Before we can walk …

(Anderson 2005)

mechanistic understanding
gained by
trait-based model development

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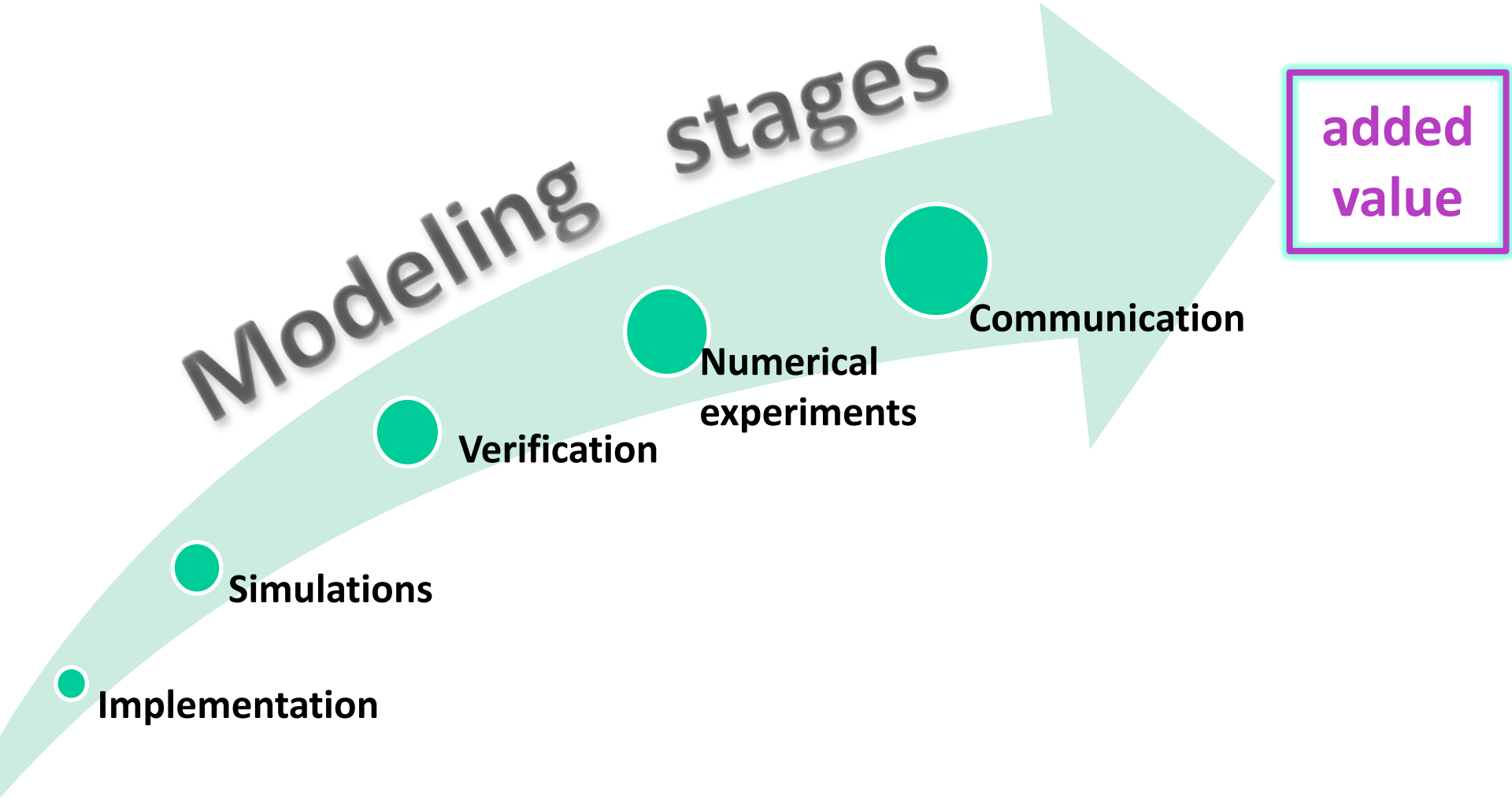
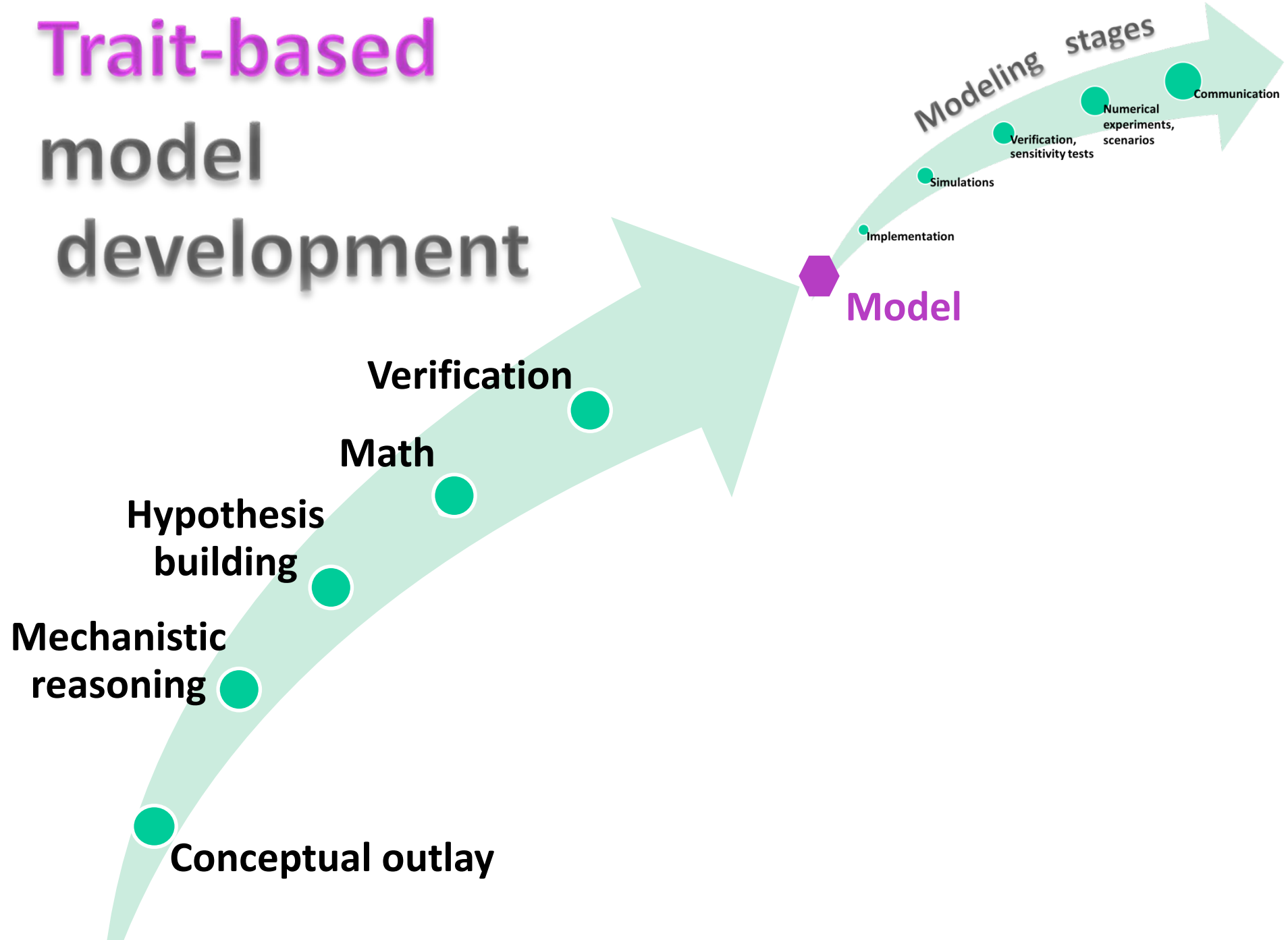
Kopenhagen Aug 2013


Modeling stages
Implementation
Simulations
Verification
Numerical experiments
Communication
added value

Trait-based model development



MANY growth related parameters

net growth rate

maximal photosynthesis

nutrient affinity

max. nutrient uptake

…

…

…

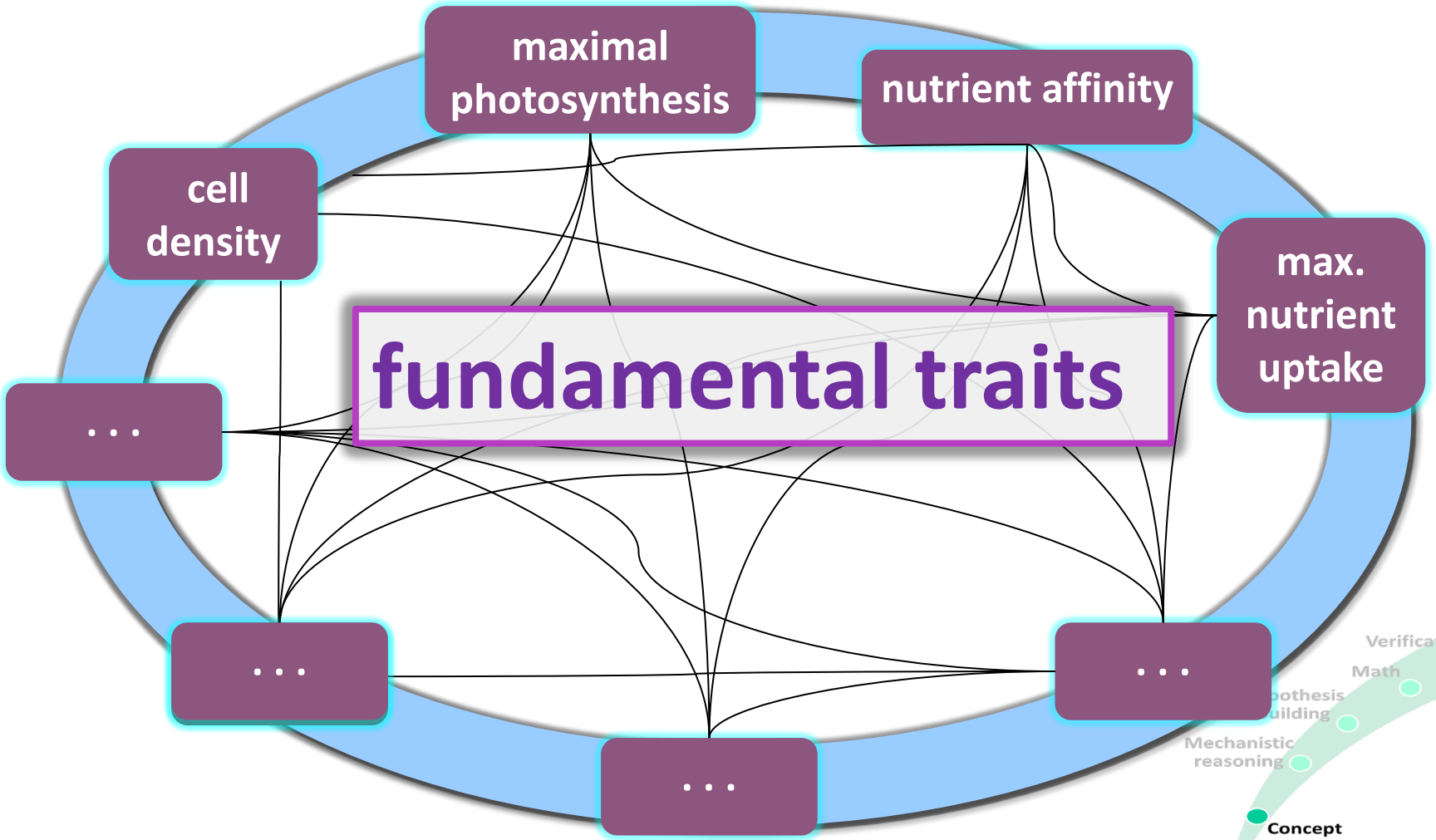
…

cell density

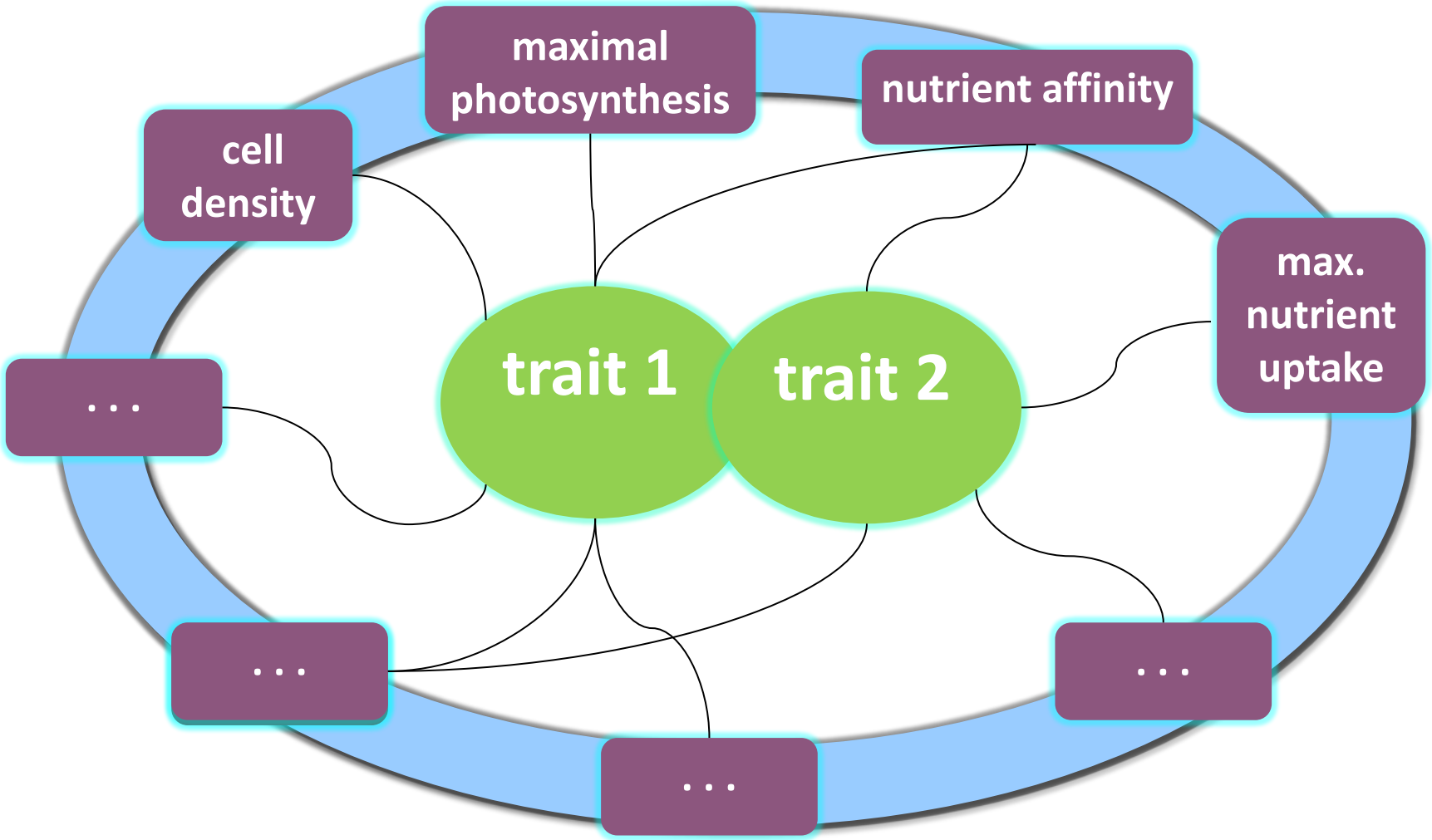
example:

unicellular autotrophs

VERY MANY trade-offs

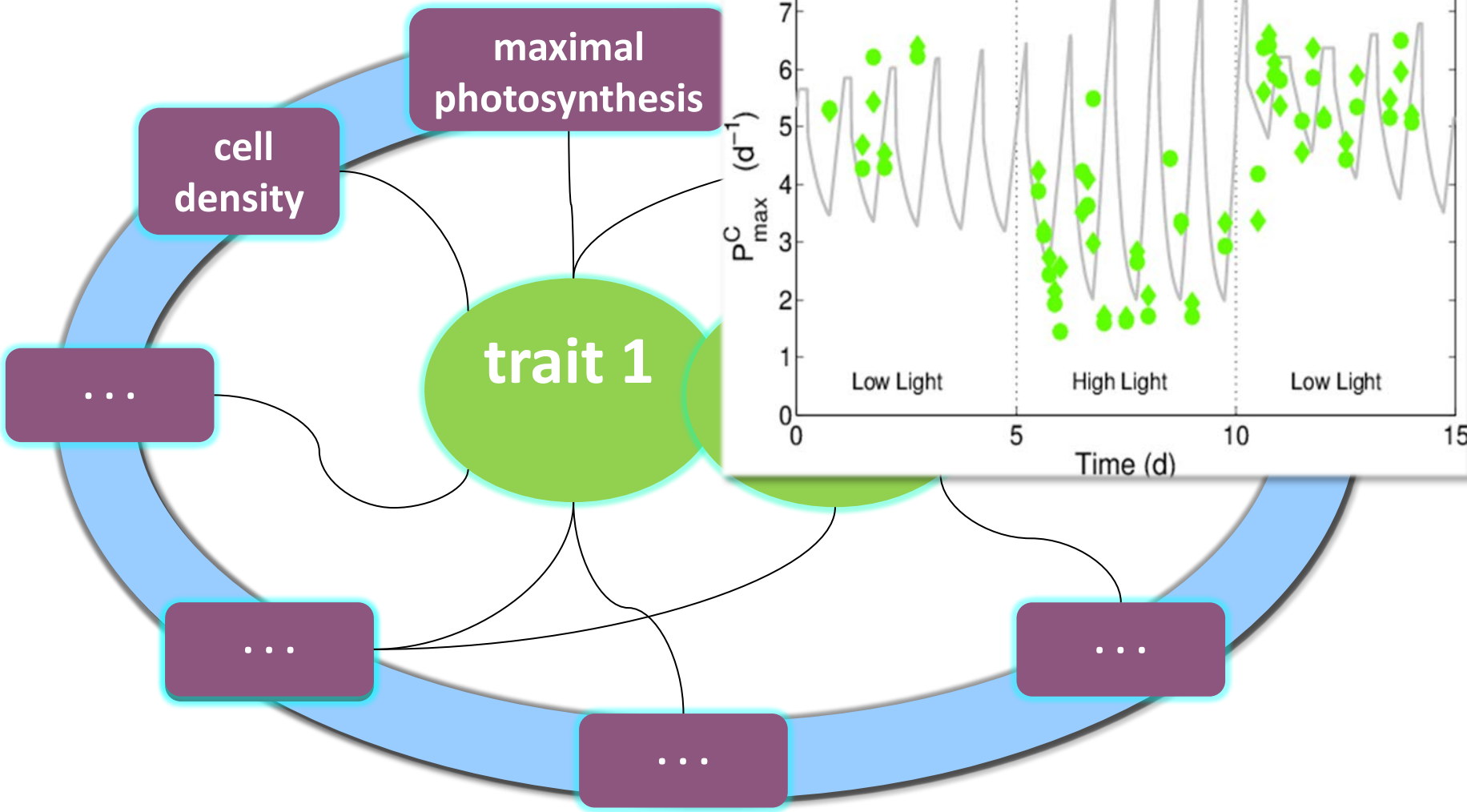


FEW fundamental traits



FEW fundamental traits

Wirtz & Pahlow 2010
Data from Geider & Anning (unpubl)



growth optimality: adaptive trait dynamics

growth rate μ

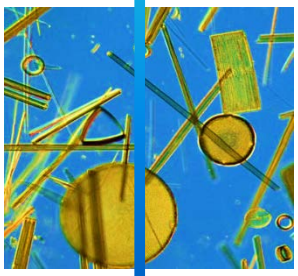
community/population level:

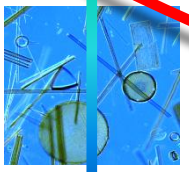
Wirtz&Eckhardt *EM* 1996, *JBT* 2002

organ/organism level:

Wirtz 1996, *AnnBot* 2000

$$\frac{d\text{Trait}}{dt} \sim \frac{d\mu}{d\text{Trait}}$$

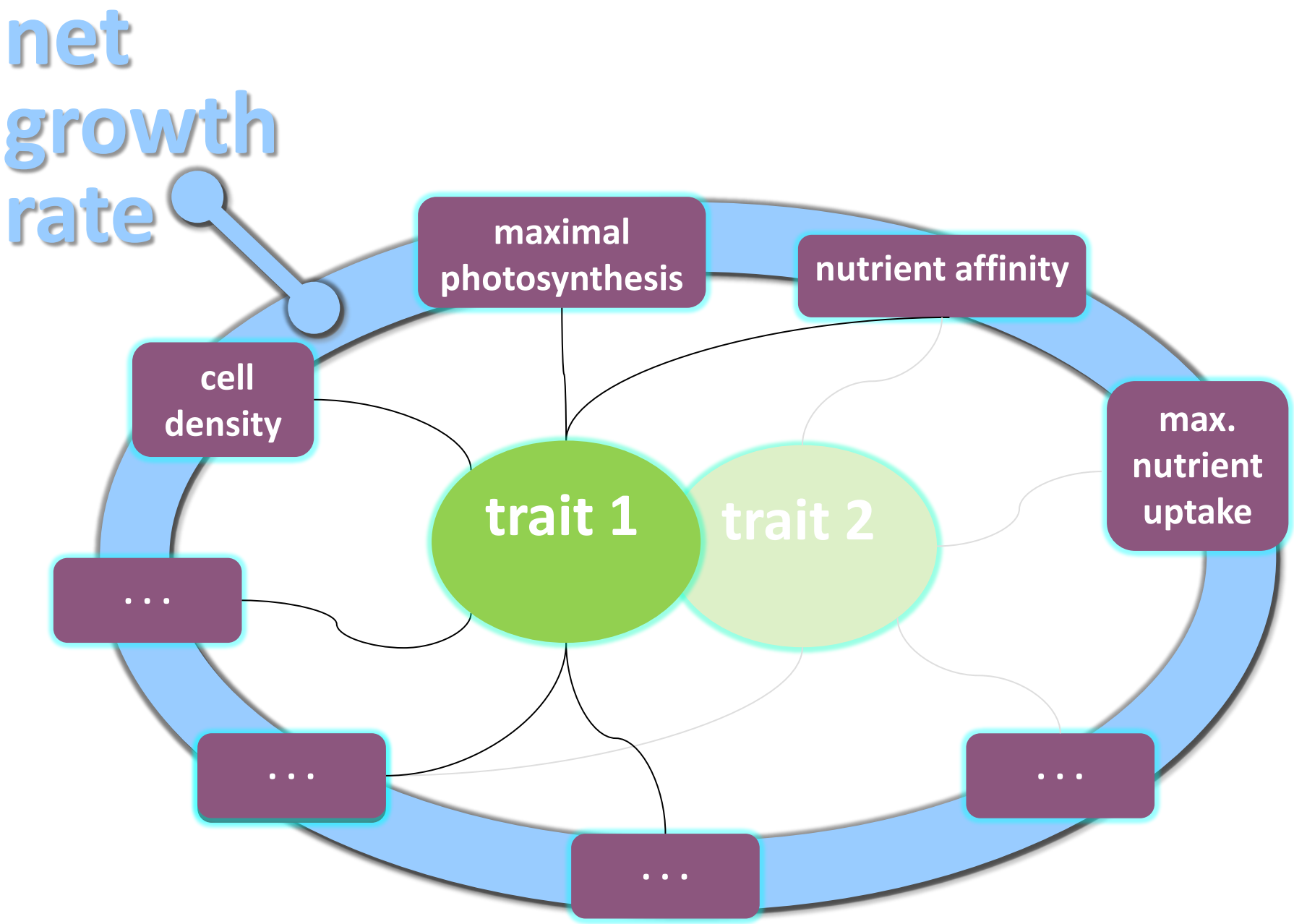


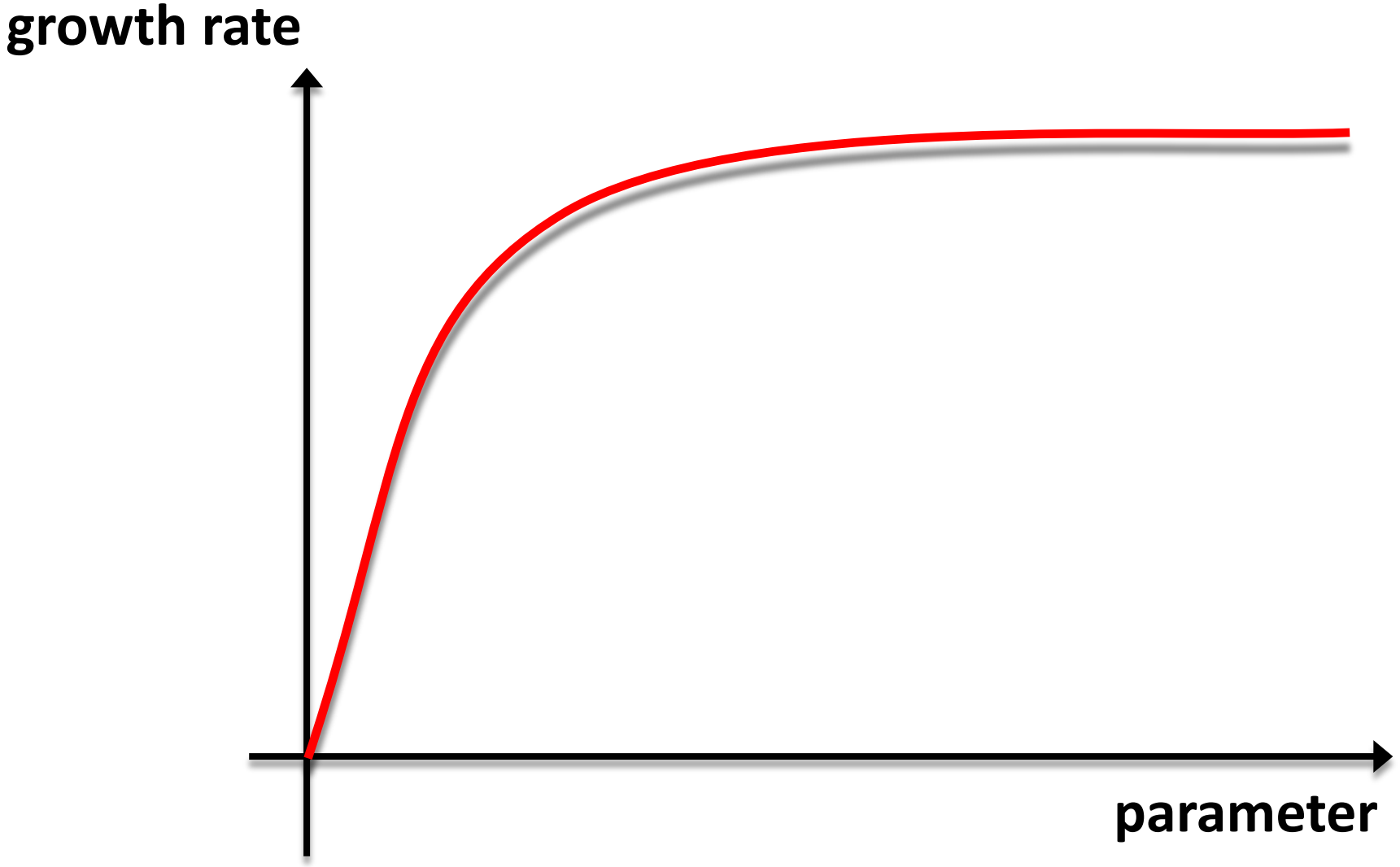


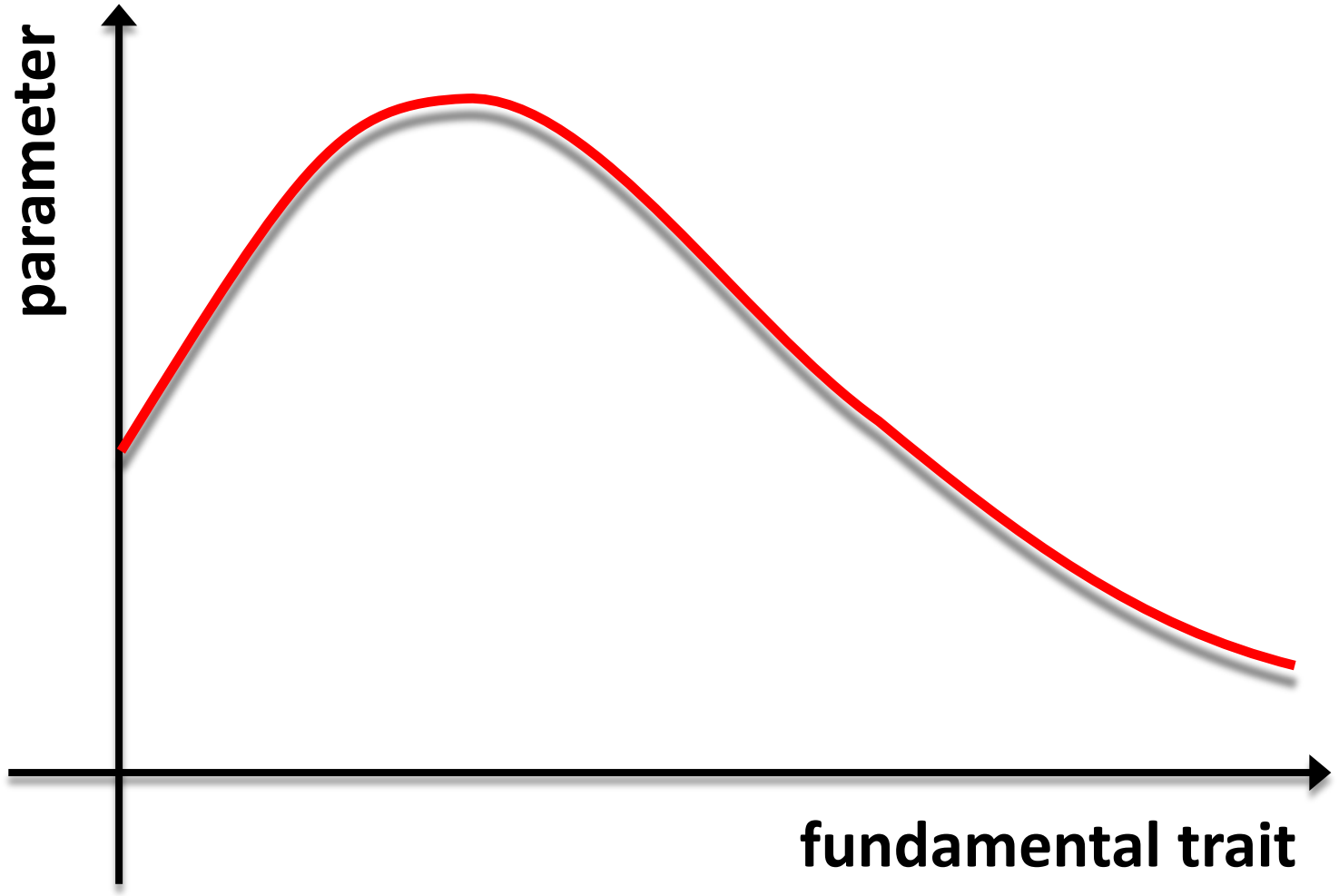
fundamental trait

Verification
Math
Hypothesis building
Mechanistic reasoning
Concept

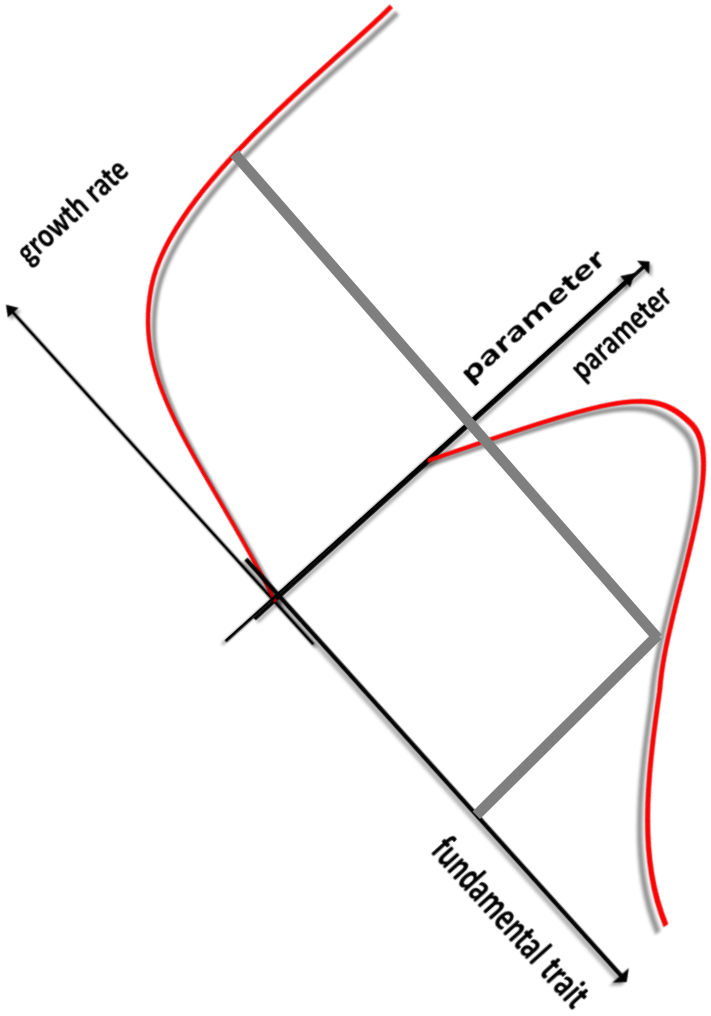
growth-trait relations

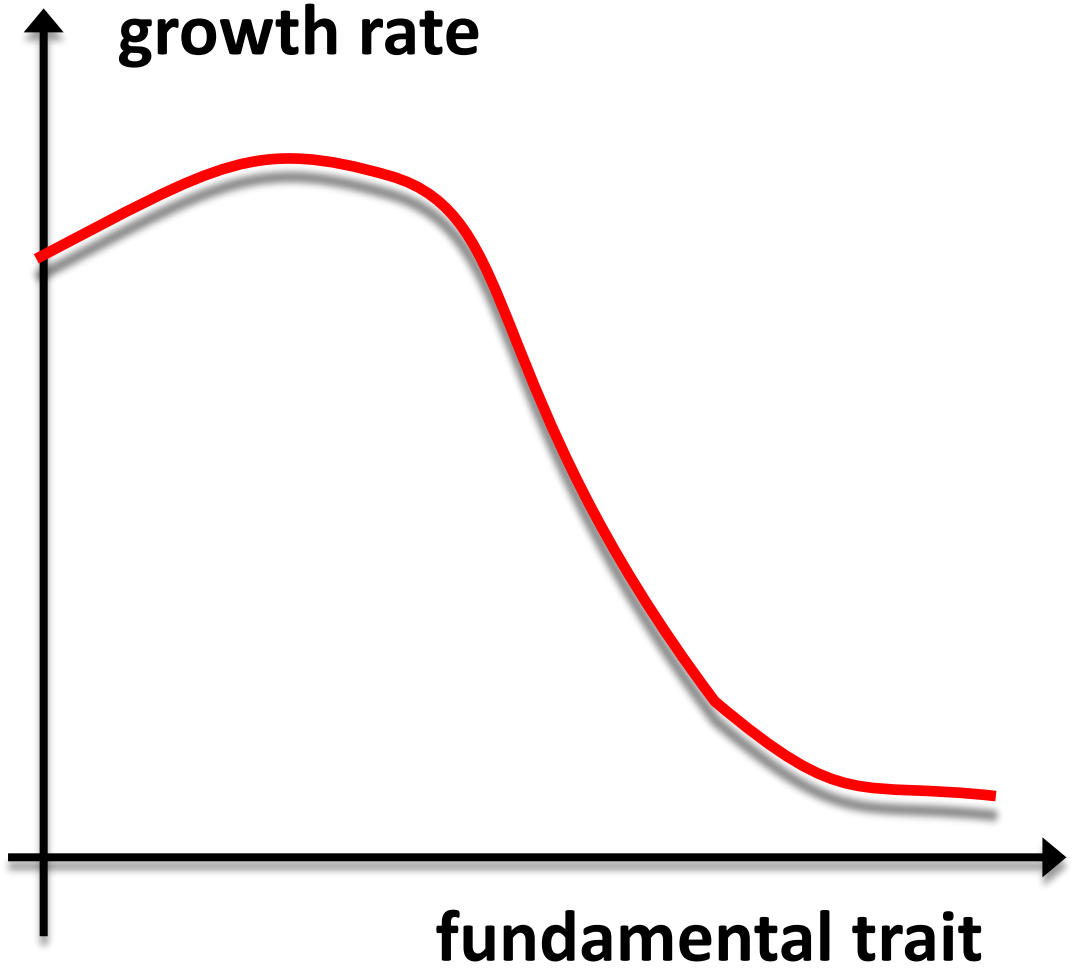



growth rate
parameter


parameter
fundamental trait

growth-trait relation





multi-criteria optimization

carbon growth

nitrogen assimilation

maximal photosynthesis

nutrient affinity

cell density

max. nutrient uptake

. . .

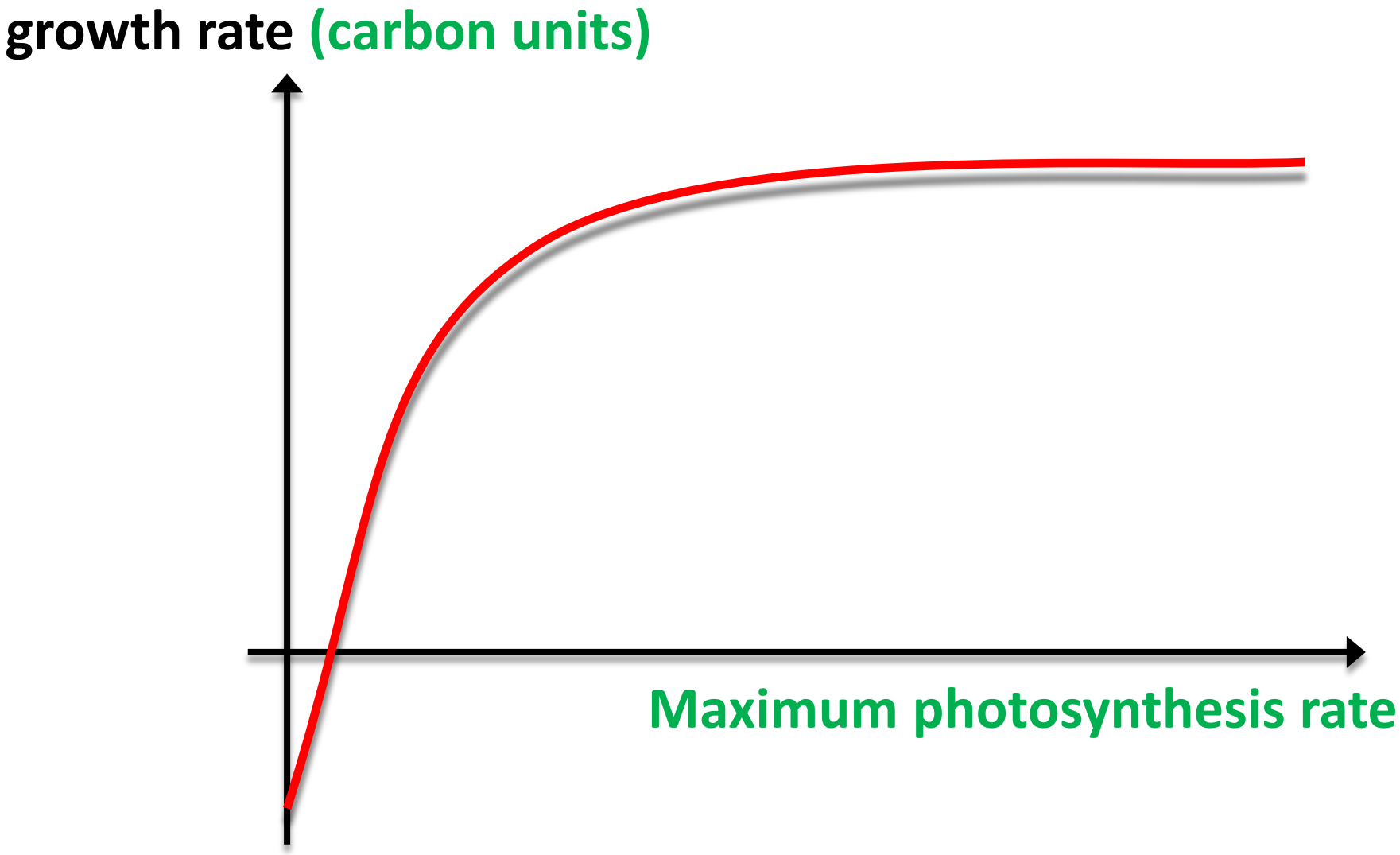
. . .

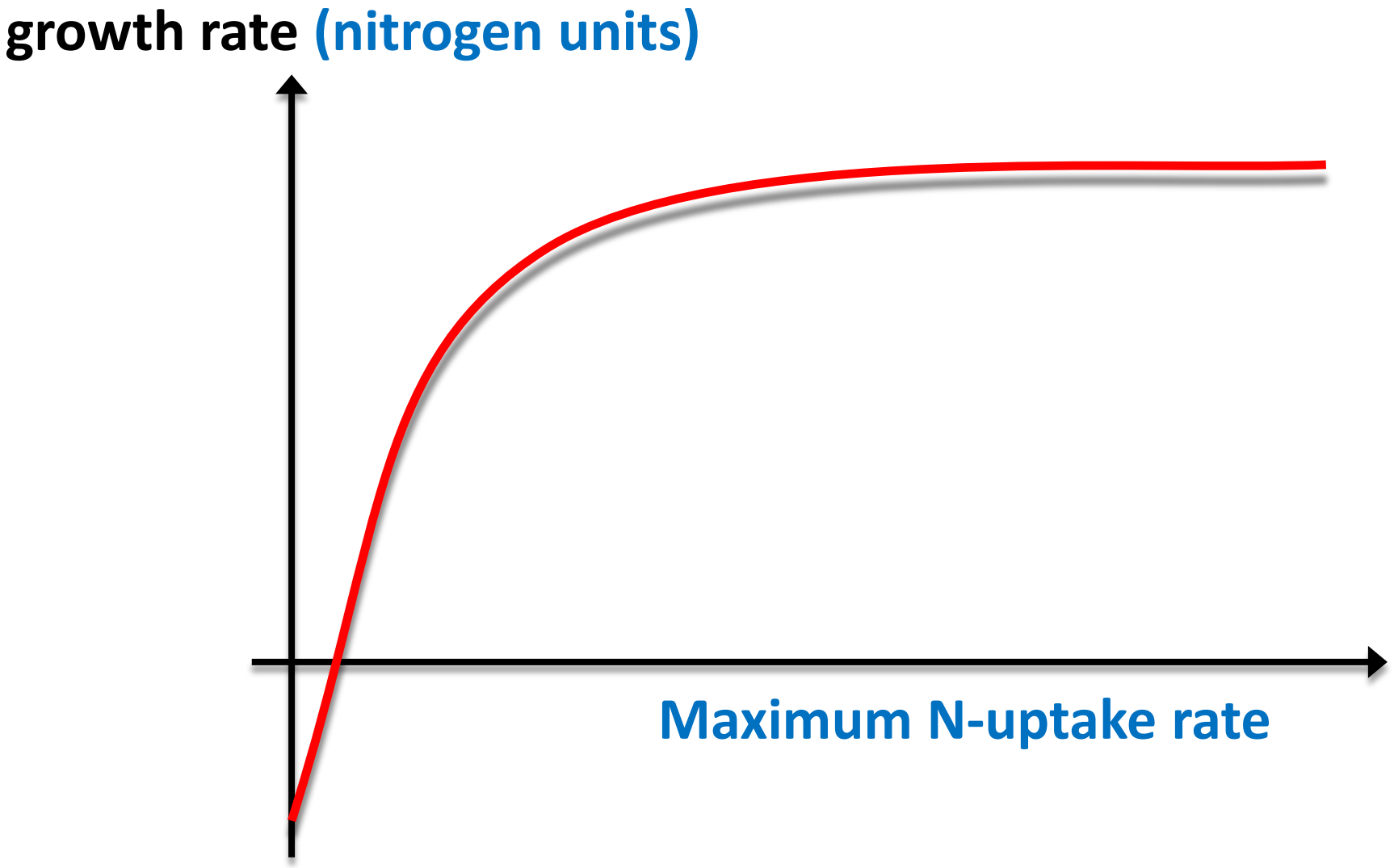
. . .

. . .

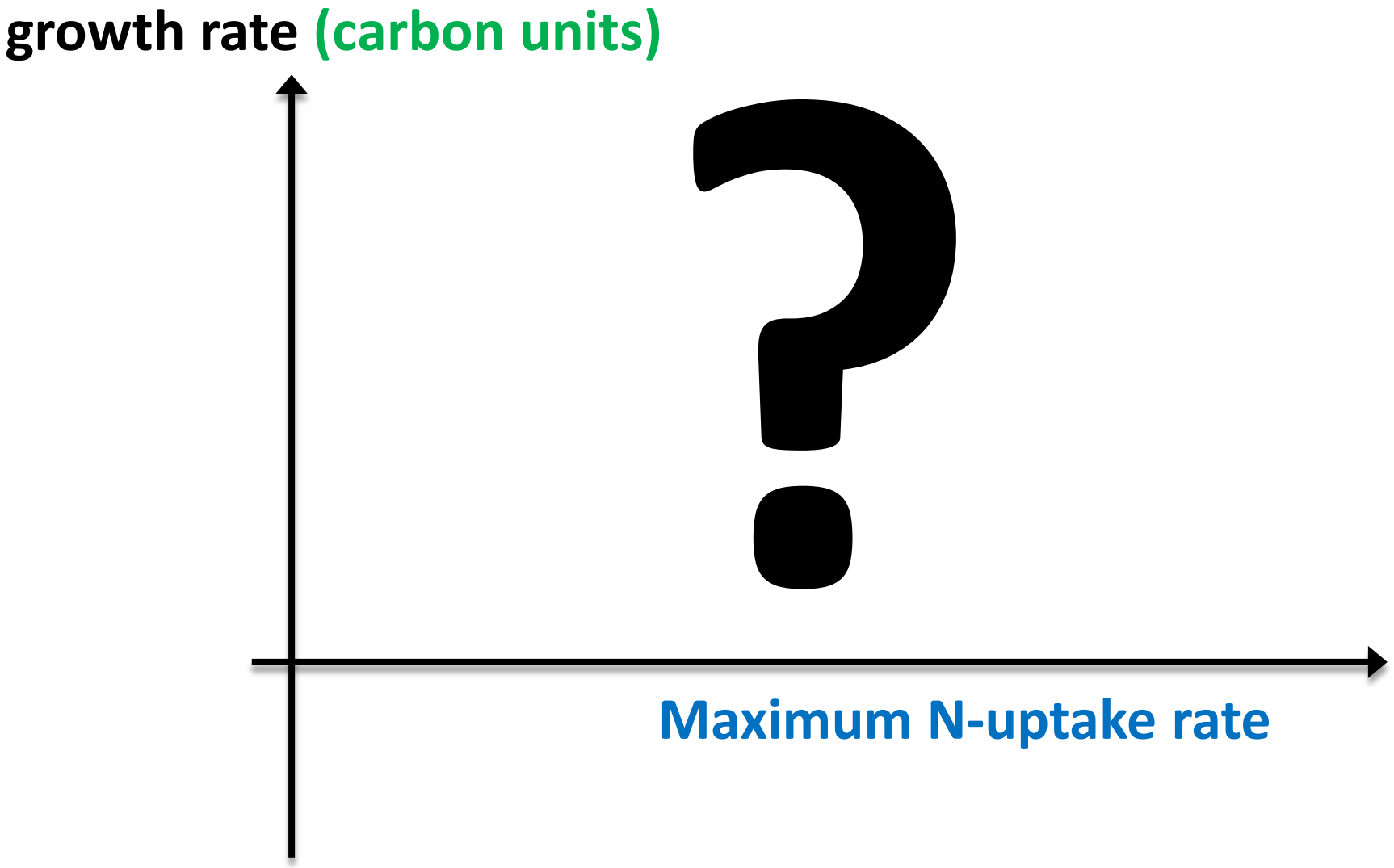
example:

unicellular autotrophs


growth rate (carbon units)
Maximum photosynthesis rate

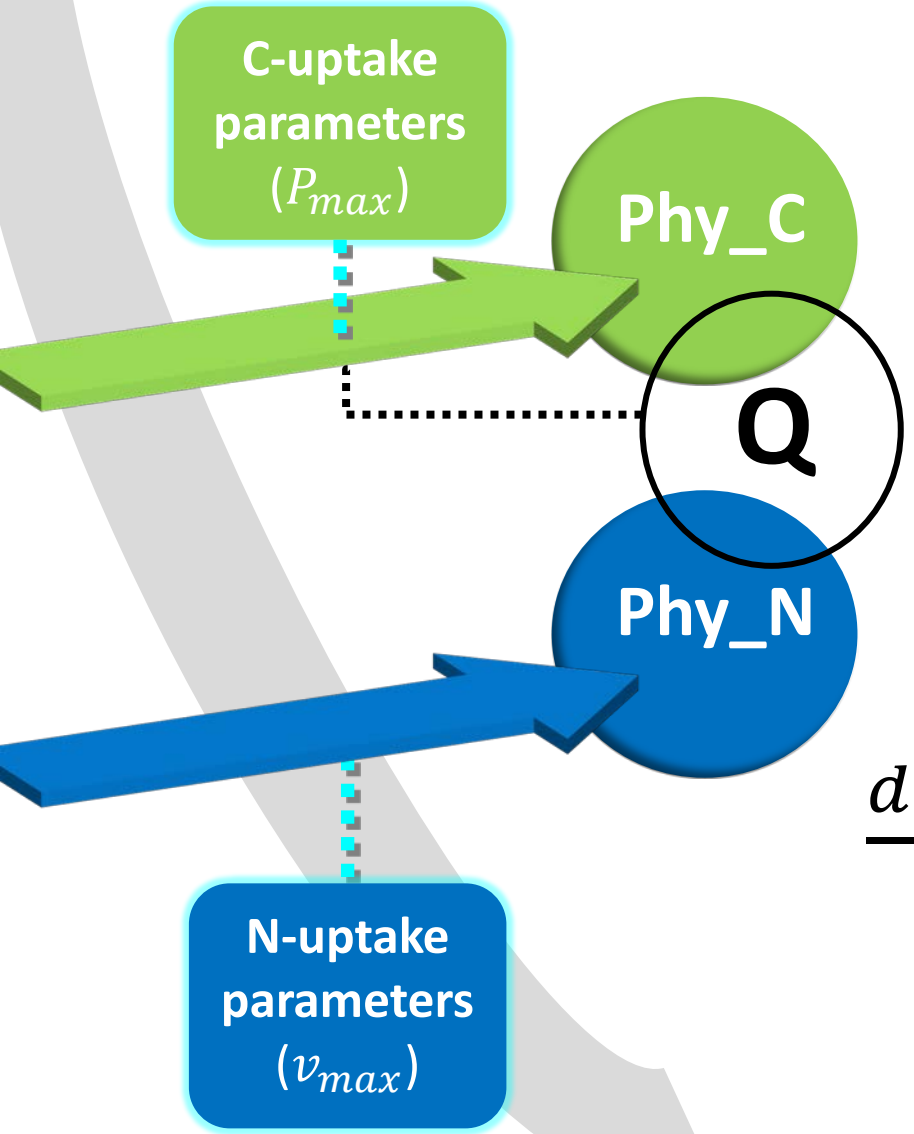

growth rate (nitrogen units)
Maximum N-uptake rate

growth-trait relation (>1 goal function)



Wirtz & Pahlow 2010

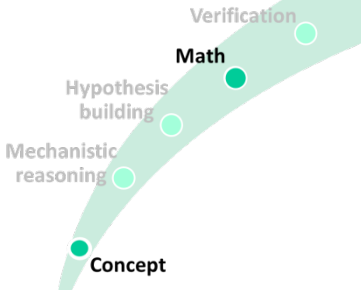
$$\frac{d\mathrm{PhyC}}{dt} = \mu(\mathrm{Q}, P_{max}) \cdot \mathrm{PhyC}$$



$$V = \mu \cdot \mathrm{Q}$$

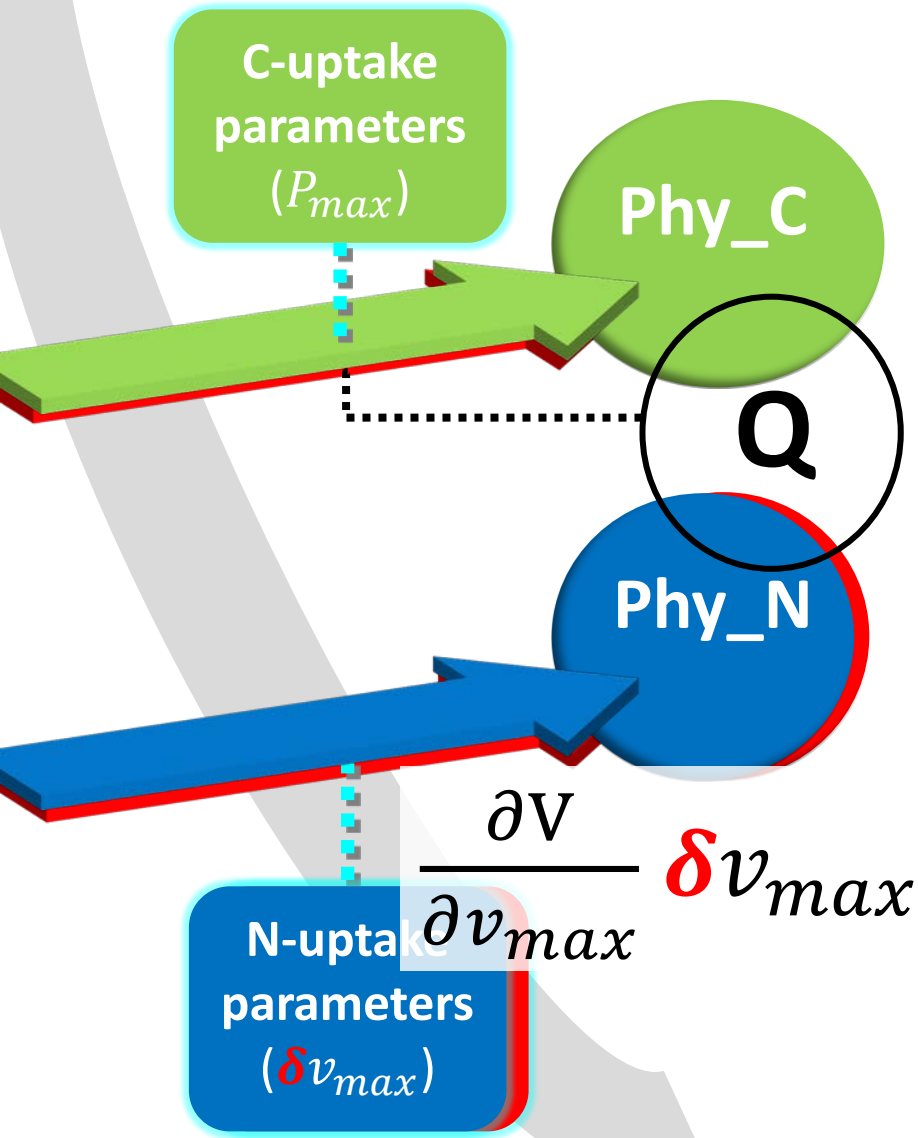
$$\mathrm{Q} = \frac{\mathrm{Phy\_N}}{\mathrm{Phy\_C}}$$

$$\frac{d\mathrm{PhyN}}{dt} = V(v_{max}) \cdot \mathrm{PhyC}$$



Wirtz & Pahlow 2010c

propagating a parameter perturbation



$$V = \mu \cdot Q$$

$$\delta V = \delta(\mu \cdot Q)$$

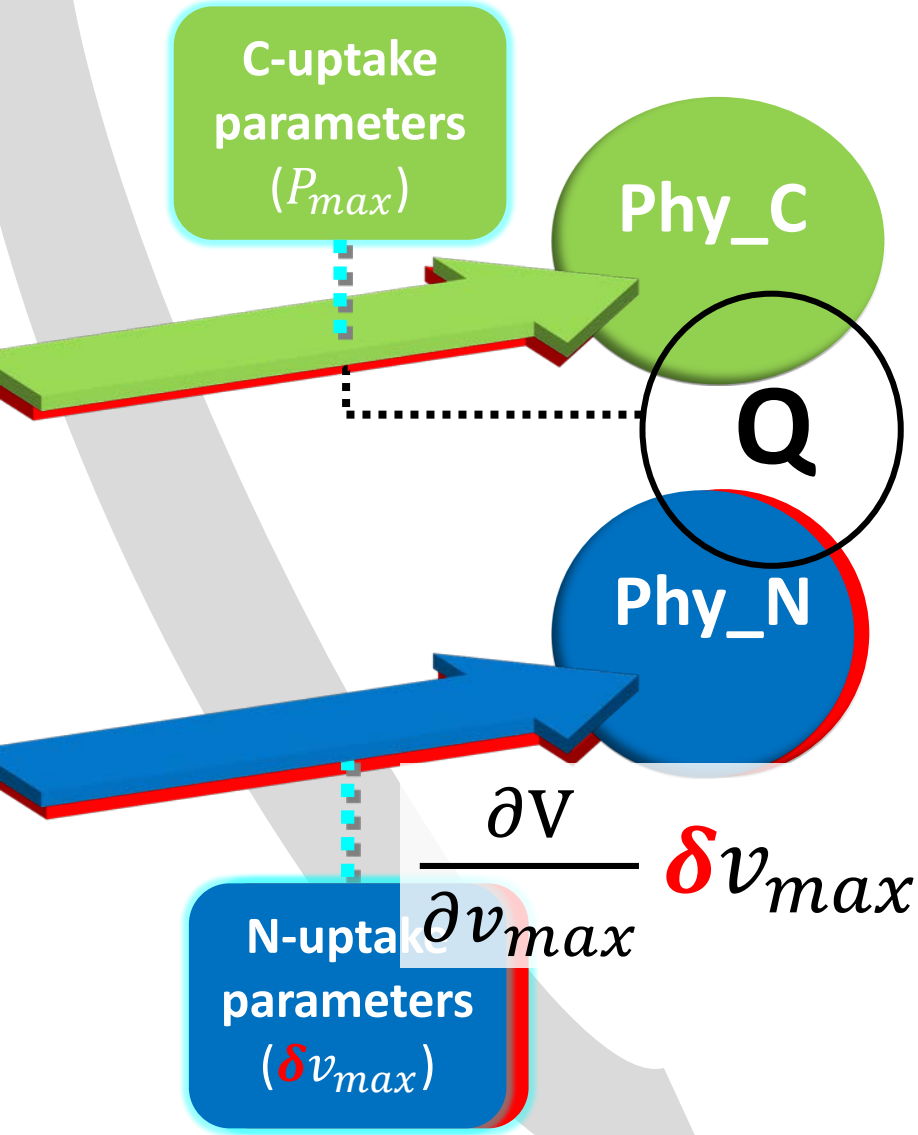
$$\delta V = \delta\mu \cdot Q + \mu \cdot \delta Q$$

$$\frac{\partial V}{\partial v_{max}} \delta v_{max} = \delta V = \frac{\partial \mu}{\partial Q} \delta Q \cdot Q + \mu \cdot \delta Q$$

$$= \left(\frac{\partial \mu}{\partial Q} Q + \mu\right) \cdot \delta Q$$

Wirtz & Pahlow 2010c

propagating a parameter perturbation



$$\frac{d\mu}{dv_{max}} = \frac{\partial \mu}{\partial Q}\frac{\delta Q}{\delta v_{max}}$$

$$\frac{\partial V}{\partial v_{max}}\,\delta v_{max} = \delta V = \frac{\partial \mu}{\partial Q}\delta Q \cdot Q + \mu \cdot \delta Q$$

$$= \left(\frac{\partial \mu}{\partial Q}\,Q + \mu\right) \cdot \delta Q$$

~~PhyC (Trait, Env)~~

$$\frac{d\mathrm{PhyC}}{dt} = \mu(\ldots, Env) \cdot \mathrm{PhyC}$$

~~$\mu(v_{max})$~~

$$\frac{dv_{max}}{dt} \sim \frac{d\mu}{dv_{max}}$$

trait history

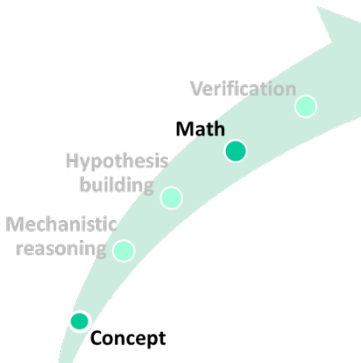
1. **not always explicit trade-offs !**
2. **interpretation of observations/experiments requires a time-explicit approach**

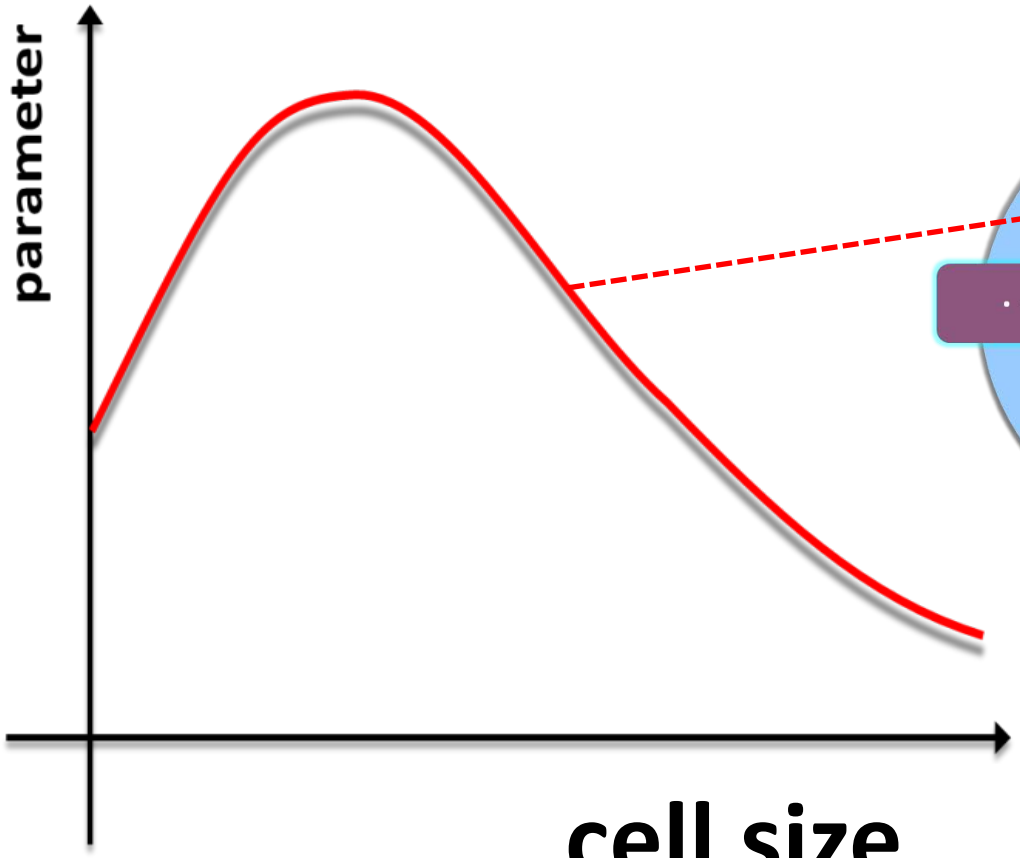
perturbation method:

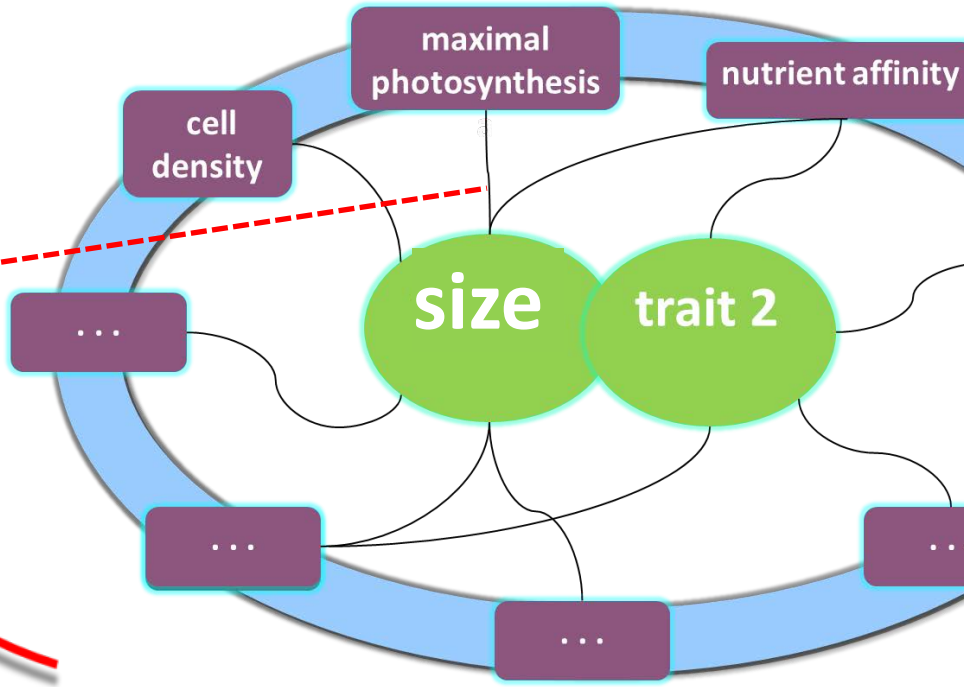
multi-criteria optimization problems

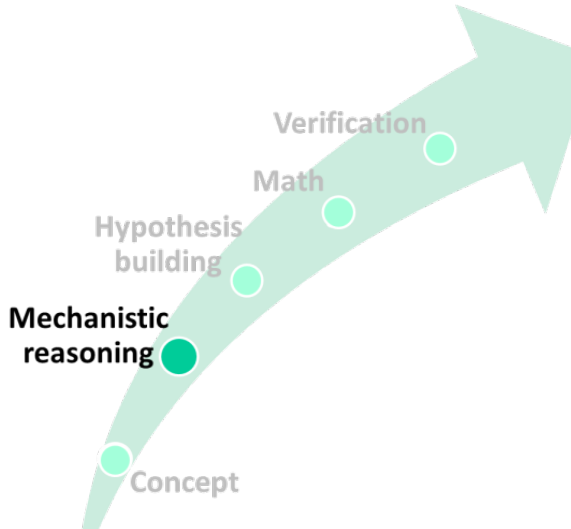
1. **nutrient uptake (N, P, …)** →**Monod** (Wirtz&Pahlow 2010)
2. **optimality in uptake activity** → ~~Q_{max}~~ (Wirtz&Sommer 2013)
3. **population vs. community structure** (Wirtz&Sommer 2013)
4. **individual growth vs. reproduction**

complete & consistent integration of growth parameters

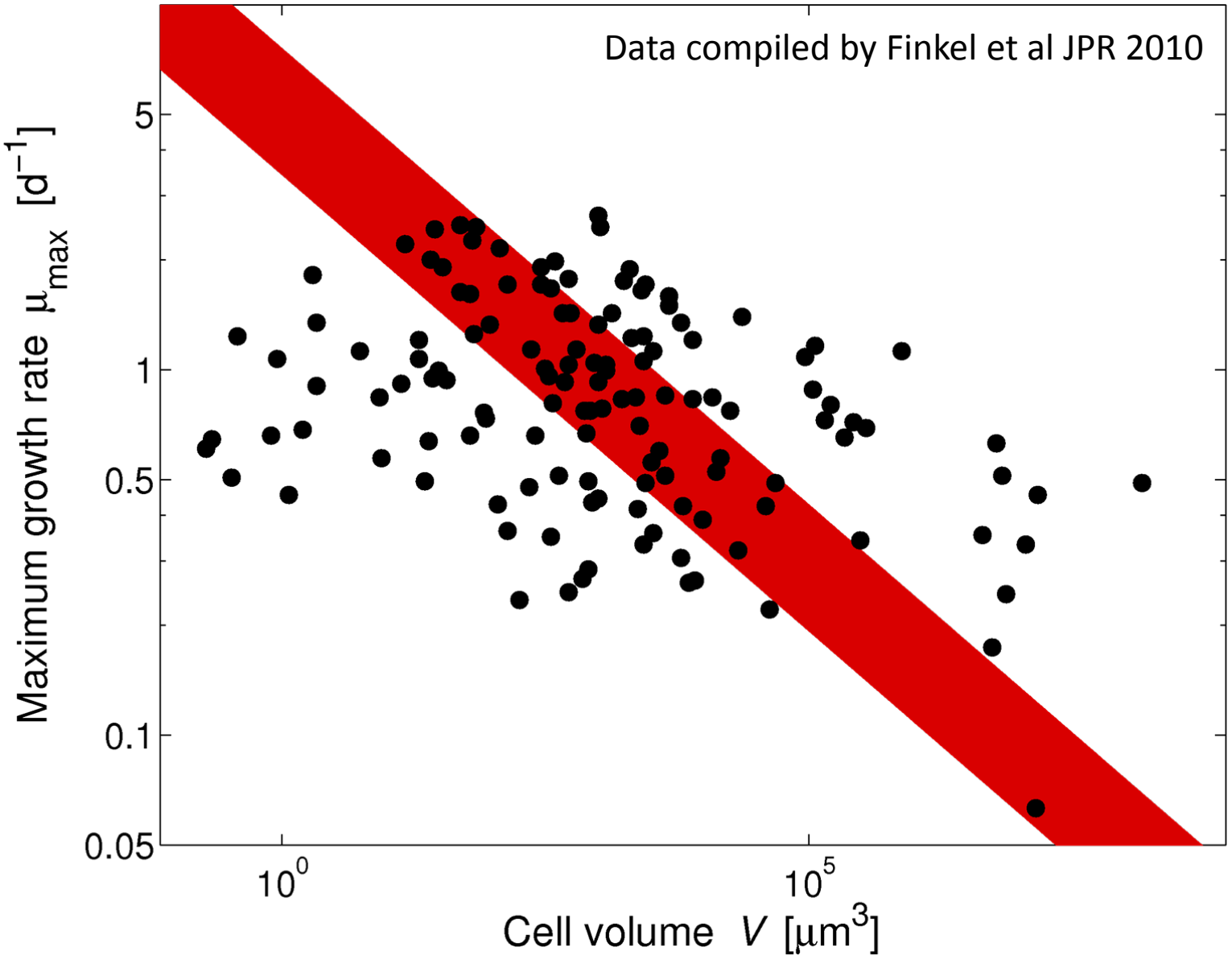



parameter
cell size


maximal photosynthesis
nutrient affinity
cell density
size
trait 2
...
...
...
..

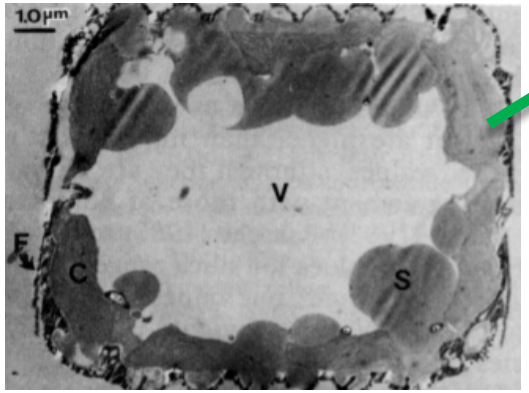

Verification
Math
Hypothesis building
Mechanistic reasoning
Concept

Maximum photosynthesis rate



Maximum photosynthesis rate

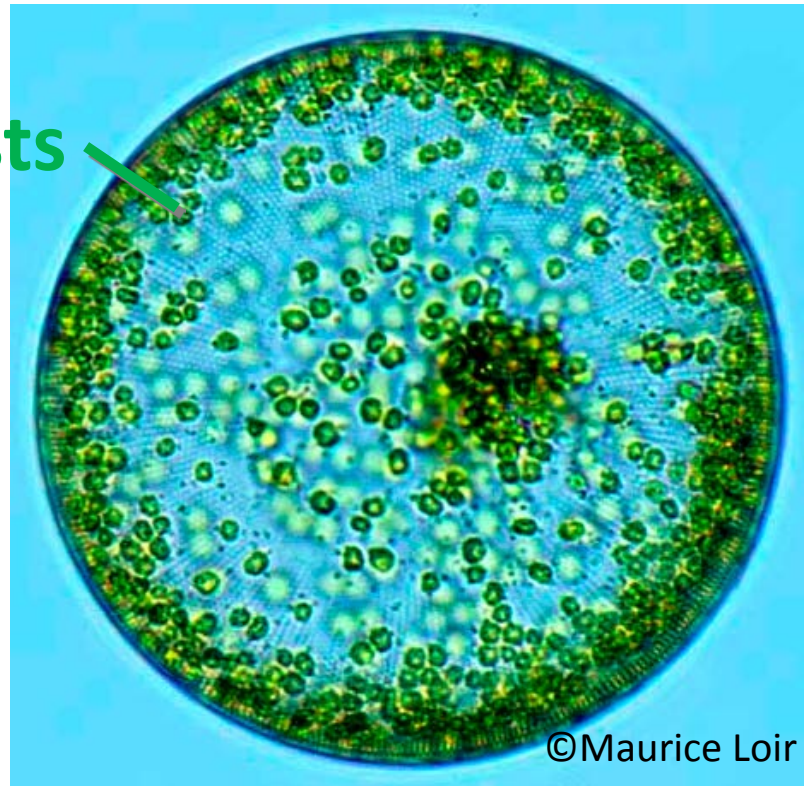
Cyclotella meneghiniana



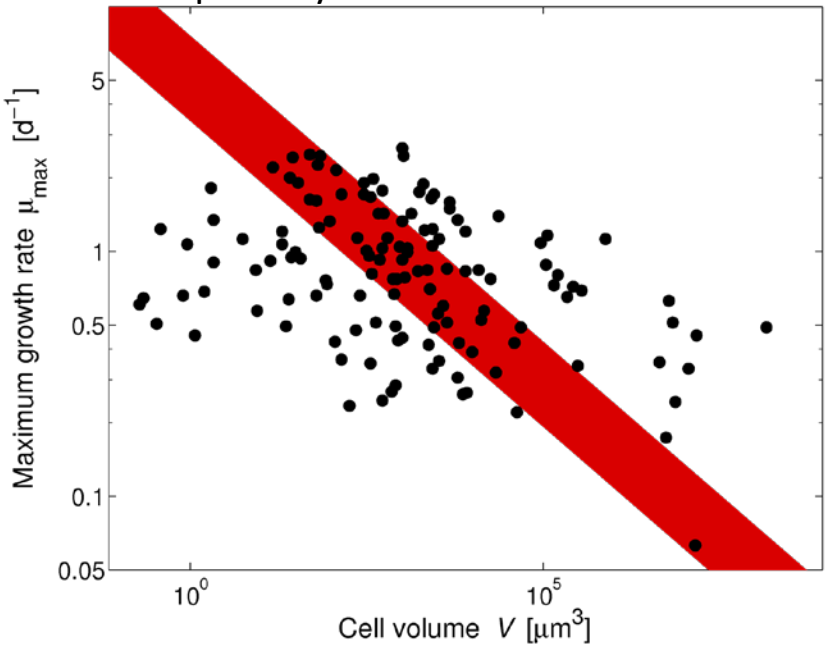
Sicko-Goad et al 1985

chloroplasts

Coscinodiscus wailesii



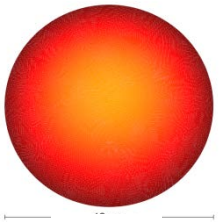
Data compiled by Finkel et al 2010



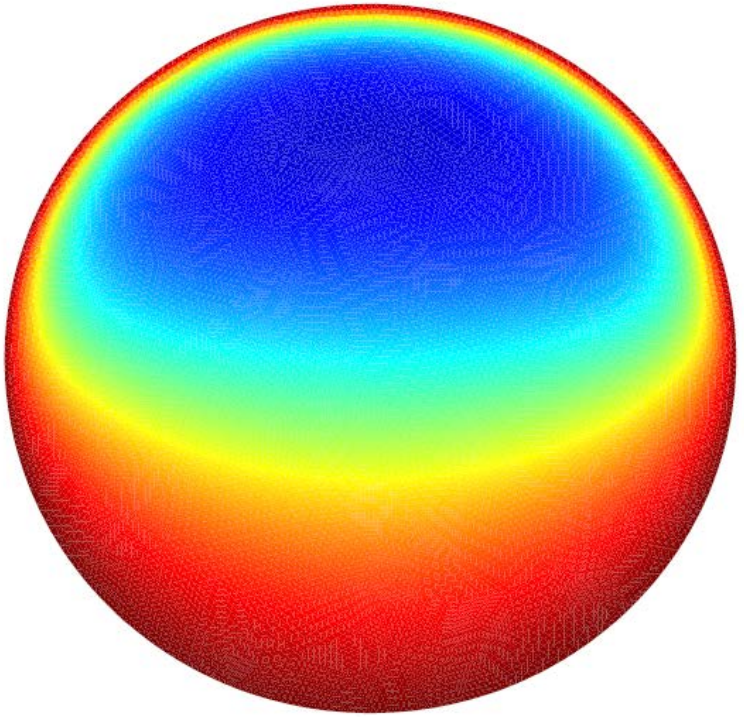
Non-uniform scaling due to intracellular transport limitation

Maximum photosynthesis rate

intracellular CO_2/light gradients

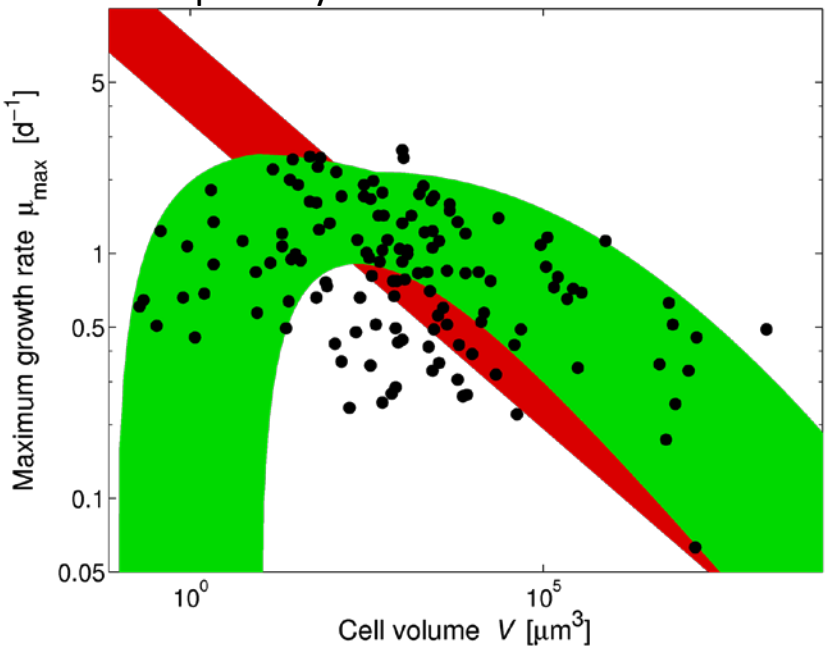


10µm



80 µm

Data compiled by Finkel et al 2010



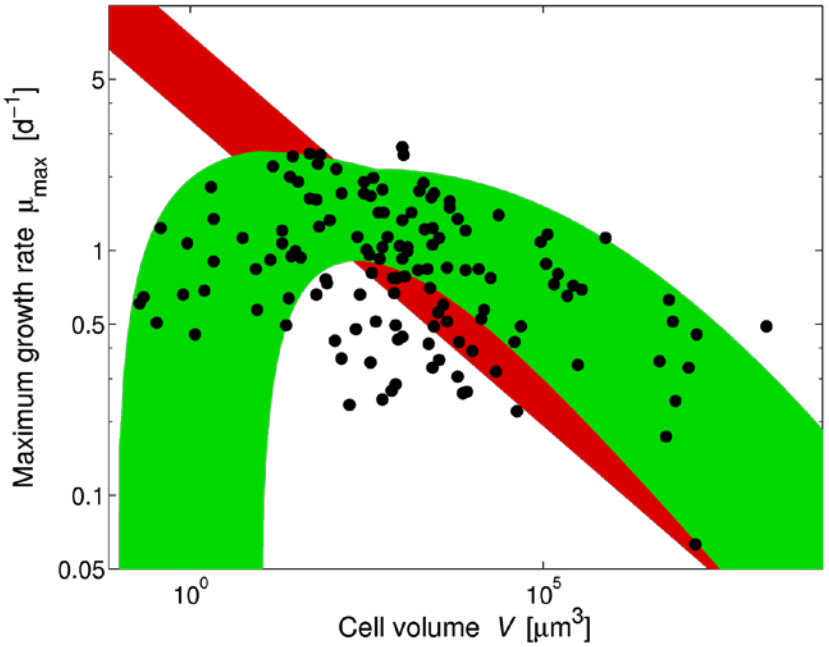
Non-uniform scaling due to intracellular transport limitation

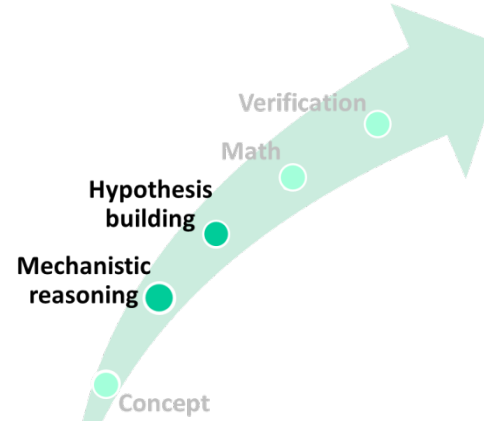
Wirtz JPR 2011

Non-uniform scaling ← intracellular transport limitation

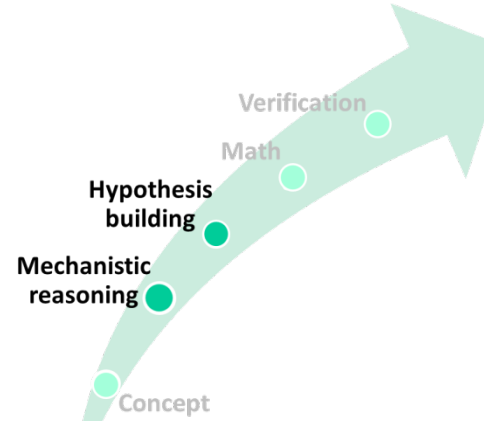
- improves accuracy of size-based models
- biophysical coefficients
- testable assumptions

  → may stimulate new experimental designs

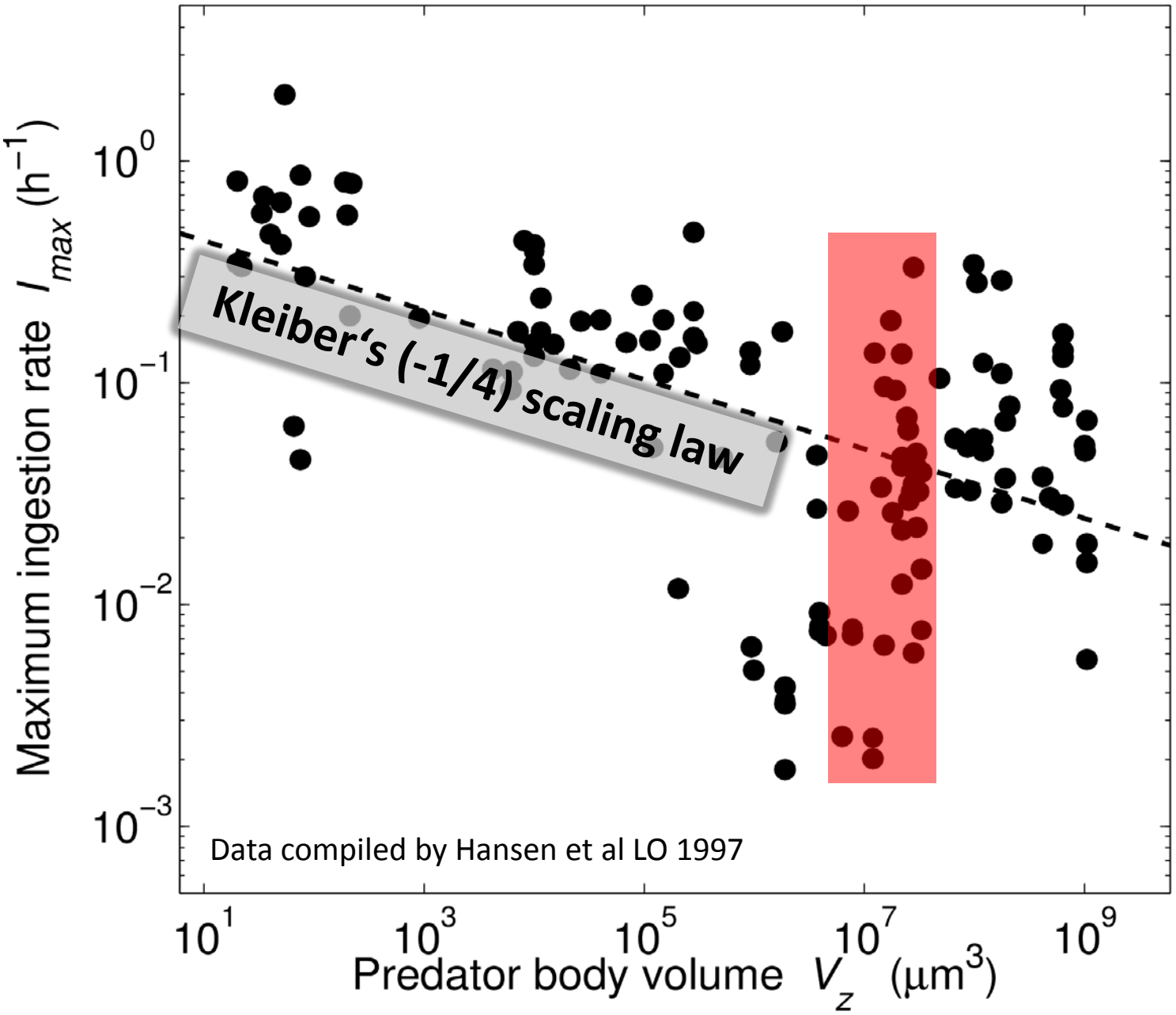




size scaling
in
growth parameters of heterotrophs



Allometry in maximum ingestion rate ?



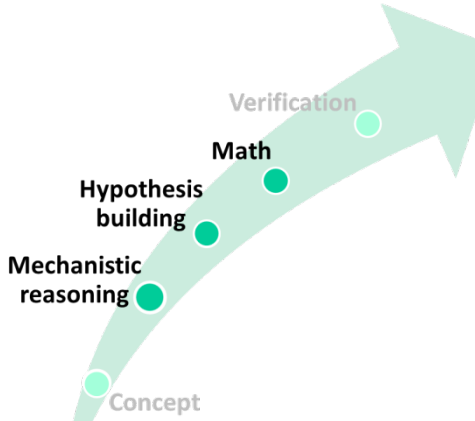
maximum ingestion rate

digestive surface area

$$I_{\max} = v_{\mathrm{dig}} \cdot \frac{A_{\mathrm{dig}}}{V_{\mathrm{z}}}$$

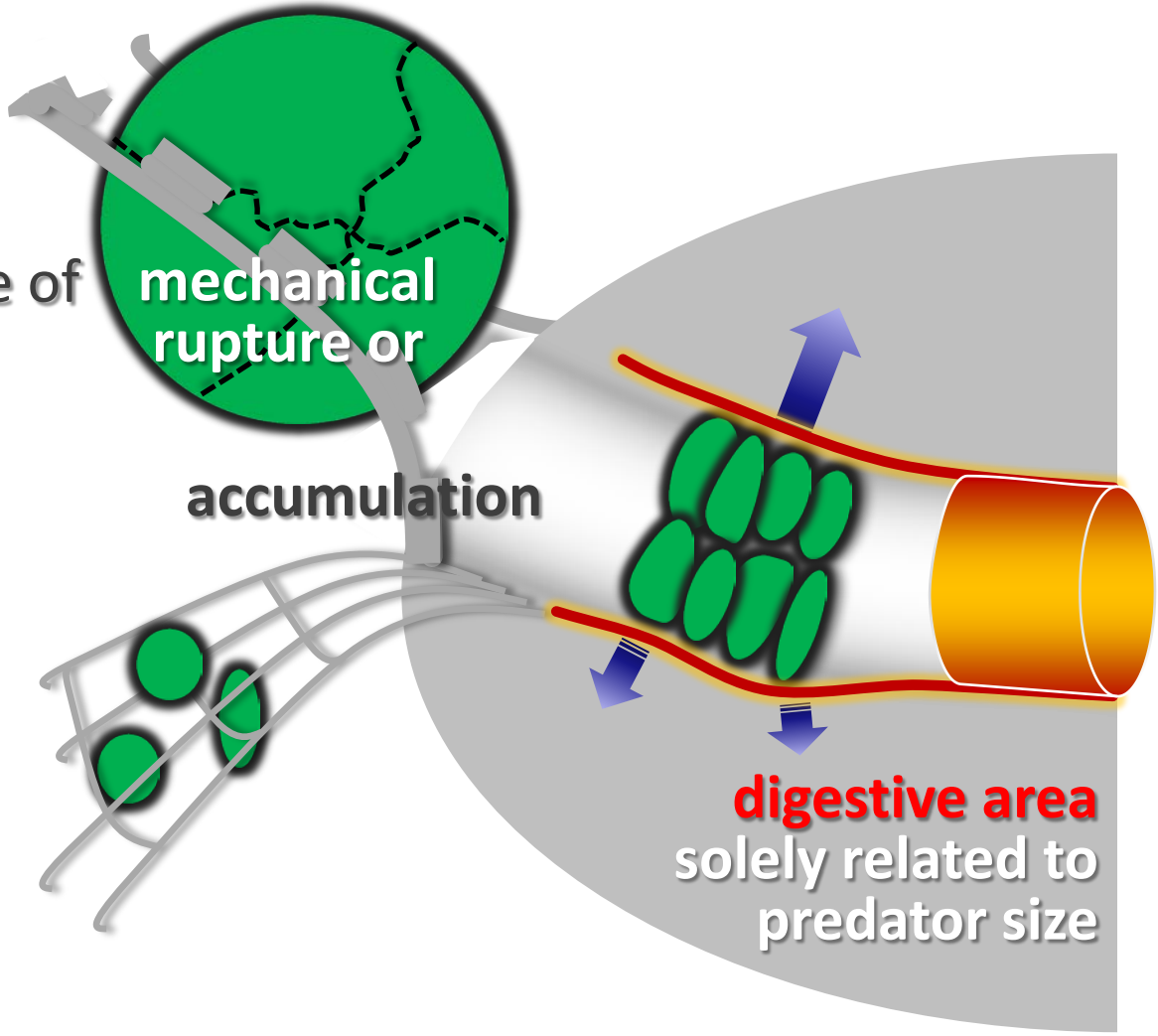
body volume

"hydrolytic velocity"



Wirtz JPR 2013

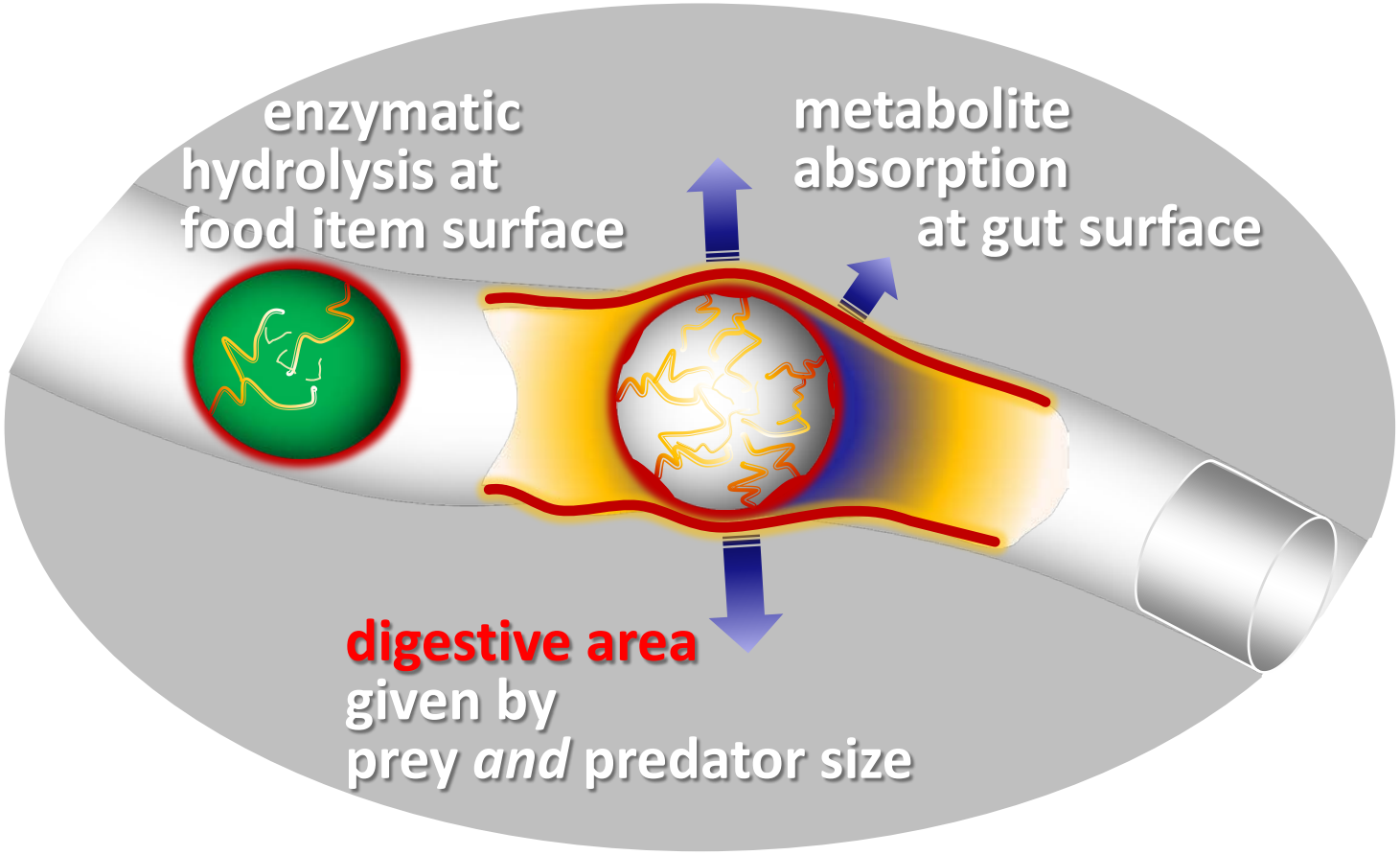
A



$$A_{\mathrm{dig}} \sim {D_z}^2$$

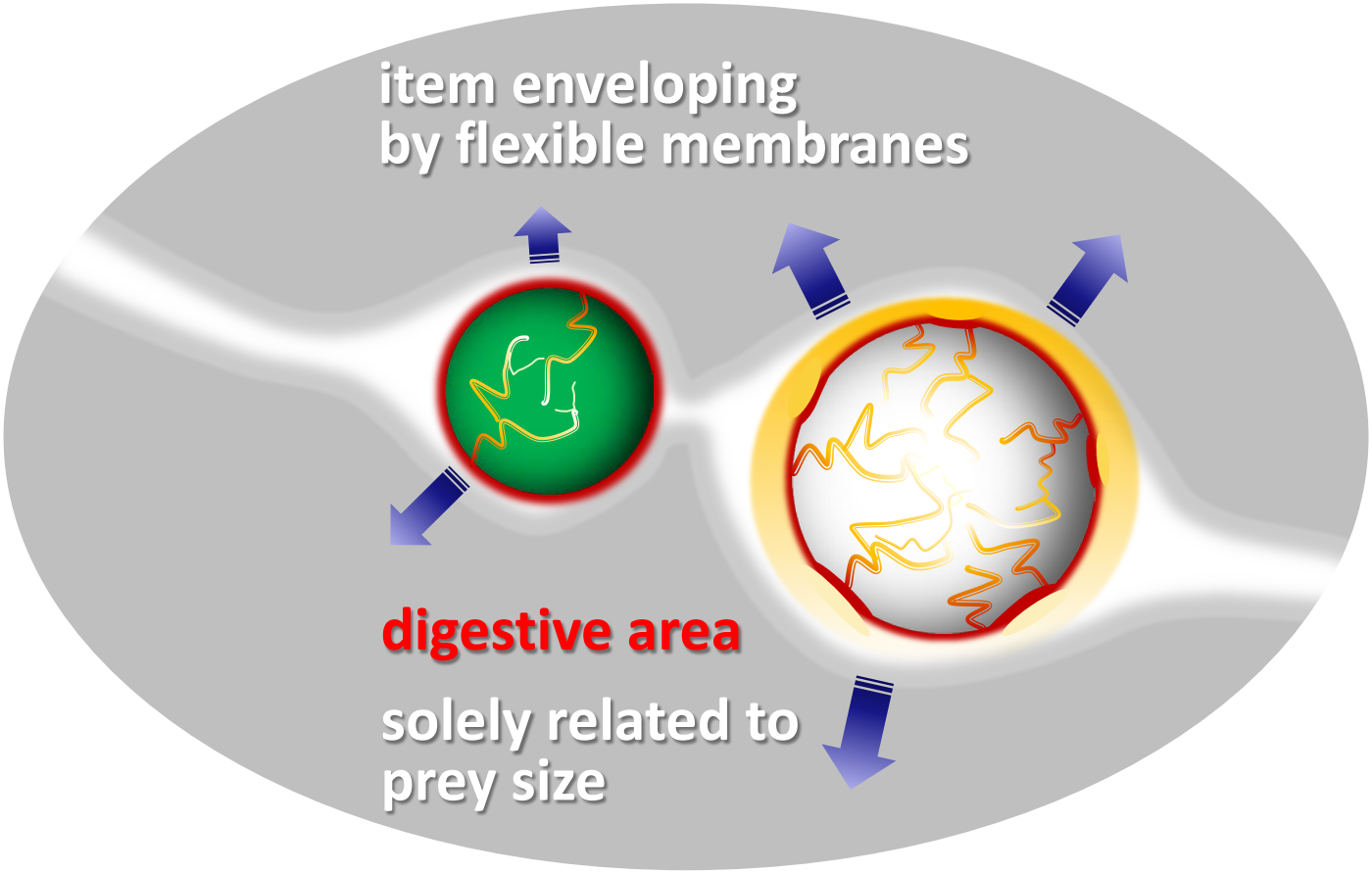
Wirtz JPR 2013

B

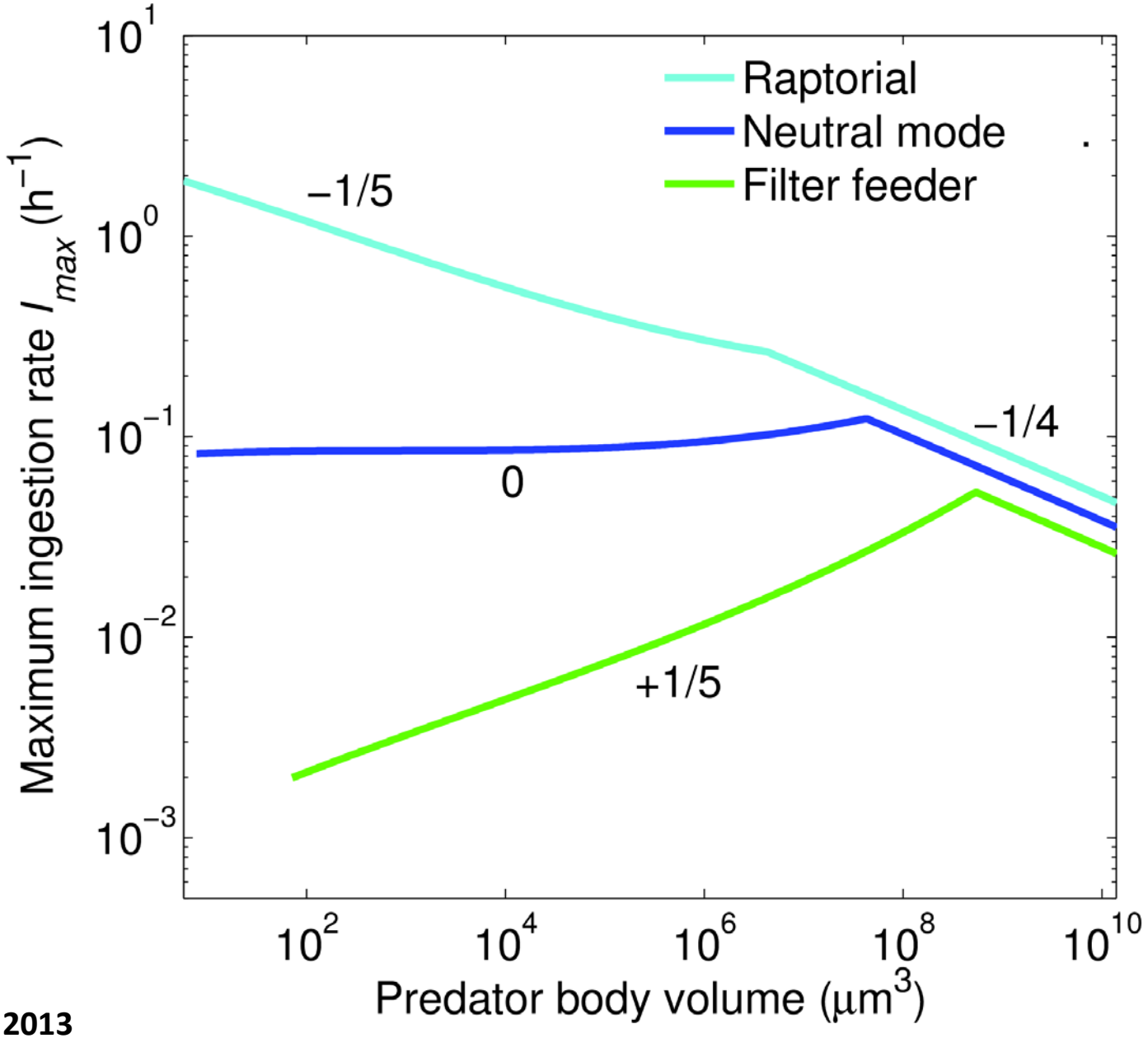


$$A_{\mathrm{dig}} \sim D_{\mathrm{z}} \cdot D_{p}$$

C

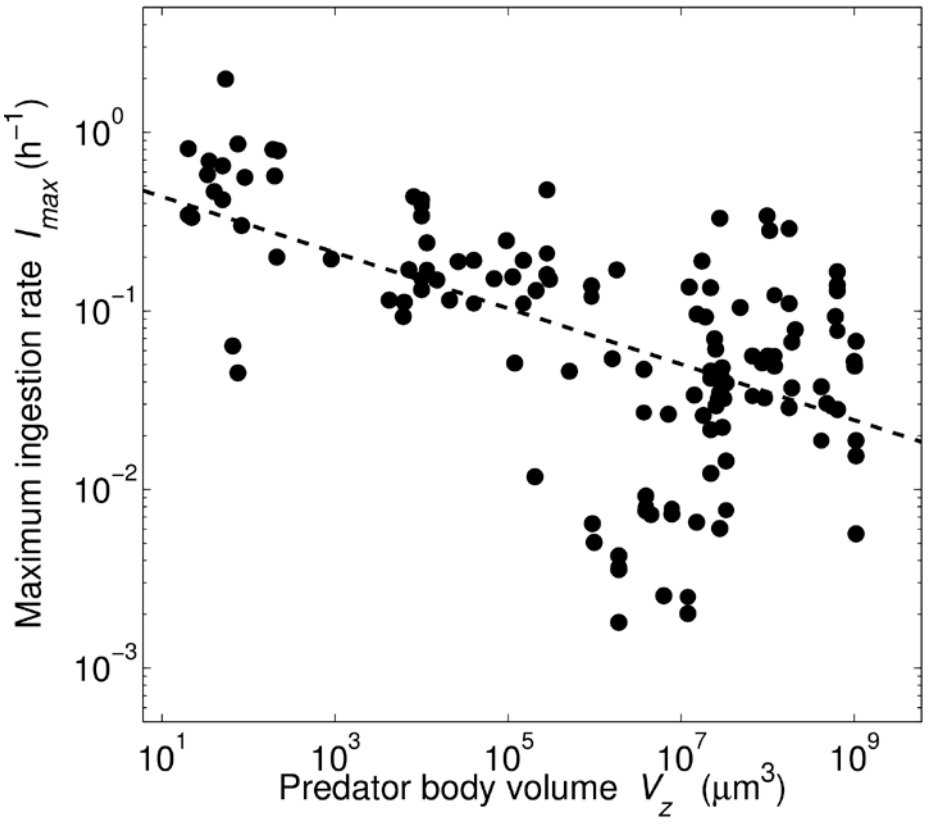


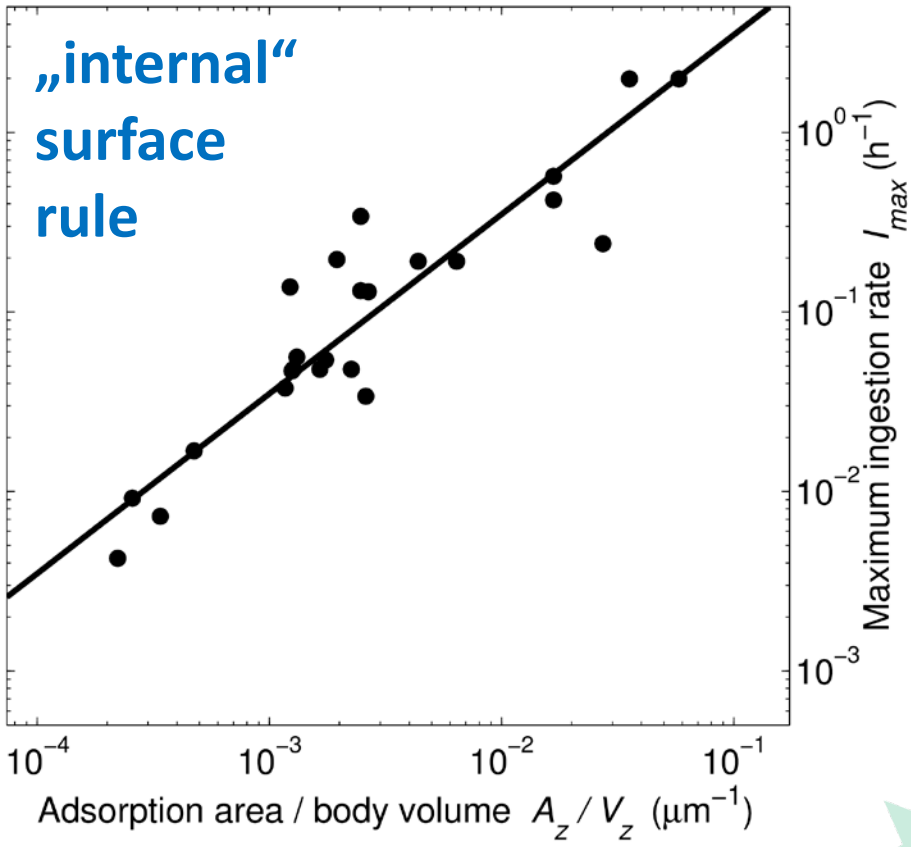
$$A_{\mathrm{dig}} \sim {D_p}^2$$



Wirtz JPR 2013

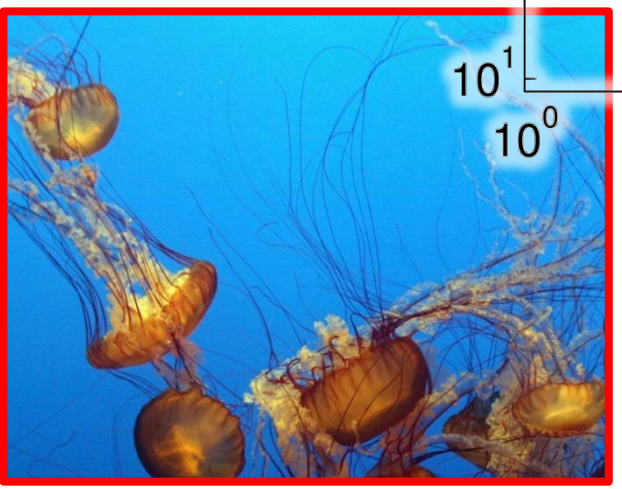
Mechanistic allometry in maximum ingestion rate

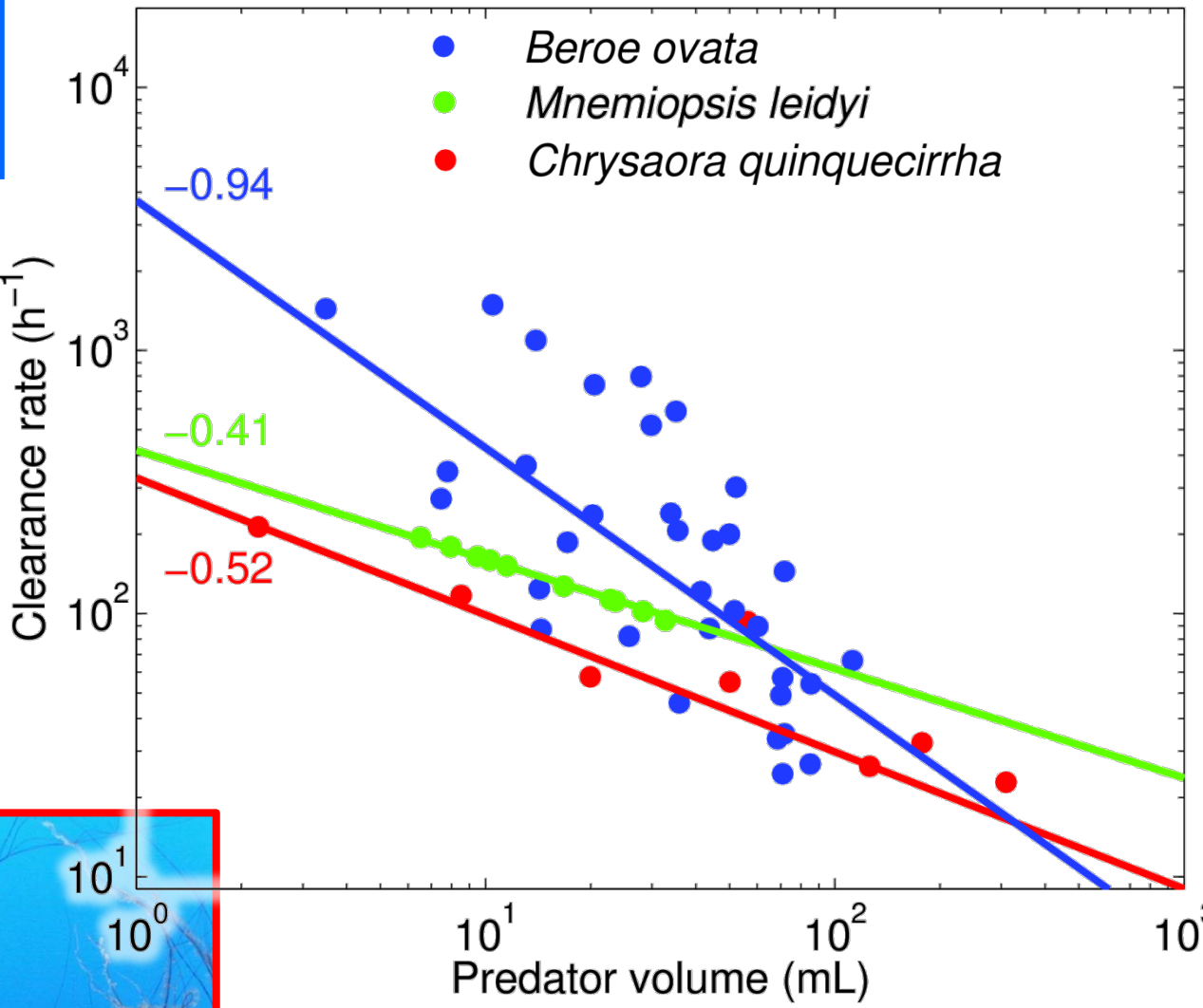


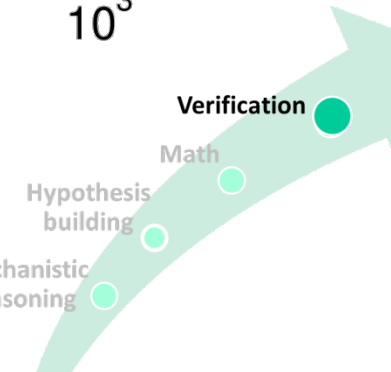


Verification
Math
Hypothesis building
Mechanistic reasoning

Wirtz JPR 2013

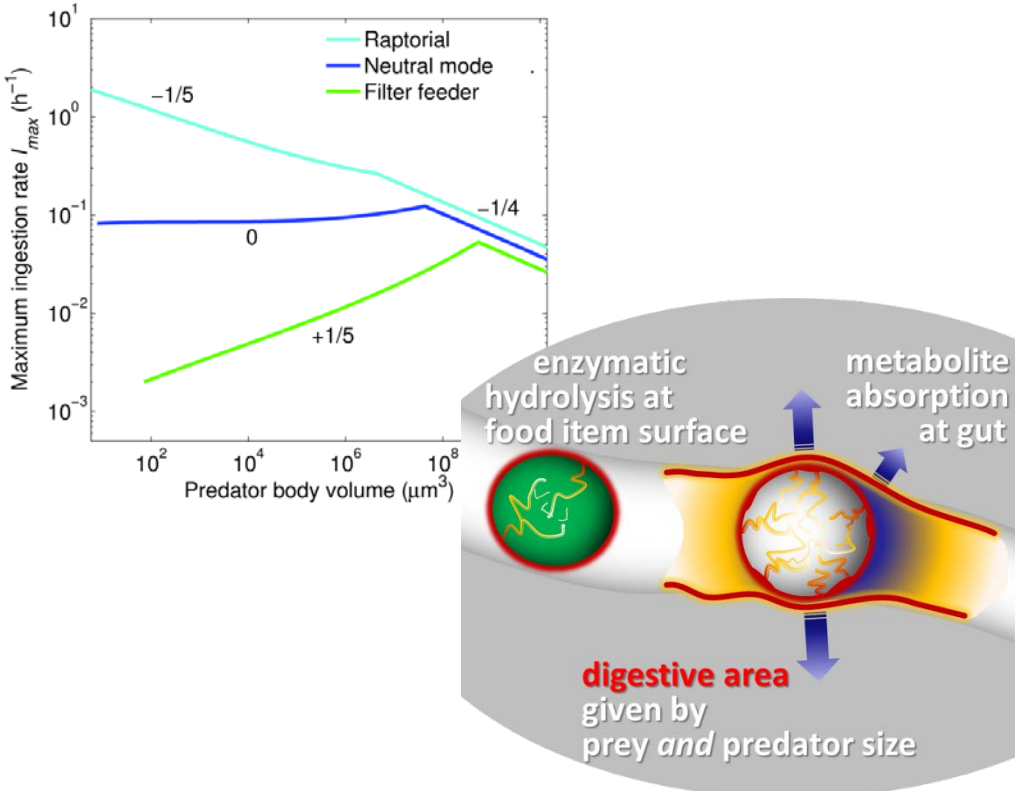



Beroe ovata
Mnemiopsis leidyi
Chrysaora quinquecirrha
−0.94
−0.41
−0.52
Clearance rate (h^{-1})
Predator volume (mL)
10^0
10^1
10^2
10^3
10^4


Verification
Math
Hypothesis building
Mechanistic reasoning

Non-uniform scaling ← intrabody transport limitation

- improves accuracy of size-based models
- biophysical coefficients
- may stimulate new experimental designs

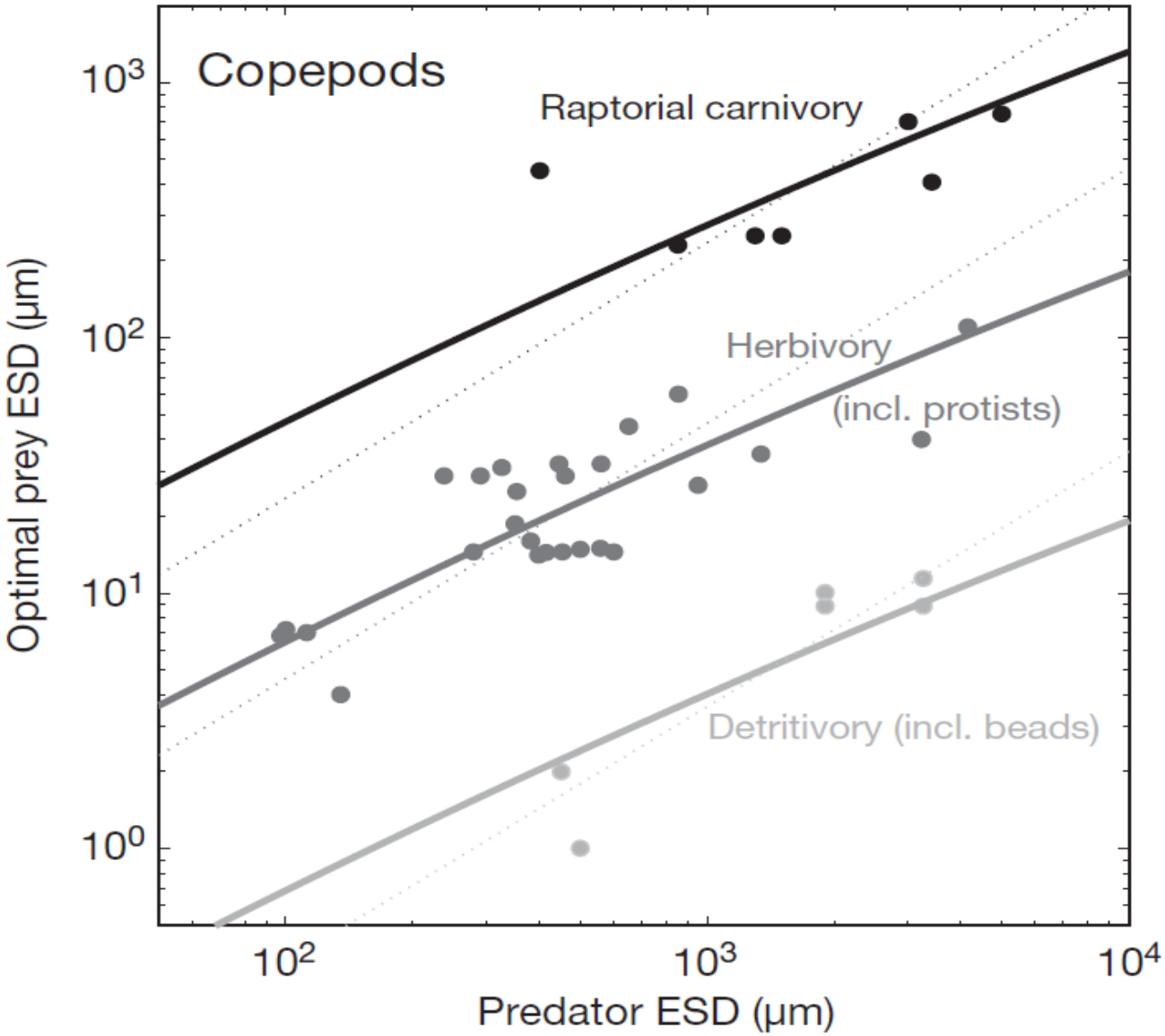


feeding mode:

2nd fundamental trait in zooplankton

feeding mode

2nd fundamental trait in zooplankton



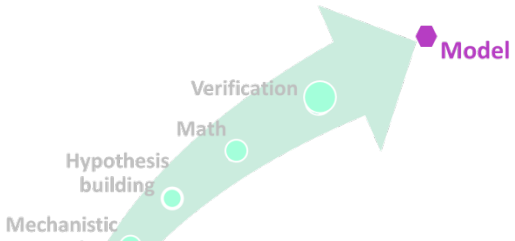
prey size

swimming speed

Wirtz MEPS 2012
(Hansen et al LO 1994)

mechanistic trait-based zooplankton model

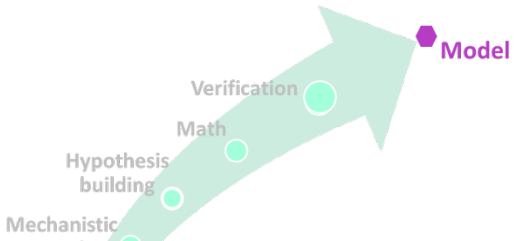
Wirtz *MaBi* 2013



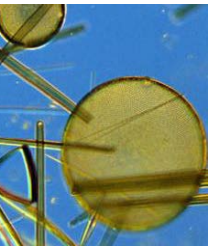
mechanistic trait-based zooplankton model

Wirtz *Oecologia* 2012

Wirtz *MaBi* 2013



mechanistic trait-based phytoplankton model



carboxy-lation

maximal photosynthesis

light harvesting

exudation

cell size

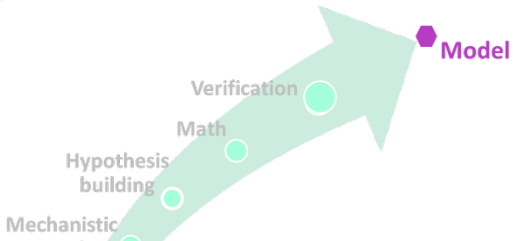
%photo-machinery

%chloroplasts

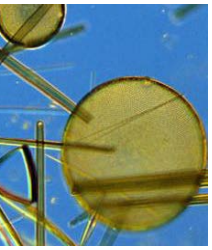
edibility

Wirtz *MaBi* 2013

Wirtz&Sommer *MaBi* 2013, subm.



mechanistic trait-based phytoplankton model

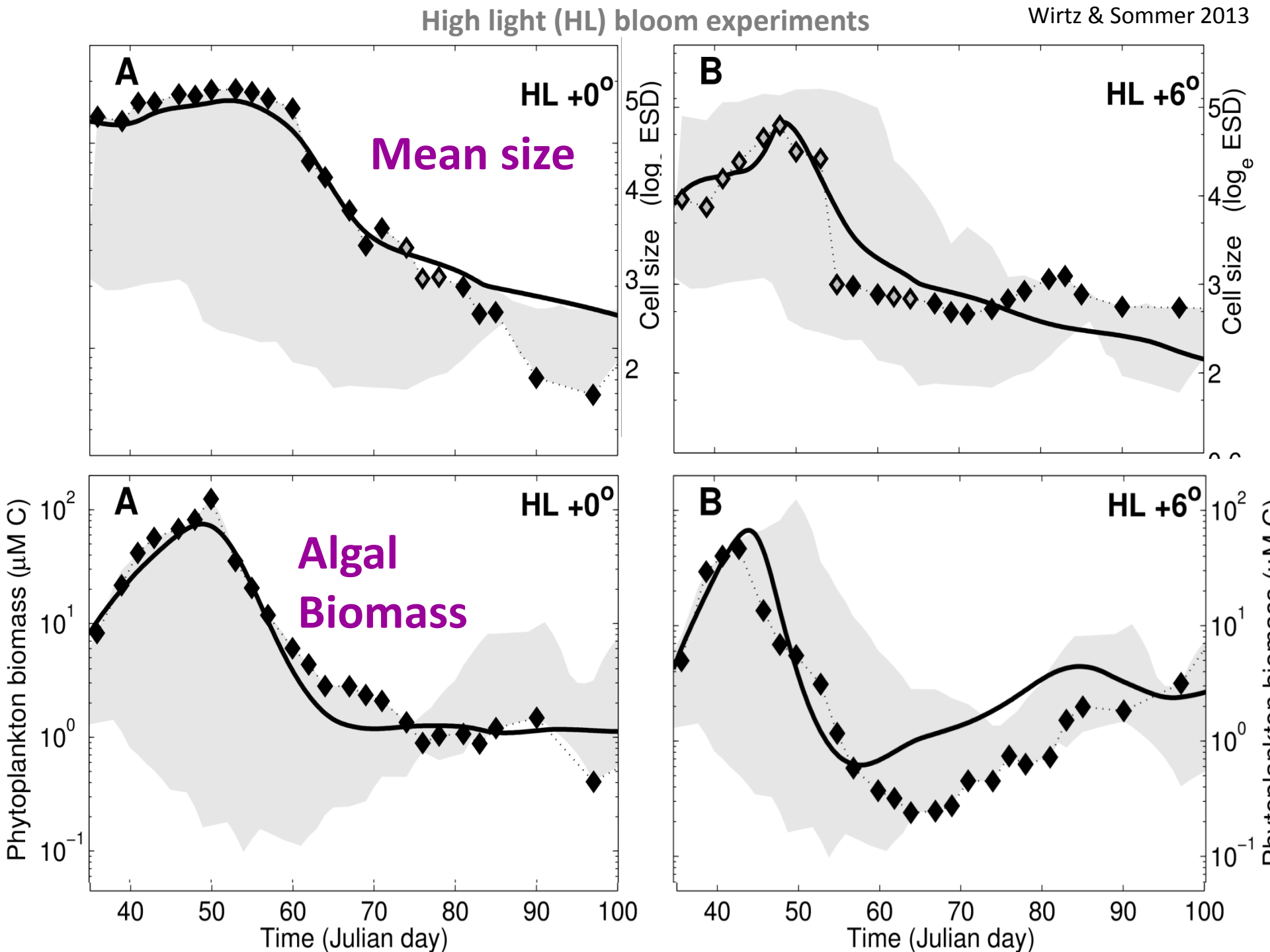


Wirtz *MaBi* 2013

Wirtz&Sommer *MaBi* 2013, subm.

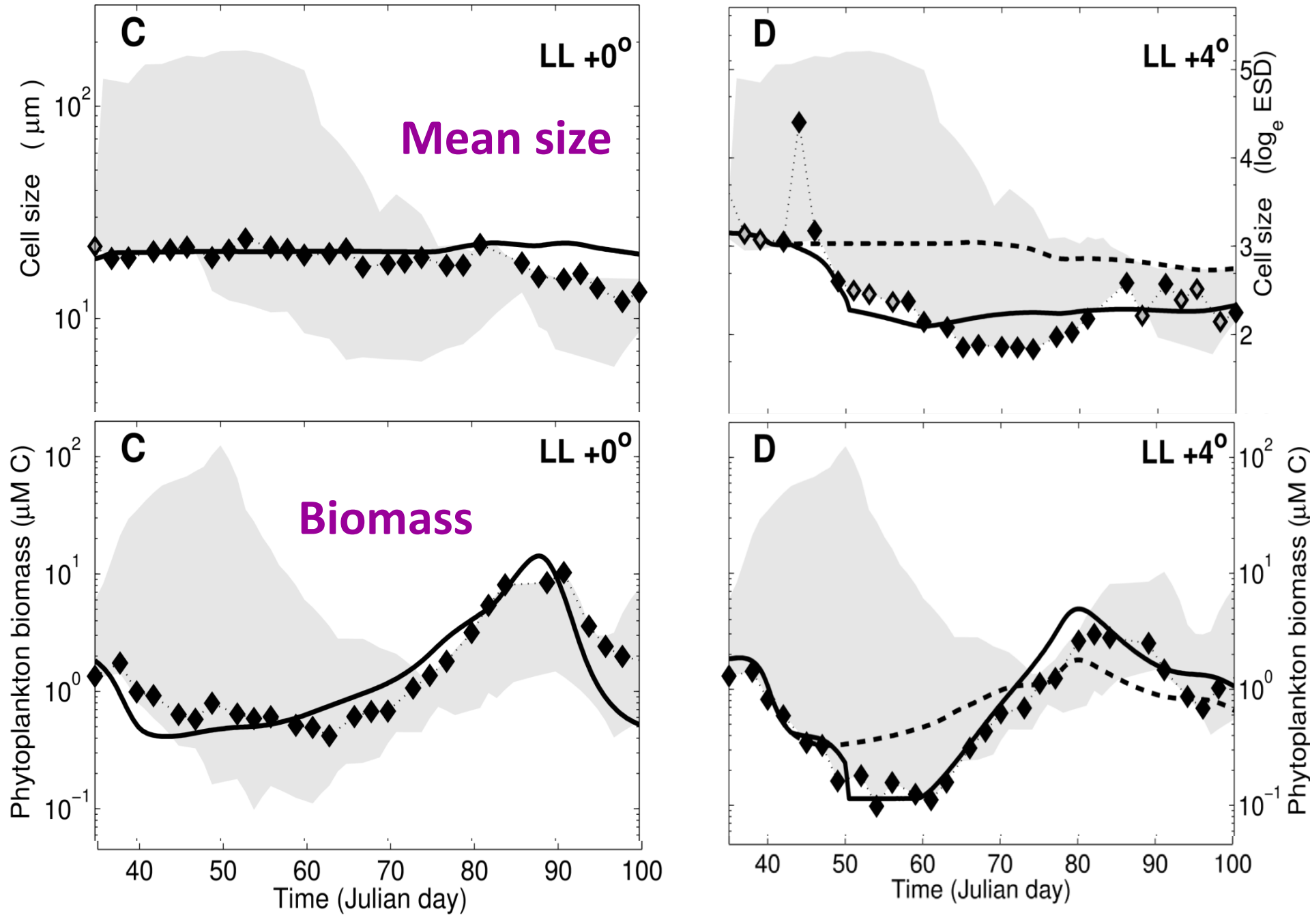
High light (HL) bloom experiments

Wirtz & Sommer 2013

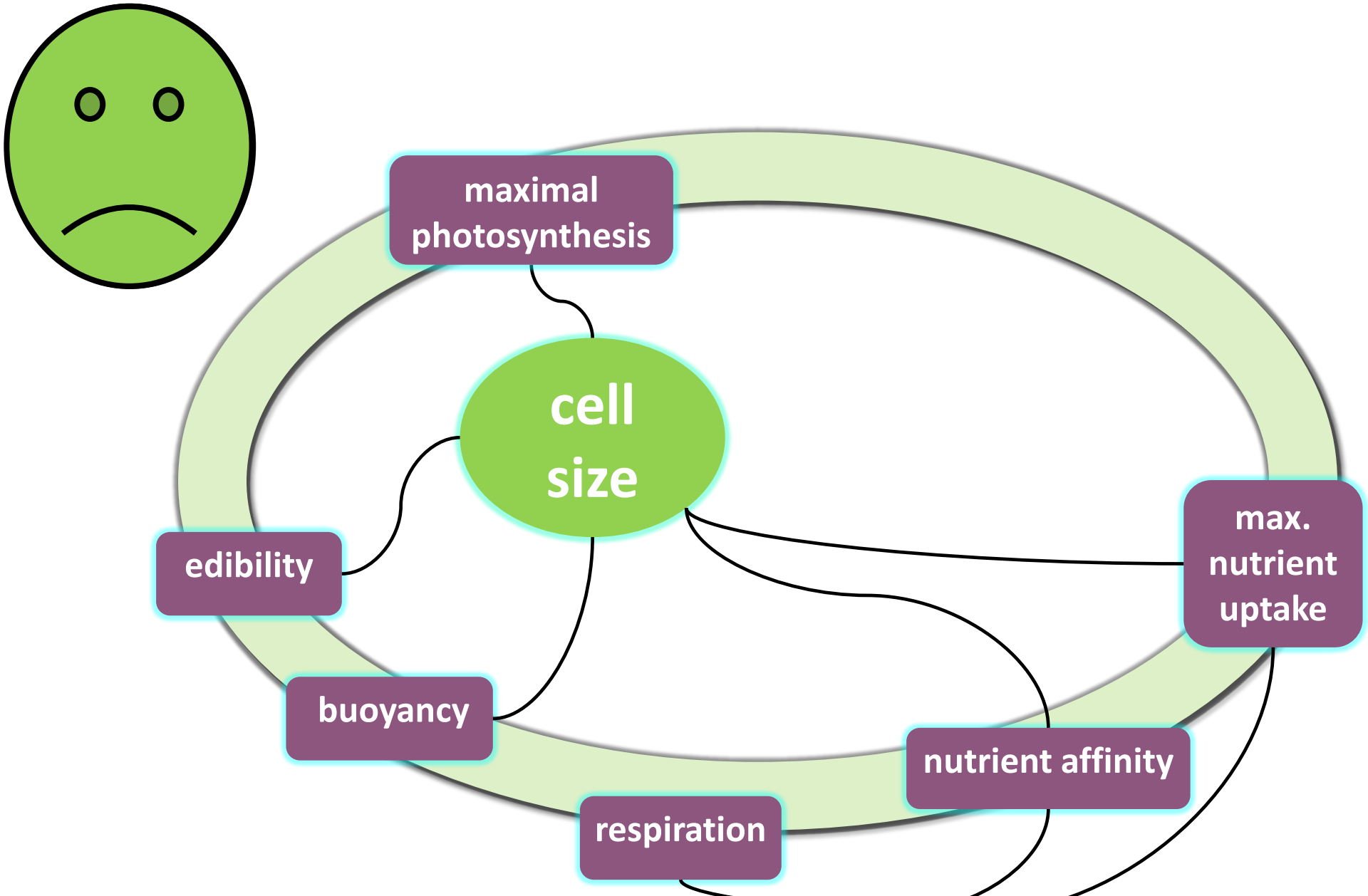


Low light (LL) experiments

Wirtz & Sommer 2013



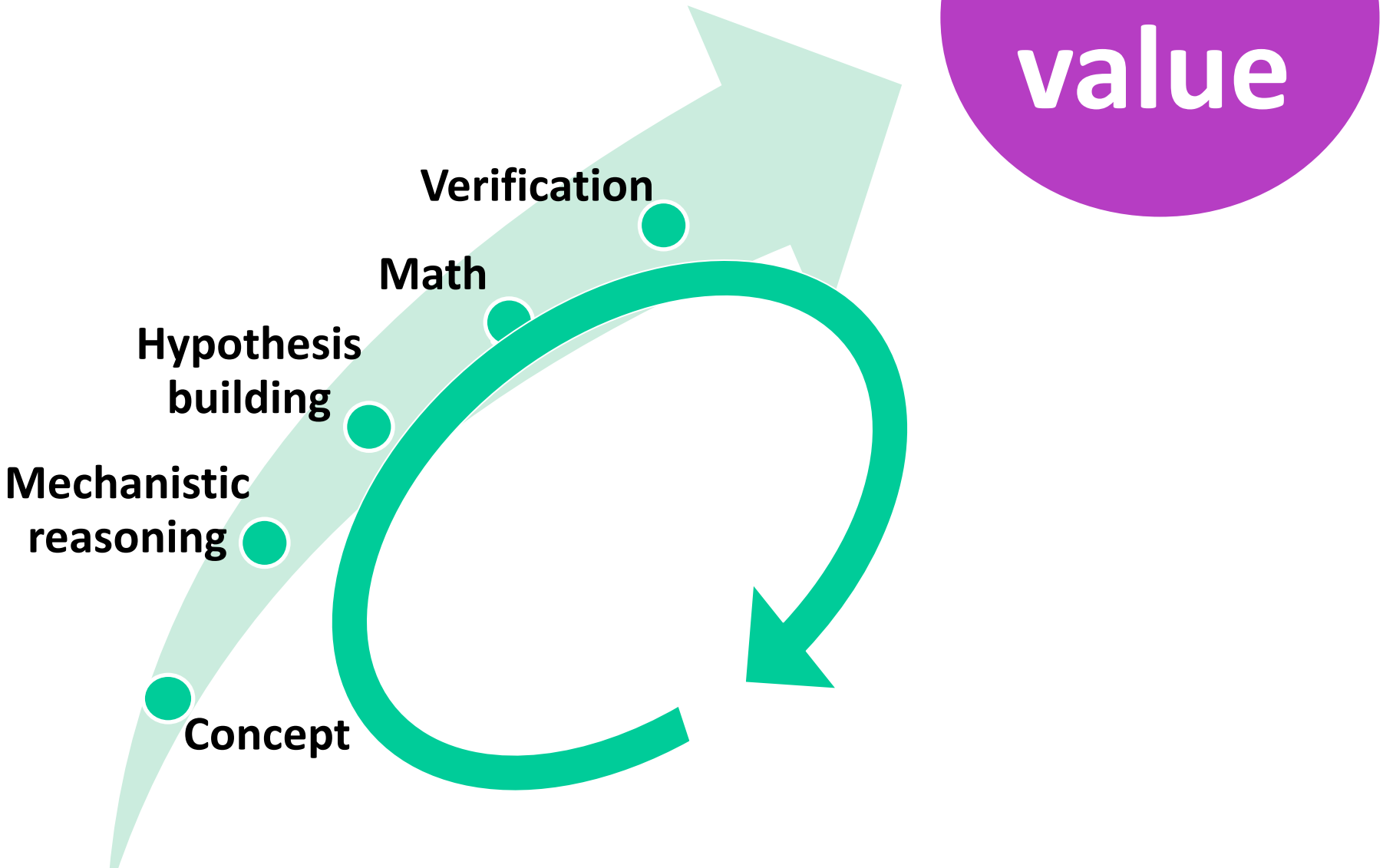
sub-critical number of trait-relations



trait-based, mechanistic model development

requires and generates

- **new trait definitions**
- **mechanistic functions** **(e.g., non-uniform scaling)**
- **new hypotheses & experimental approaches**
- **integral view on ecophysiology (*differential* „trade-offs“)**

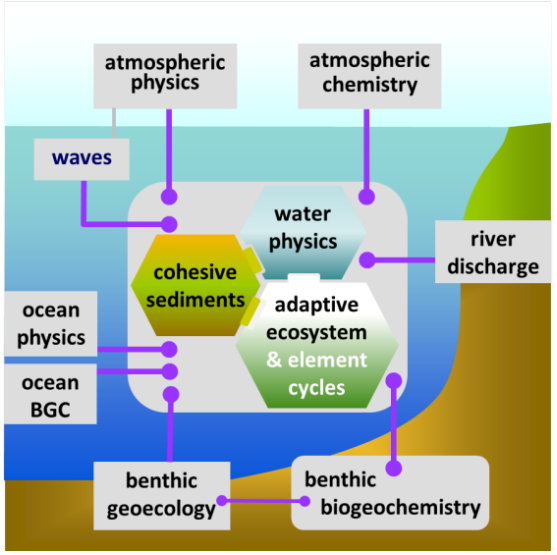

added value
Verification
Math
Hypothesis building
Mechanistic reasoning
Concept

Thanks
for your attention

and to

Richard Hofmeister, Carsten Lemmen, Onur Kerimoglu, Lan Smith, Jorn Bruggeman, Uli Sommer

modular coupling



$$\frac{d\mathrm{Trait}}{dt} \sim \frac{d\mu}{d\mathrm{Trait}}$$

southern North Sea

trait: C-fraction related to C-assimilation