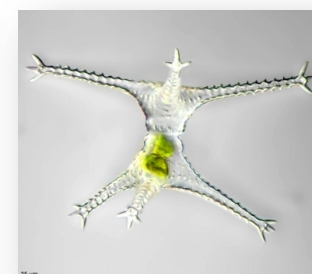
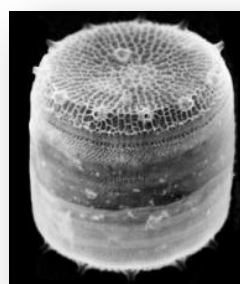
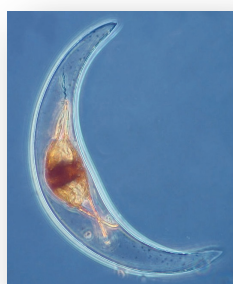
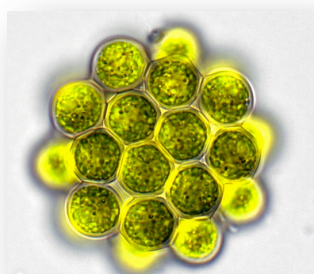


Opportunities and challenges for quantifying functional tradeoffs



Kyle F. Edwards*, Elena Litchman, Christopher A. Klausmeier
Kellogg Biological Station, Michigan State University

*starting Jan 2014:

Assistant Professor, Dept of Oceanography
University of Hawaii Manoa

Why tradeoffs?

Organismal: what phenotypes are possible

Evolutionary: how is selection constrained

Community Ecology: how is diversity maintained, what determines community structure

Ecosystem Ecology: how does functional variation affect ecosystem processes



Spike Walker, Wellcome Images



ARC Centre of Excellence

Why tradeoffs?

How can we test / quantify tradeoffs?

- Interspecific trait correlations
- Quantitative genetics (intraspecific genetic trait correlations)
- Selection experiments



Spike Walker, Wellcome Images

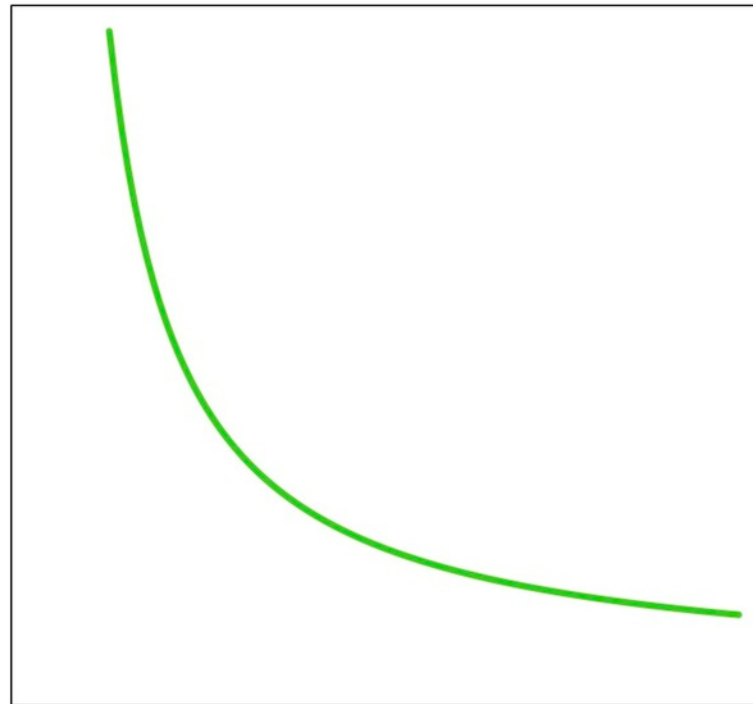


ARC Centre of Excellence

How can we quantify tradeoffs?

Interspecific trait correlation

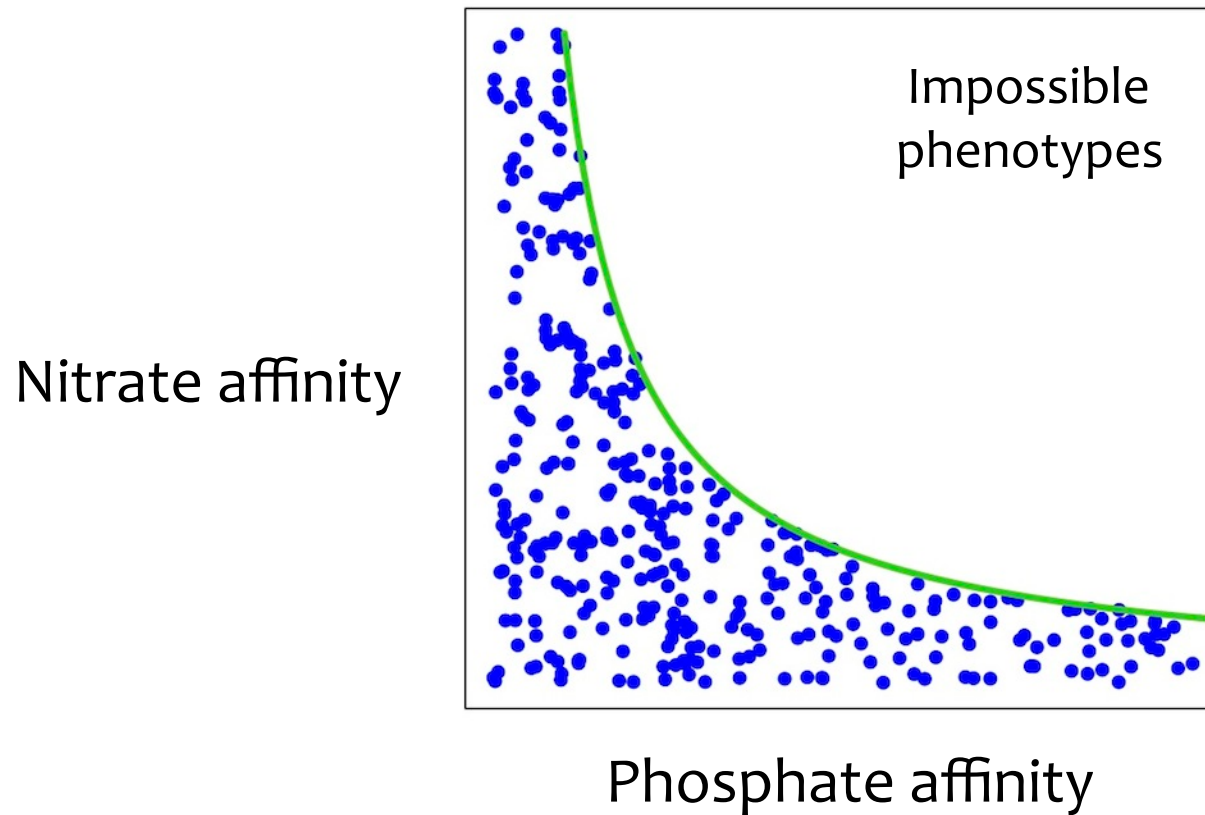
Nitrate affinity



Phosphate affinity

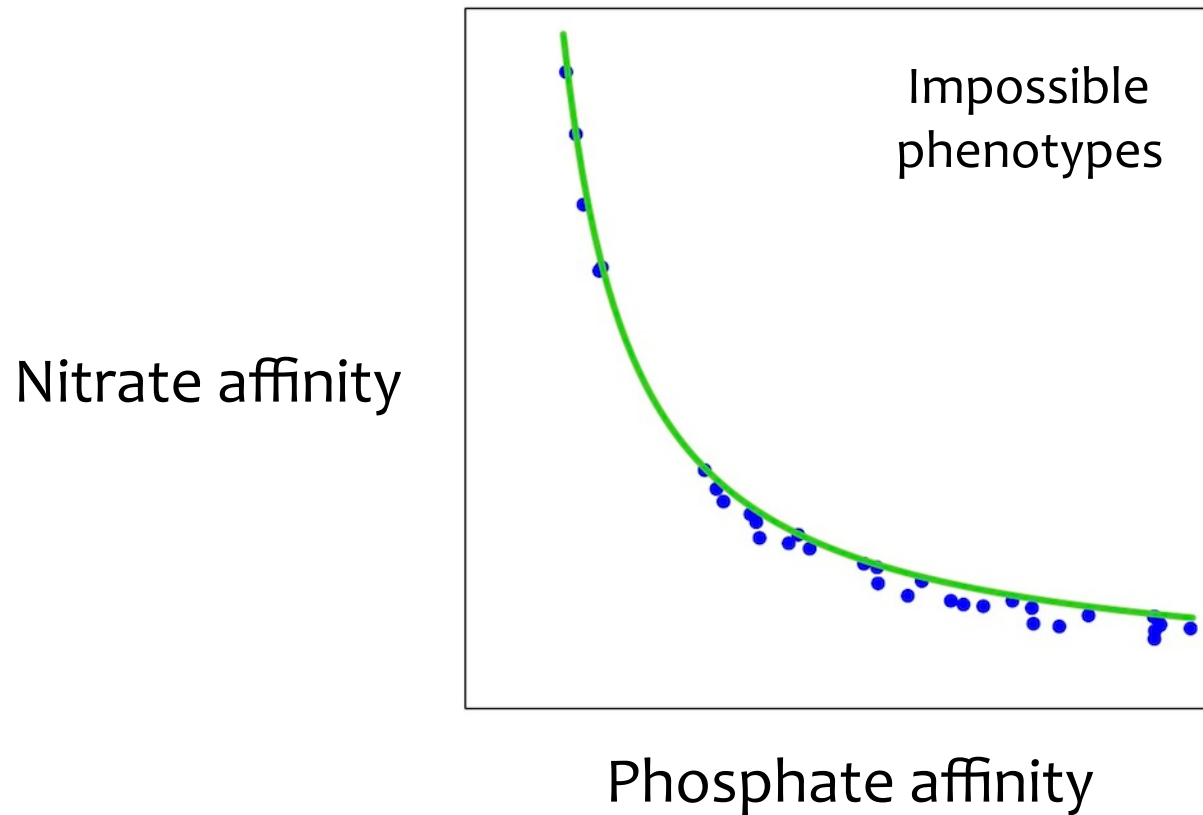
How can we quantify tradeoffs?

Interspecific trait correlation



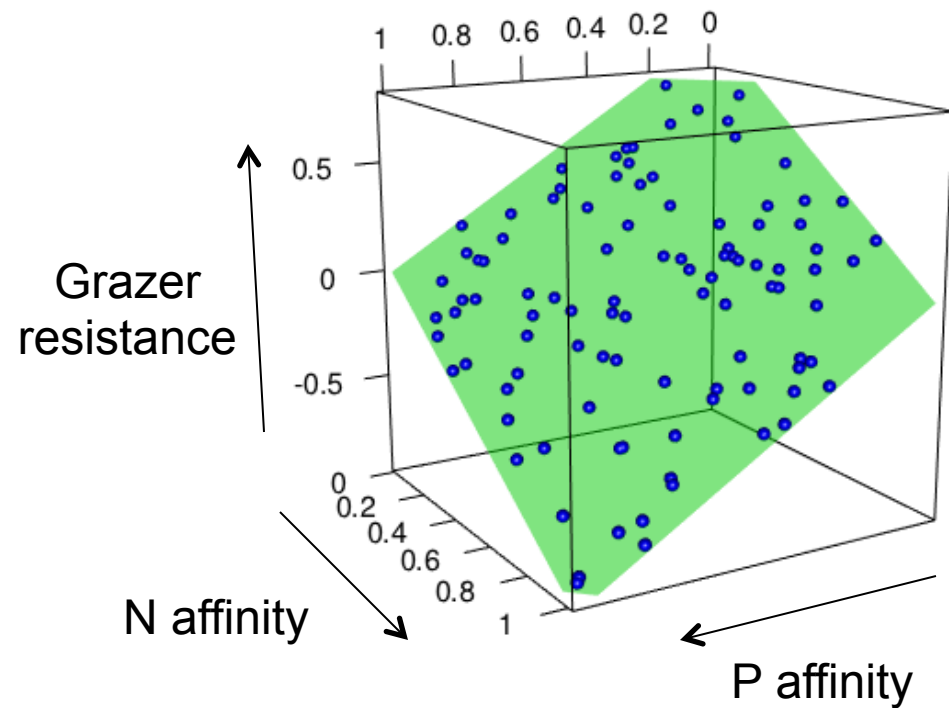
How can we quantify tradeoffs?

Interspecific trait correlation



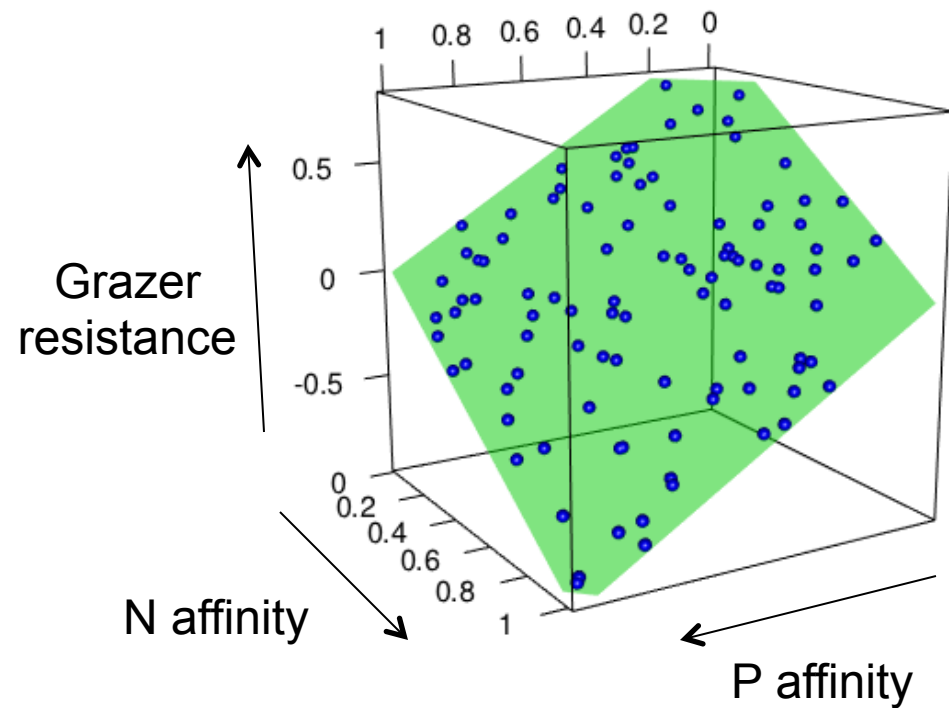
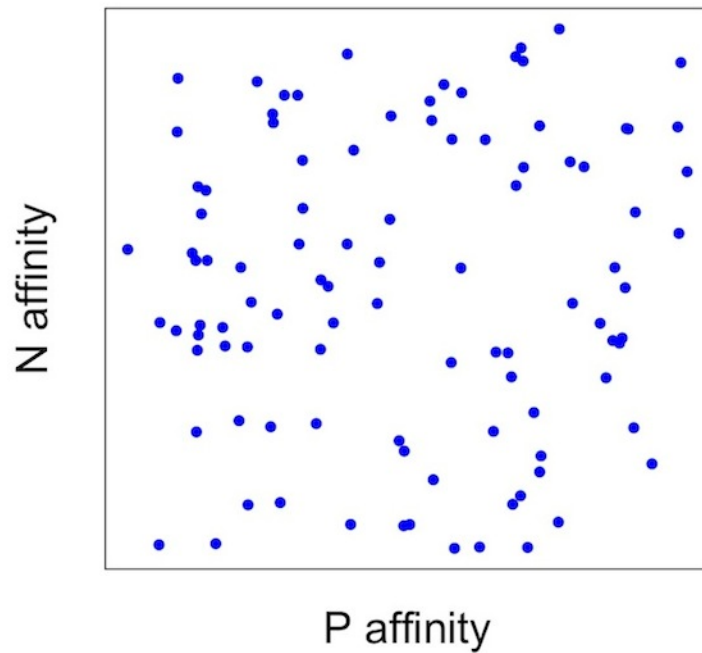
How can we quantify tradeoffs?

Tradeoffs are probably multidimensional



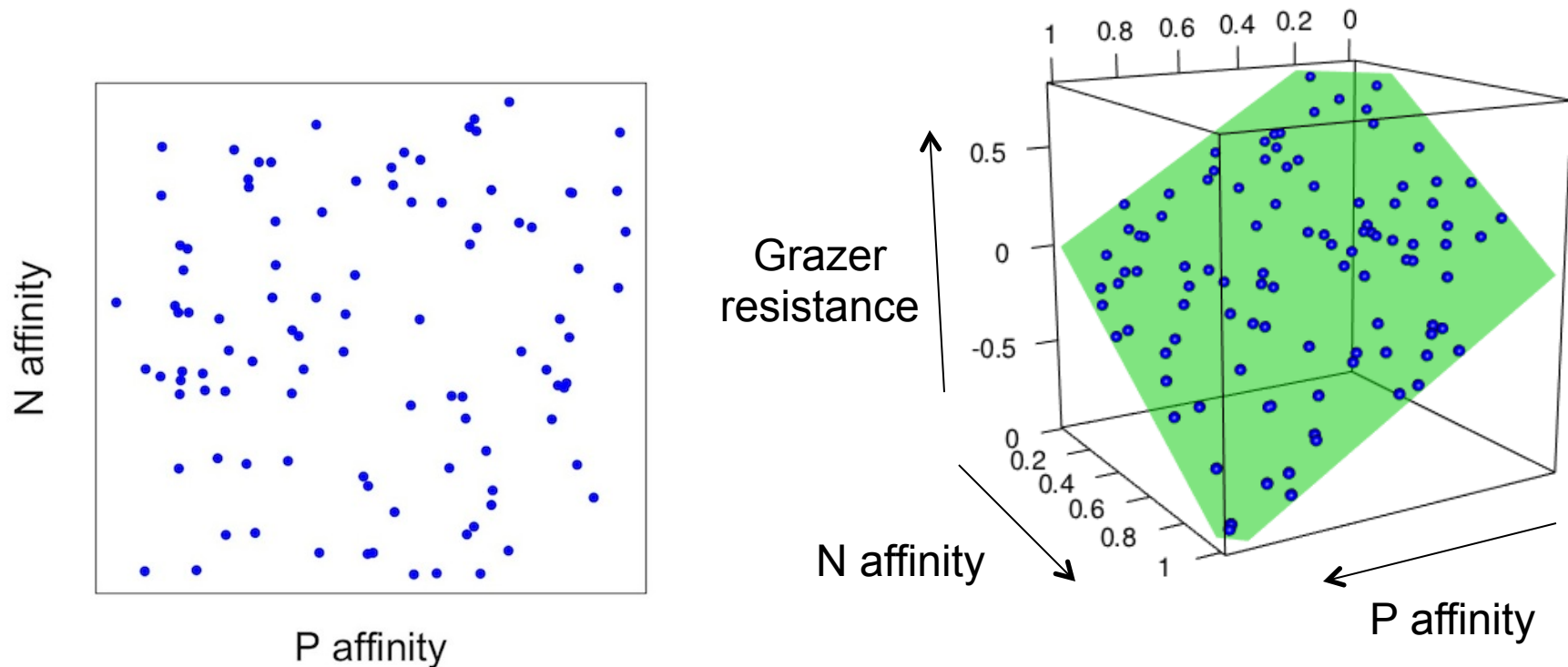
How can we quantify tradeoffs?

Tradeoffs are probably multidimensional



How can we quantify tradeoffs?

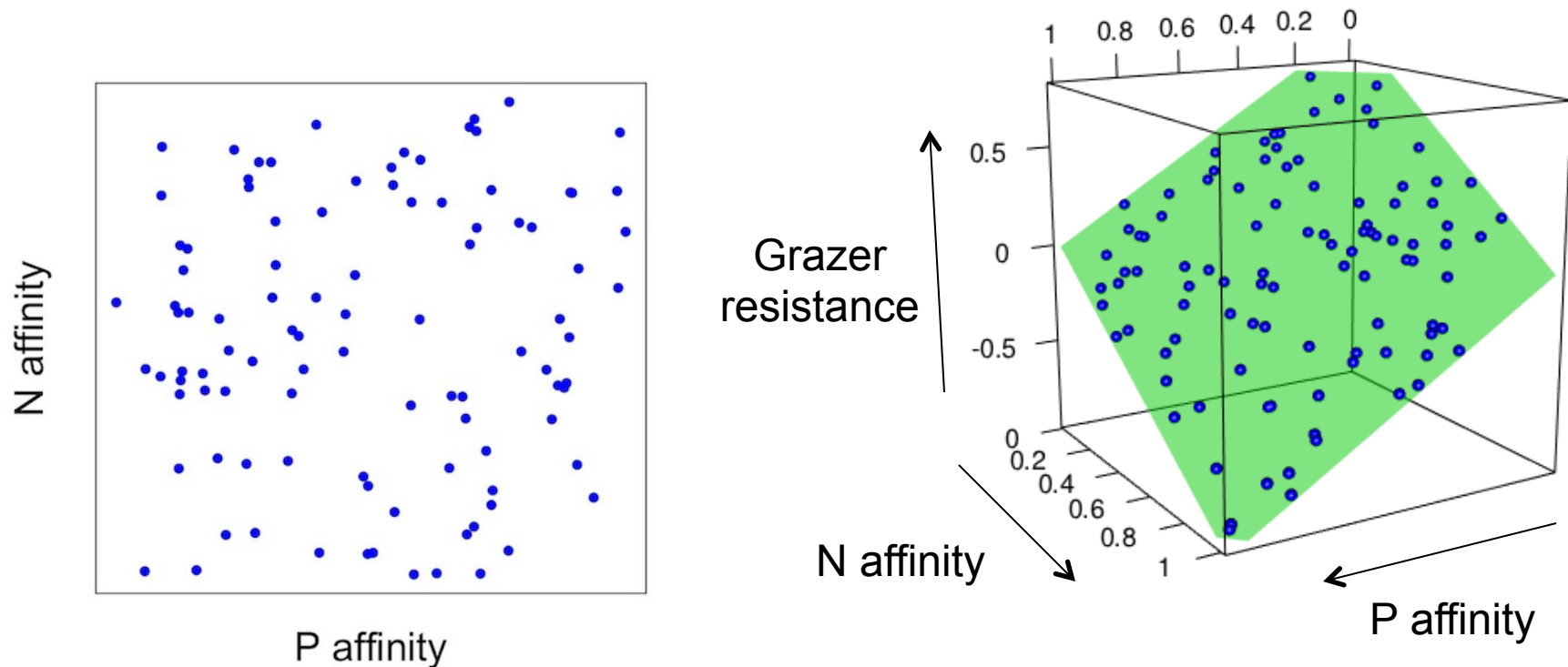
Tradeoffs are probably multidimensional



The good news: Partial correlations can test this
(but need multiple important traits)

How can we quantify tradeoffs?

Tradeoffs are probably multidimensional

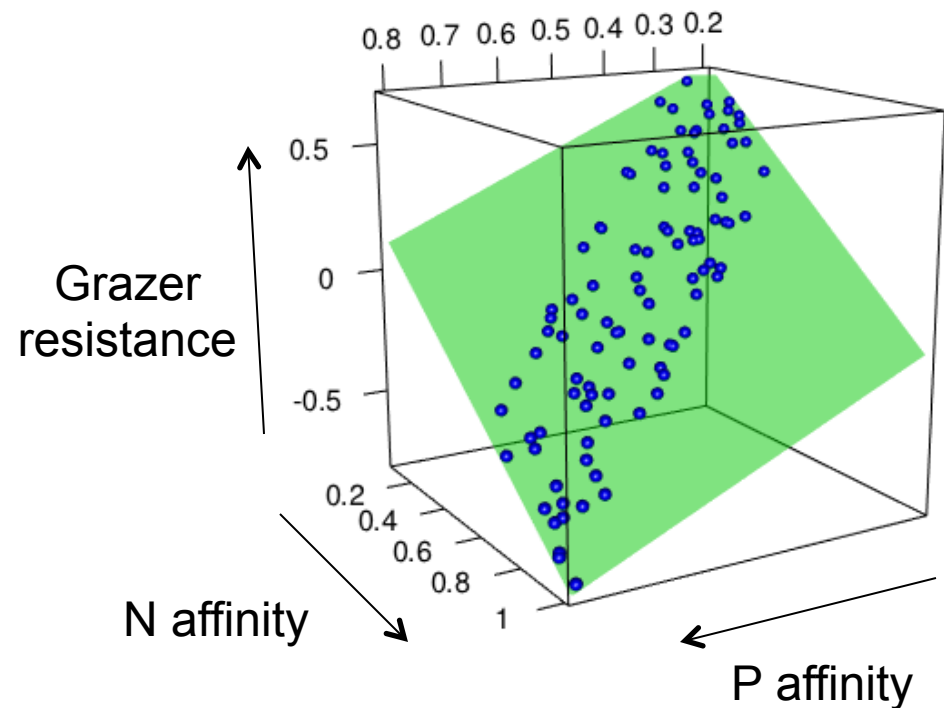


What kind of environment?

Relative importance of N, P, grazers vary a lot

How can we quantify tradeoffs?

Environmental variation determines which dimensions are important

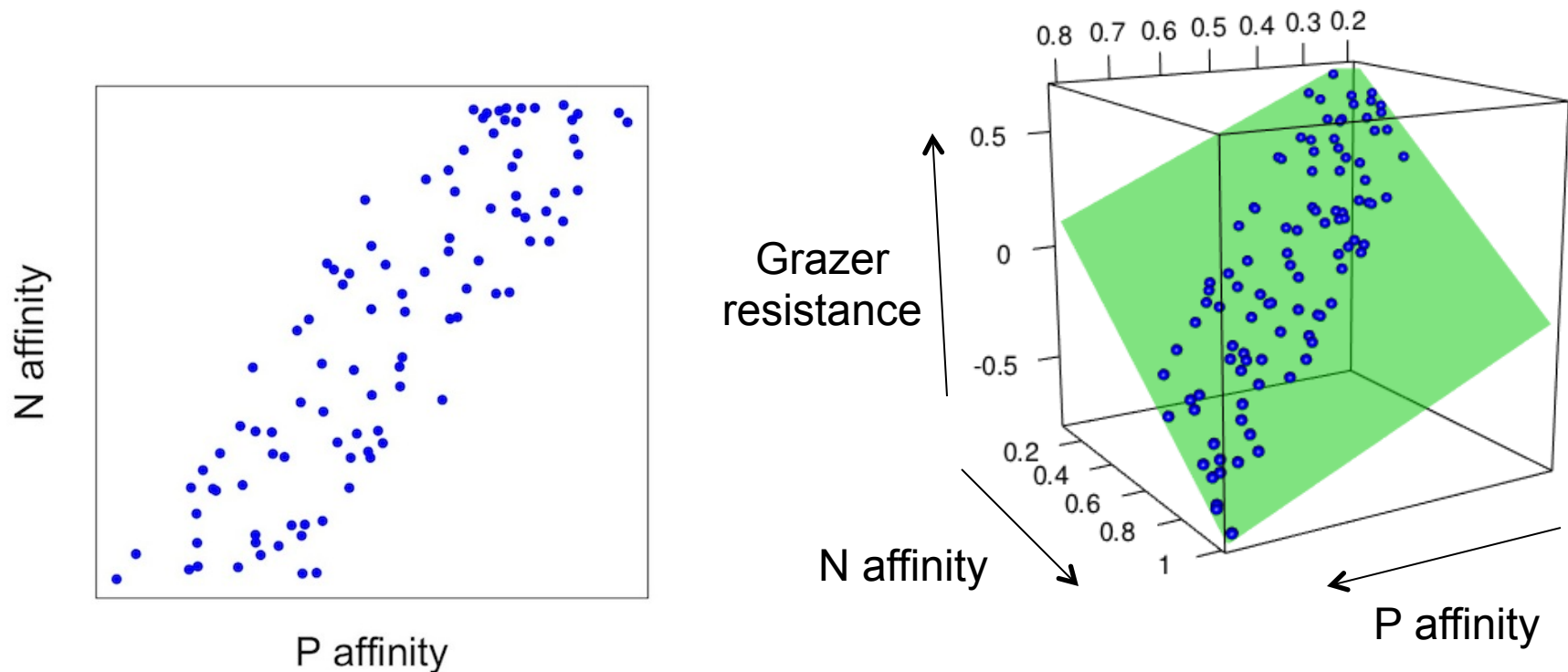


What kind of environment?

Little N:P variation, much variation in grazing pressure

How can we quantify tradeoffs?

Environmental variation determines which dimensions are important

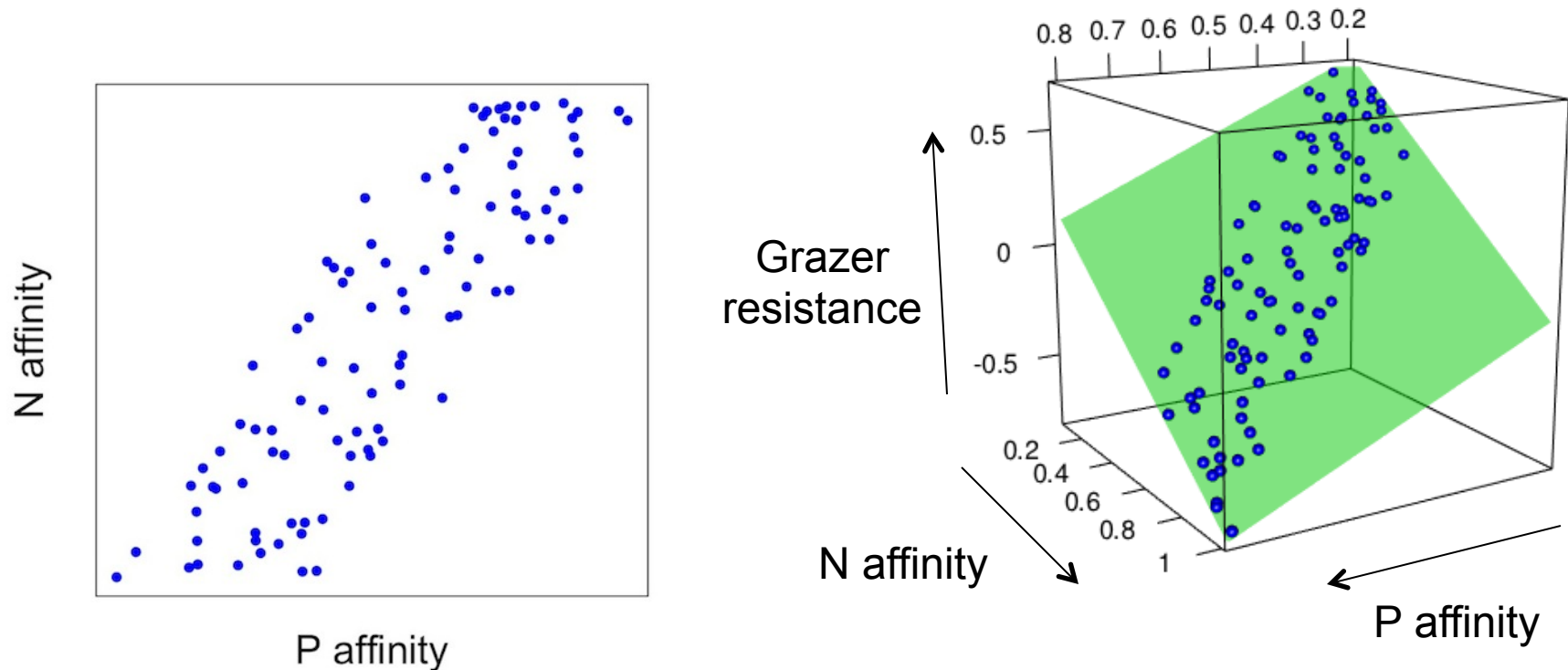


What kind of environment?

Little N:P variation, much variation in grazing pressure

How can we quantify tradeoffs?

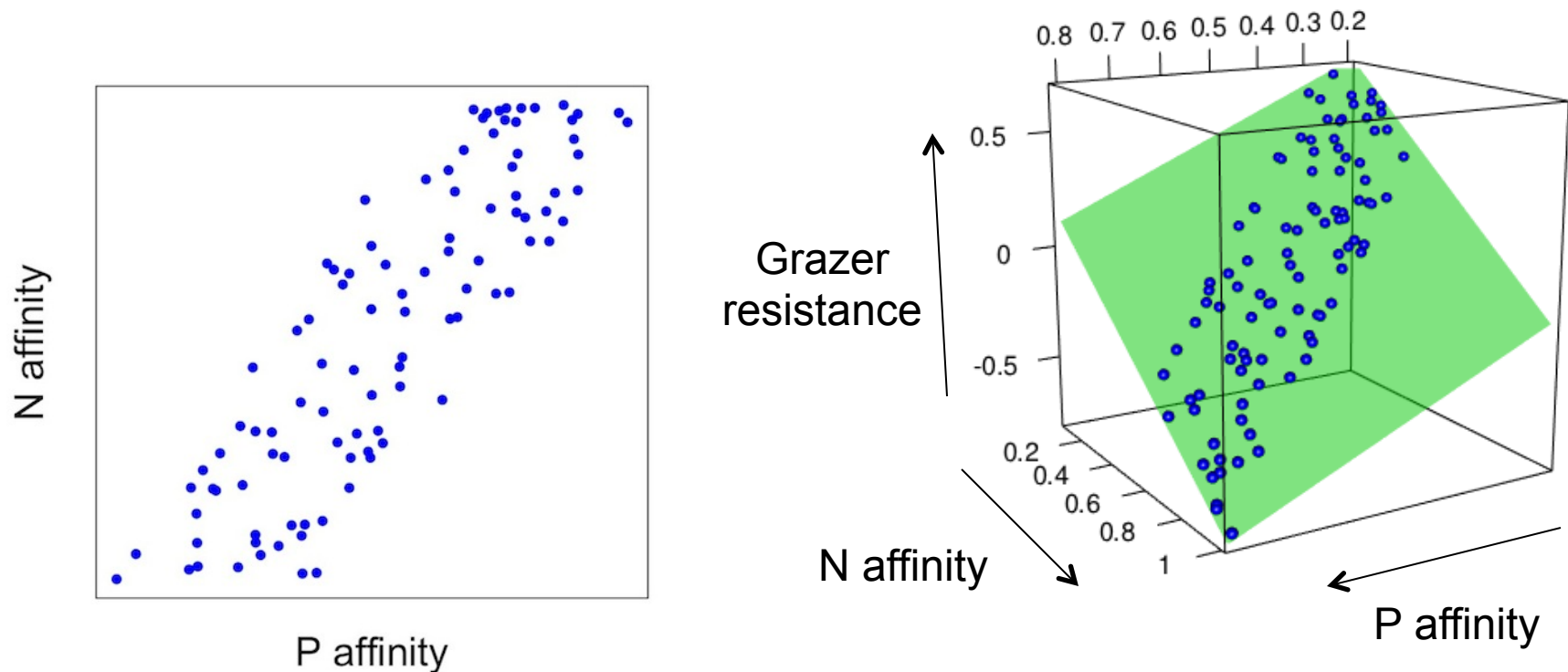
Environmental variation determines which dimensions are important



The good news: Tradeoffs associated with the most important environmental variation should be most evident.

How can we quantify tradeoffs?

Environmental variation determines which dimensions are important



N affinity and P affinity still have negative partial correlation
(requires good data to see)

Velocity / Affinity / Storage

Testing for a **velocity-affinity-storage** tradeoff (Sommer 1984)

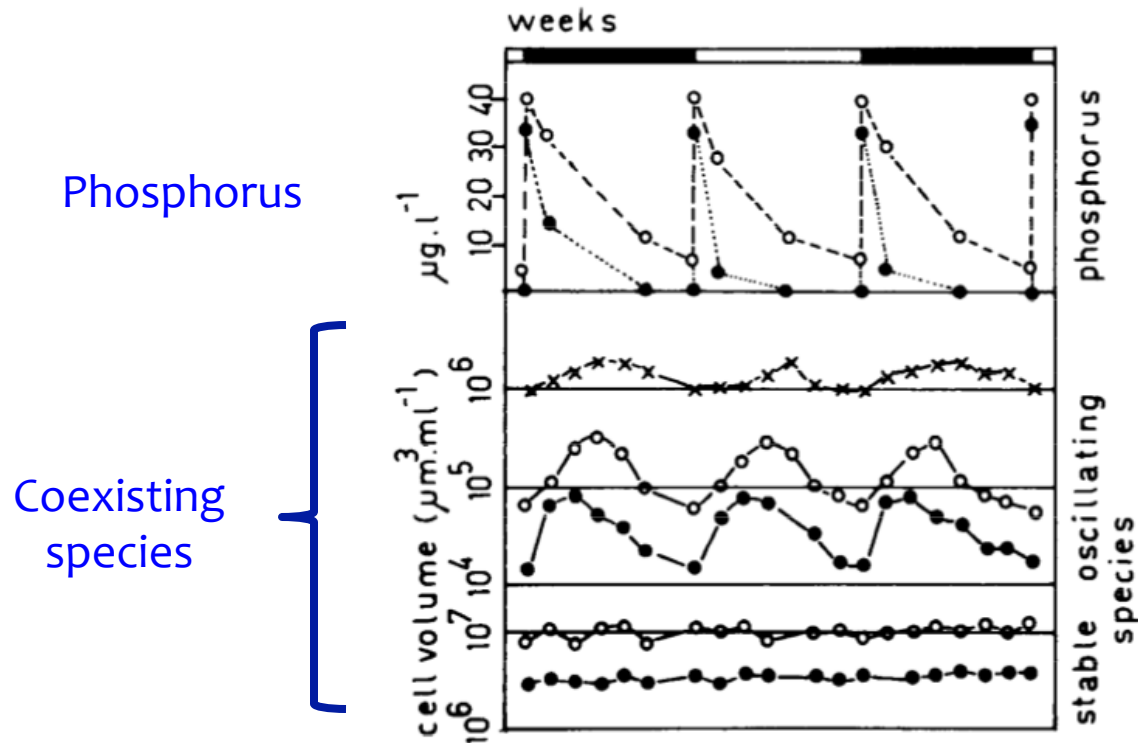
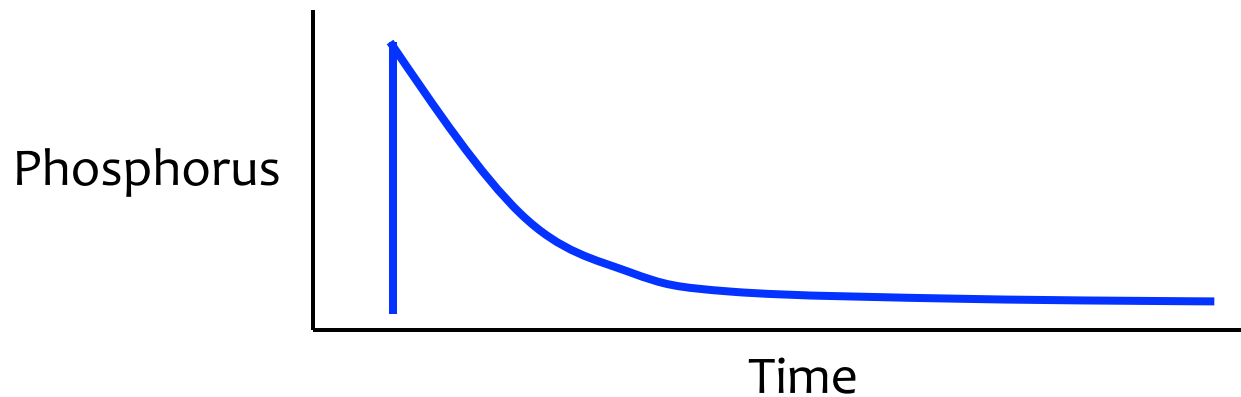


Fig. 1. Example of oscillating equilibrium (experiment with Si:P = 200:1). Upper panel—concentration of total (○) and soluble reactive (●) phosphorus. Middle panel—cell volume of oscillating species, *Mougeotia thylespora* (×), *Scenedesmus quadricauda* (○), and *Chlorella* sp. (●). Lower panel—cell volume of stable species, *Synedra acus* (○), *Diatoma elongatum* (●).

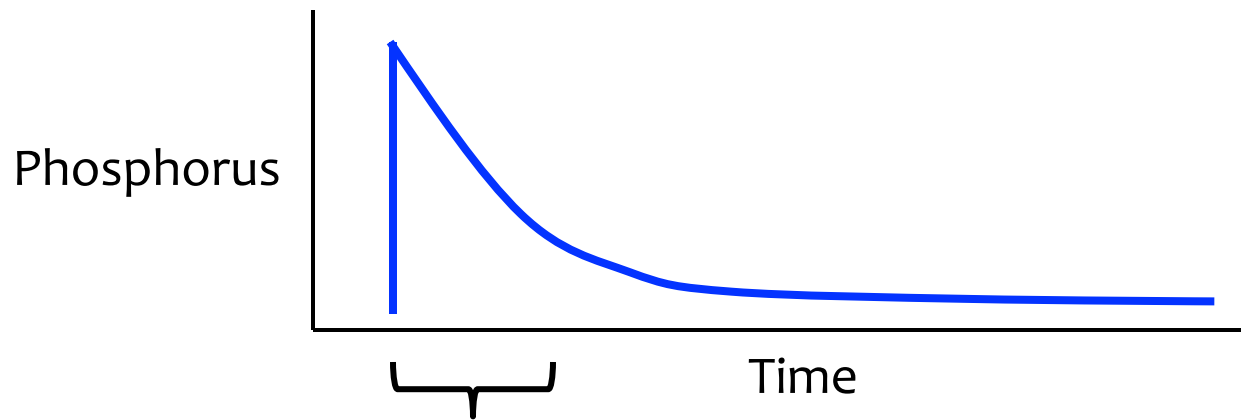
Velocity / Affinity / Storage

Three ways to adapt to fluctuating nutrient supply



Velocity / Affinity / Storage

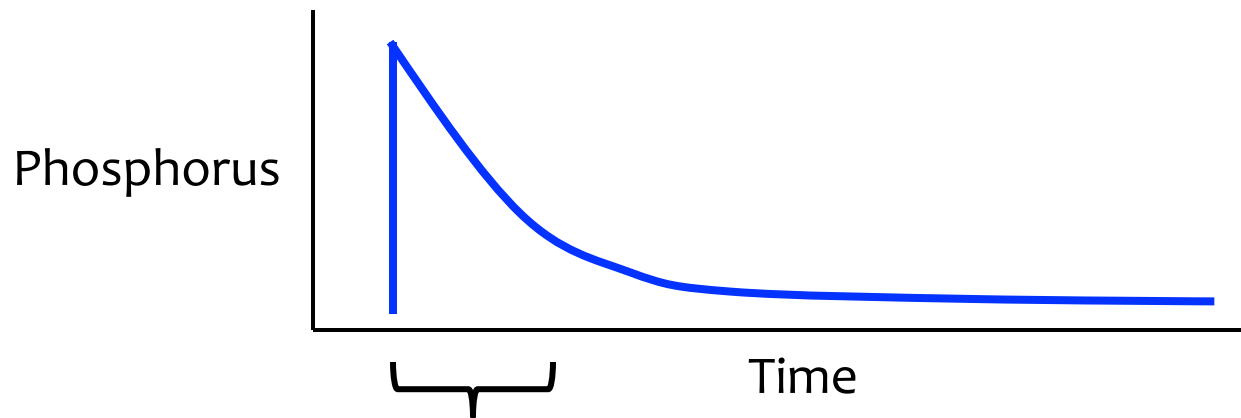
Three ways to adapt to fluctuating nutrient supply



“Velocity” = grow fast when resource abundant

Velocity / Affinity / Storage

Three ways to adapt to fluctuating nutrient supply

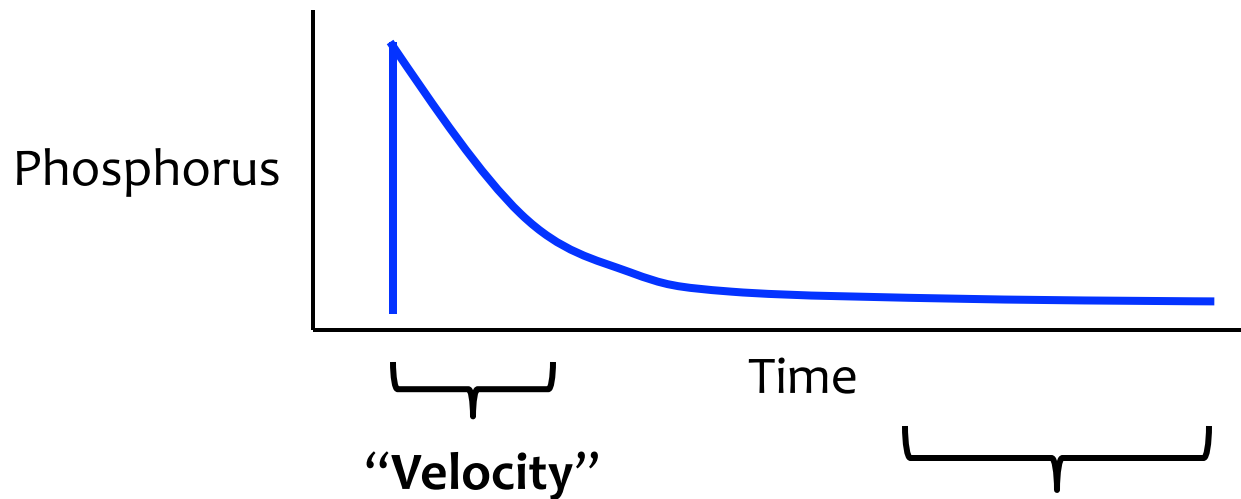


“**Velocity**” = grow fast when resource abundant

- maximum growth rate = $\mu_{\max}$

Velocity / Affinity / Storage

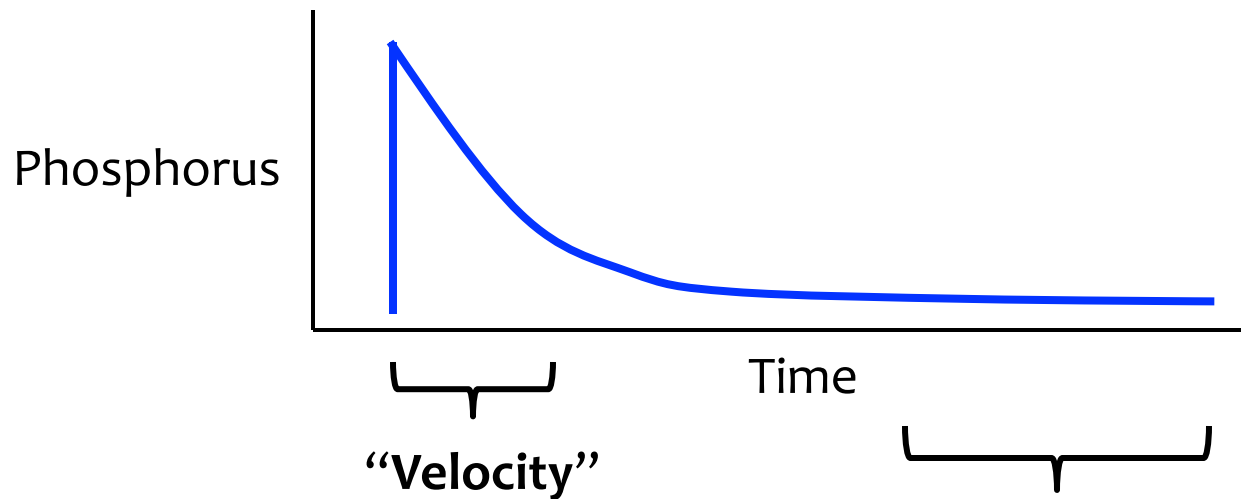
Three ways to adapt to fluctuating nutrient supply



“Affinity” = maintain growth when resource low

Velocity / Affinity / Storage

Three ways to adapt to fluctuating nutrient supply

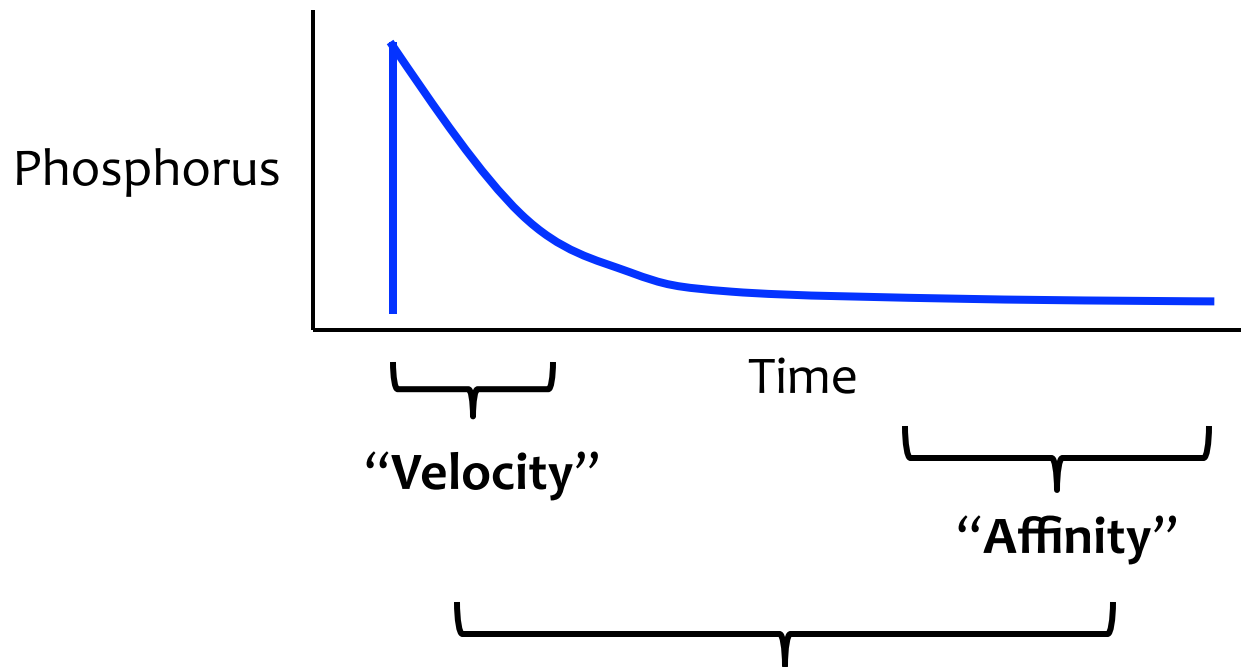


“**Affinity**” = maintain growth when resource low

- scaled P affinity = P_{saff} = competitive ability for low P

Velocity / Affinity / Storage

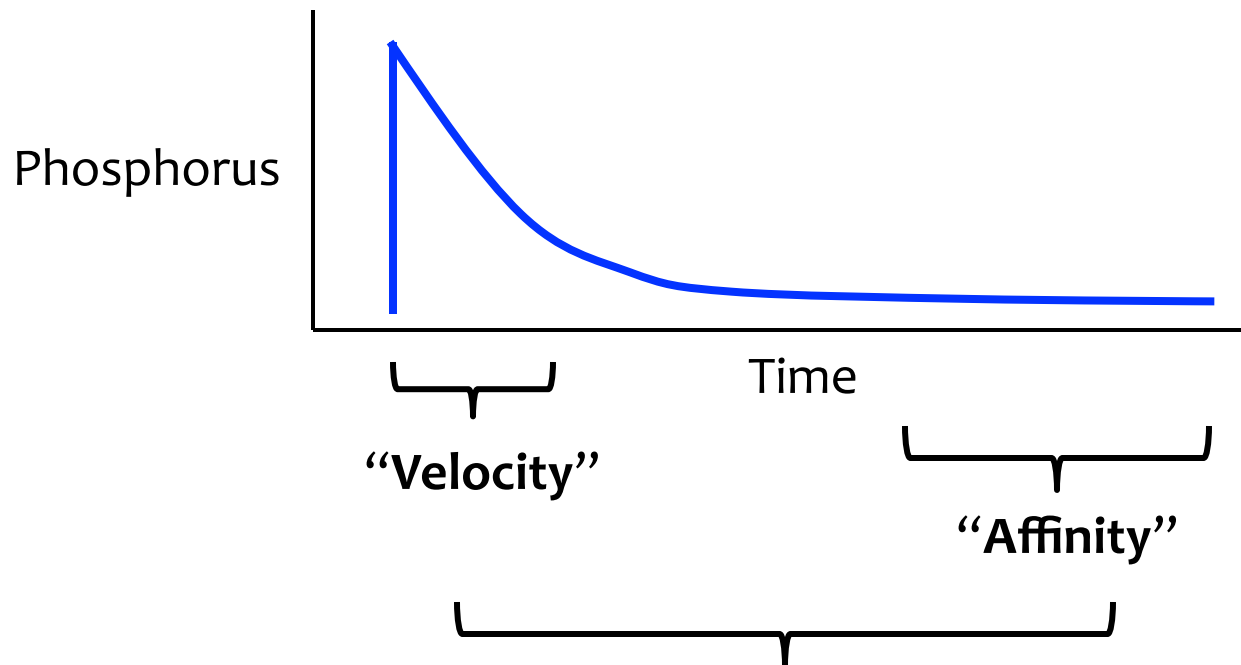
Three ways to adapt to fluctuating nutrient supply



“Storage” = store abundant resource for growth later

Velocity / Affinity / Storage

Three ways to adapt to fluctuating nutrient supply



“**Storage**” = store abundant resource for growth later

- P storage capacity = $Q_{\max}$

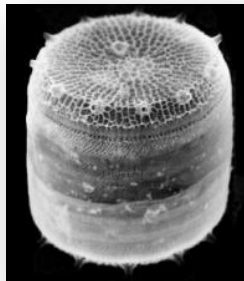
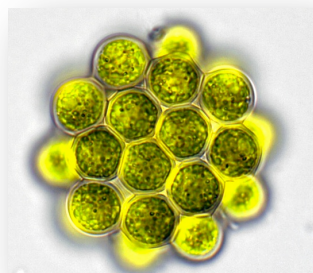
Multidimensional tradeoffs and phytoplankton coexistence

Data from published lab experiments

Multivariate data are often incomplete

29 species for which at least 2 traits were measured

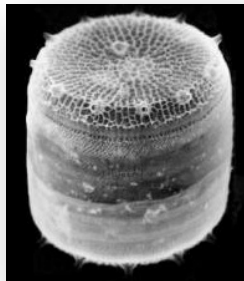
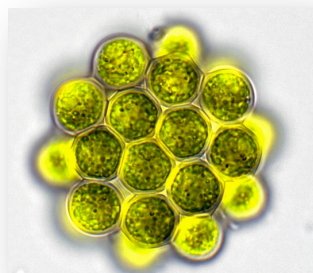
mu.max	P.saff	Q.max
0.4580000	634.920635	3.18e-09
0.7020000	168.622913	1.59e-08
0.9390000	7.554346	7.70e-09
0.8110000	353.684211	1.16e-08
0.5710000	38.047138	1.45e-06
0.7310000	1182.266010	6.60e-09
0.9080000	68.000000	6.78e-08
0.6310000	244.831918	1.59e-08
NA	3.182403	3.25e-08
NA	4.549120	2.24e-08
0.8680000	43.881857	3.06e-08
0.4860000	241.269841	4.69e-08
0.5980000	173.674918	1.52e-08
NA	1201.142709	4.15e-08
1.2860000	387.096774	8.33e-09
0.7880000	182.648402	4.14e-08
1.3700000	2.385950	1.45e-08
NA	43.060913	7.31e-07
0.5230000	16.216216	5.35e-07
NA	14.396135	6.45e-09
1.0862508	63.699469	7.31e-08
0.6677209	642.402184	NA
1.4985399	21.077844	NA
0.9705773	14.671053	NA
0.5795237	47.384220	7.33e-08
1.3460621	116.514691	1.16e-08
0.5704568	354.261364	NA
NA	235.014620	7.33e-08
NA	24.449878	5.25e-07



Multidimensional tradeoffs and phytoplankton coexistence

Methods for quantifying multivariate patterns with missing data

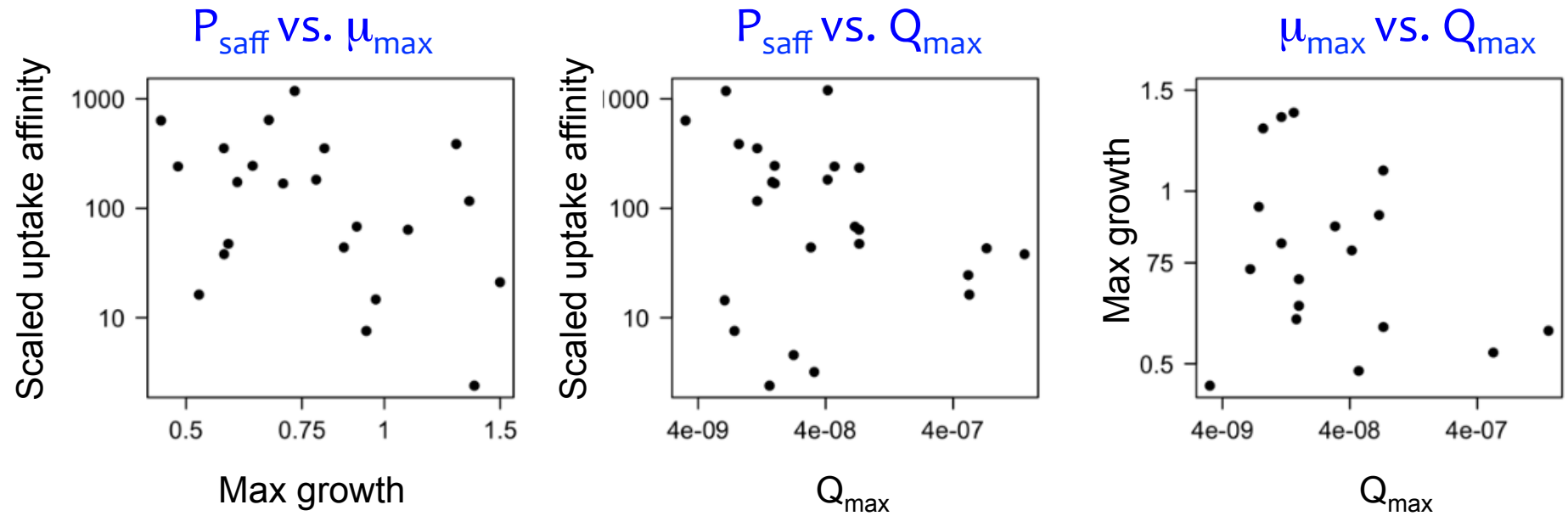
Which underlying multivariate distribution is most likely, given the observed data.



mu.max	P.saff	Q.max
0.4580000	634.920635	3.18e-09
0.7020000	168.622913	1.59e-08
0.9390000	7.554346	7.70e-09
0.8110000	353.684211	1.16e-08
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1.2860000	387.096774	8.33e-09
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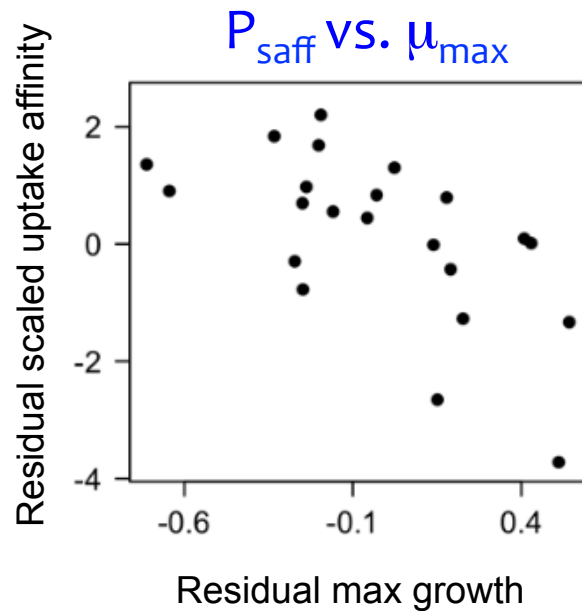
Testing for multidimensional tradeoffs

Raw data

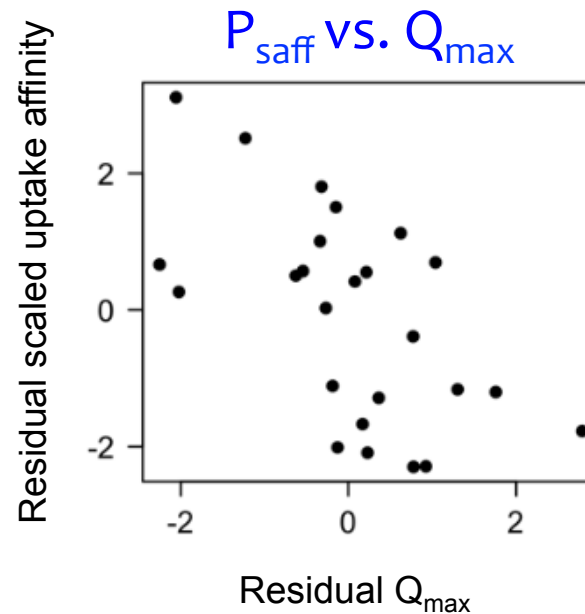


Testing for multidimensional tradeoffs

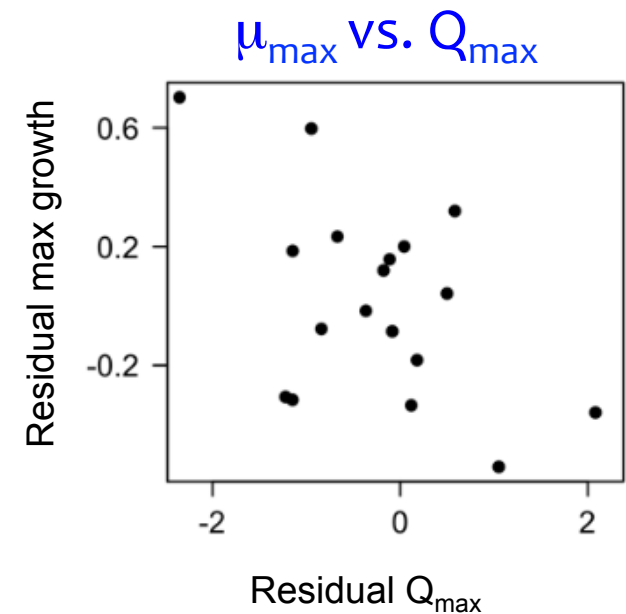
Partial correlations



95% CI: (-0.86, -0.35)



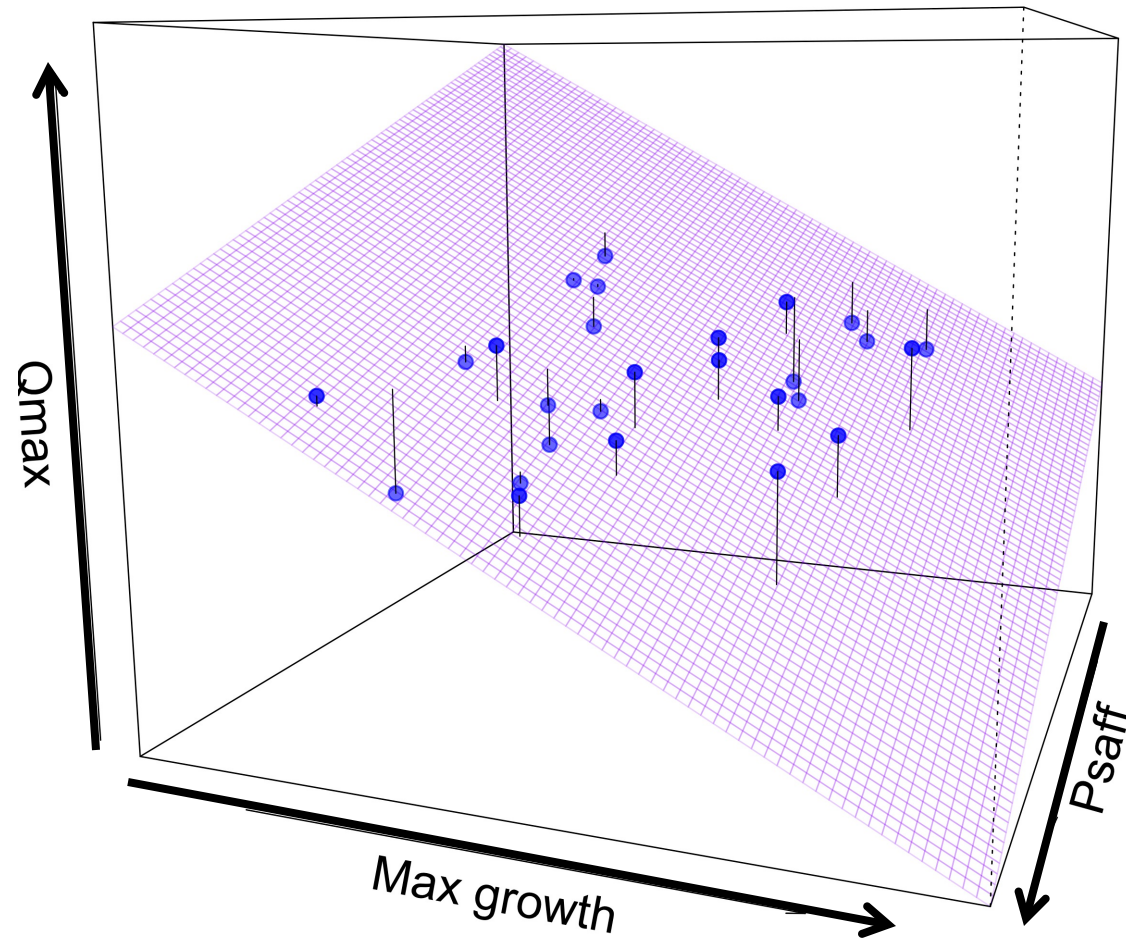
(-0.79, -0.20)



(-0.86, -0.20)

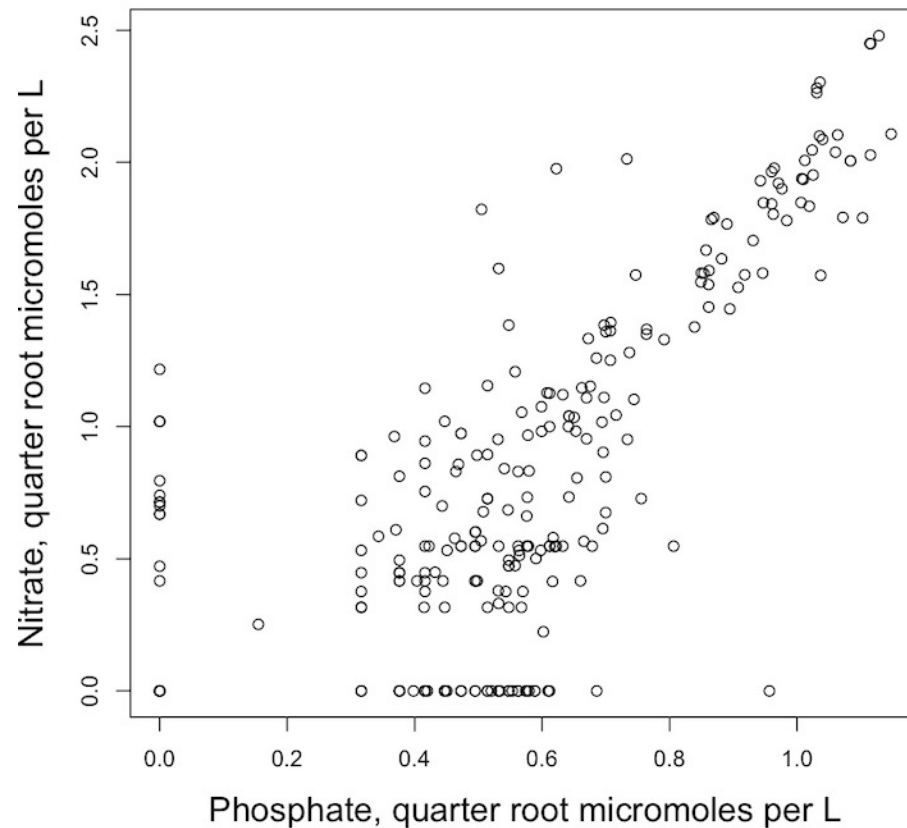
Evidence for a three-way tradeoff:
A multivariate approach is essential

Tradeoffs -> Mechanistic Model



How can we quantify tradeoffs?

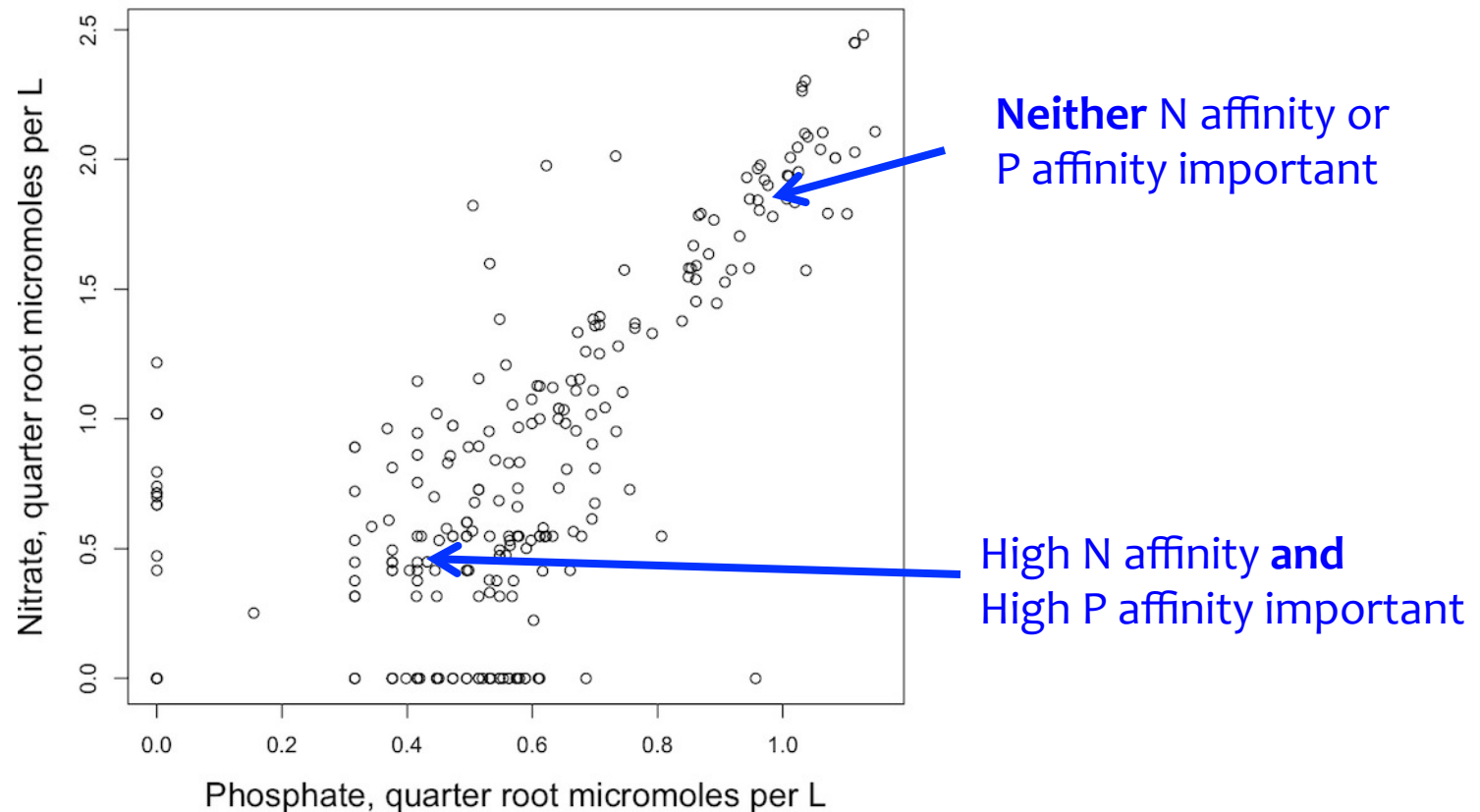
Environmental variation determines which dimensions are important



Atlantic Meridional Transects 1-6
Data from Sal et al. 2013, *Ecology*

How can we quantify tradeoffs?

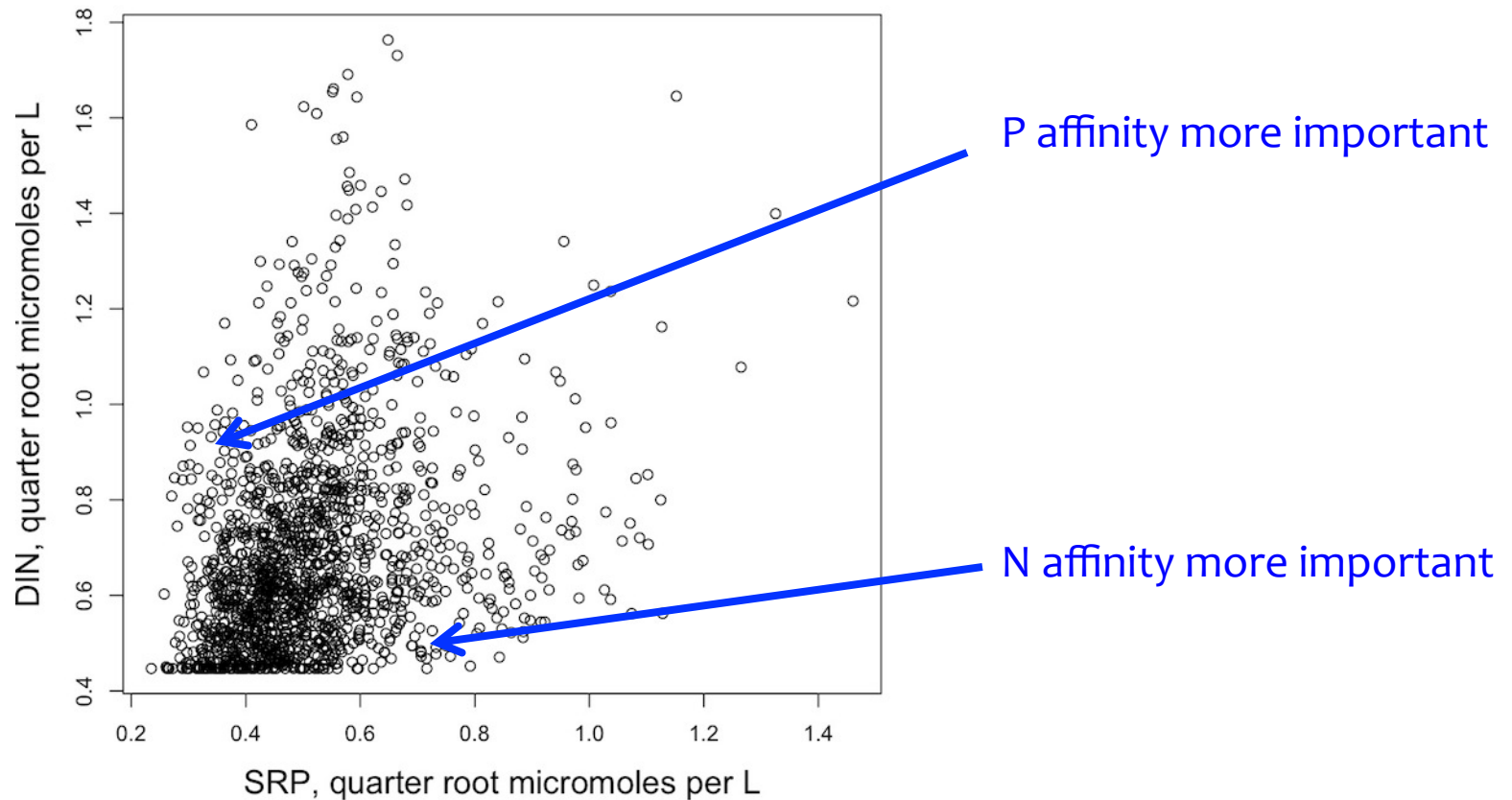
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Atlantic Meridional Transects 1-6
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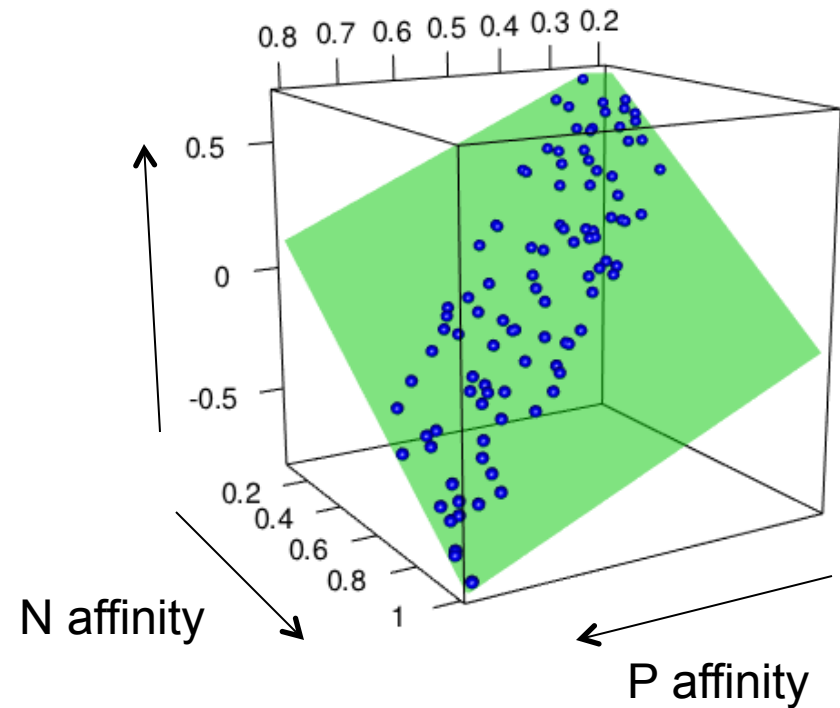
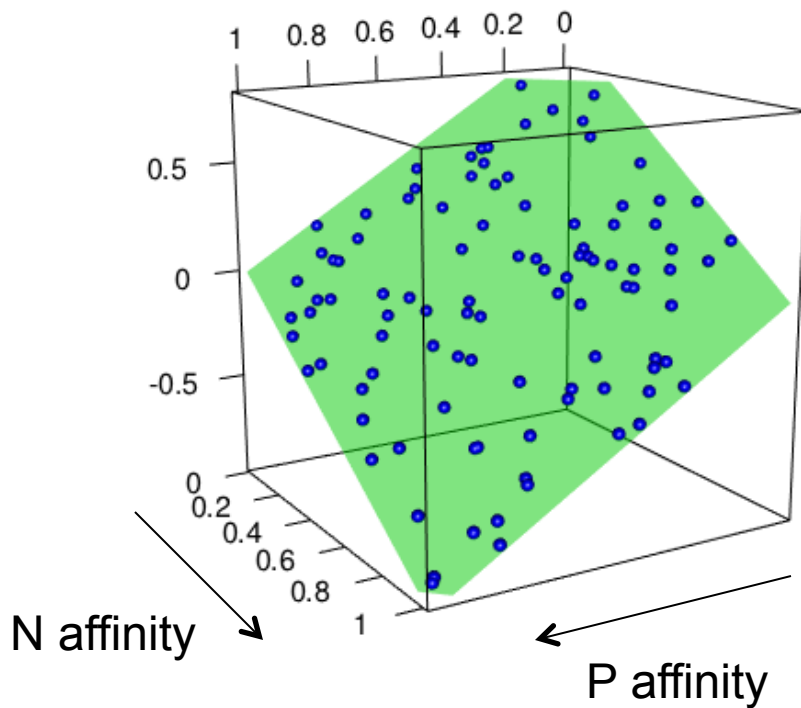
Environmental variation determines which dimensions are important



Continental US Lakes
Data from US EPA

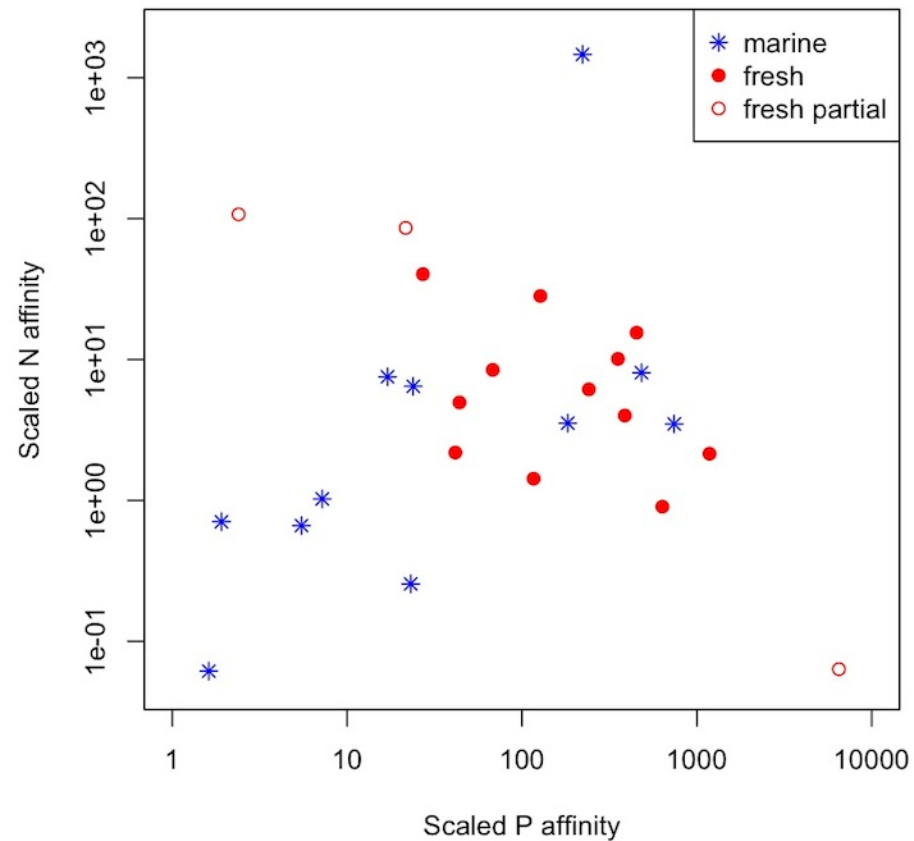
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Environmental variation determines which dimensions are important



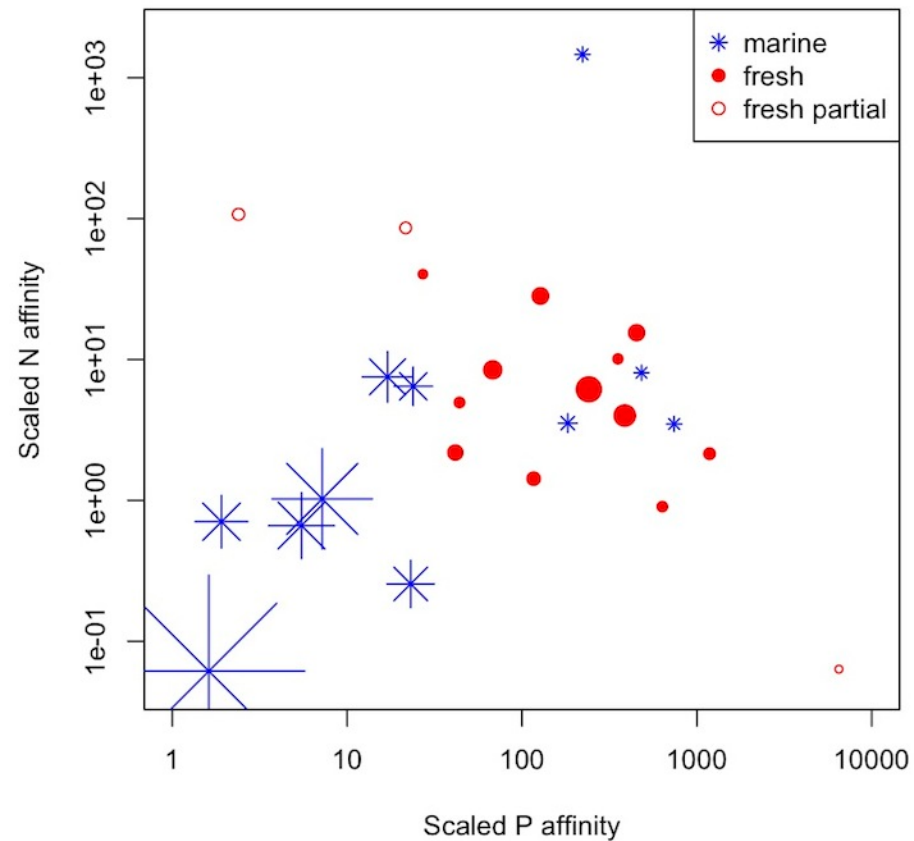
How can we quantify tradeoffs?

Environmental variation determines which dimensions are important



How can we quantify tradeoffs?

Environmental variation determines which dimensions are important



How can we quantify tradeoffs?

Key challenges in tradeoff identification/quantification

- tradeoffs among multiple traits
- trait variation across species depends on variation and correlation of environmental factors
- existing trait information is biased (coastal, larger phytos)

The bad news:

- raw trait correlations can be misleading

The good news:

- tradeoffs associated with important environmental variation should be most evident
- multivariate approaches seem to help

We need multiple traits measured on the same species,
from the full range of taxa / environments

How can we quantify tradeoffs?

Acknowledgements

NSF

Litchman-Klausmeier lab, Kellogg Biological Station, Fred Adler, three anonymous reviewers

