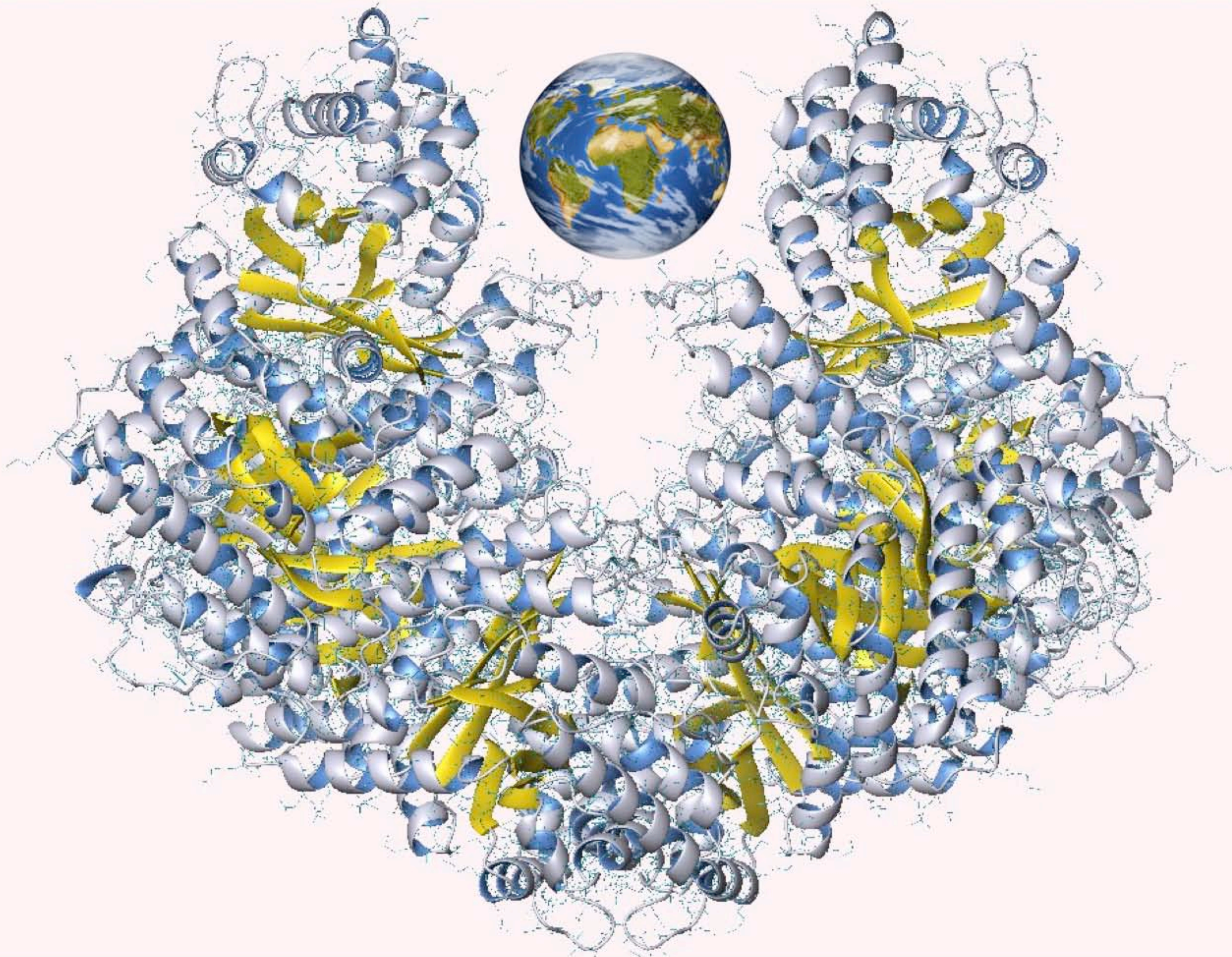


Large-scale EEA Patterns: Linking Paradigms

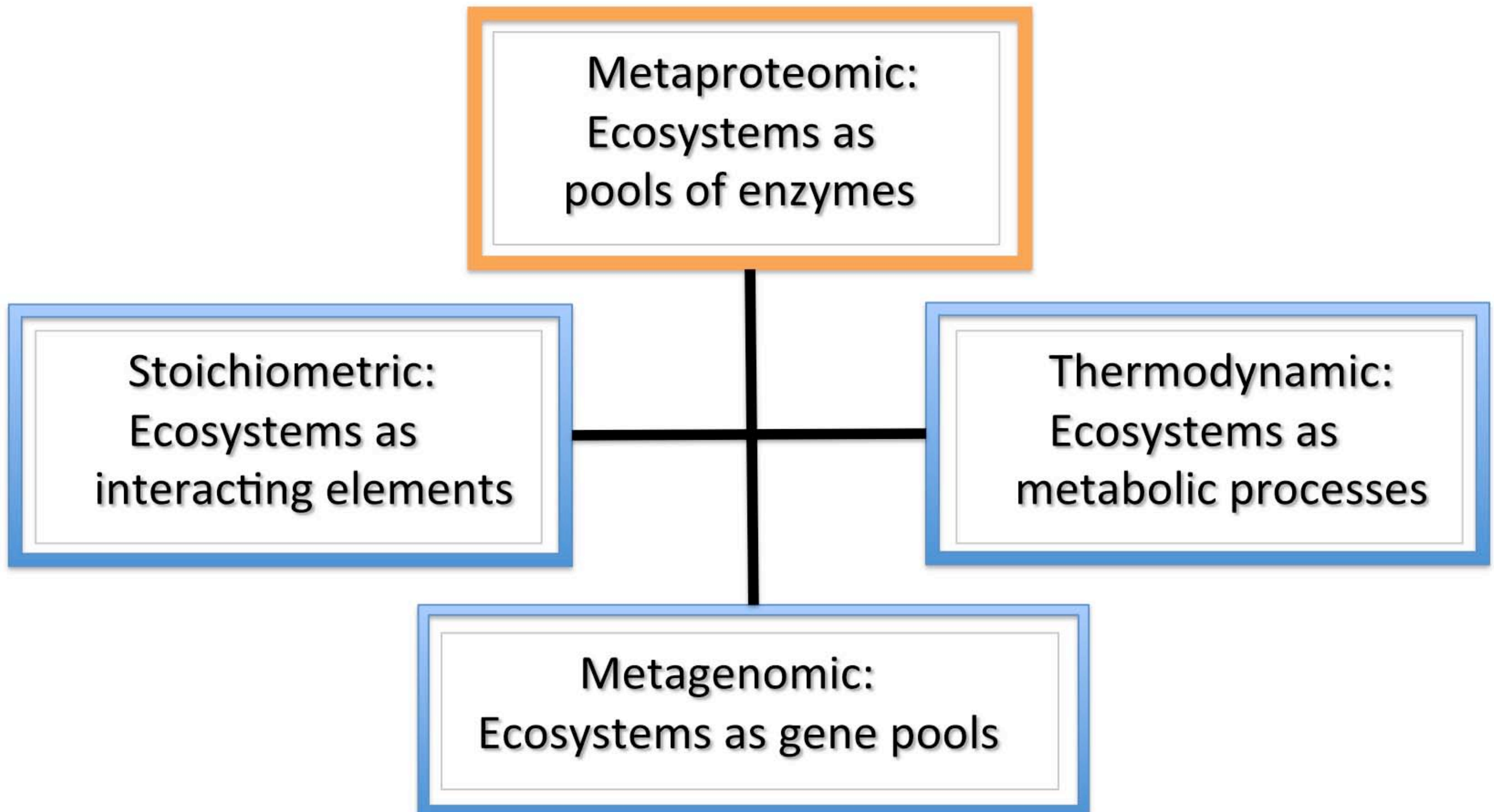
RL Sinsabaugh
JJ Follstad Shah



A GE
TER
B M
C:N
C:P μ
N:P
pH
T Q
S R
Vmax
Km
Ea

Perspectives on Ecosystem Organization

Ecosystem: All organisms that live in a geographic area together with abiotic components that affect or exchange materials with the organisms



EEA Generalizations

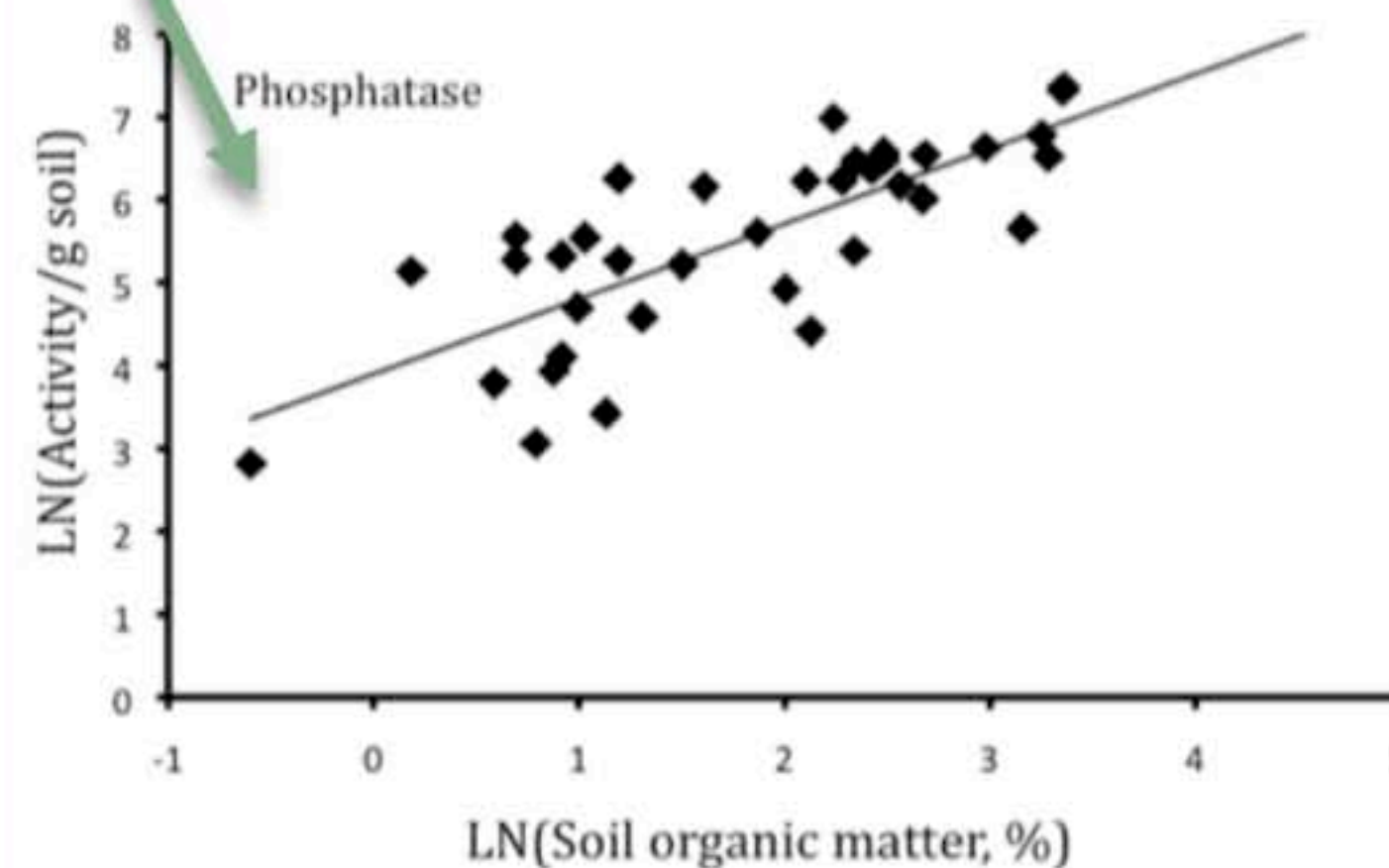
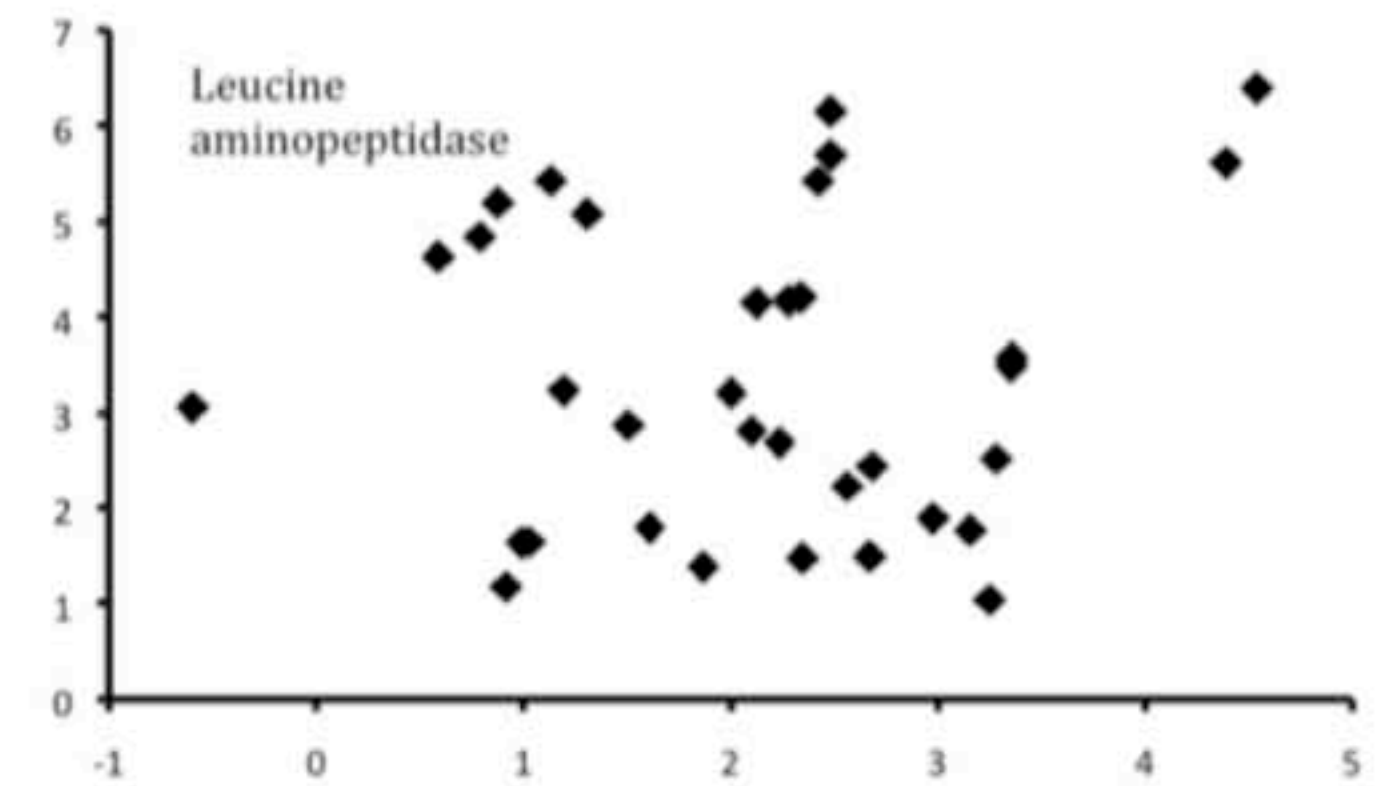
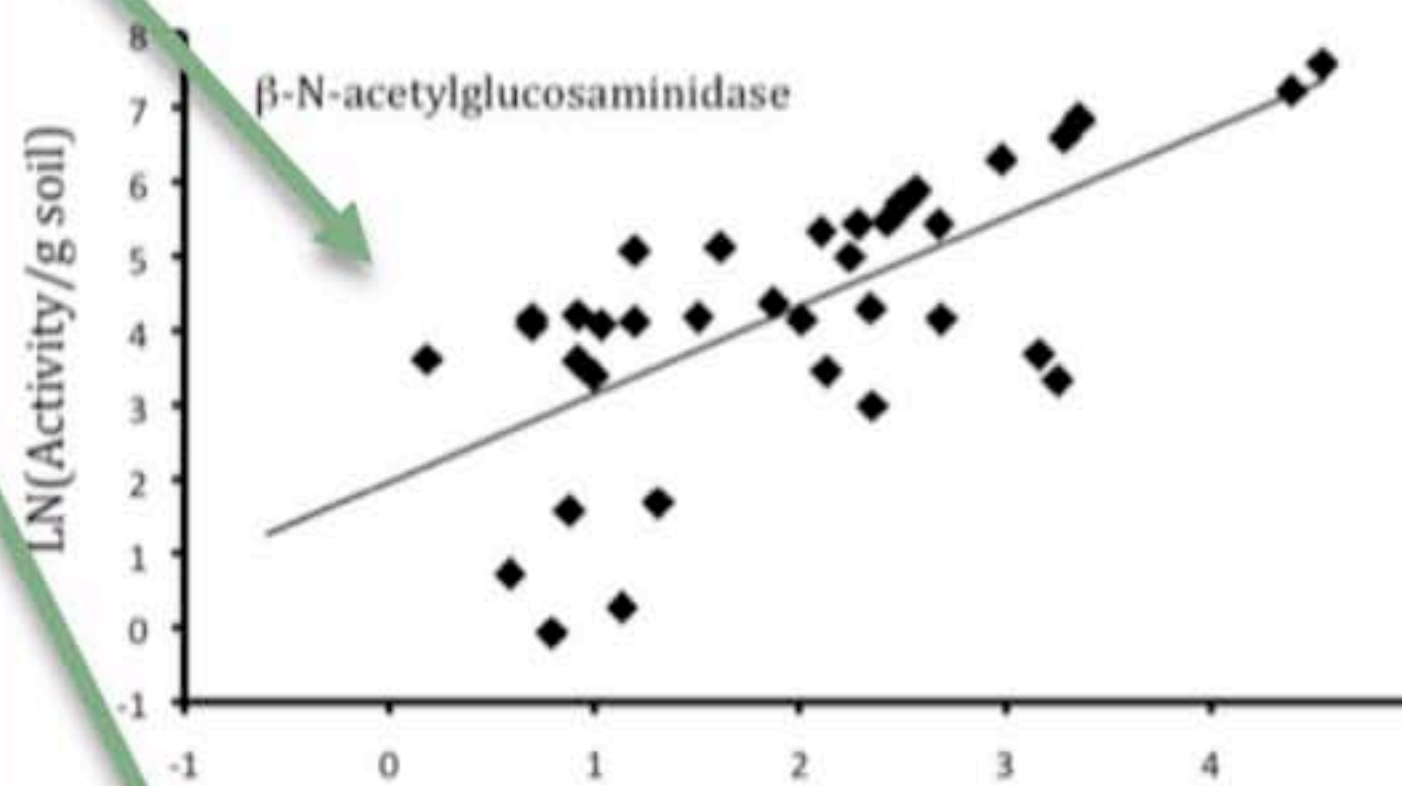
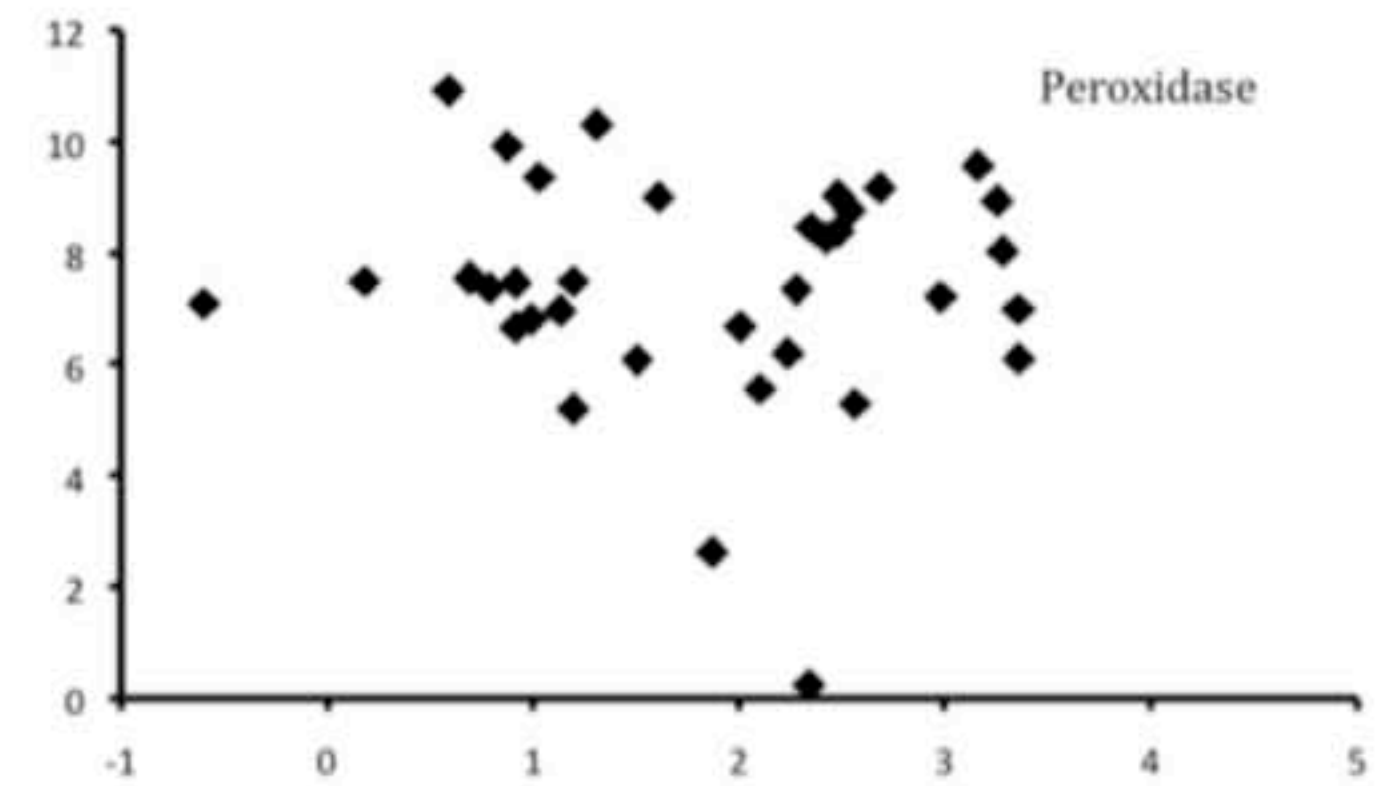
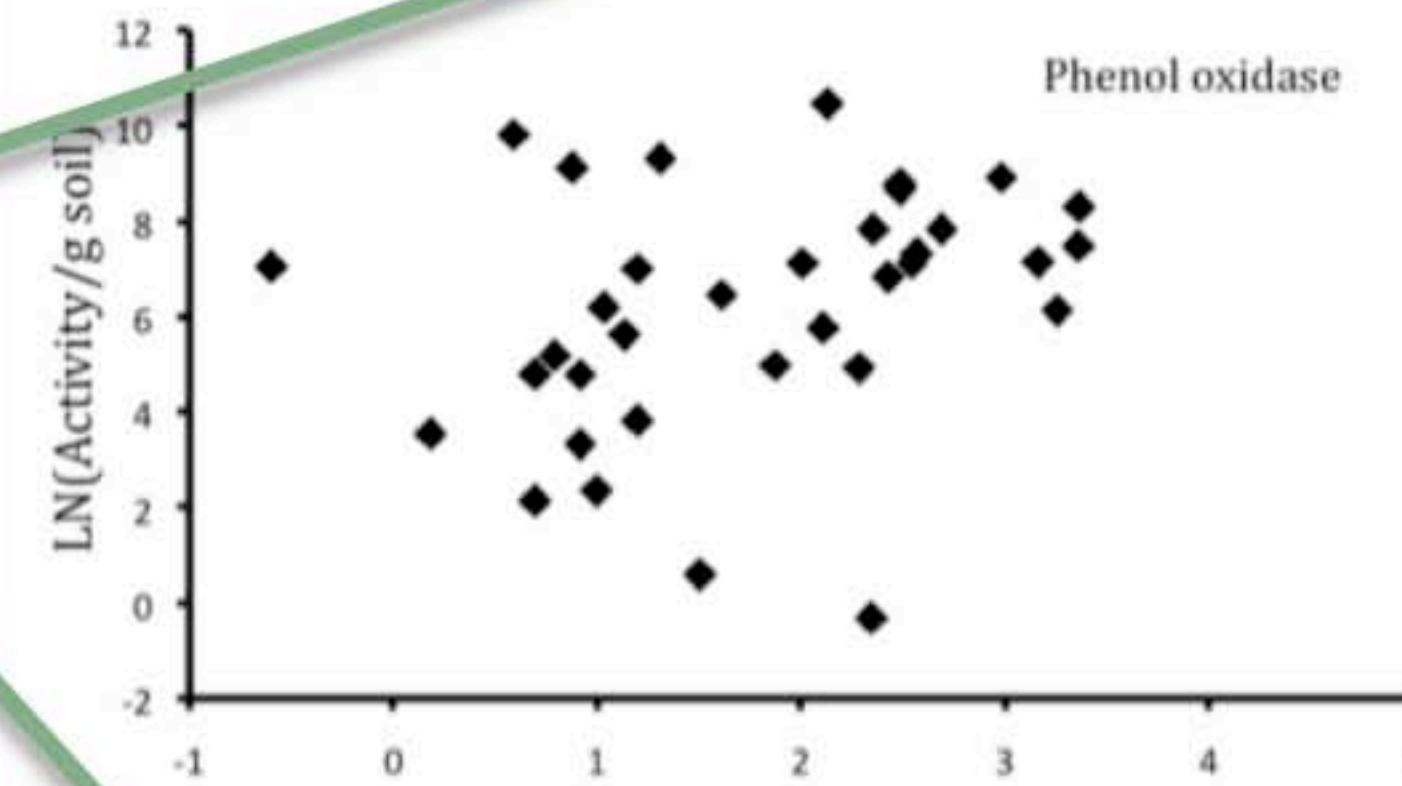
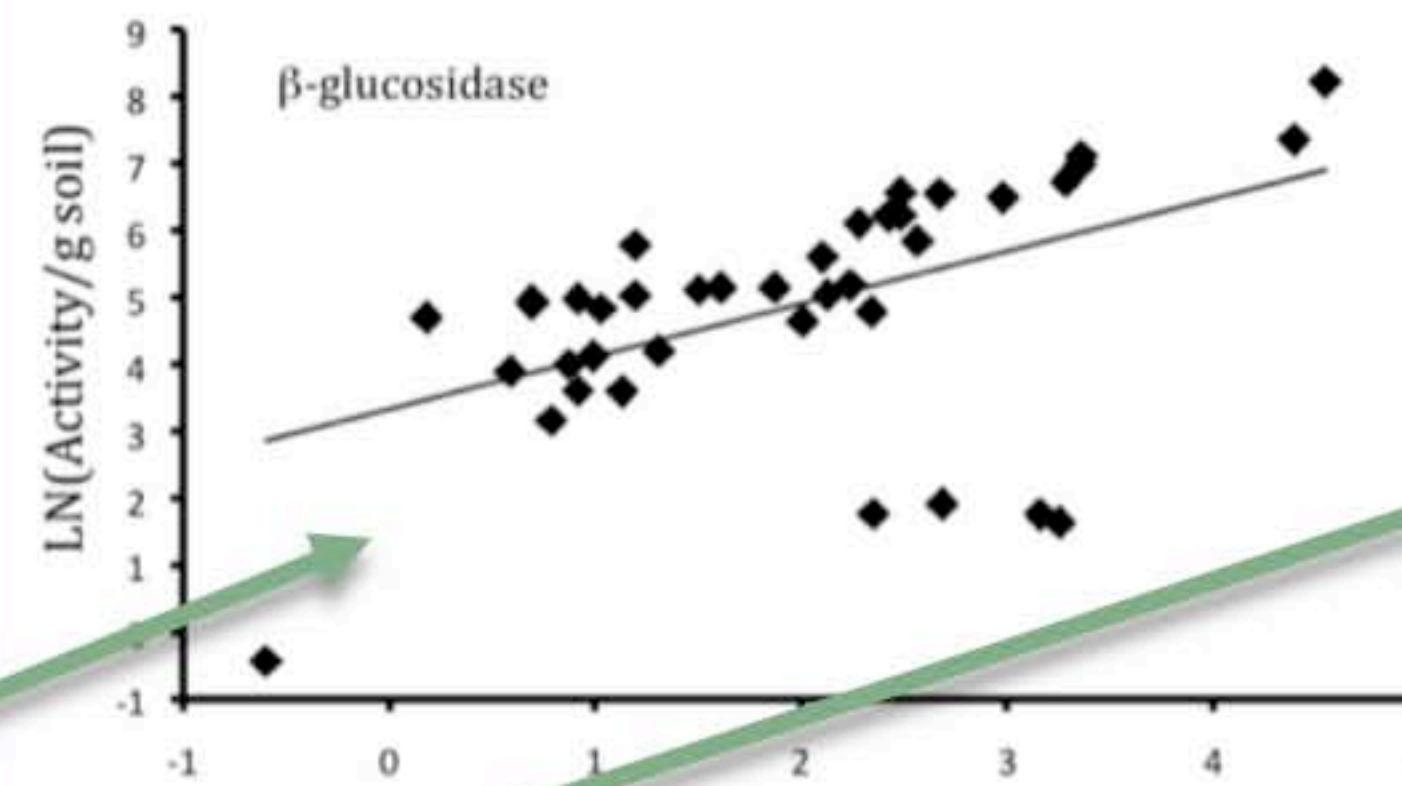
- EEA is positively related to rates of microbial metabolism [production, respiration, decomposition].
- Ratios of hydrolytic activities [glucosidase, aminopeptidase, phosphatase] can be related to resource availability.
- Oxidative activities [phenol oxidase] do not covary with hydrolytic activities.
- Activation energies for EEA are lower than those for microbial metabolism.

Other Big Scale EEA trends: Soil organic matter

B-glucosidase
Cellobiohydrolase
N-acetylglucoaminidase
Phosphatase

Activities covary with soil organic matter content

Sinsabaugh RL, CL Lauber, MN Weintraub, B Ahmed, SD Allison, C Crenshaw, AR Contosta, D Cusack, S Frey, ME Gallo, TB Gartner, Sarah E. Hobbie, Keri Holland, BL Keeler, JS Powers, M Stursova, C Takacs-Vesbach, M Waldrop, M Wallenstein, DR Zak, LH Zeglin. 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11:1252-1264.



LN(Soil organic matter, %)

Other Big Scale EEA trends: Soil pH

Phenol oxidase

Peroxidase

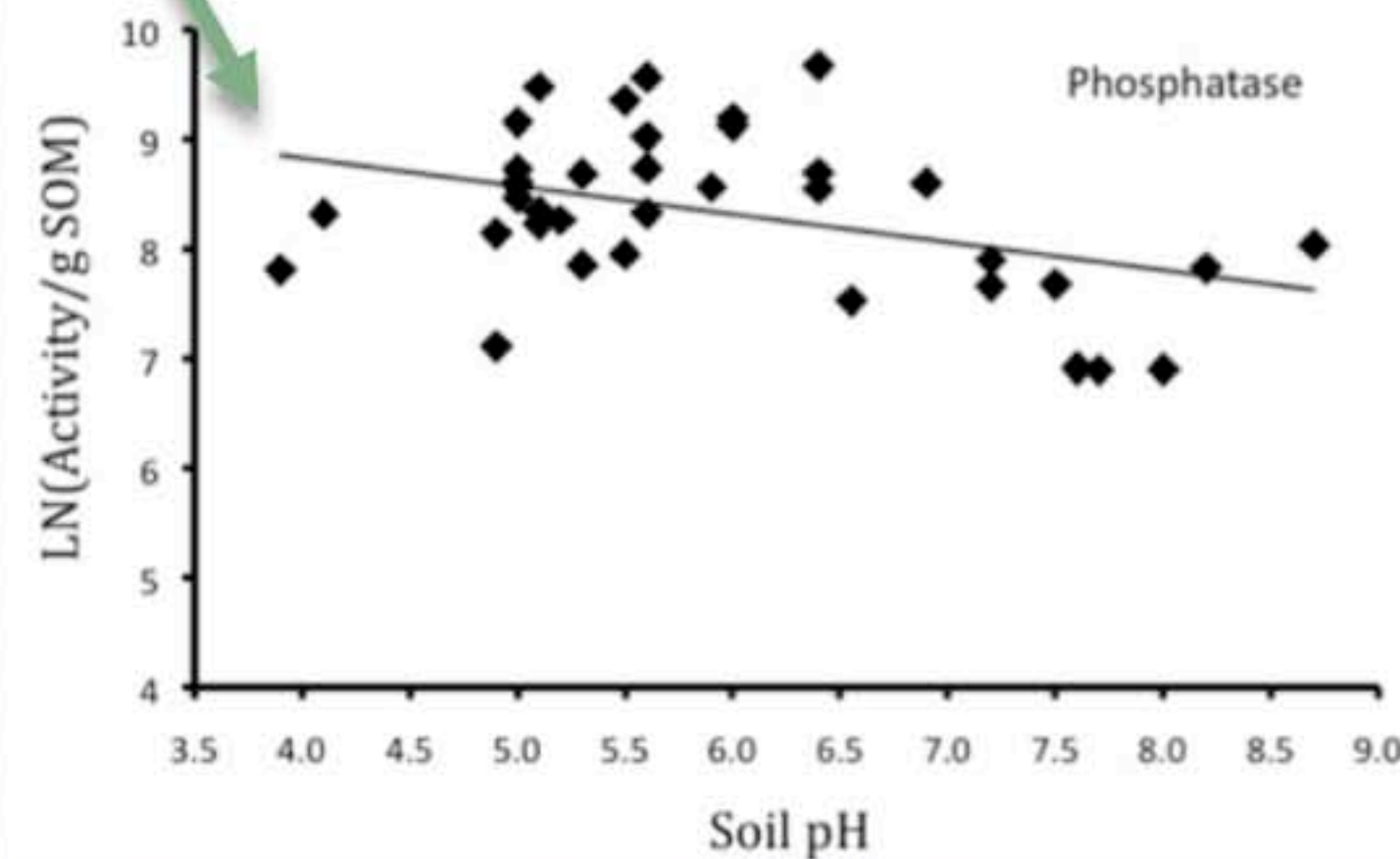
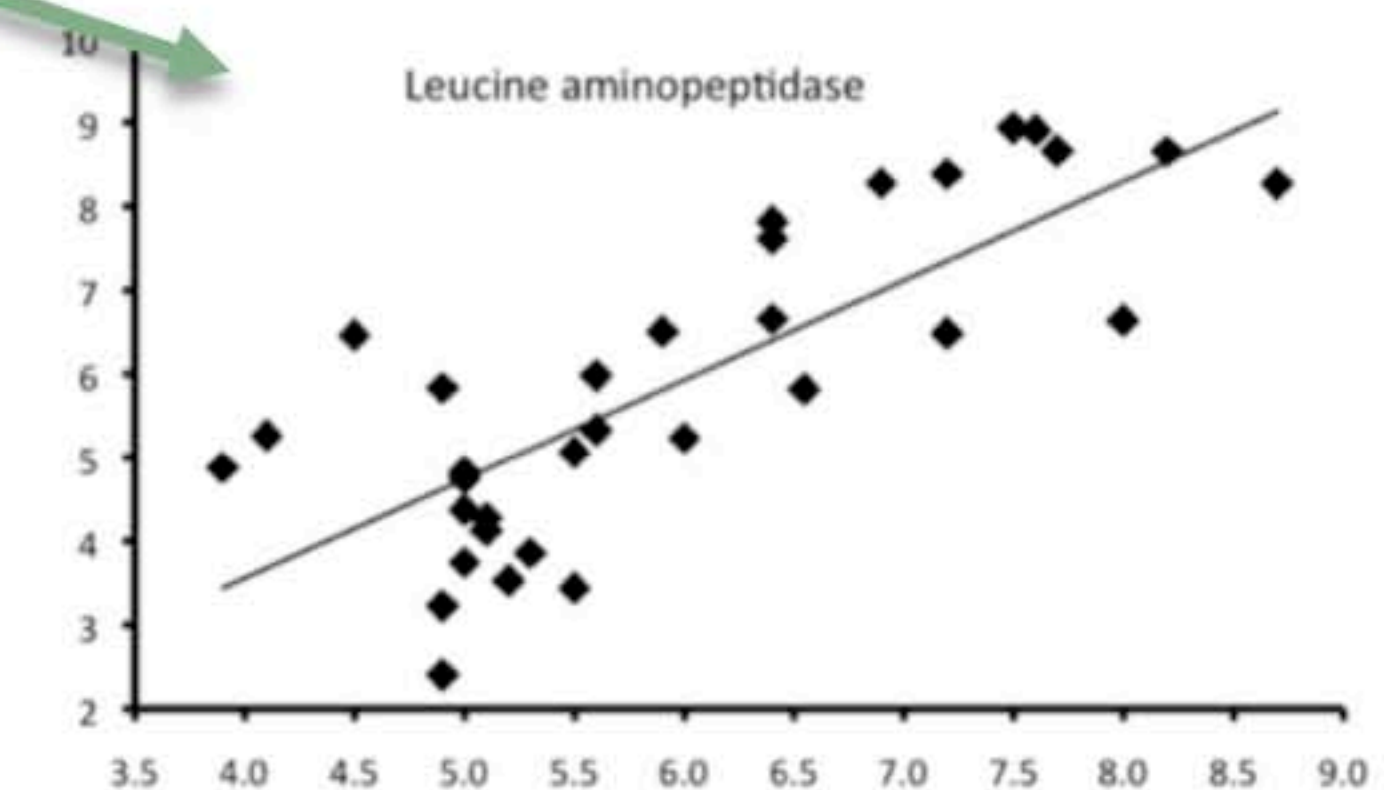
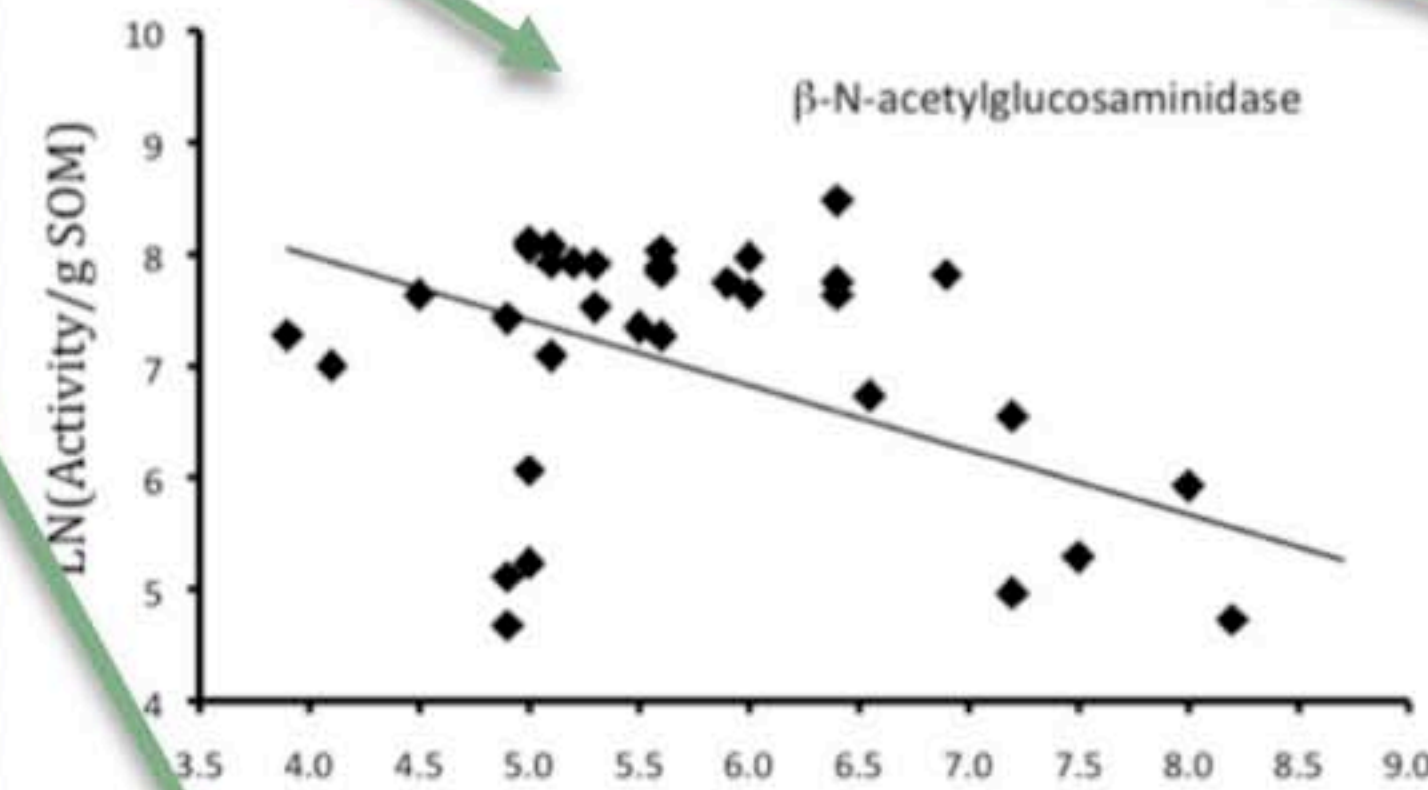
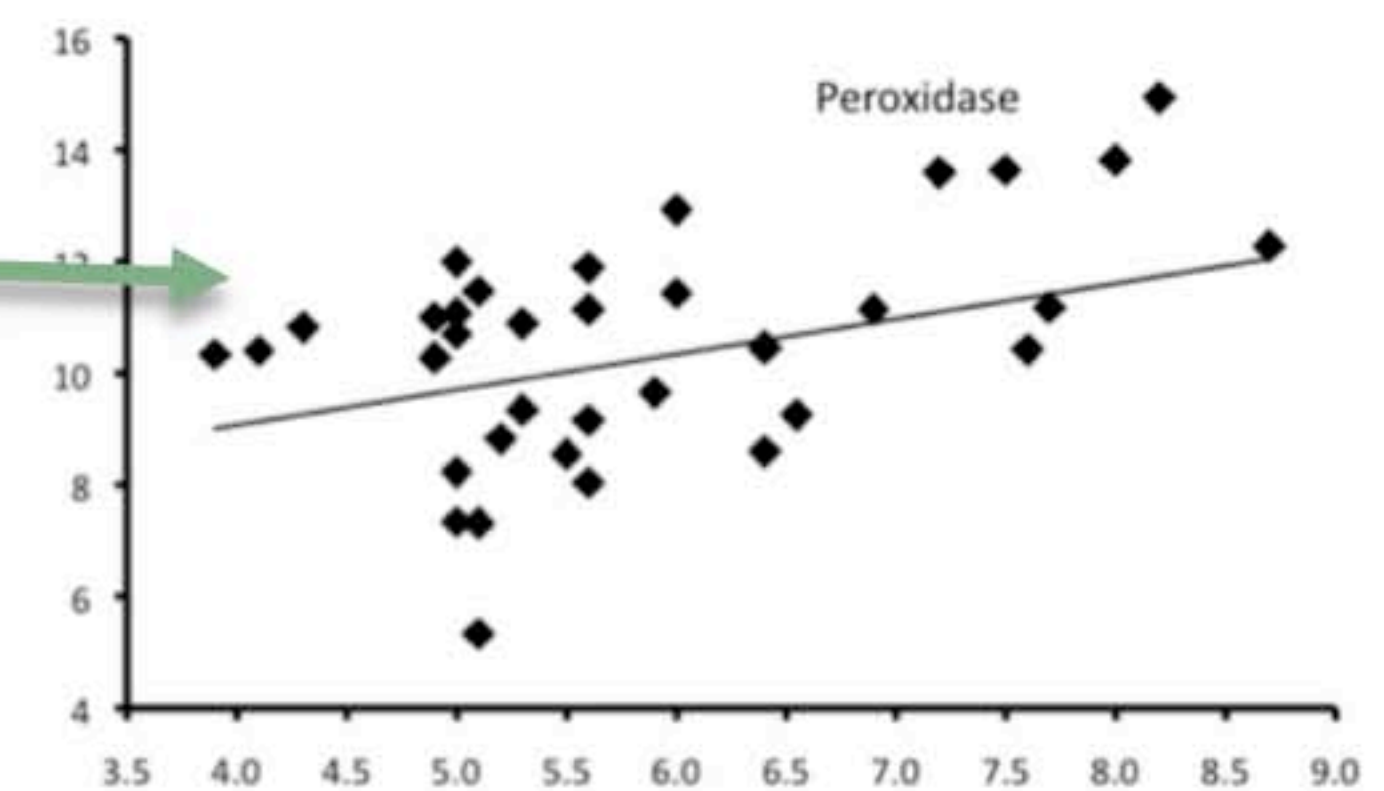
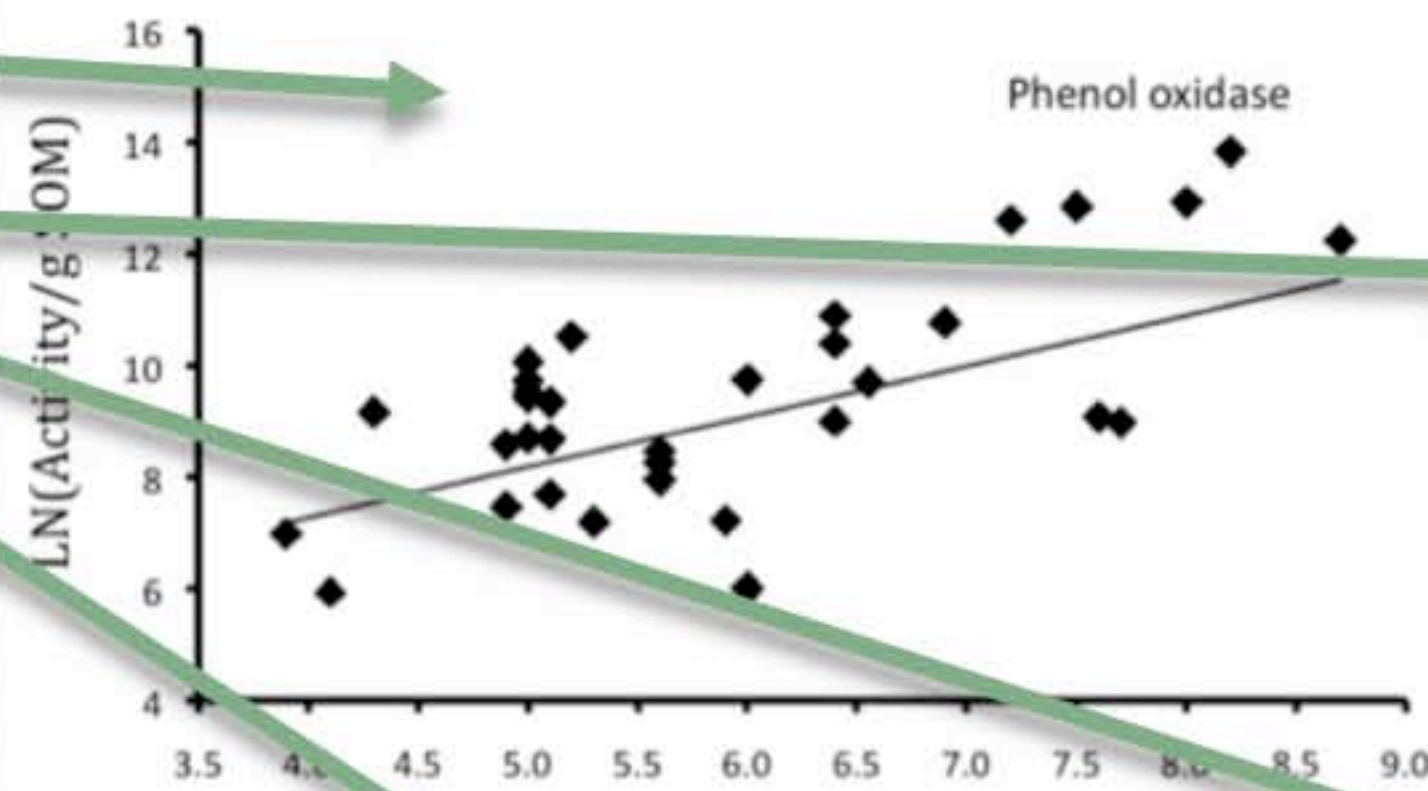
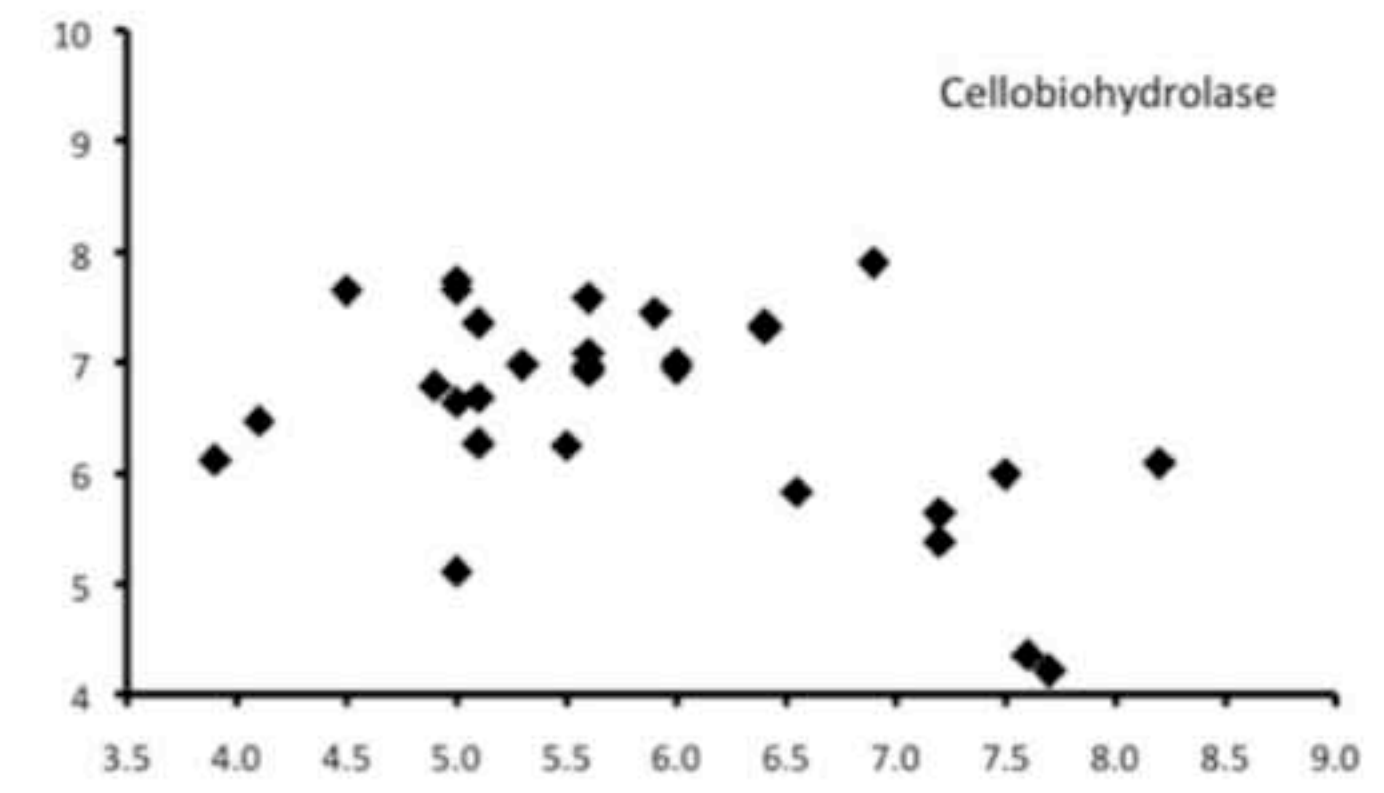
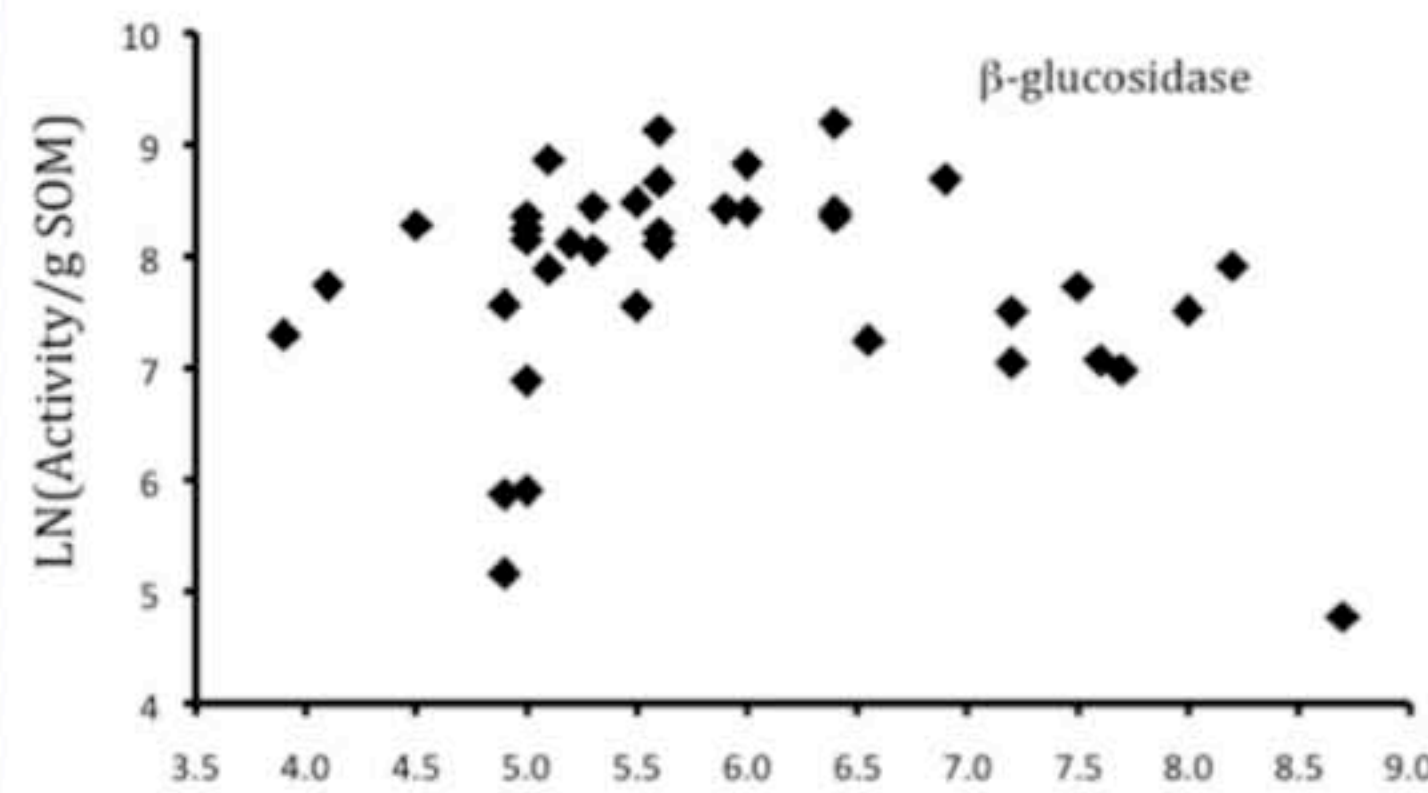
Leucine aminopeptidase

N-acetylglucosaminidase

Phosphatase

Activities covary with Soil pH

Sinsabaugh RL, CL Lauber, MN Weintraub, B Ahmed, SD Allison, C Crenshaw, AR Contosta, D Cusack, S Frey, ME Gallo, TB Gartner, Sarah E. Hobbie, Keri Holland, BL Keeler, JS Powers, M Stursova, C Takacs-Vesbach, M Waldrop, M Wallenstein, DR Zak, LH Zeglin. 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11:1252-1264.



Pushing our paradigm: Stoichiometry

● Michaelis-Menten model: Substrate generation

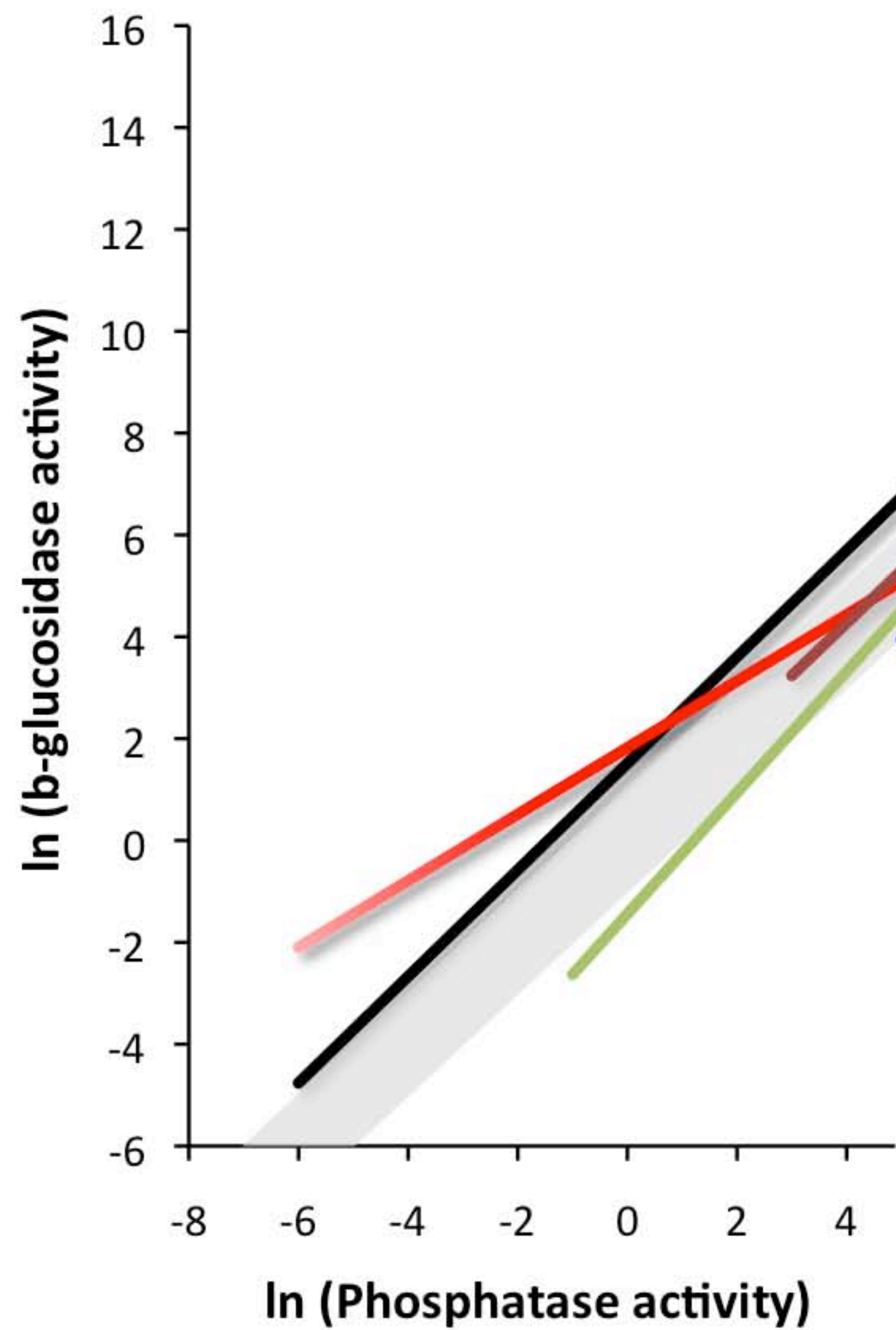
- $V = V_{\max} * S/[S + K_m]$
 - V = rate, V_{\max} = max rate, S = substrate conc., K_m = half saturation constant

● Monod model: Organismal growth

- $\mu = \mu_{\max} * R/[R + K_{\mu}]$
 - μ = growth rate, μ_{\max} = max growth rate, R = resource conc., K_{μ} = half saturation constant

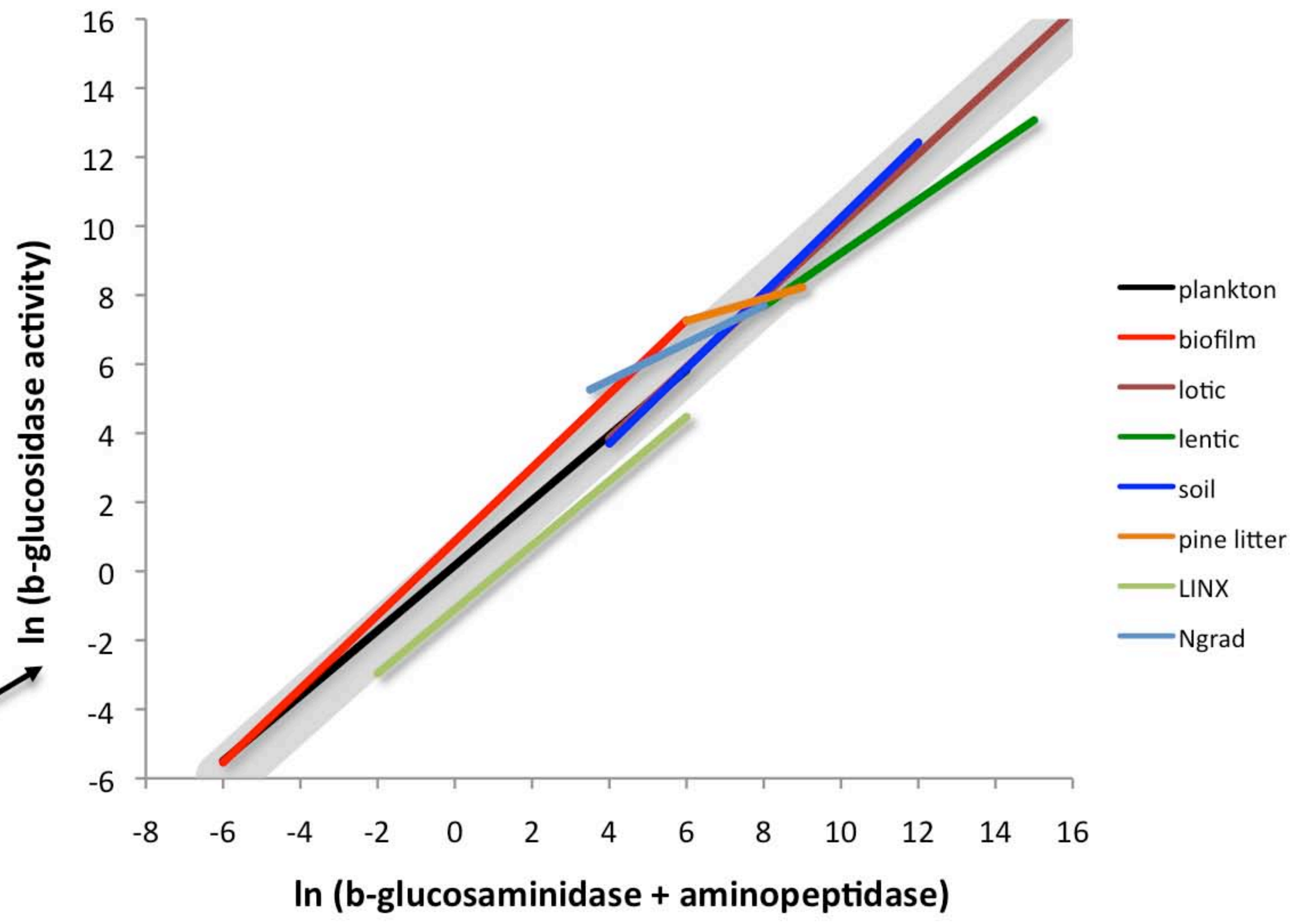
● Droop model: Stoichiometric growth

- $\mu = \mu_{\max} * 1 - [Q_{\min}/Q]$
 - Q_{\min} = element content/cell at zero growth rate, Q = element content/cell



Ecoenzymatic C:P hydrolysis ratio

- plankton
- biofilm
- lotic
- lentic
- soil

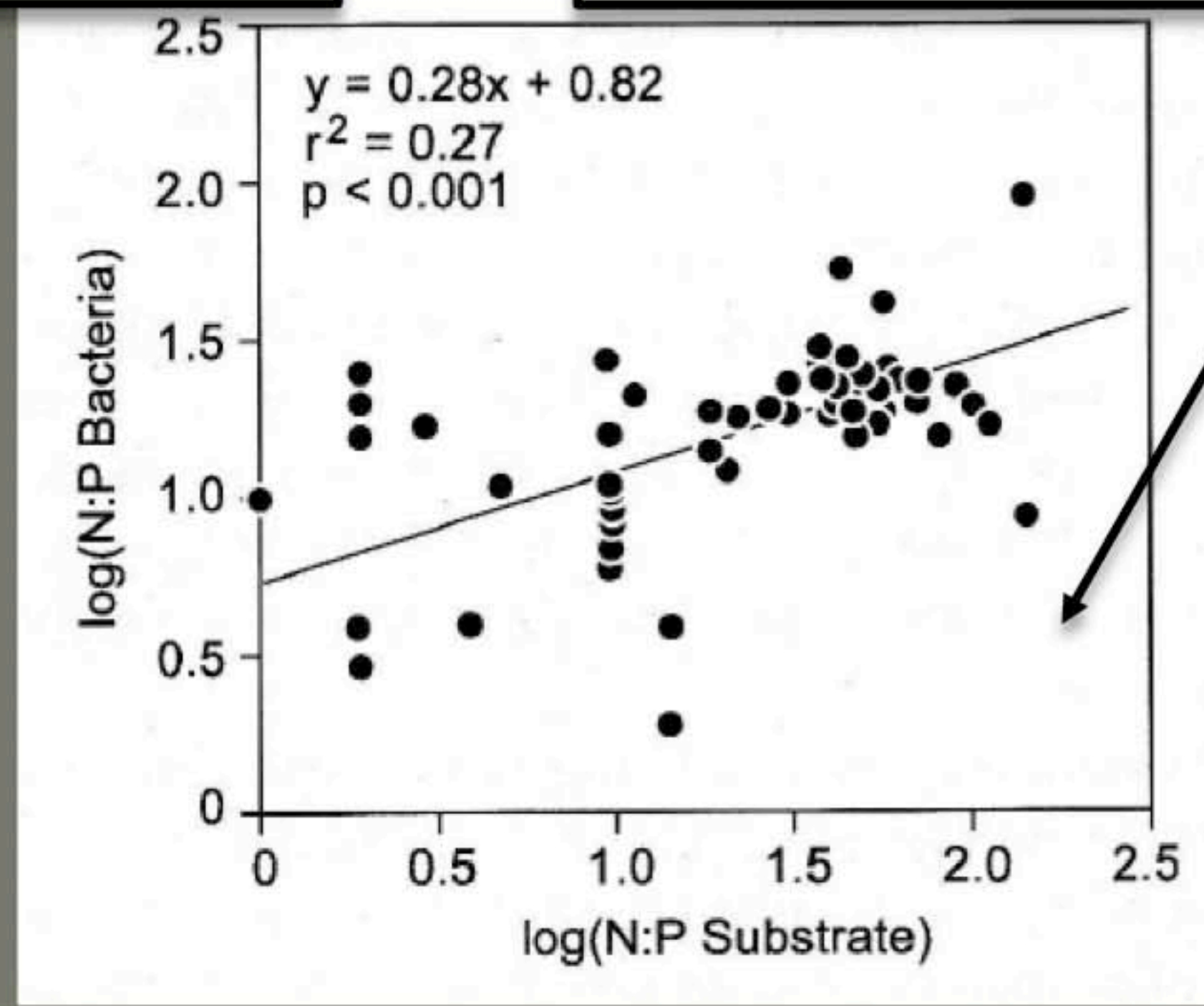
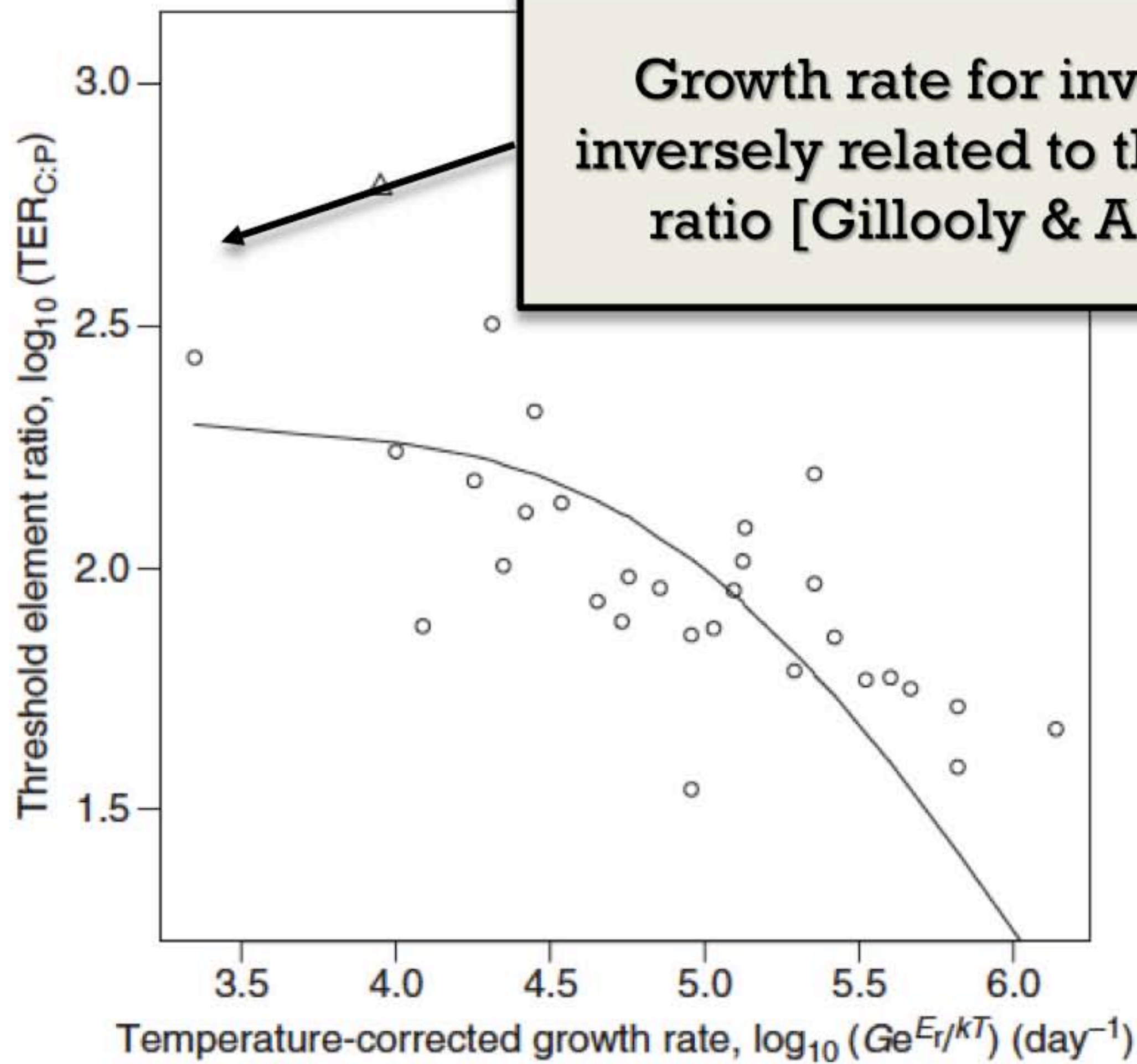


- plankton
- biofilm
- lotic
- lentic
- soil
- pine litter
- LINX
- Ngrad

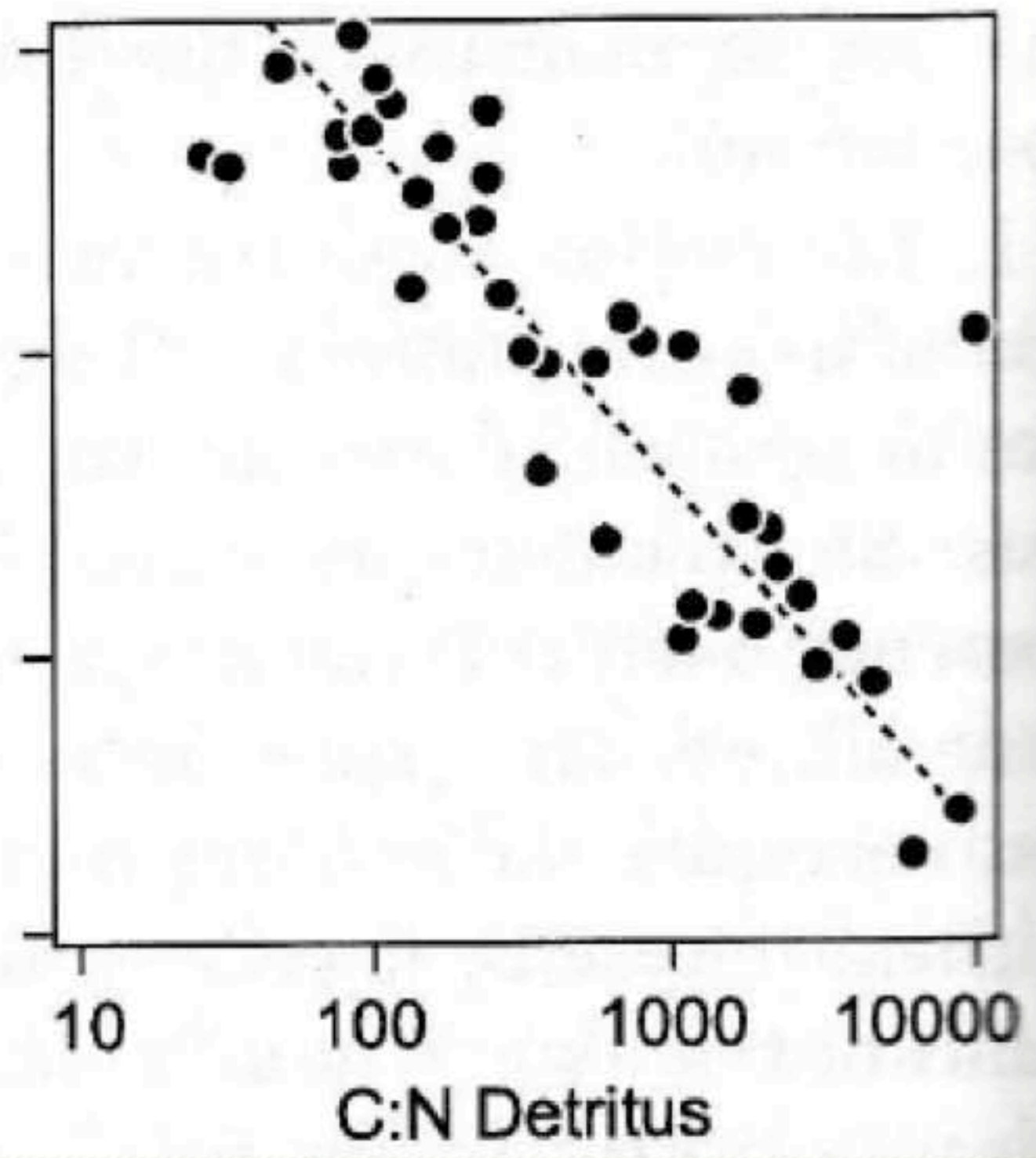
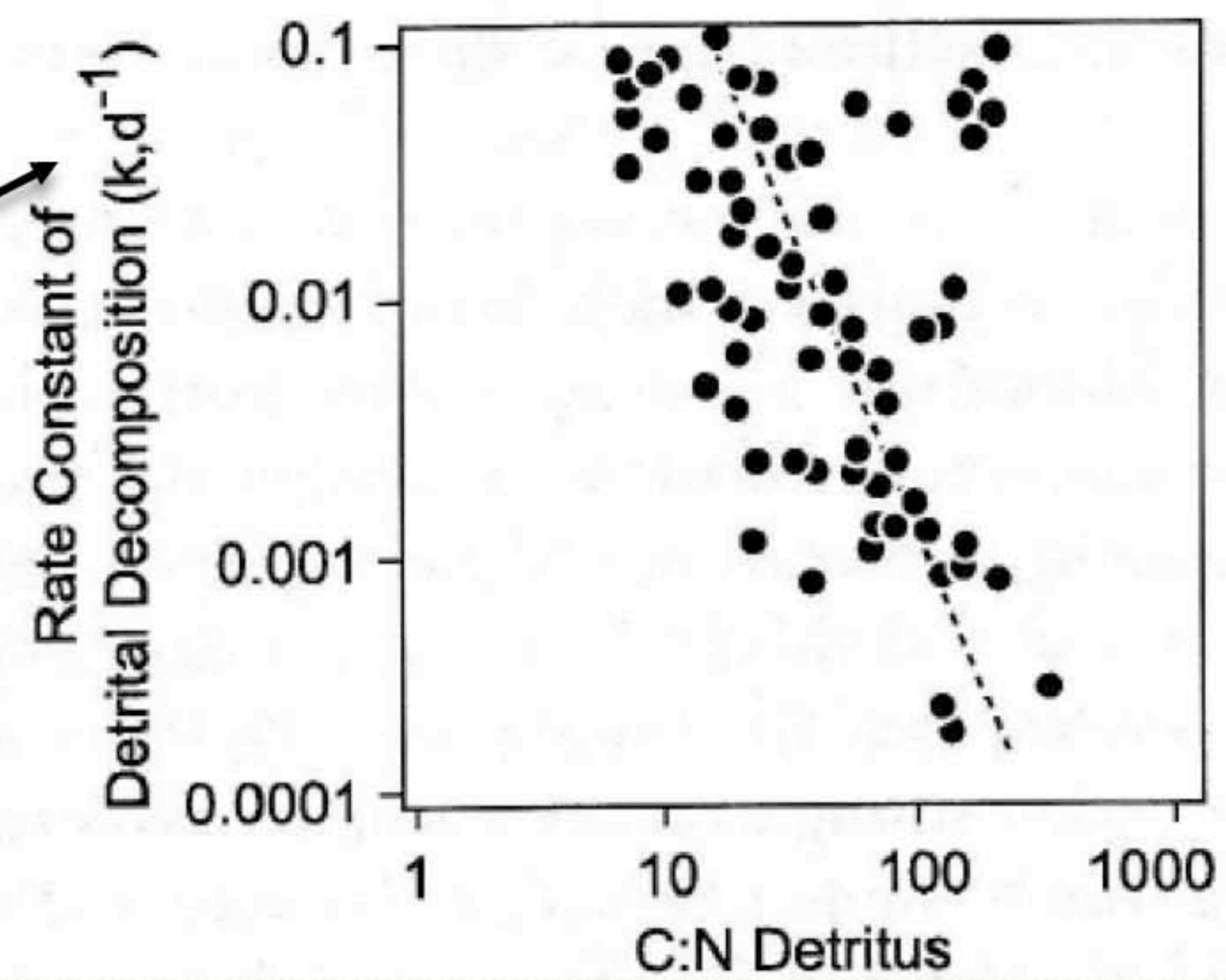
Ecoenzymatic C:N hydrolysis ratio

Growth rate hypothesis

- Specific growth rate $[\mu]$ is a function of the rRNA [ribosome] content of cells.
- As μ increases, cellular P content $[Q_P]$ increases, biomass N:P $[B_{N:P}]$ decreases.
- As μ increases threshold element ratio for N:P decreases $[TER_{N:P}]$.
 - TER is the threshold element ratio for optimal (stoichiometrically balanced) growth.
- $TER_{C:P}/B_{C:P} = A_P/GE$
- $TER_{C:N}/B_{C:N} = A_N/GE$



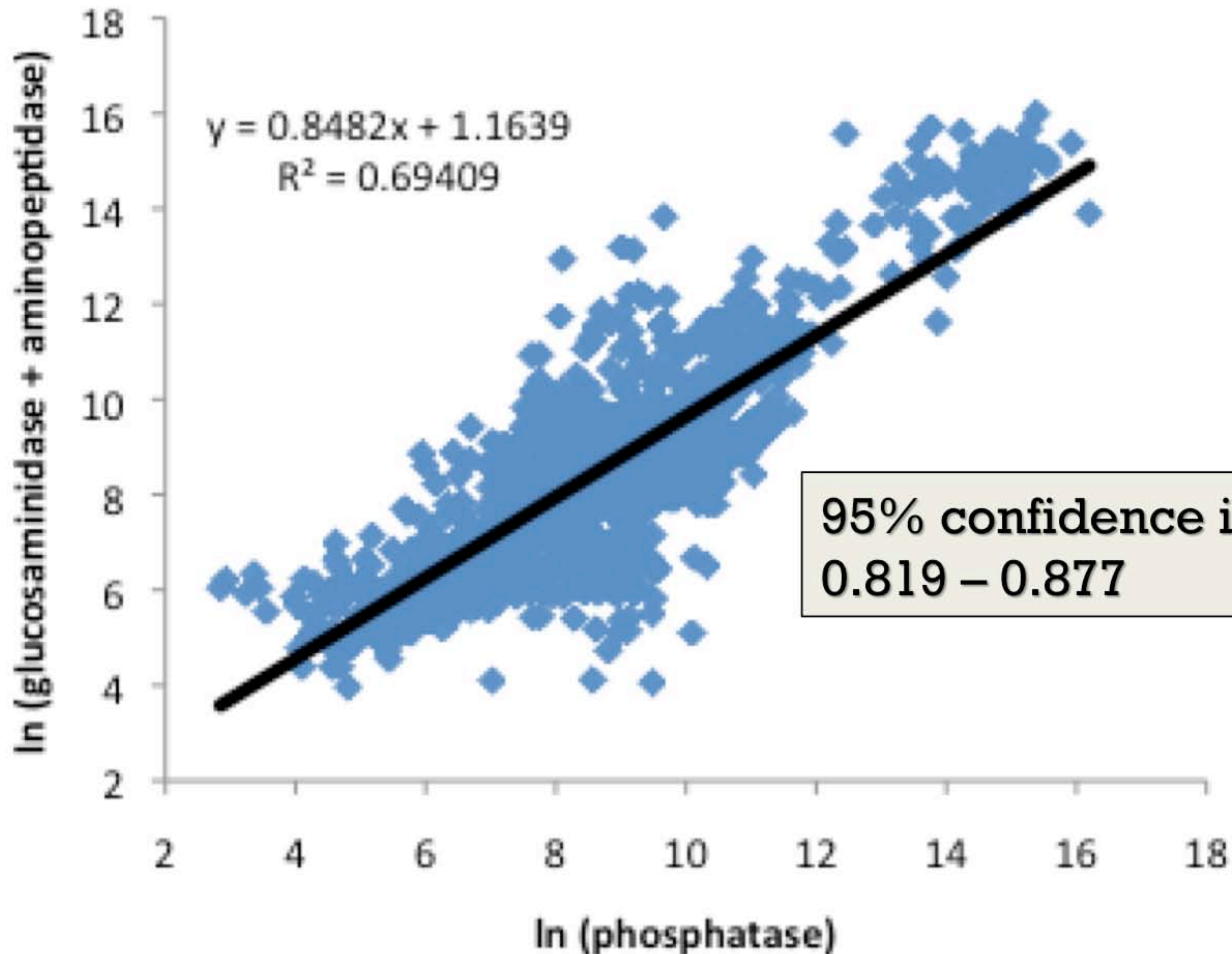
Litter decomposition rate inversely related to litter C:N and C:P ratios [Sterner & Elser 2002]



EEA Predictions for Growth Rate Hypothesis

- $BG/AP \propto TER_{C:P}/B_{C:P} \propto A_P/GE$
- $BG/(LAP+NAG) \propto TER_{C:N}/B_{C:N} \propto A_N/GE$
 - Sinsabaugh, Hill, Follstad Shah. 2009. Nature 462:795-798
- $TER_{N:P}$ for microbial communities associated with decomposing litter declines from 45 to 2 with increasing nutrient supply
 - Gusewell & Gessner. 2009. Functional Ecology 23:211-219
- Magnitude of EEA is proportional to rate of nutrient supply
- Slope of N:P regression $(LAP+NAG)/AP$ is < 1.0.

For soils and sediments, scaling relationship for N-acquiring and P-acquiring hydrolytic activities is consistent with growth rate hypothesis of ecological stoichiometry: EEA N:P slope < 1.



95% confidence interval:
0.819 – 0.877

Sinsabaugh, Hill,
Follstad Shah.
2009. Nature
462:795-798

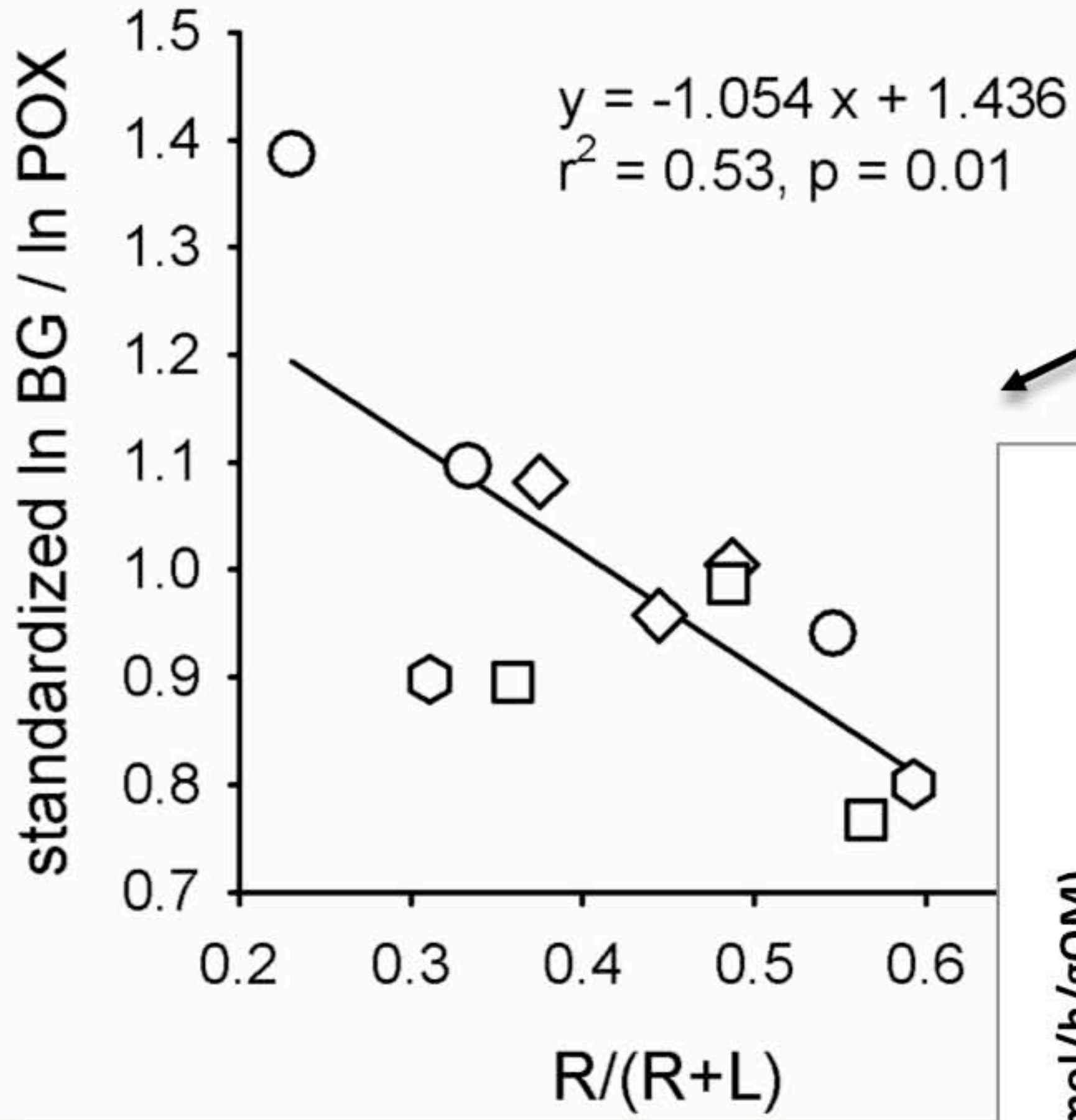
Litter decomposition and the growth rate hypothesis

● Increasing organic matter recalcitrance reverses the growth rate hypothesis

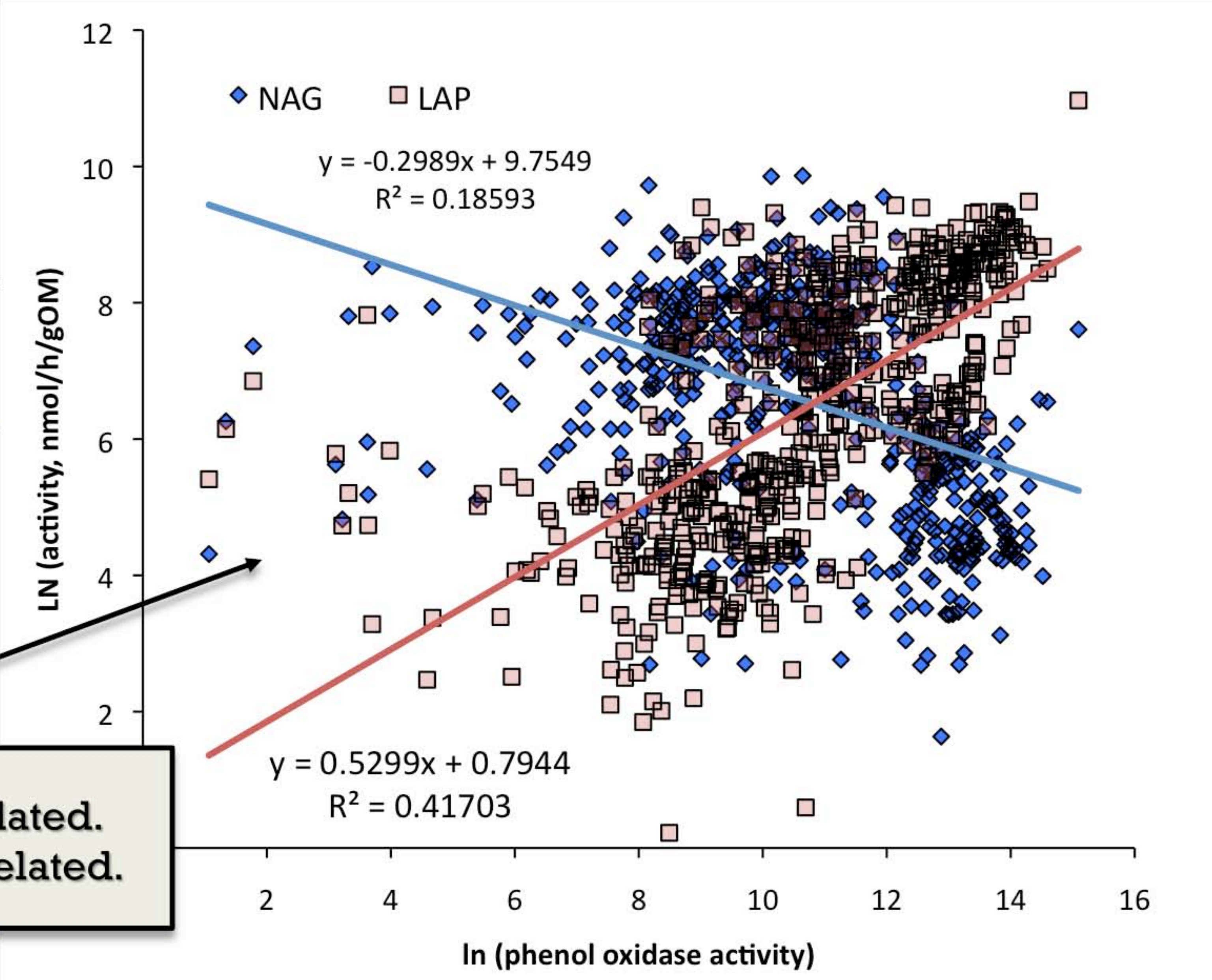
- Sinsabaugh & Follstad Shah. 2010. Biogeochemistry
- Nutrient availability declines as residual OM becomes increasingly recalcitrant
- Growth rates slow
- $TER_{N:P}$ should increase
- $TER_{C:P}$ and $TER_{C:N}$ should decrease
- Critical $R_C/[R_C + L_C]$ ratio ~ 0.45

EEA test for GRH reversal

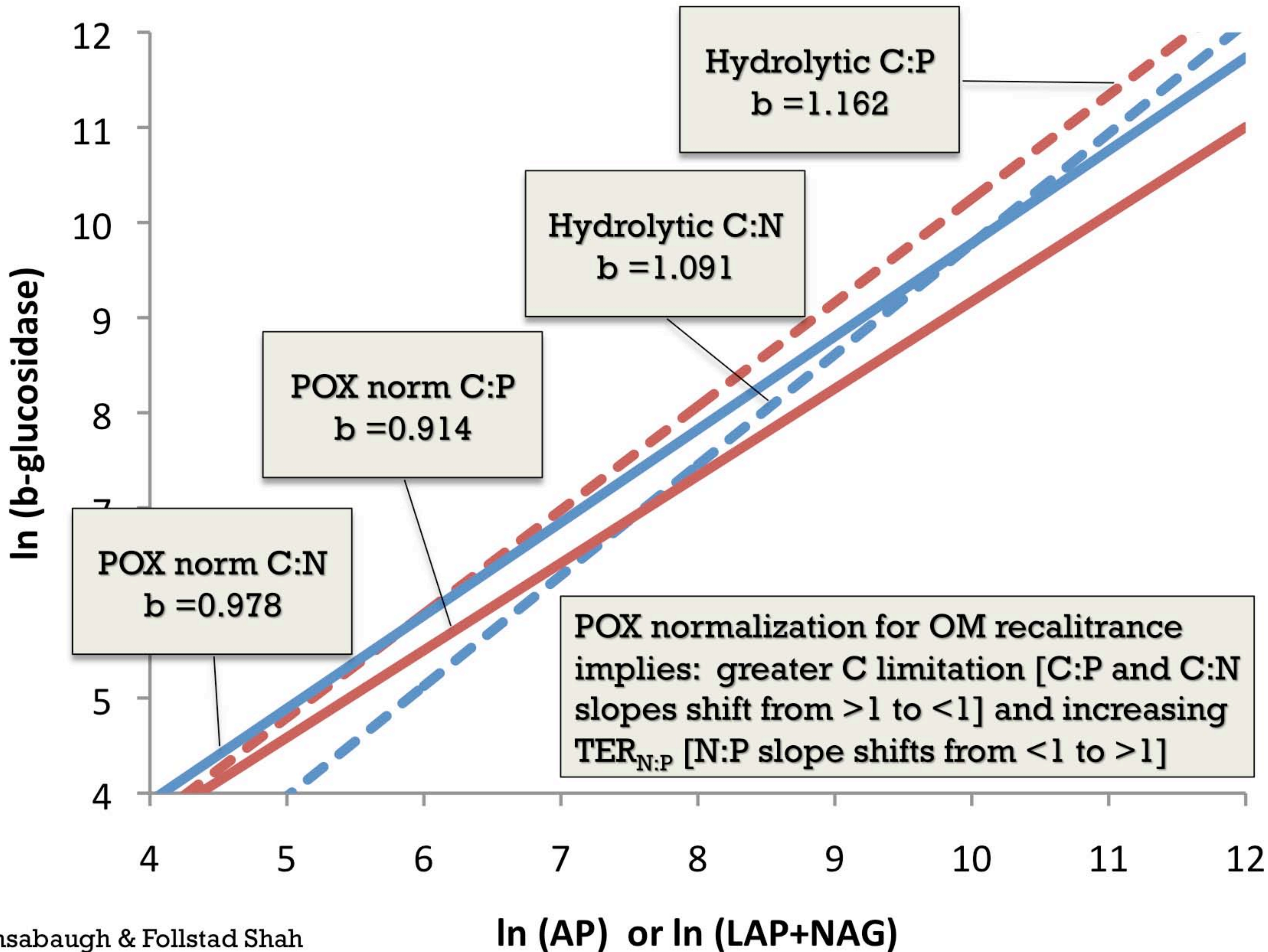
- $BG/POX \propto 1/[(R+L)/R]$
 - R = recalcitrant organic matter, L = labile OM
- BG & POX uncorrelated
- AP & POX have weak +correlation
- (LAP+NAG) & POX have +correlation
 - POX & LAP have strong +correlation
 - POX & NAG have –correlation
- Normalizing hydrolytic activities to POX captures the declining availability of C and nutrients associated with humification.



BG/POX negatively correlated with SOM recalcitrance



**POX and LAP positively correlated.
 POX and NAG negatively correlated.**



EEA and biomass stoichiometry (B)

- $BG/AP \propto TER_{C:P}/B_{C:P}$
- $BG/(LAP+NAG) \propto TER_{C:N}/B_{C:N}$
 - C:N:P of soil microbial biomass: 60:7:1
 - [Cleveland & Liptzin. 2006. Biogeochemistry 85:235-252]
 - C:N:P of planktonic microbial biomass: 106:16:1
 - [Redfield 1958 and many others]
- EEA prediction: slopes of BG/AP and BG/(LAP+NAG) regressions should be related to difference in B of attached and planktonic microbial communities.

EEA is normalized to microbial productivity (P).

Mean $B_{C:P}$ for plankton and biofilm: $106/60 = 1.77$

EEA C:P slopes: $1.046/0.653 = 1.60$

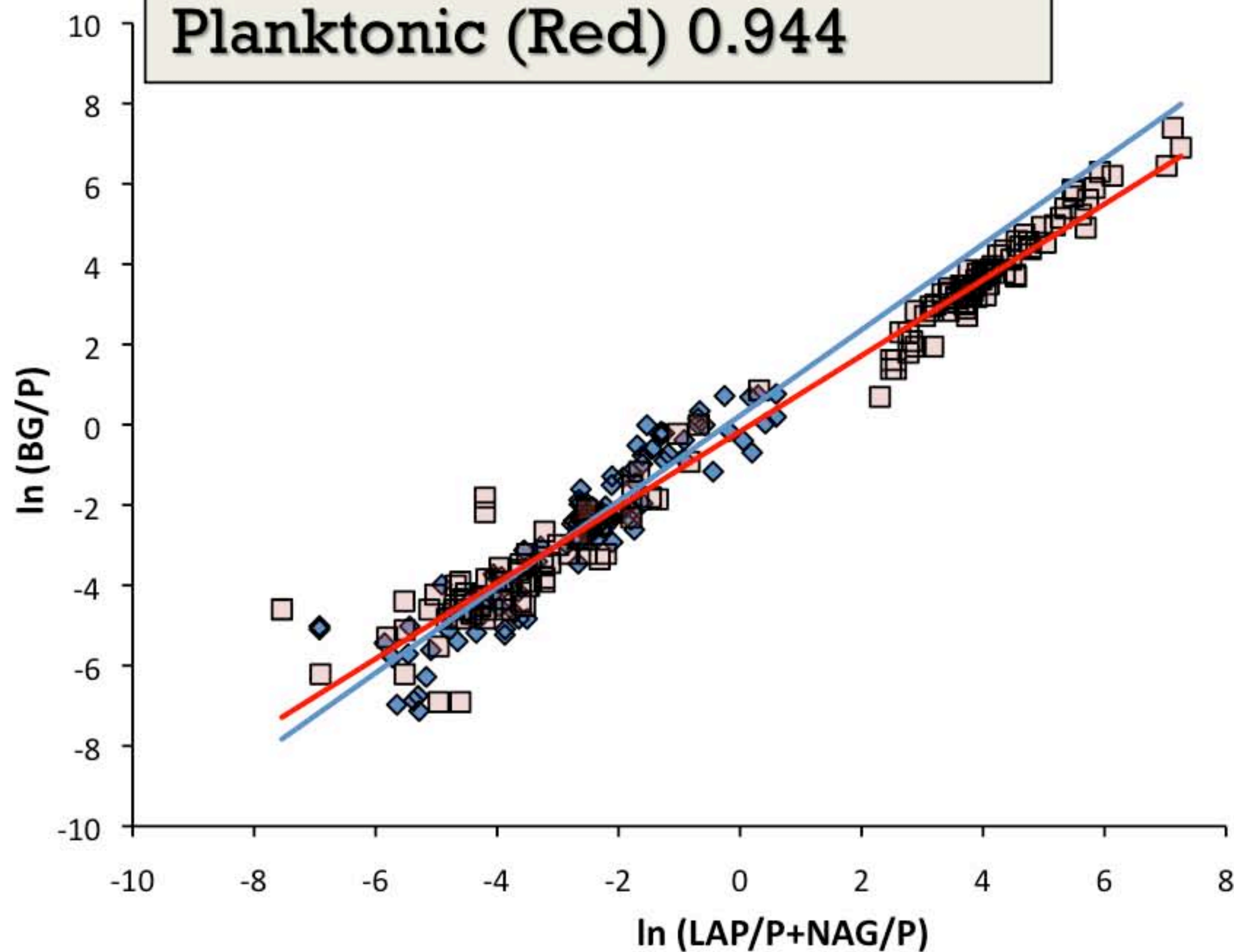
Mean $B_{C:N}$ for plankton and biofilm: $6.6/8.6 = 0.77$

EEA C:N slopes: $0.944/1.068 = 0.88$

BG/(LAP+NAG) slopes: C:N

Attached (Blue) 1.068

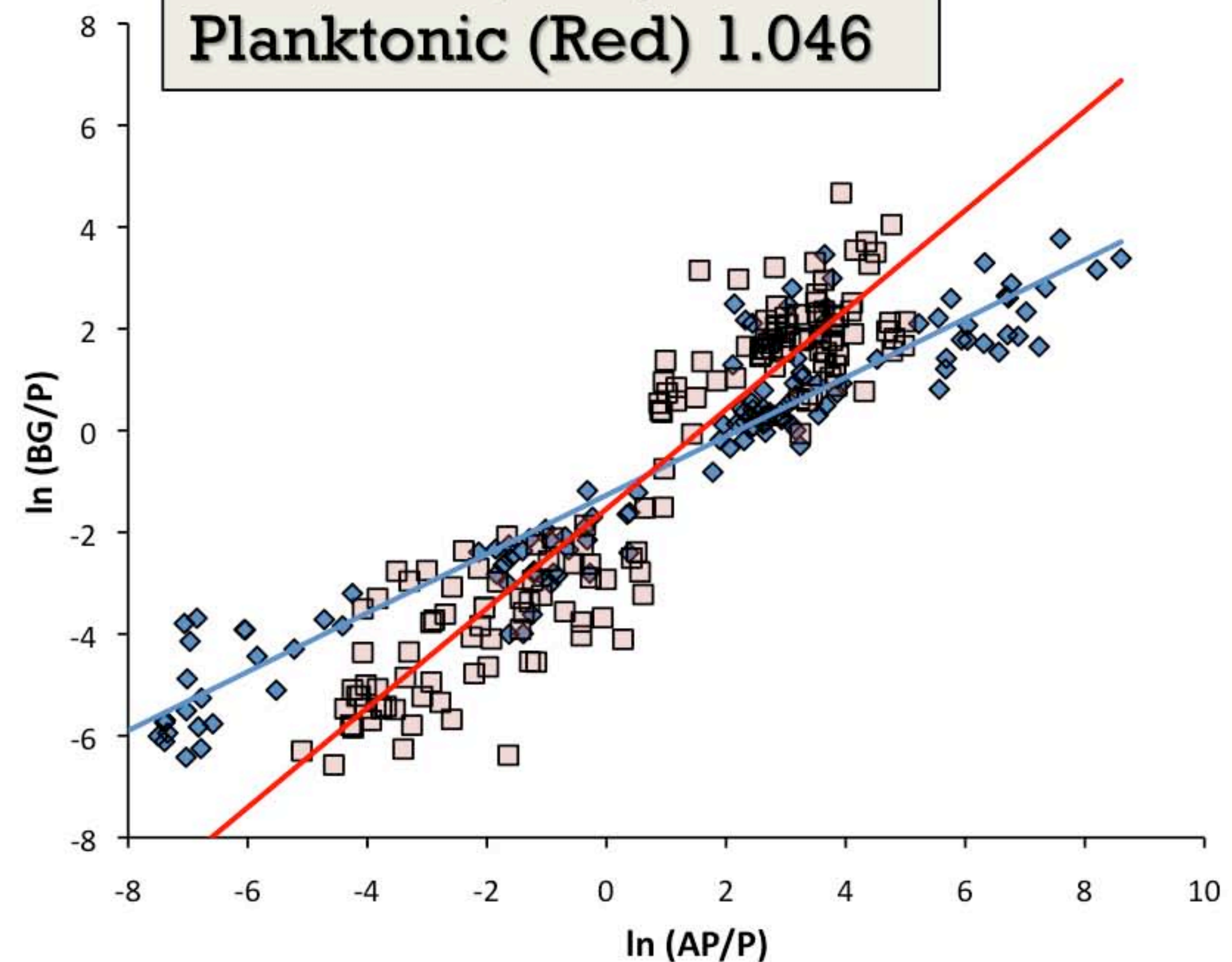
Planktonic (Red) 0.944



BG/AP slopes: C:P

Attached (Blue) 0.653

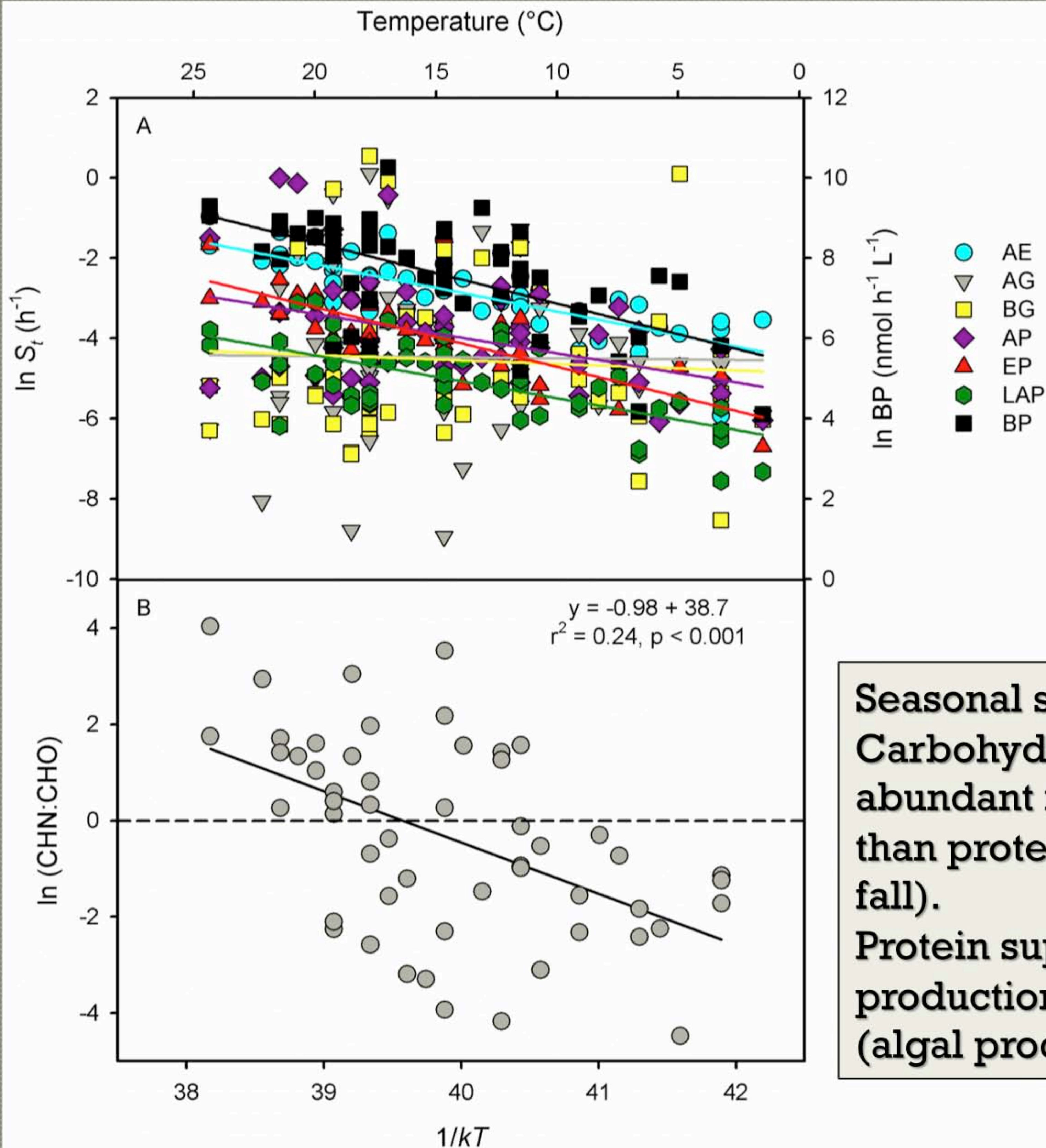
Planktonic (Red) 1.046



EEA and metabolic theory

$$P_{tot} \left(\sum_{j=1}^n \text{App} V_{\max_j} / 2 \right)^{-\sigma} = b_0 \langle M_i \rangle^b e^{-E_a / k \langle T \rangle} N$$

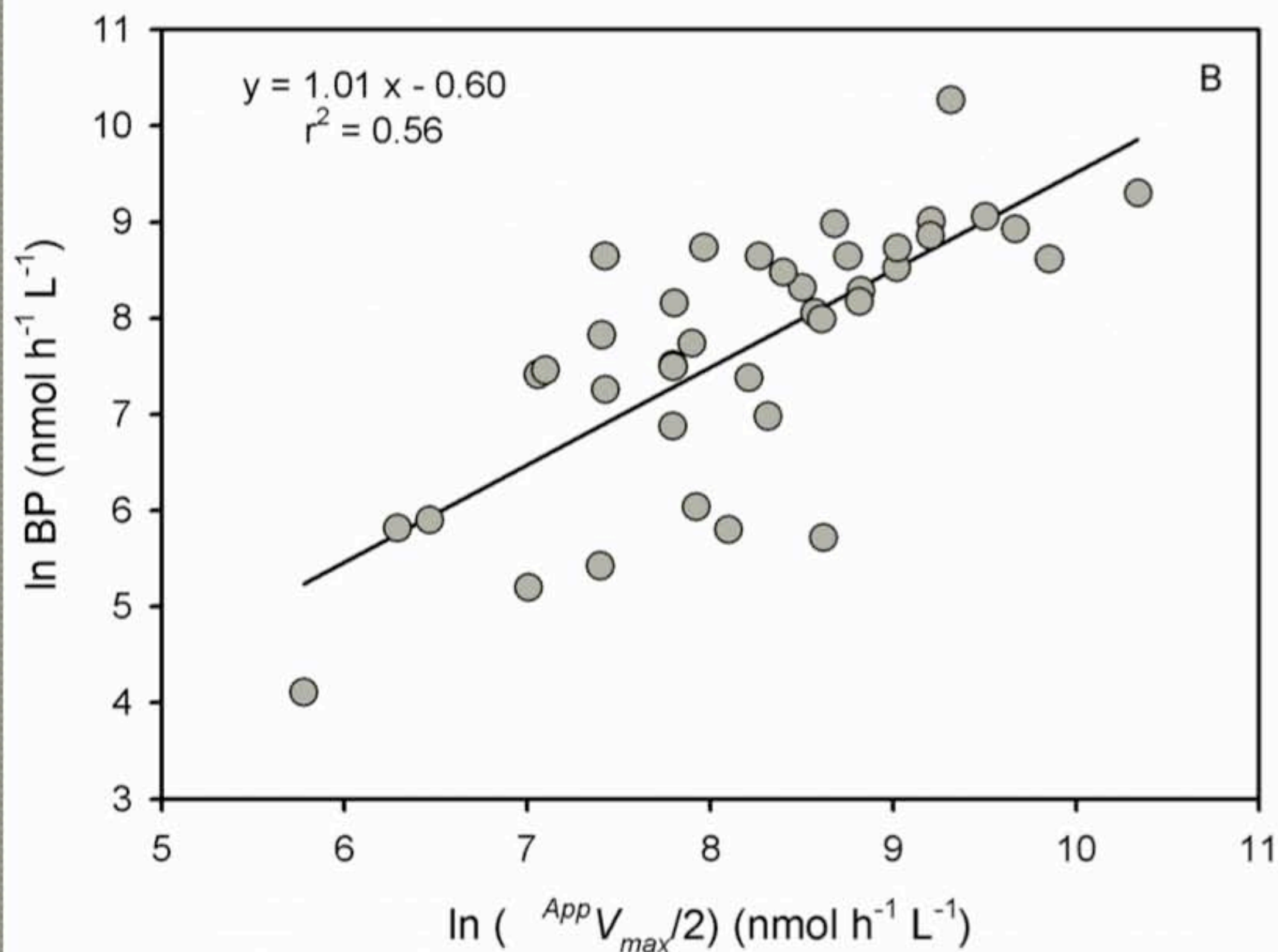
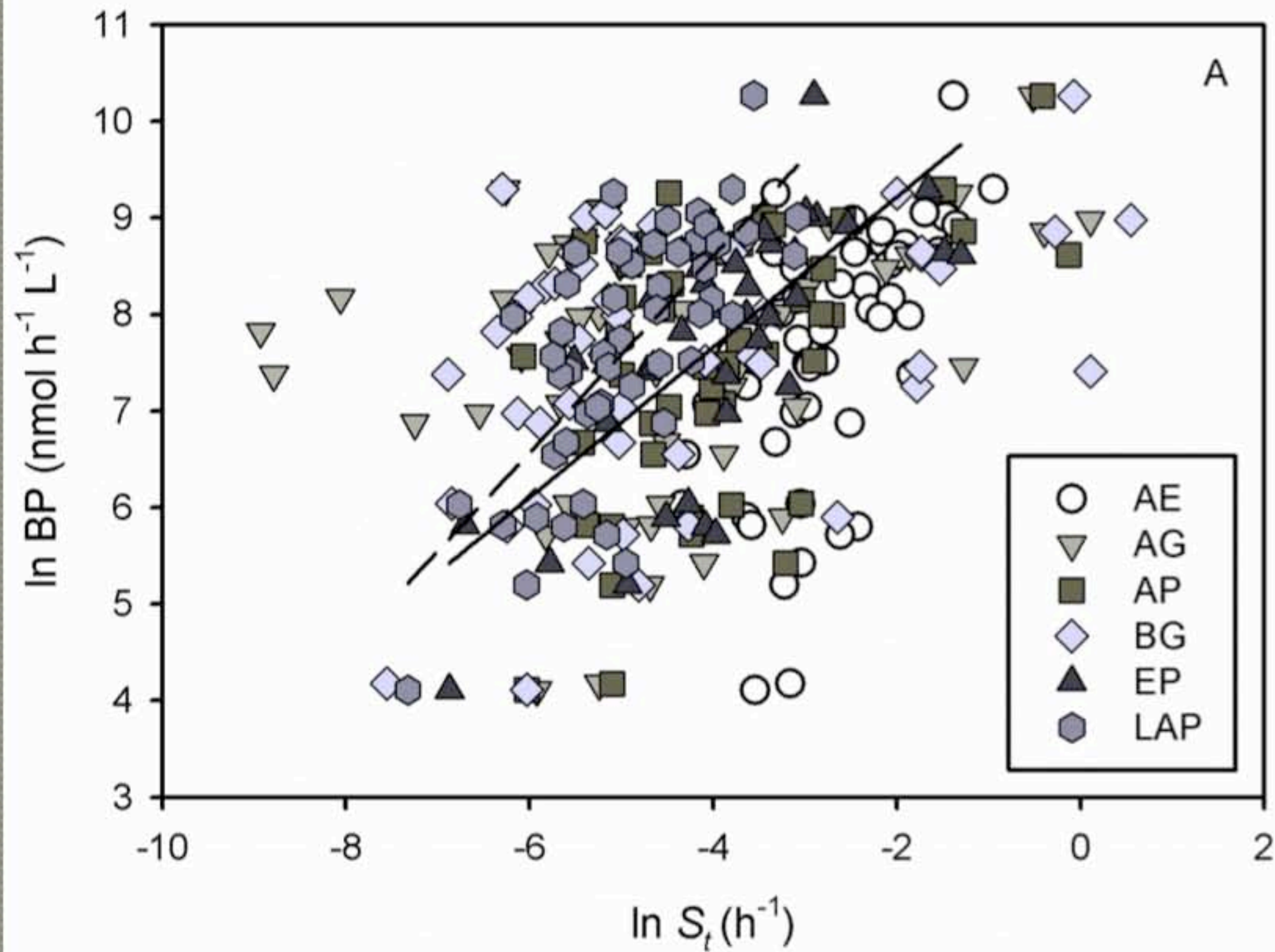
- Left: Production normalized to resource supply which is expressed as the summed flows of nutrients from major EEA resource pools.
- Right: Metabolism normalized to body size, number of individuals and temperature.



Resource supply from 6 enzymes ($V_{max}/2 K_m$) as a function of temperature.

Over the year, apparent activation energies (E_a) for resource supply are lower than the apparent E_a of bacterial production (in black).

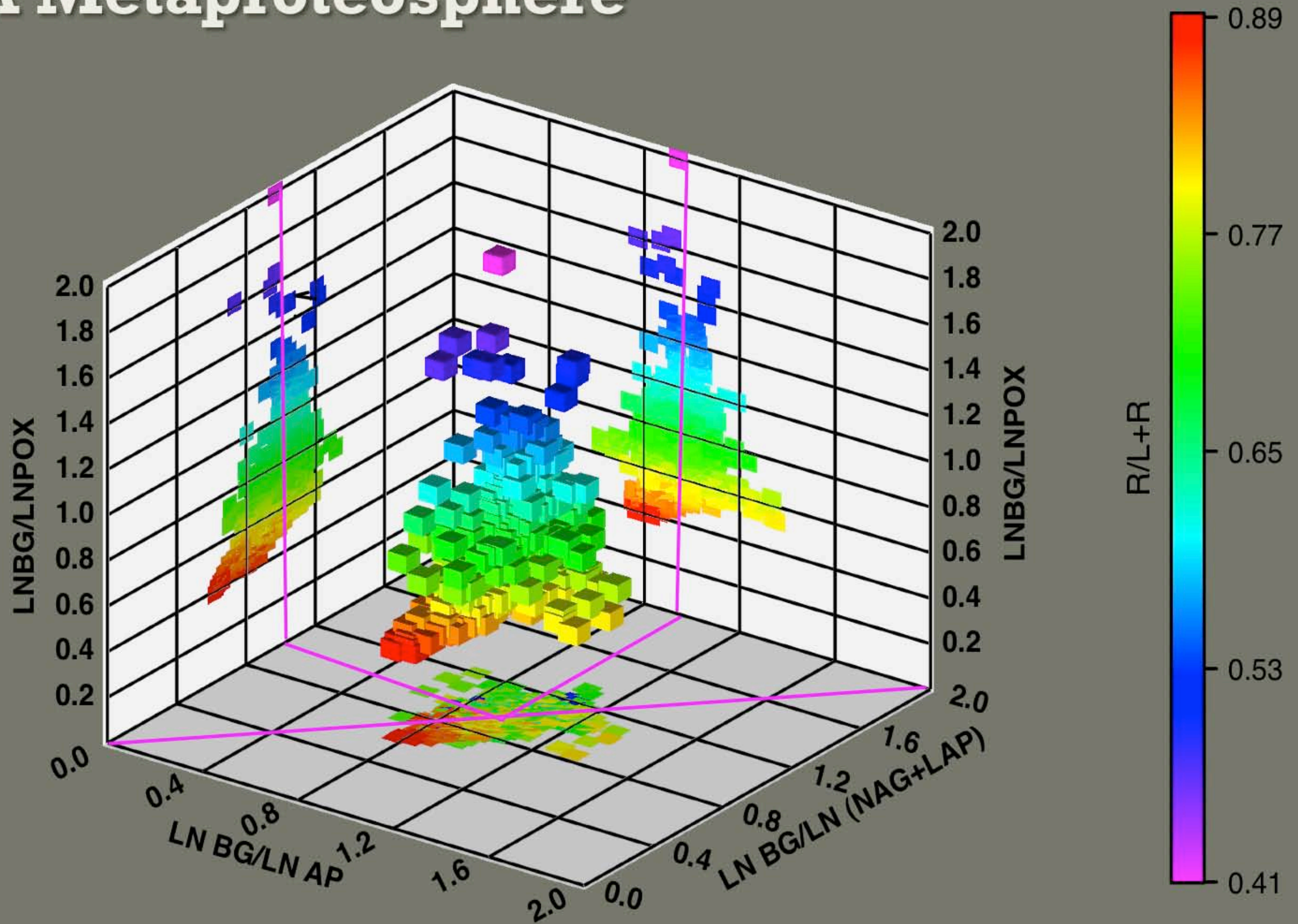
Seasonal shift in resource supply: Carbohydrates are relatively more abundant resources for production than proteins in fall and winter (litter fall). Protein supports relatively more production in spring and summer (algal production).



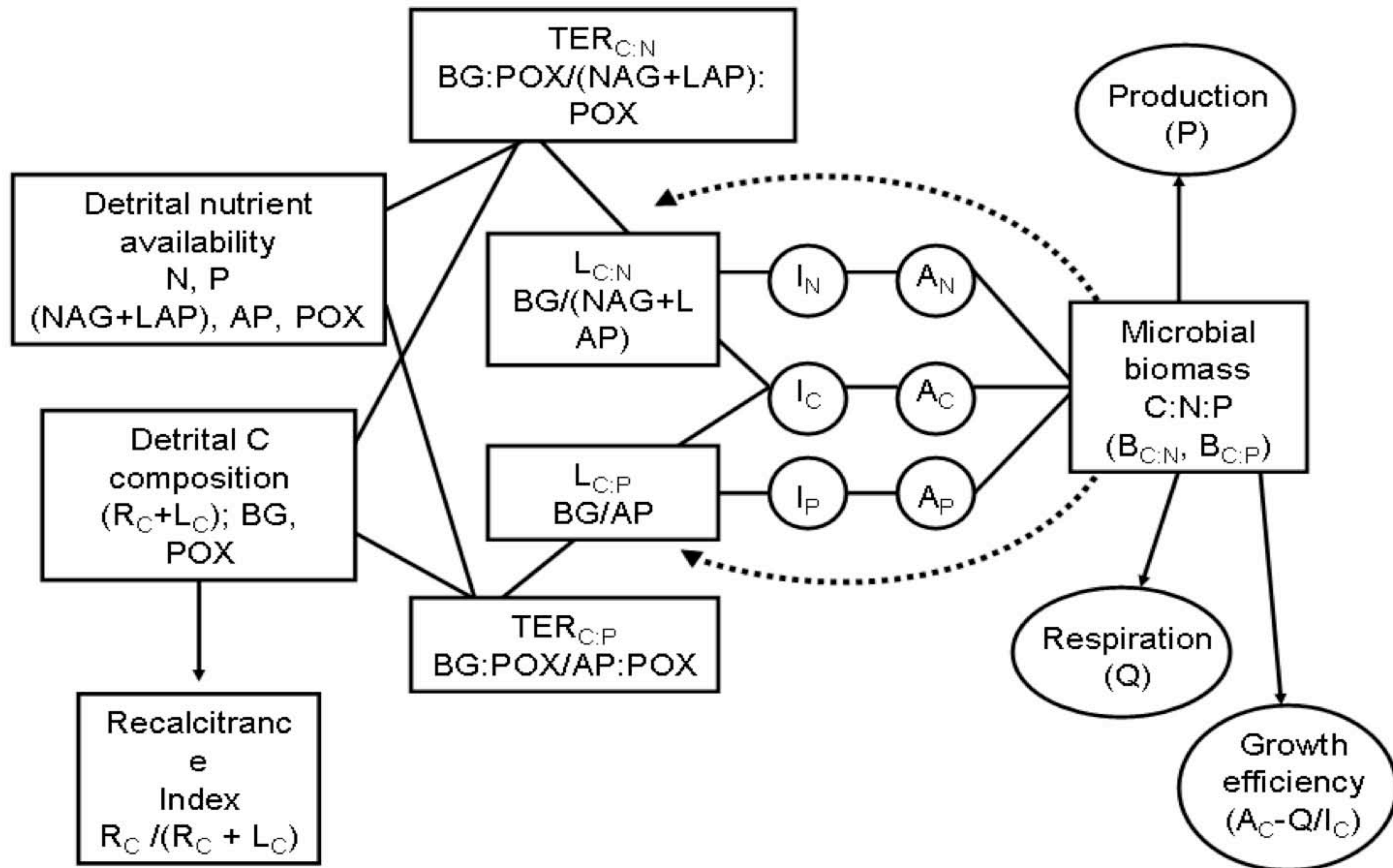
→ Over an annual cycle, temperature corrected resource supply from EEA is correlated with temperature corrected bacterial production.

→ Apparent E_a of resource supply matches the apparent E_a of production.

EEA Metaproteosphere



EEA-up Decomposition Model?



Summary

- Functional metaproteomics is a big part of stoichiometric and metabolic theories of ecology.
 - Focus has been intracellular enzymes
 - ribosomes, RuBisCo, nitrogenase, hydrogenase, glutamine synthetase, etc.
- EEA has a lot of potential to resolve issues related to resource vs. thermodynamic control of community metabolism.
 - Easy to measure at high spatiotemporal resolution.
 - Relevant to community composition and diversity.
 - Presenting our work more explicitly in the context of general theory will extend interest.