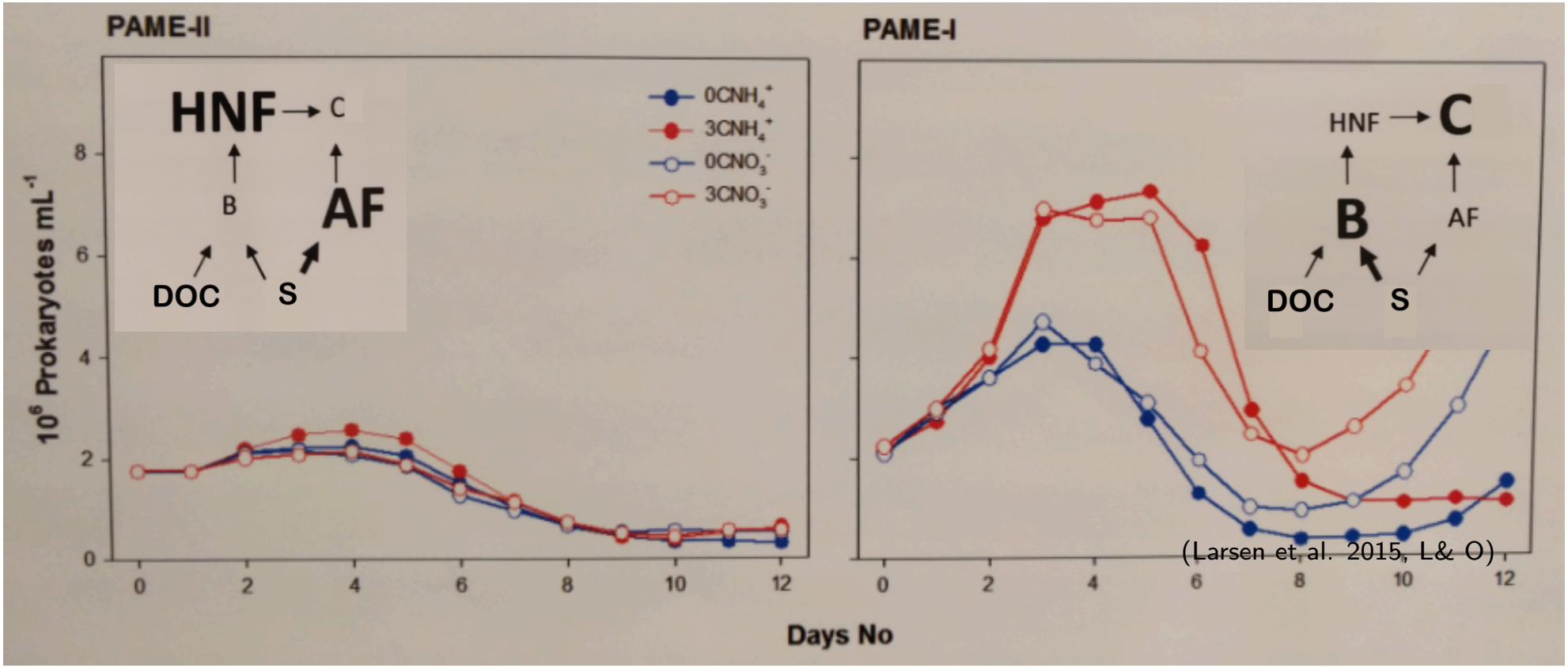
(Larsen et al. 2015, L& O)

selina.vage@uib.no

External control: Central role of ciliates



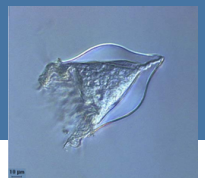
(Photo J. Rose)



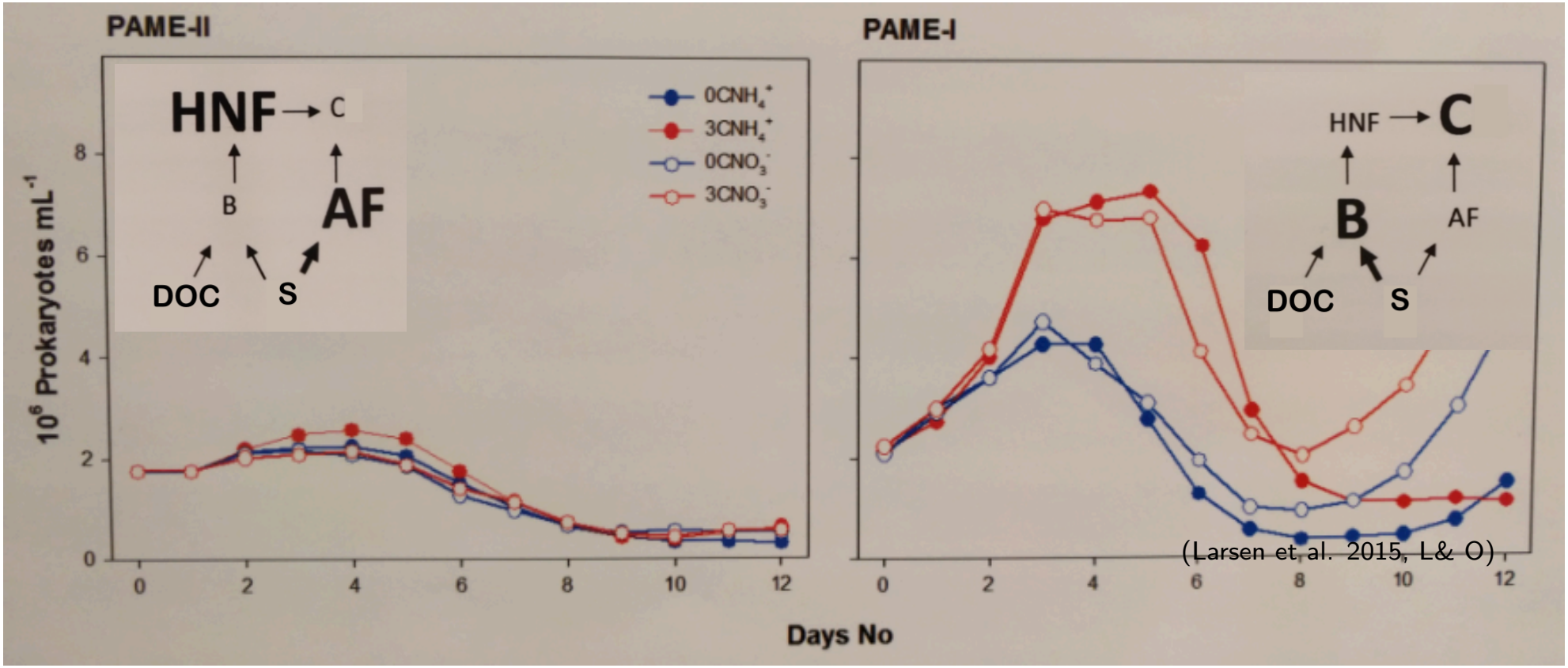
(Larsen et al. 2015, L& O)

selina.vage@uib.no

External control: Central role of ciliates



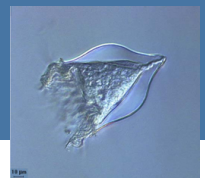
(Photo J. Rose)



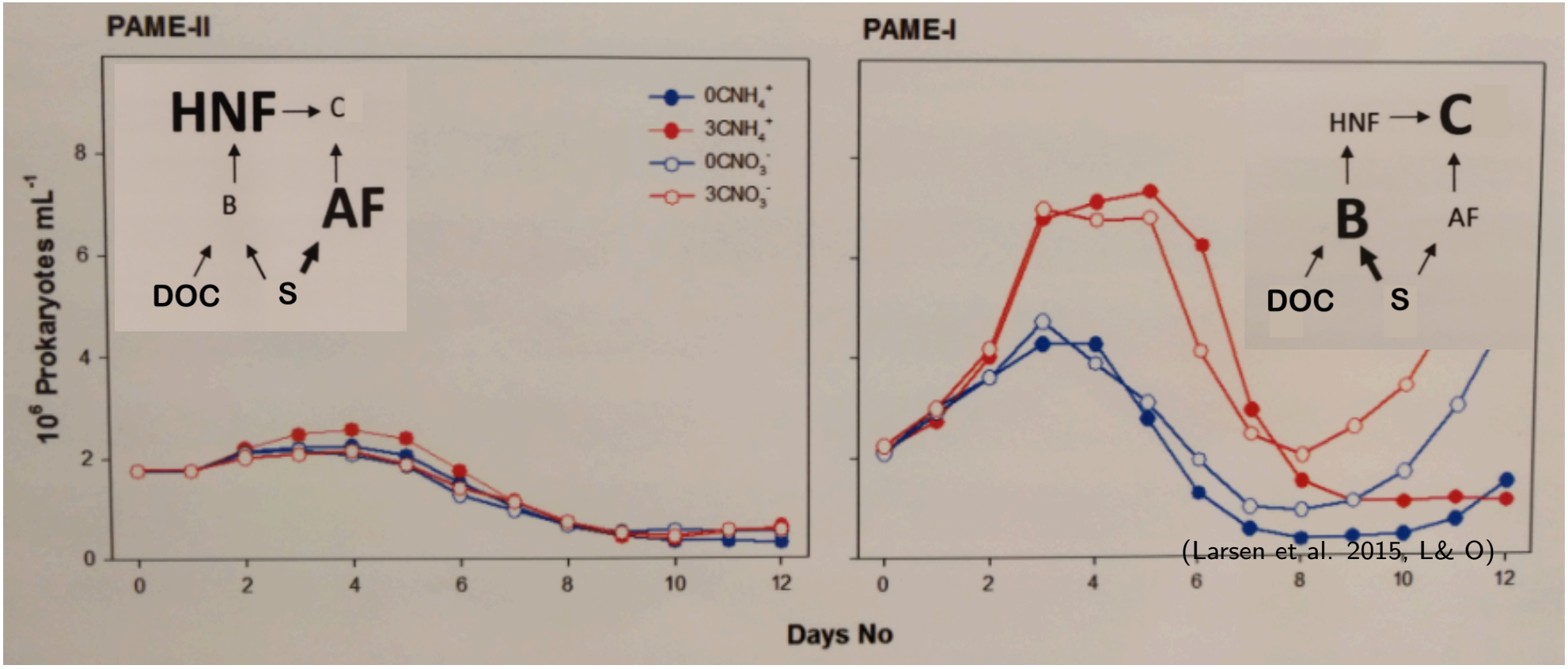
- **Low ciliate concentration**
  $\Rightarrow$ No response to carbon addition due to **mineral nutrient limitation** ($C \propto S$)

selina.vage@uib.no

External control: Central role of ciliates



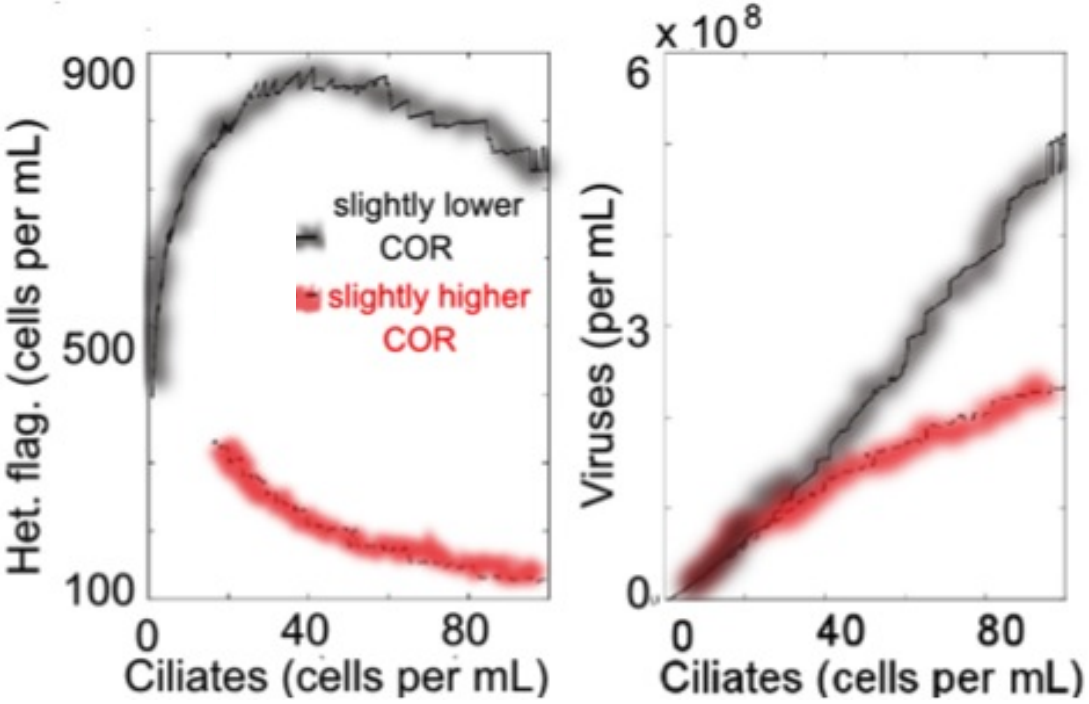
(Photo J. Rose)



- **Low ciliate concentration**
  ⇒ No response to carbon addition due to **mineral nutrient limitation** ($C \propto S$)
- **High ciliate concentration**
  ⇒ Bacterial bloom after carbon addition due to **carbon limitation** ($C \propto B_T$)

selina.vage@uib.no

Strong **interactions** between internal and external control

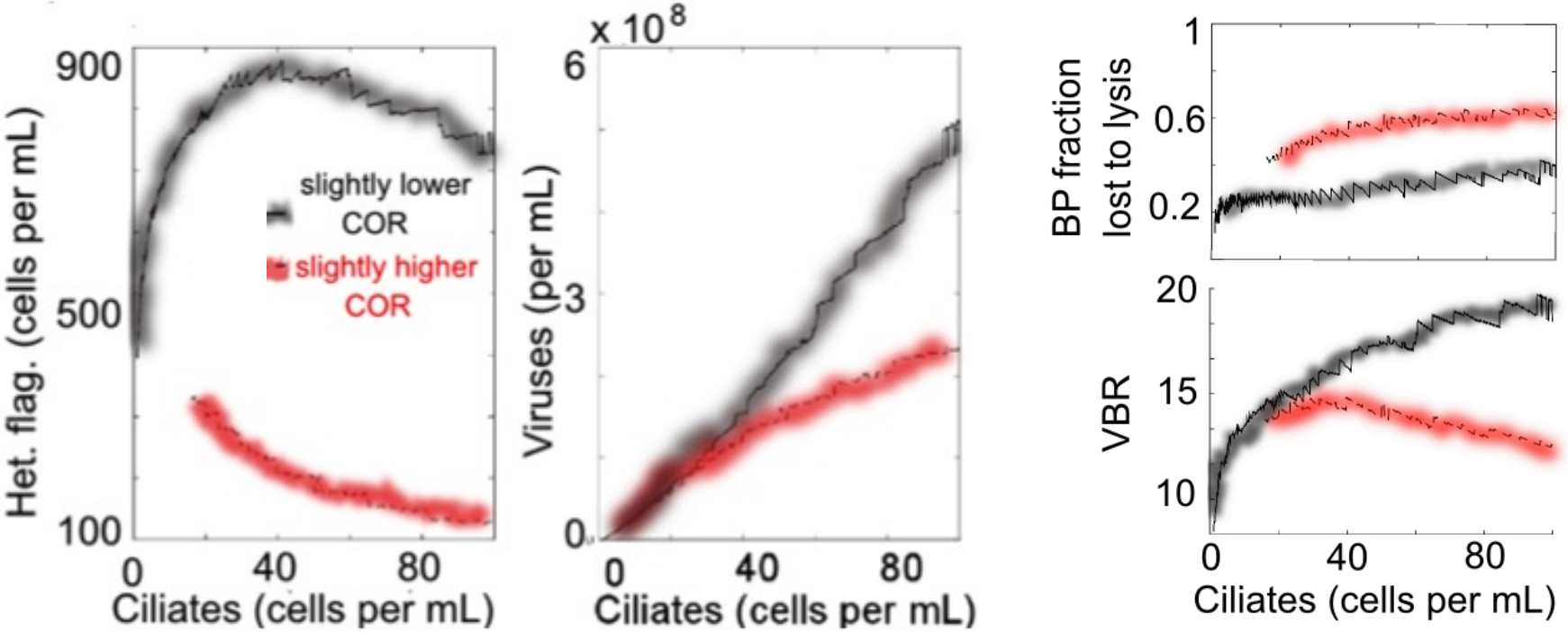


(submitted)

- **Grazer community** and **viral abundance** highly **sensitive to COR**

selina.vage@uib.no

Strong **interactions** between internal and external control

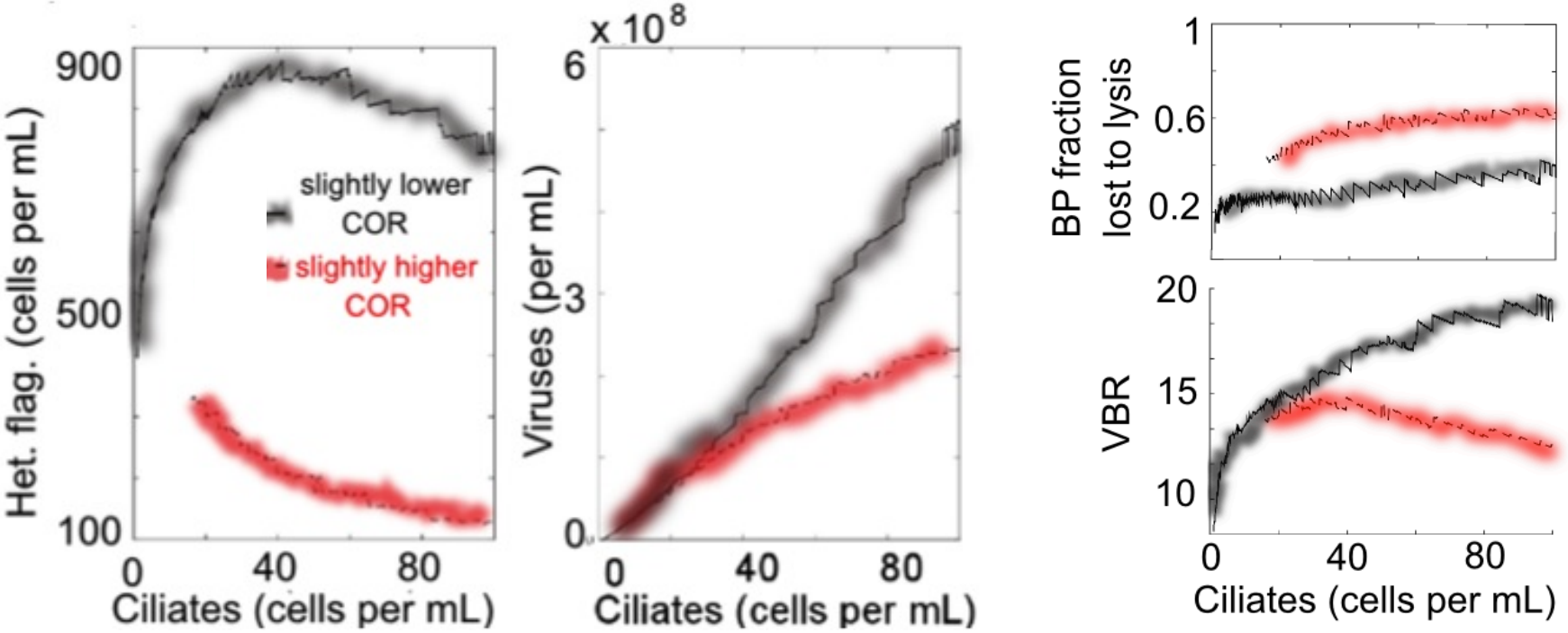


(submitted)

- **Grazer community** and **viral abundance** highly **sensitive to COR**
- Fraction of bacterial **production lost to lysis sensitive to COR**

selina.vage@uib.no

Strong **interactions** between internal and external control

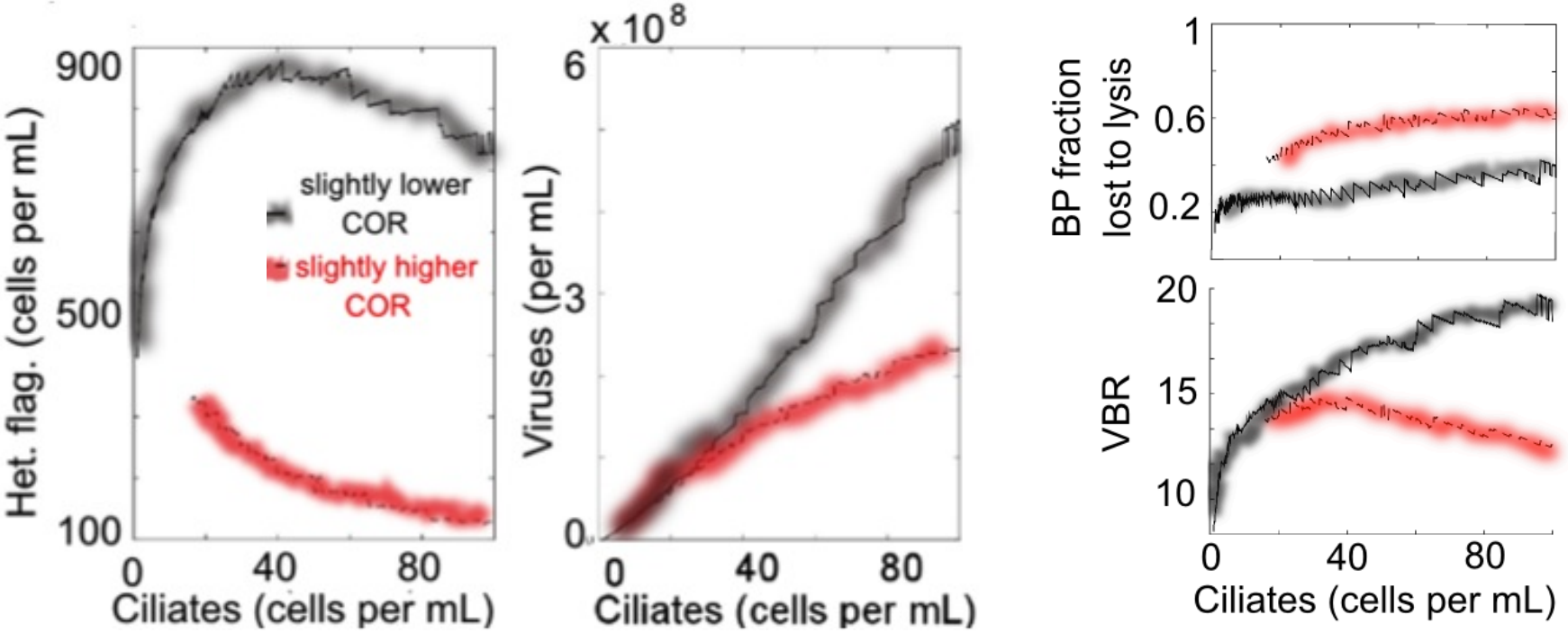


(submitted)

- **Grazer community** and **viral abundance** highly **sensitive to COR**
- Fraction of bacterial **production lost to lysis sensitive to COR**
- High COR $\rightarrow$ Low μ_{min} $\rightarrow$ Fewer grazers $\rightarrow$ More viruses
  $\Rightarrow$ Less transport up the food chain

selina.vage@uib.no

Strong **interactions** between internal and external control



(submitted)

- **Grazer community** and **viral abundance** highly **sensitive to COR**
- Fraction of bacterial **production lost to lysis sensitive to COR**
- High COR $\rightarrow$ Low μ_{min} $\rightarrow$ Fewer grazers $\rightarrow$ More viruses
  $\Rightarrow$ Less transport up the food chain

$\Rightarrow$ **Molecular basis of COR** linked to **grazer abundance** and **food web efficiency** $\Rightarrow$ Mechanistic framework for VBR

selina.vage@uib.no

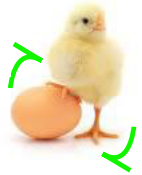
Conclusions

- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends

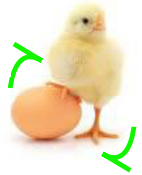
Conclusions

- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**

Conclusions

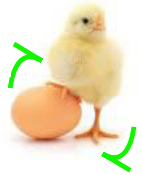
- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**
-  Growth rate differences compensated for by lysis, but differences determined by COR

Conclusions

- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**
-  Growth rate differences compensated for by lysis, but differences determined by COR

$\Rightarrow$ VBR seen as the ratio between mechanisms generating bacterial diversity and those controlling community size

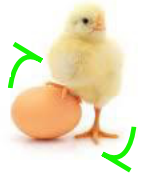
Conclusions

- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**
-  Growth rate differences compensated for by lysis, but differences determined by COR

$\Rightarrow$ VBR seen as the ratio between mechanisms generating bacterial diversity and those controlling community size

- Viruses win over flagellate grazers at high COR
  $\rightarrow$ Less transfer of BP to higher trophic levels

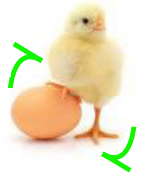
Conclusions

- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**
-  Growth rate differences compensated for by lysis, but differences determined by COR

$\Rightarrow$ VBR seen as the ratio between mechanisms generating bacterial diversity and those controlling community size

- Viruses win over flagellate grazers at high COR
  $\rightarrow$ Less transfer of BP to higher trophic levels
- Microbial diversity and food web structure highly sensitive to life strategy trade-offs (e.g. COR)

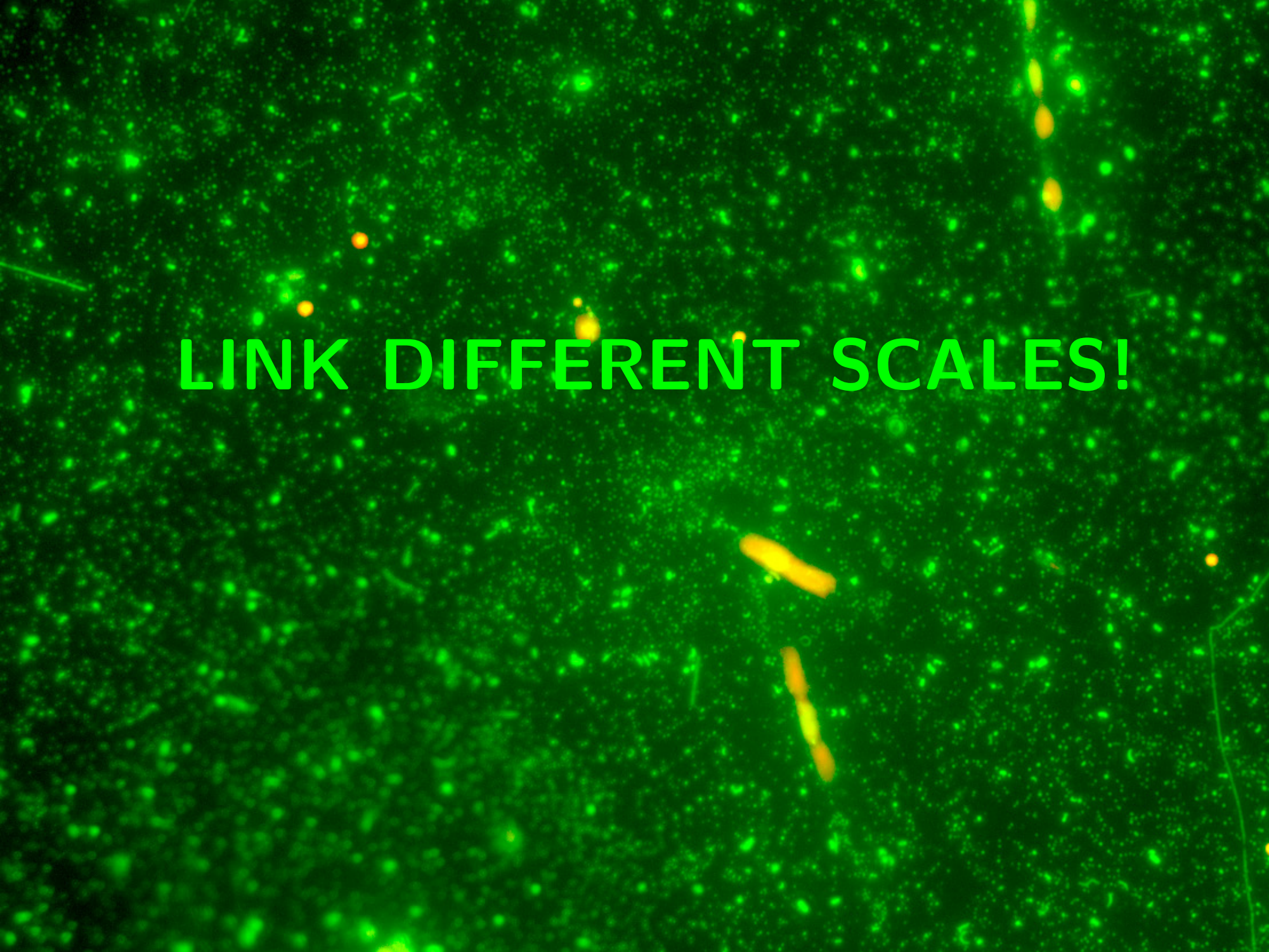
Conclusions

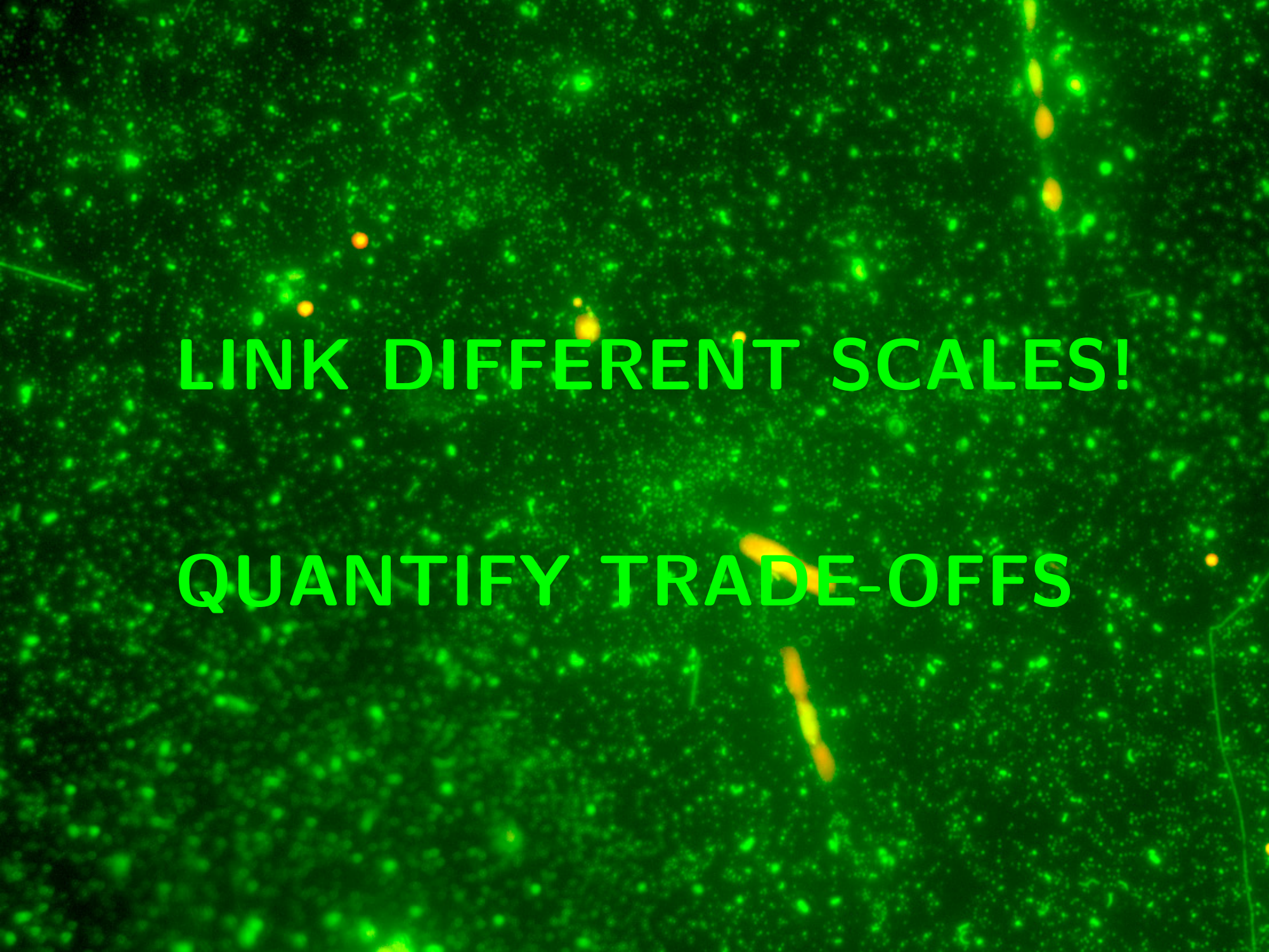
- *Genetic make-up affects ecosystem functioning*
  $\rightarrow$ Coupled model touches both ends
- Microzooplankton control total **bacterial abundance**, **state of limitation** and **minimum growth rate**
-  Growth rate differences compensated for by lysis, but differences determined by COR

$\Rightarrow$ VBR seen as the ratio between mechanisms generating bacterial diversity and those controlling community size

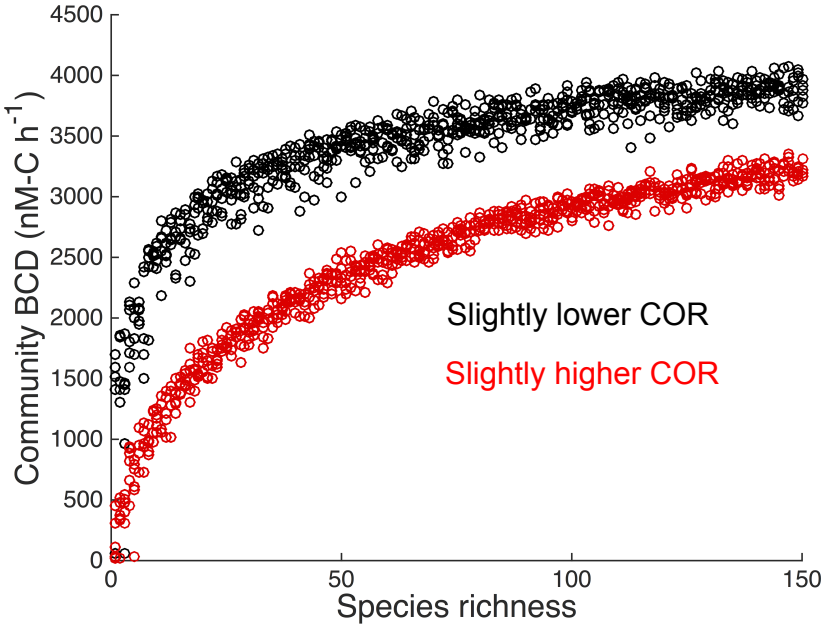
- Viruses win over flagellate grazers at high COR
  $\rightarrow$ Less transfer of BP to higher trophic levels
- Microbial diversity and food web structure highly sensitive to life strategy trade-offs (e.g. COR)

$\Rightarrow$ **Take-home message for all marine ecologists:**


LINK DIFFERENT SCALES!


LINK DIFFERENT SCALES!
QUANTIFY TRADE-OFFS

Linking biodiversity to ecosystem functioning

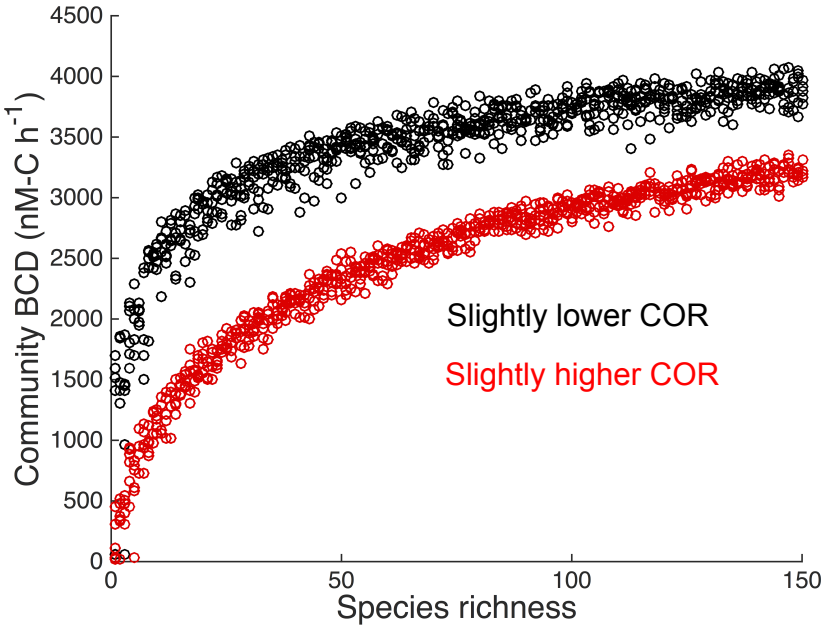


(submitted)

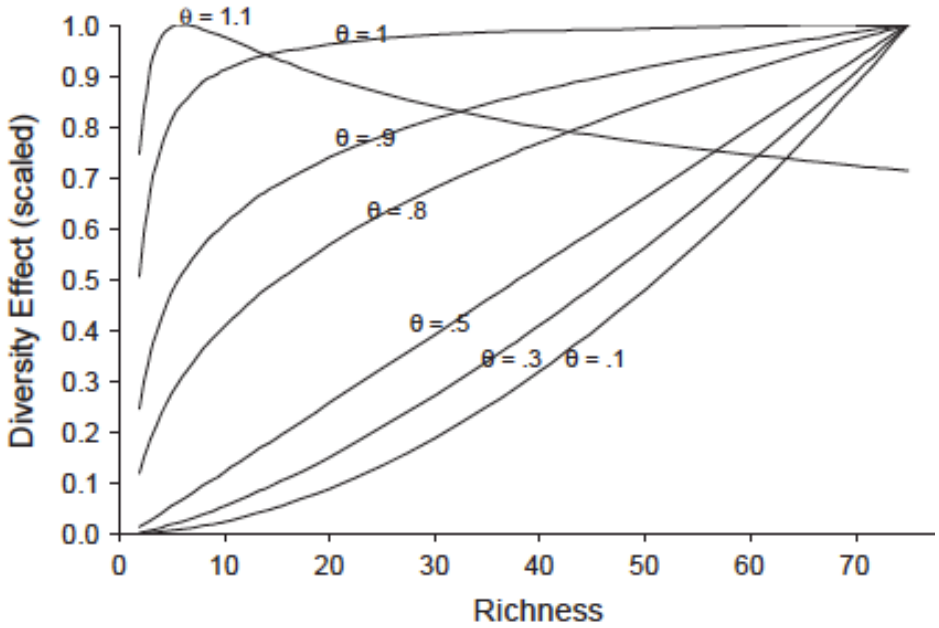
- Links **species diversity** to **community carbon consumption** and hence ecosystem functioning

selina.vage@uib.no

Linking biodiversity to ecosystem functioning



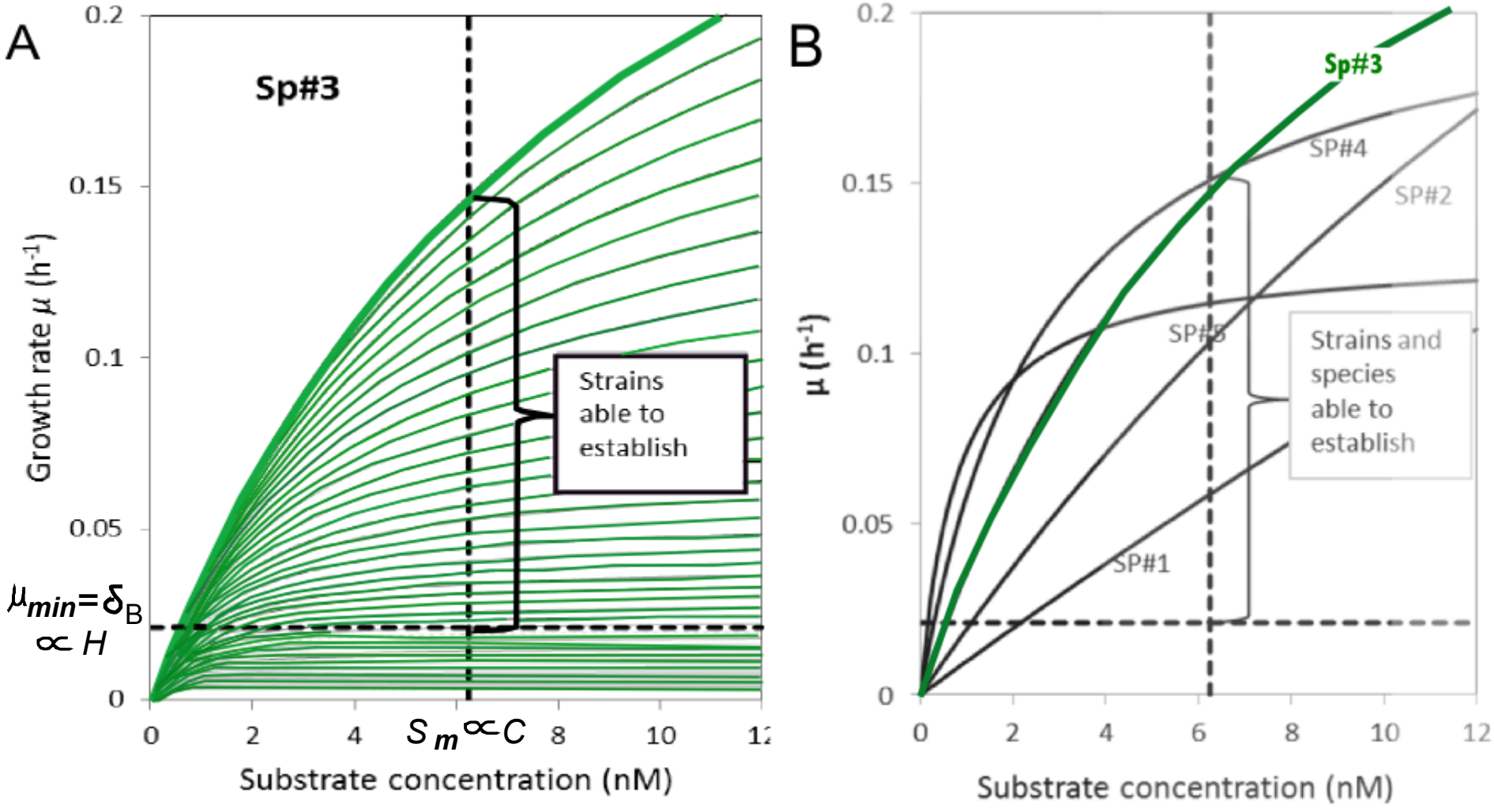
(submitted)

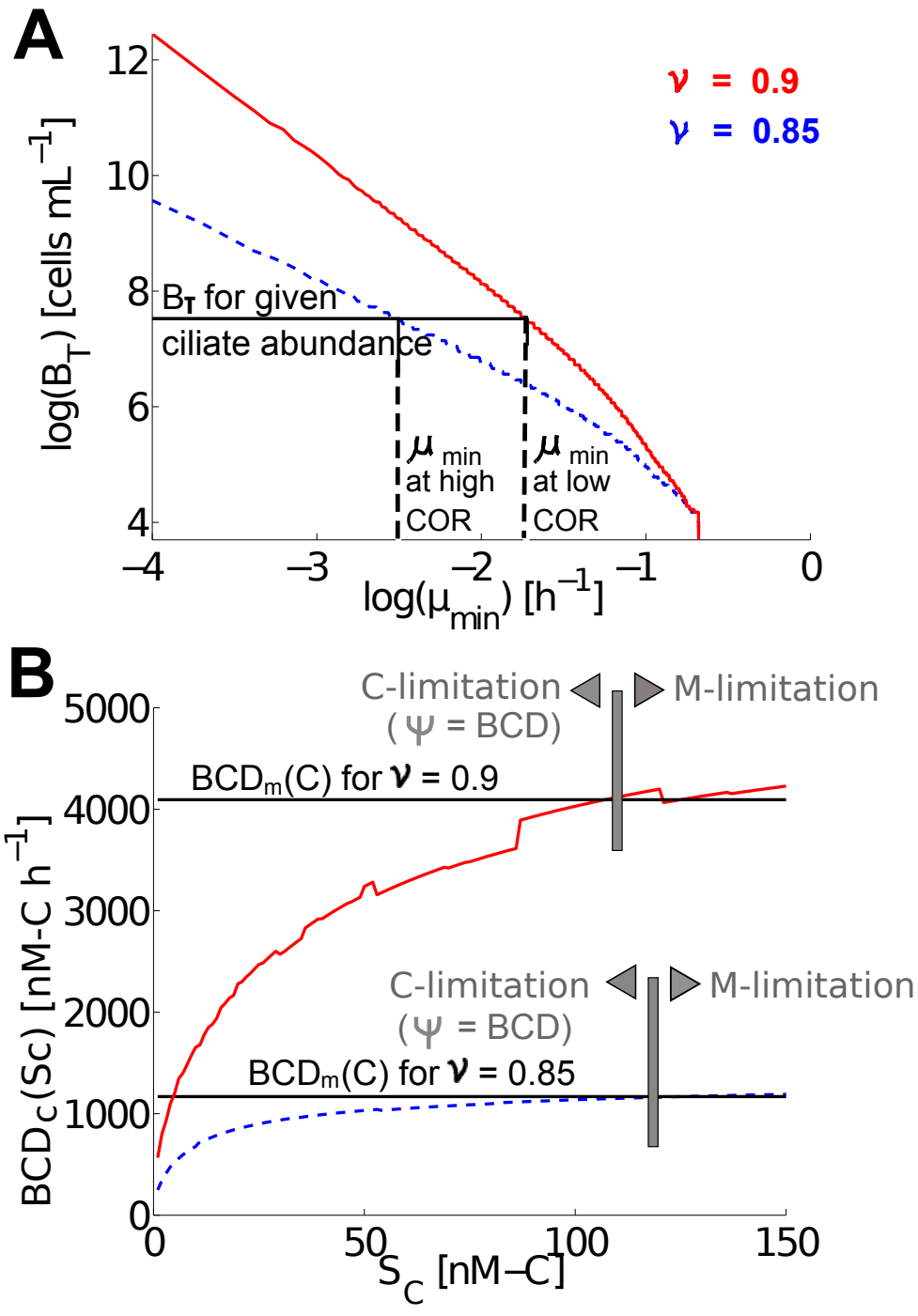


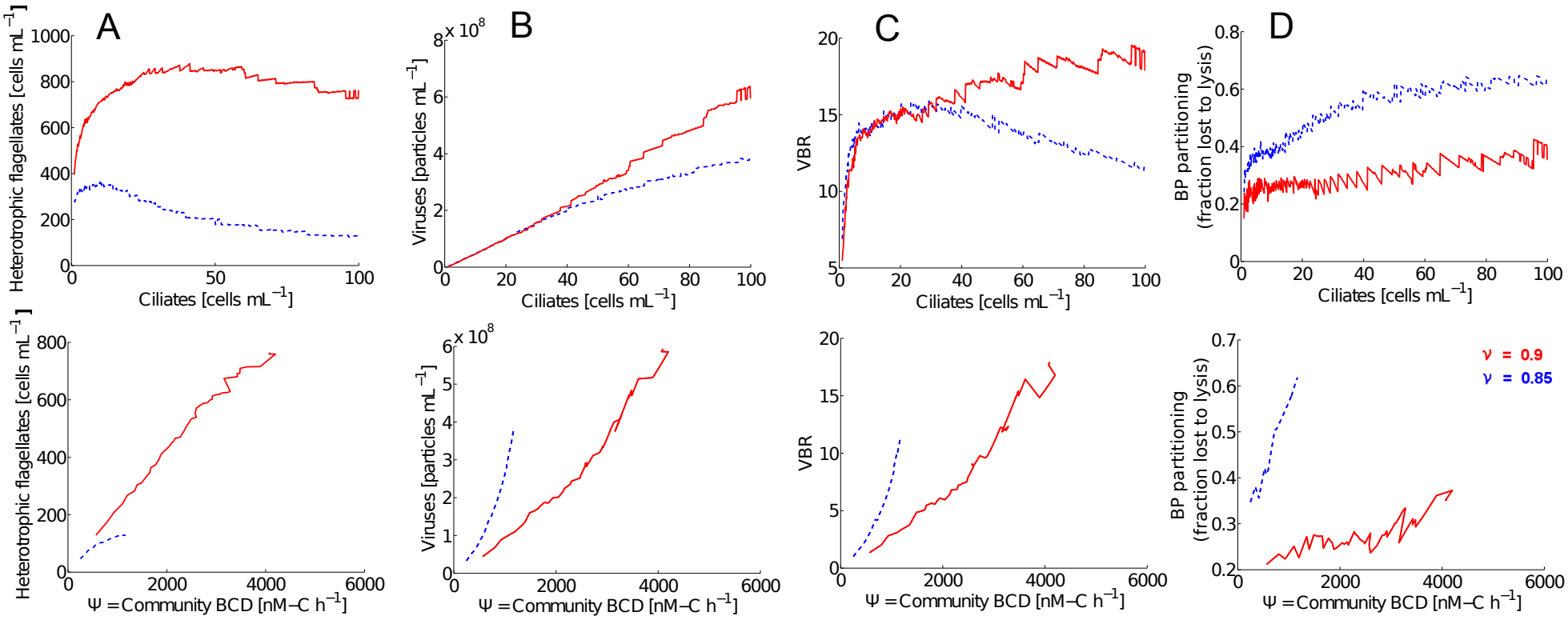
(Connolly et al 2013)

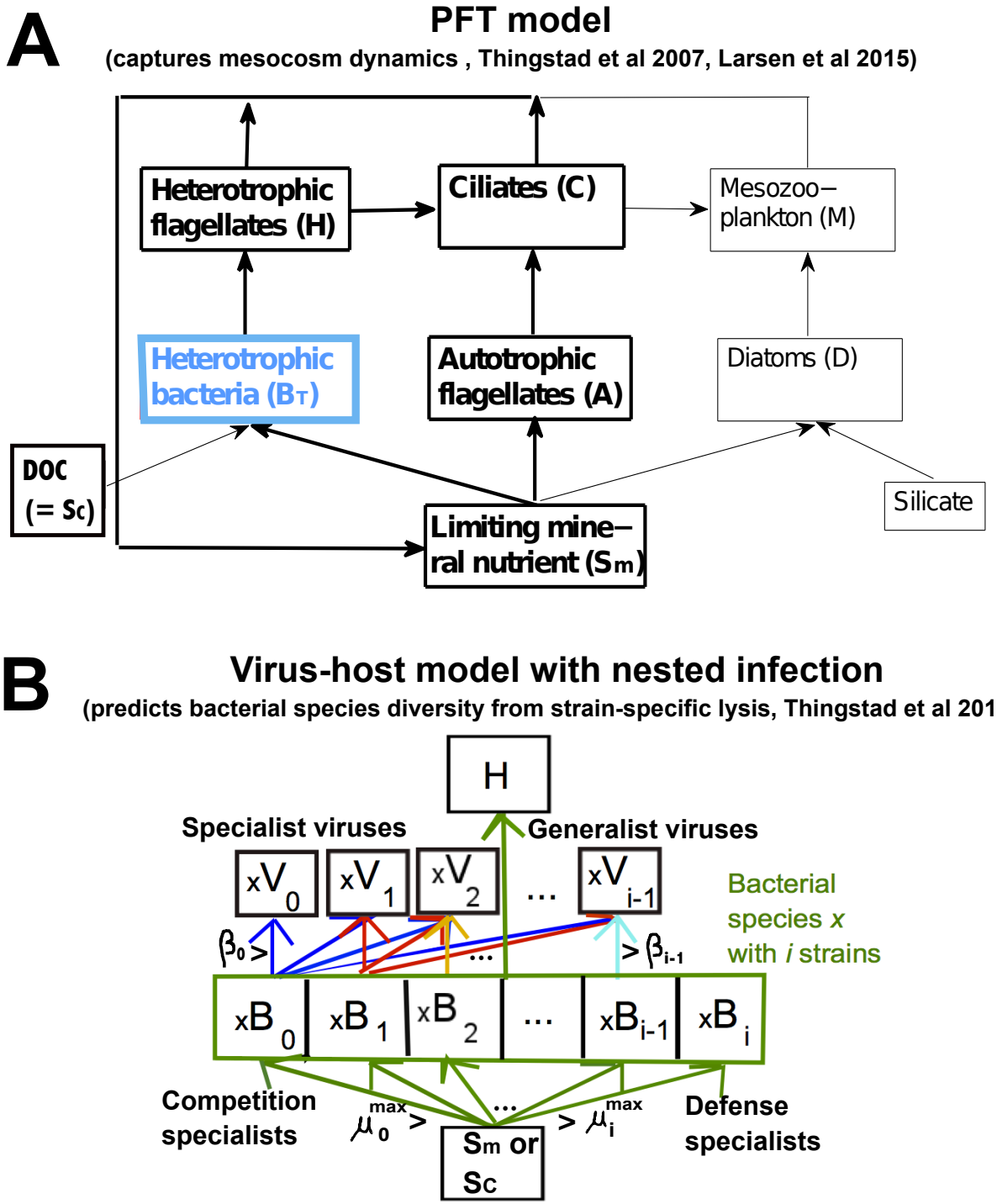
- Links **species diversity** to **community carbon consumption** and hence ecosystem functioning
- Resembles generalized diversity-interaction models with some species redunancy at high richness (i.e. $\Theta \leq 1$, 'species-pair contributions to ecosystem function' slightly stronger than expected, Connolly et al 2013)

selina.vage@uib.no


A
Sp#3
Growth rate μ (h-1)
0.2
0.15
0.1
0.05
0
μmin=δB
∝ H
Strains
able to
establish
0
2
4
Sm∝C
8
10
12
Substrate concentration (nM)
B
Sp#3
SP#4
SP#2
SP#3
SP#1
Strains and
species
able to
establish
μ (h-1)
0.2
0.15
0.1
0.05
0
0
2
4
6
8
10
12
Substrate concentration (nM)


A
ν = 0.9
γ = 0.85
12
10
8
6
4
log(B_T) [cells mL^-1]
B_T for given
ciliate abundance
μ min at high COR
μ min at low COR
–4
–3
–2
–1
0
log(μ_min) [h^-1]
B
C-limitation
(Ψ = BCD)
M-limitation
BCD_m(C) for ν = 0.9
5000
4000
3000
2000
1000
0
BCD_c(Sc) [nM-C h^-1]
C-limitation
(Ψ = BCD)
M-limitation
BCD_m(C) for ν = 0.85
0
50
100
150
S_C [nM–C]


A
B
C
D
Heterotrophic flagellates [cells mL^{-1}]
Viruses [particles mL^{-1}]
x 10^8
VBR
BP partitioning
(fraction lost to lysis)
Ciliates [cells mL^{-1}]
Ψ =Community BCD [nM–C h^{-1}]
ν = 0.9
ν = 0.85


A
PFT model
(captures mesocosm dynamics , Thingstad et al 2007, Larsen et al 2015)
Heterotrophic flagellates (H)
Ciliates (C)
Mesozoo–plankton (M)
Heterotrophic bacteria (BT)
Autotrophic flagellates (A)
Diatoms (D)
DOC (= Sc)
Limiting mine–ral nutrient (Sm)
Silicate
B
Virus-host model with nested infection
(predicts bacterial species diversity from strain-specific lysis, Thingstad et al 2014)
H
Specialist viruses
Generalist viruses
xV0
xV1
xV2
...
xVi-1
Bacterial species x with i strains
β0 >
> βi-1
xB0
xB1
xB2
...
xBi-1
xBi
Competition specialists
μ0max >
...
> μimax
Defense specialists
Sm or Sc