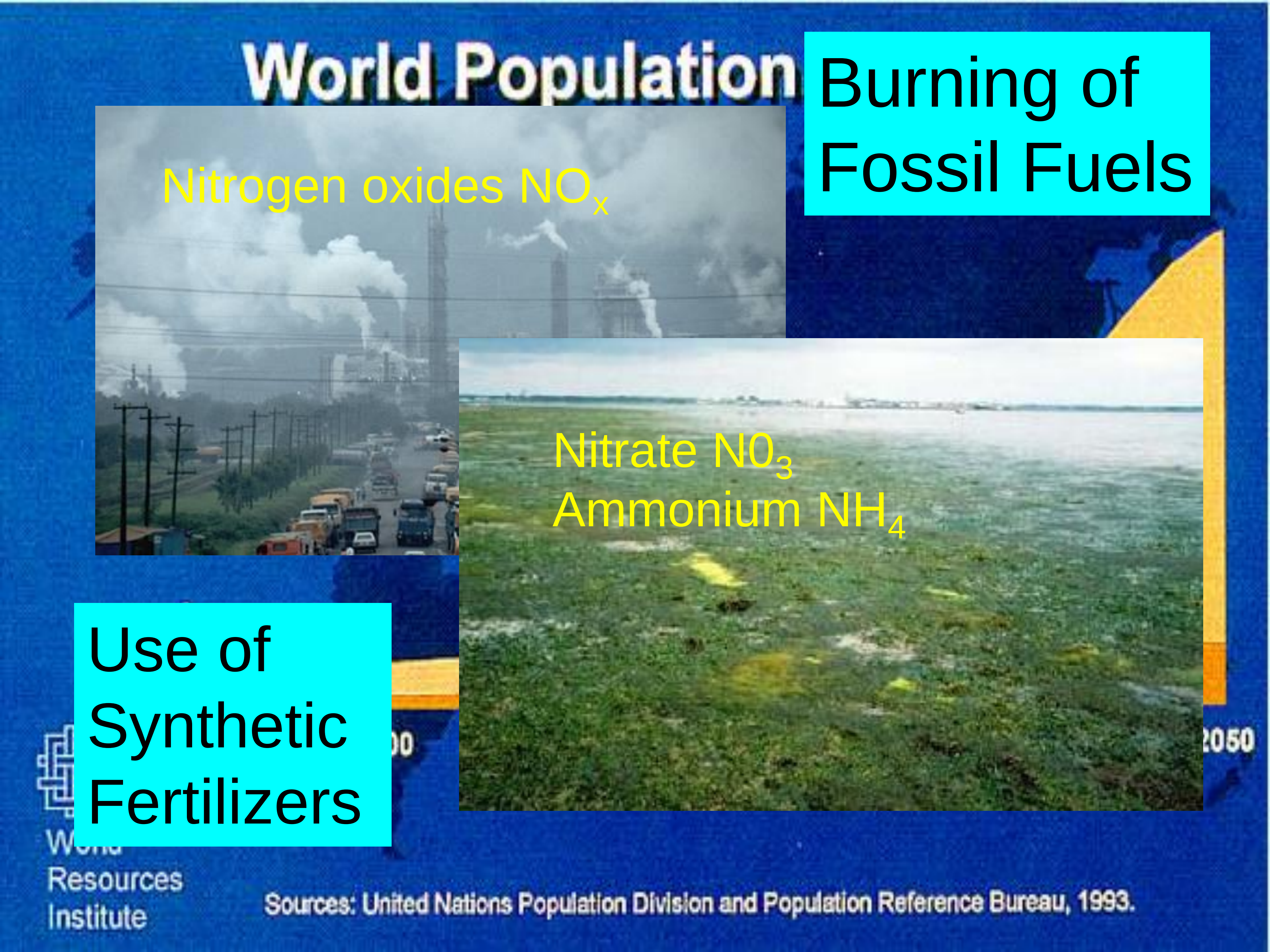
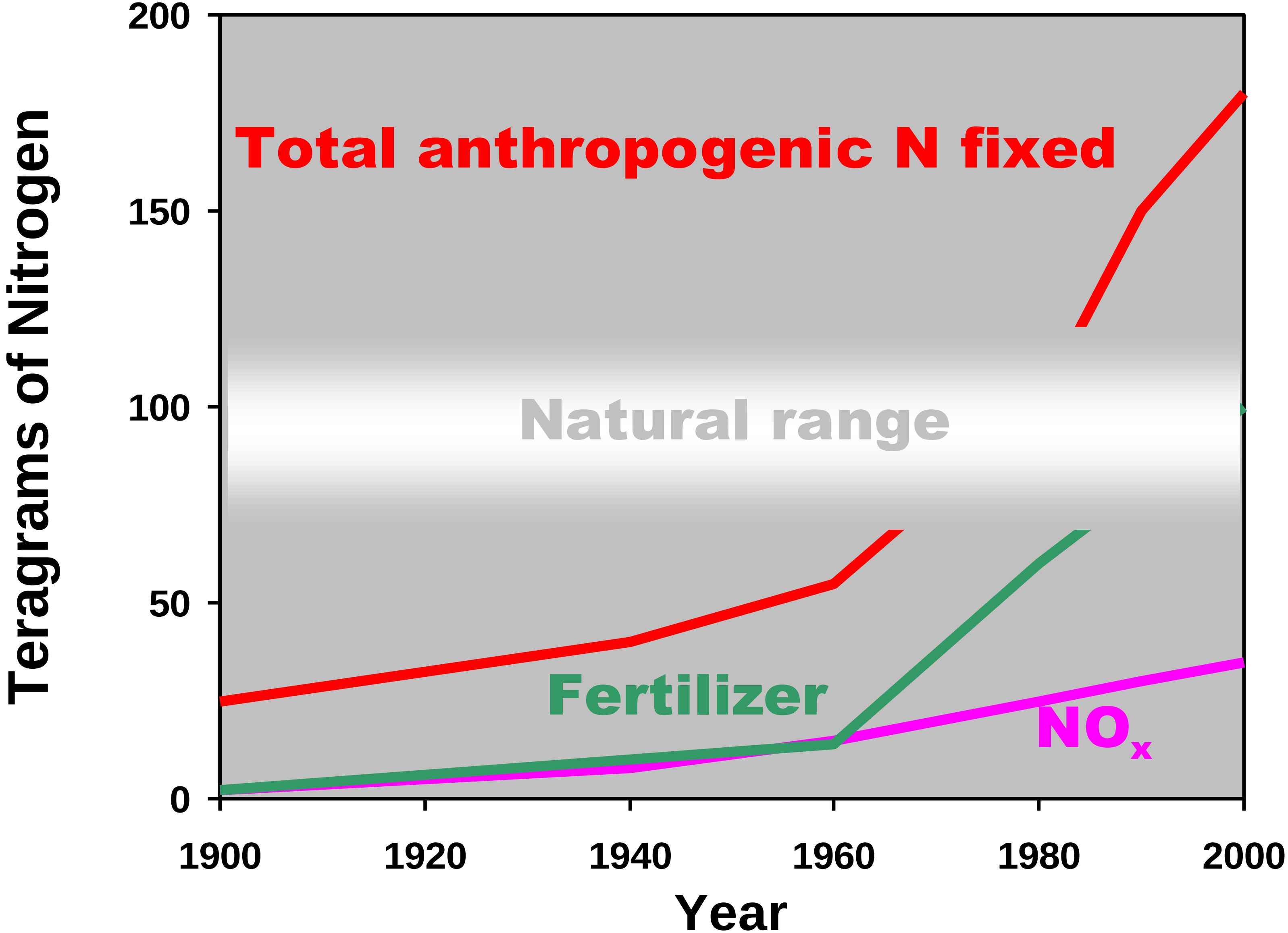
# The Ecological Impacts Of Nitrogen Deposition: Insights From The Carnivorous Pitcher Plant *Sarracenia purpurea*

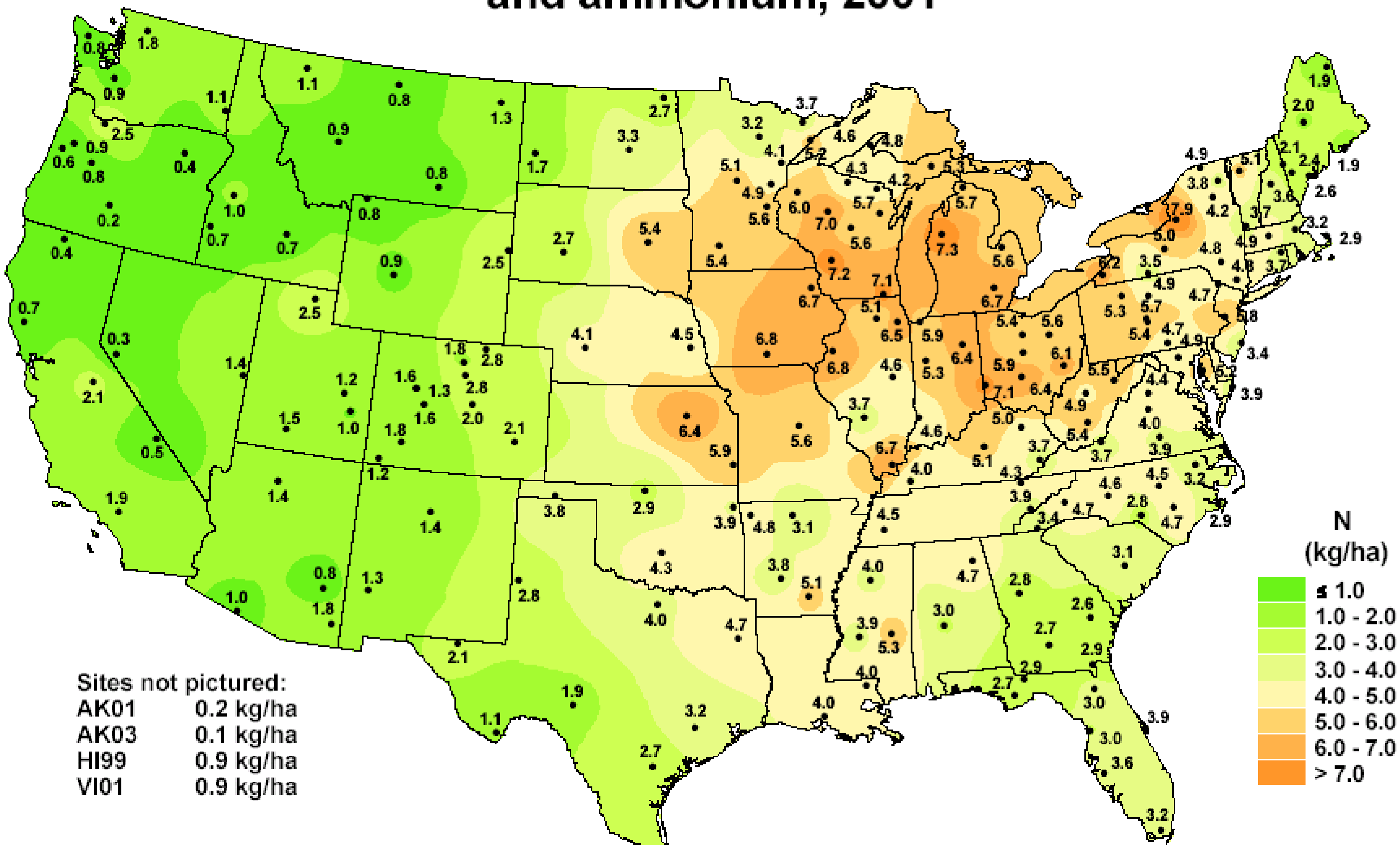
Nicholas J. Gotelli
Department of Biology
University of Vermont
Burlington, VT 05405
U.S.A.


World Population
Burning of Fossil Fuels
Nitrogen oxides $NO_x$
Nitrate $N0_3$
Ammonium $NH_4$
Use of Synthetic Fertilizers
00
2050
Resources
Institute
Sources: United Nations Population Division and Population Reference Bureau, 1993.



Total anthropogenic N fixed
Natural range
Fertilizer
$NO_x$
Teragrams of Nitrogen
200
150
100
50
0
1900
1920
1940
1960
1980
2000
Year

# Inorganic nitrogen wet deposition from nitrate and ammonium, 2001

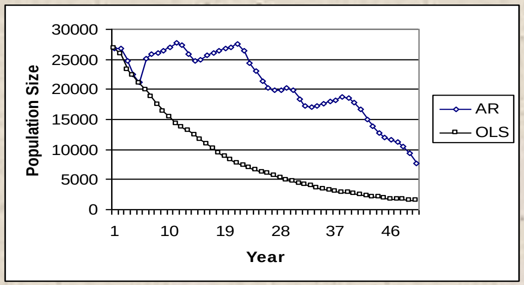



National Atmospheric Deposition Program/National Trends Network
http://nadp.sws.uiuc.edu

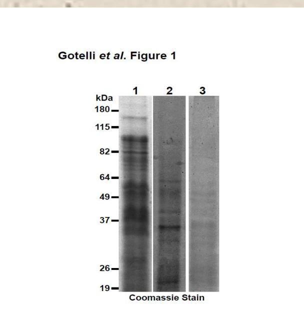
*Sarracenia purpurea*
The Northern Pitcher Plant

# Effects of N Deposition

- Individual
  - ➢ Altered morphology
  - ➢ Changes in reproduction, survivorship




- Population
  - ➢ Increased long-term extinction risk
  - ➢ Changes in short-term dynamics
- Community
  - ➢ Changes in abundance and composition
  - ➢ Proteomic early-warning indicators



# Effects of N Deposition on Carnivorous Plants

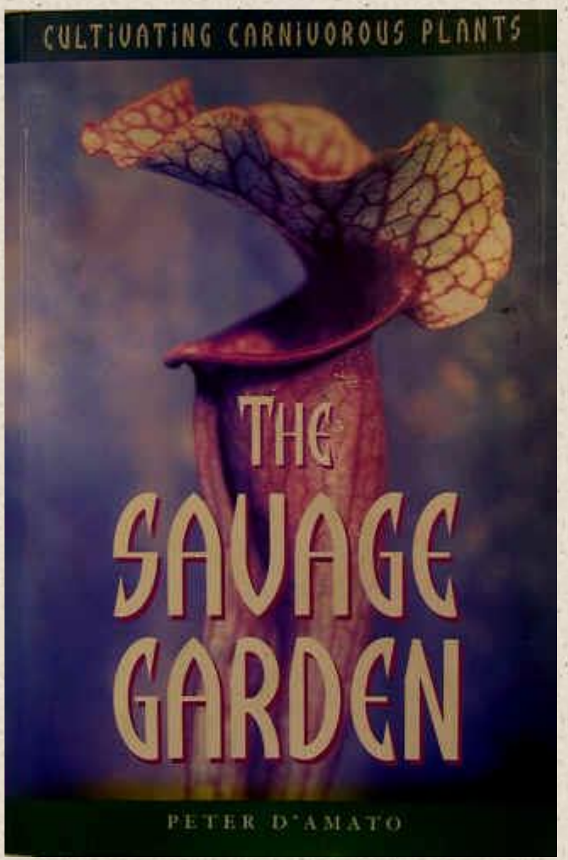
- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

# Effects of N Deposition on Carnivorous Plants

- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

# Carnivorous plants: well-known, but poorly studied





# Carnivory in plants

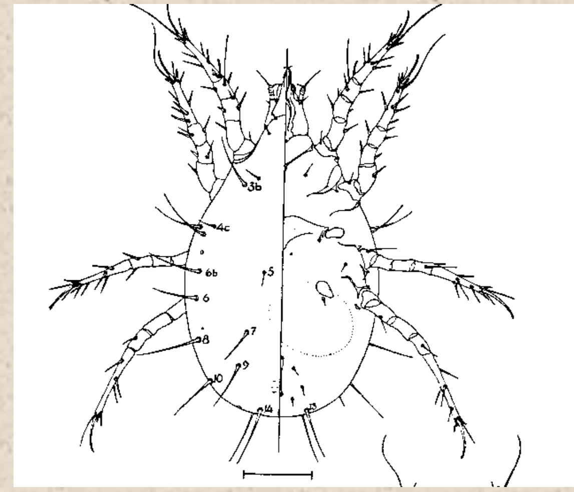
- Phylogenetically diverse
- Morphological, chemical adaptations for attracting, capturing, digesting arthropods
- Common in low N habitats
- Poor competitors for light, nutrients

# The Northern Pitcher Plant
# *Sarracenia purpurea*

- Perennial plant of low-N peatlands
- Lifespan 30-50 y
- Arthropod prey capture in water-filled pitchers
- Diverse inquiline community in pitchers

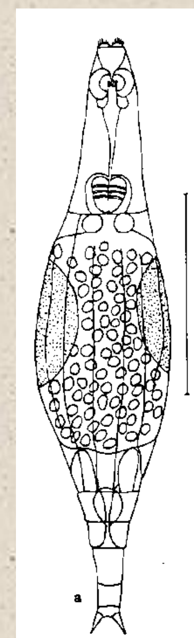
# The Inquilines

***Sarraceniopus gibsoni***



***Wyeomyia smithii***

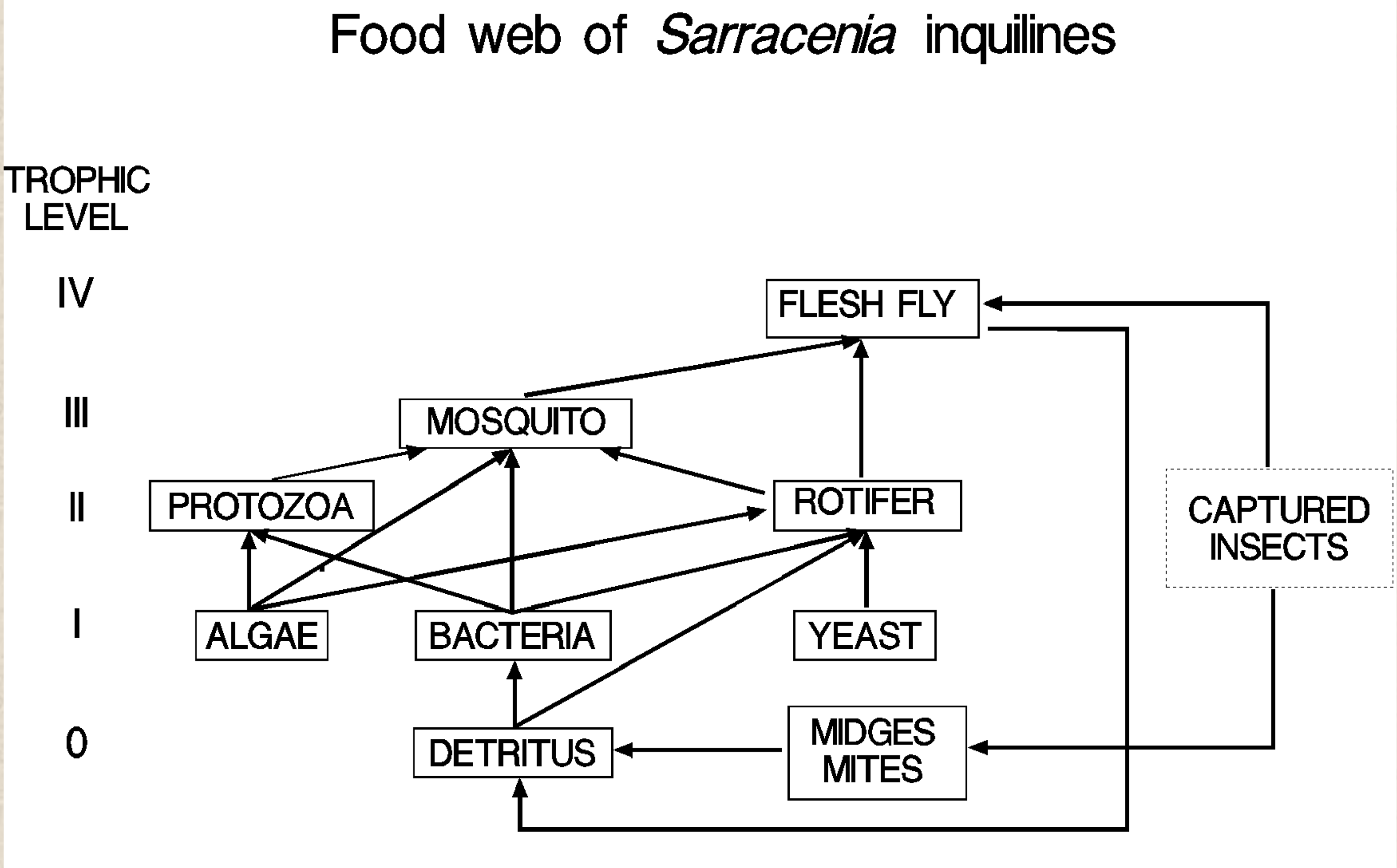
***Blaesoxipha fletcheri***



***Habrotrocha rosa***

***Metriocnemus knabi***

# Inquiline food web



# Phyllodia

- Flat leaves
- No prey capture
- High concentration of chlorophyll, stomates
- Photosynthetically more efficient than pitchers

# Flowering Stalks

- Single stalk per rosette
- Flowering after 3 to 5 years
- Bumblebee, fly pollinated
- Short-distance dispersal of seeds

# Leaf Senescence

- Leaves persist 2-3 years
- Production of new leaves in following spring
- Annual increase in rosette diameter

# Effects of N Deposition on Carnivorous Plants

- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

# Anthropogenic N additions alter growth and morphology

# Nutrient Treatments

- Distilled $H_20$
- Micronutrients
- Low N (0.1 mg/L)
- High N (1.0 mg/L)
- Low P (0.025 mg/L)
- High P (0.25 mg/L)

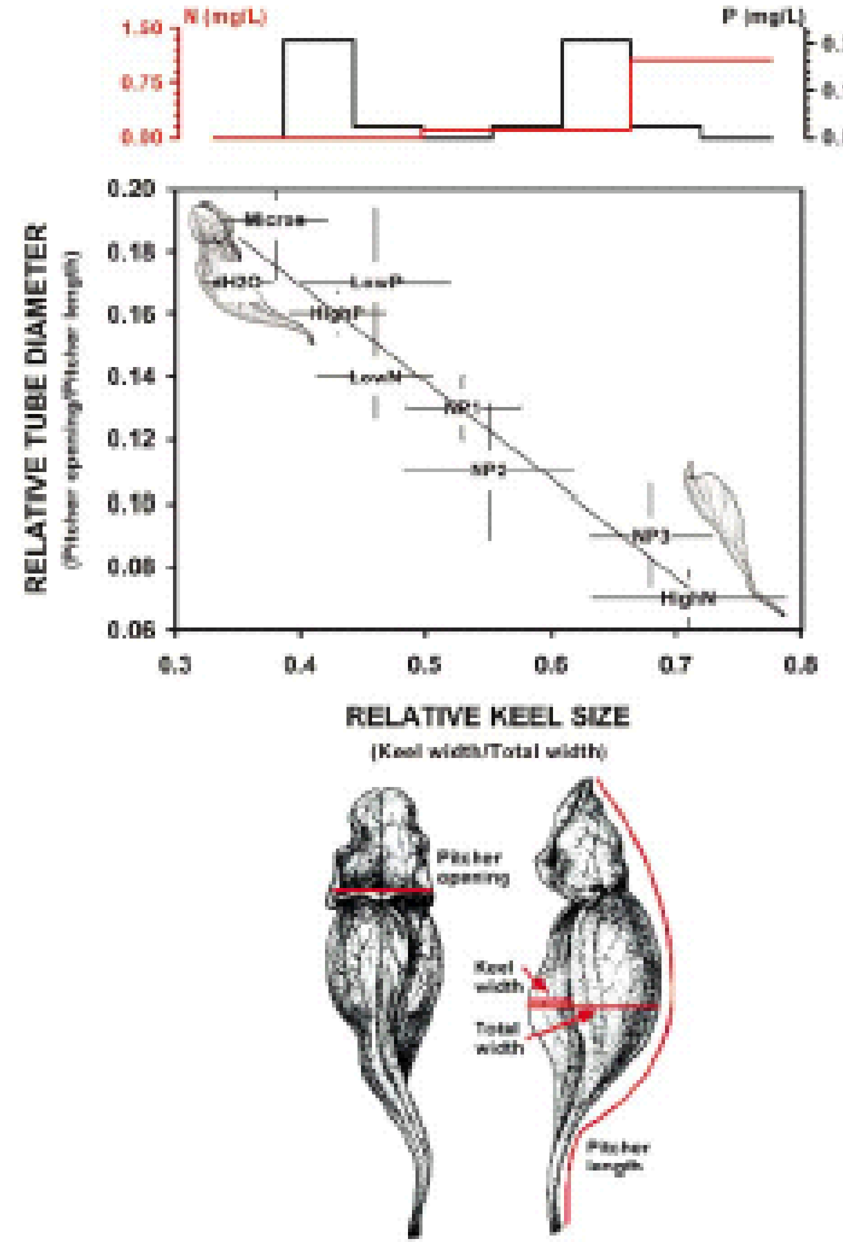
- N:P(1) Low N + Low P
- N:P(2) Low N + High P
- N:P(3) High N + Low P

*Nutrient Source:*

*Micronutrients: Hoaglands*

*N: $NH_4Cl$*

*P: $NaH_2PO_4$*



N (mg/L)
P (mg/L)
1.50
0.75
0.00
0.30
0.15
0.00
RELATIVE TUBE DIAMETER
(Pitcher opening/Pitcher length)
Micro
dH2O
LowP
HighP
LowN
NP1
NP2
NP3
HighN
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.3
0.4
0.5
0.6
0.7
0.8
RELATIVE KEEL SIZE
(Keel width/Total width)
Pitcher opening
Keel width
Total width
Pitcher length

# Anthropogenic N additions alter growth and morphology

Increasing N

# Effects of Anthropogenic N additions

- Increased production of phyllodia
- Phenotypic shift from carnivory to photosynthesis
- Increased probability of flowering

# Contrasting effects of anthropogenic N vs. N derived from prey


Wakefield, A. E., N. J. Gotelli, S. E. Wittman,
and A. M. Ellison. 2005. Prey addition alters
nutrient stoichiometry of the carnivorous
plant *Sarracenia purpurea*. Ecology 86:
1737-1743.

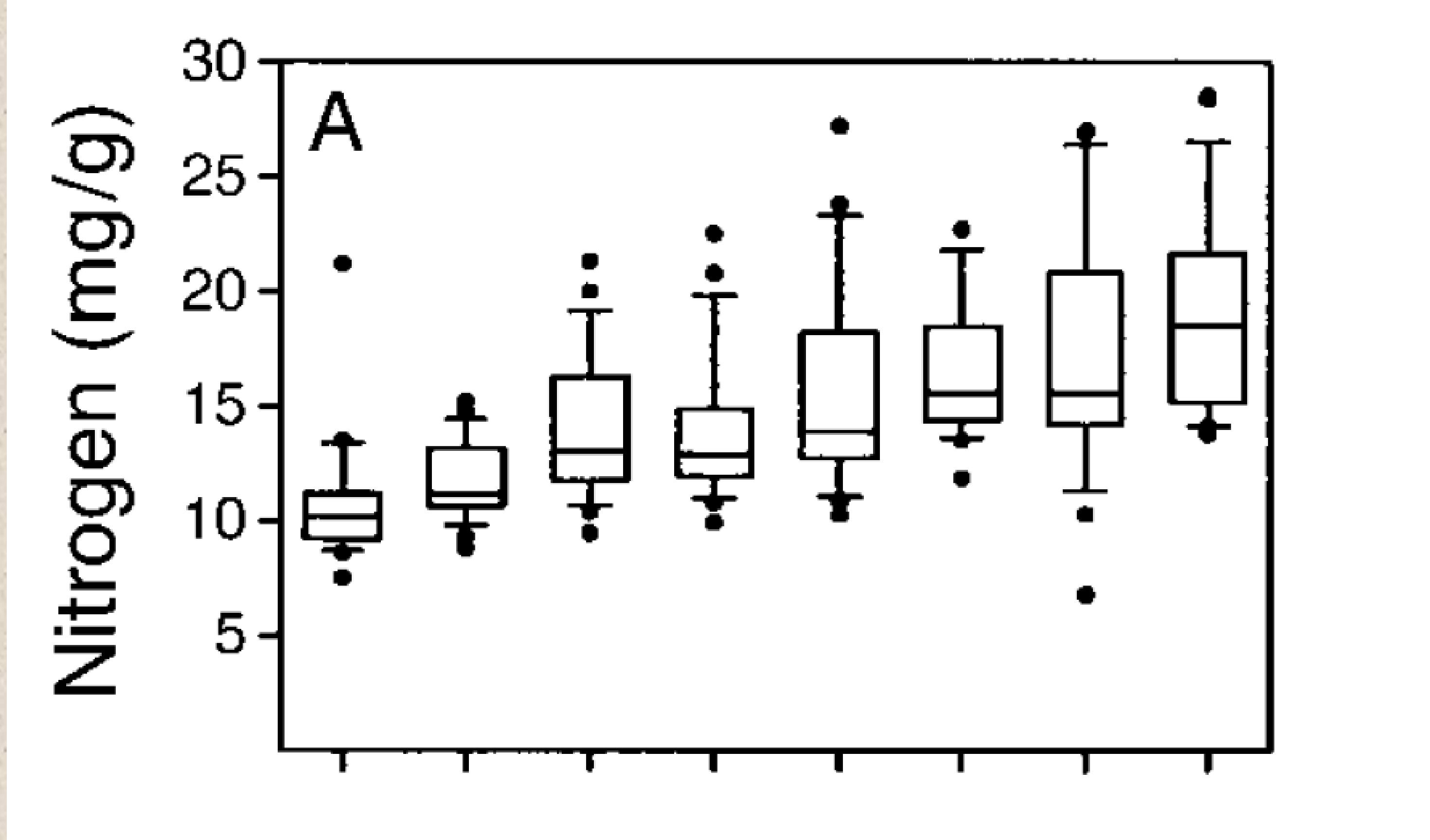
# Food Addition Experiment

- Ecological “press” experiment
- Food supplemented with house flies
- Treatments: 0, 2, 4 ,6, 8,10,12, 14 flies/week
- Plants harvested after one field season

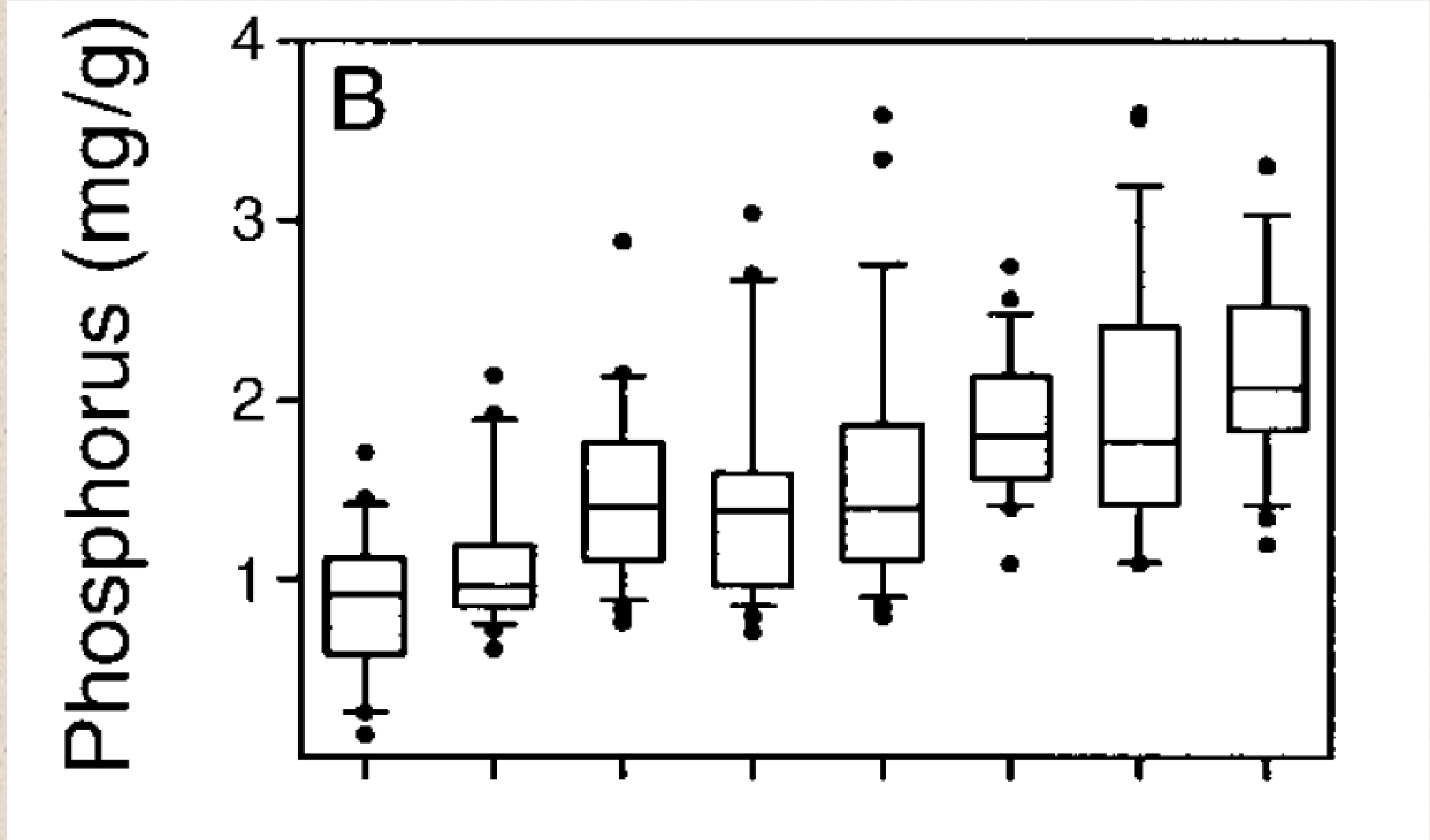
# Food additions do not alter growth and morphology

Increasing prey

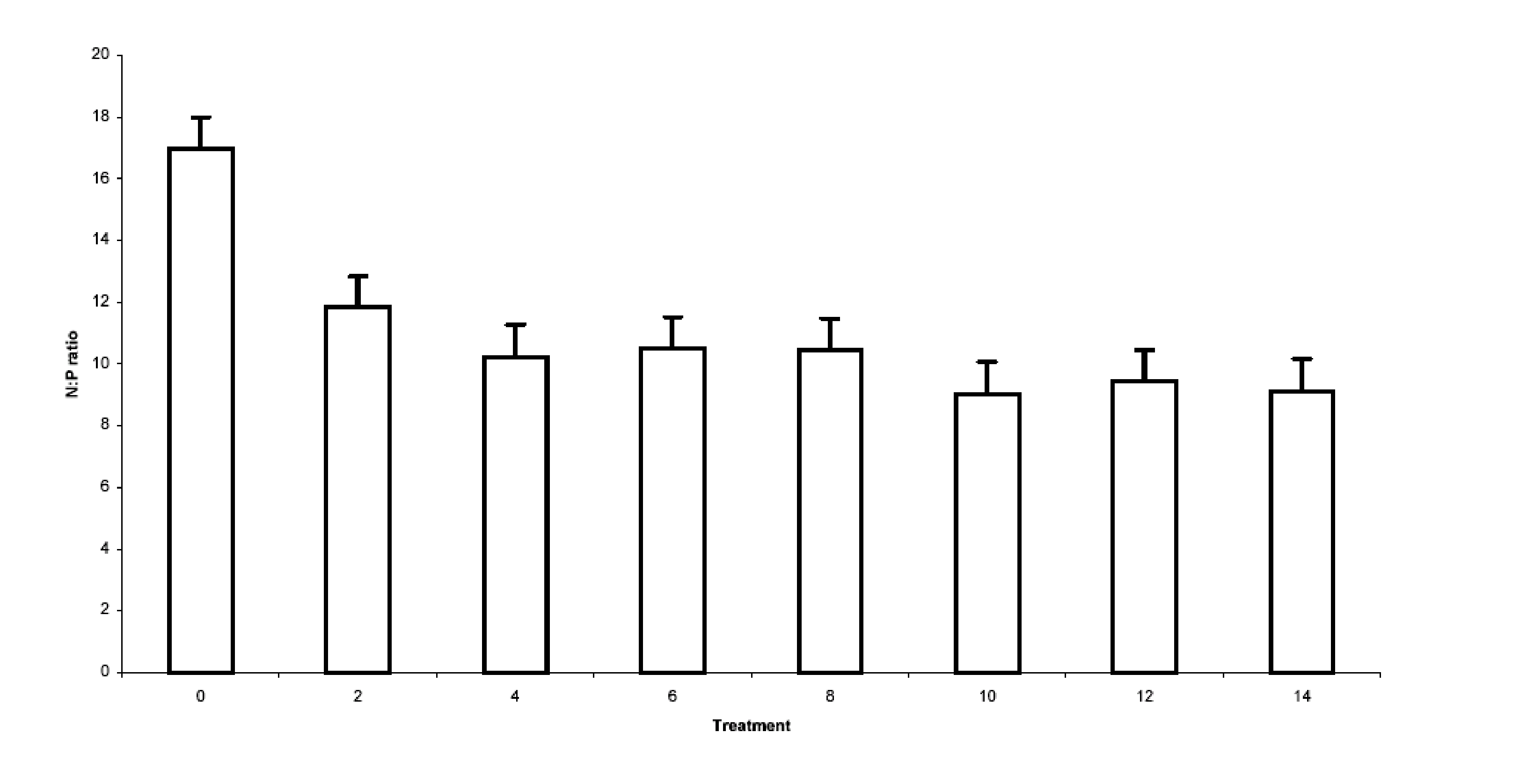
# N uptake <u>increases</u> with food level



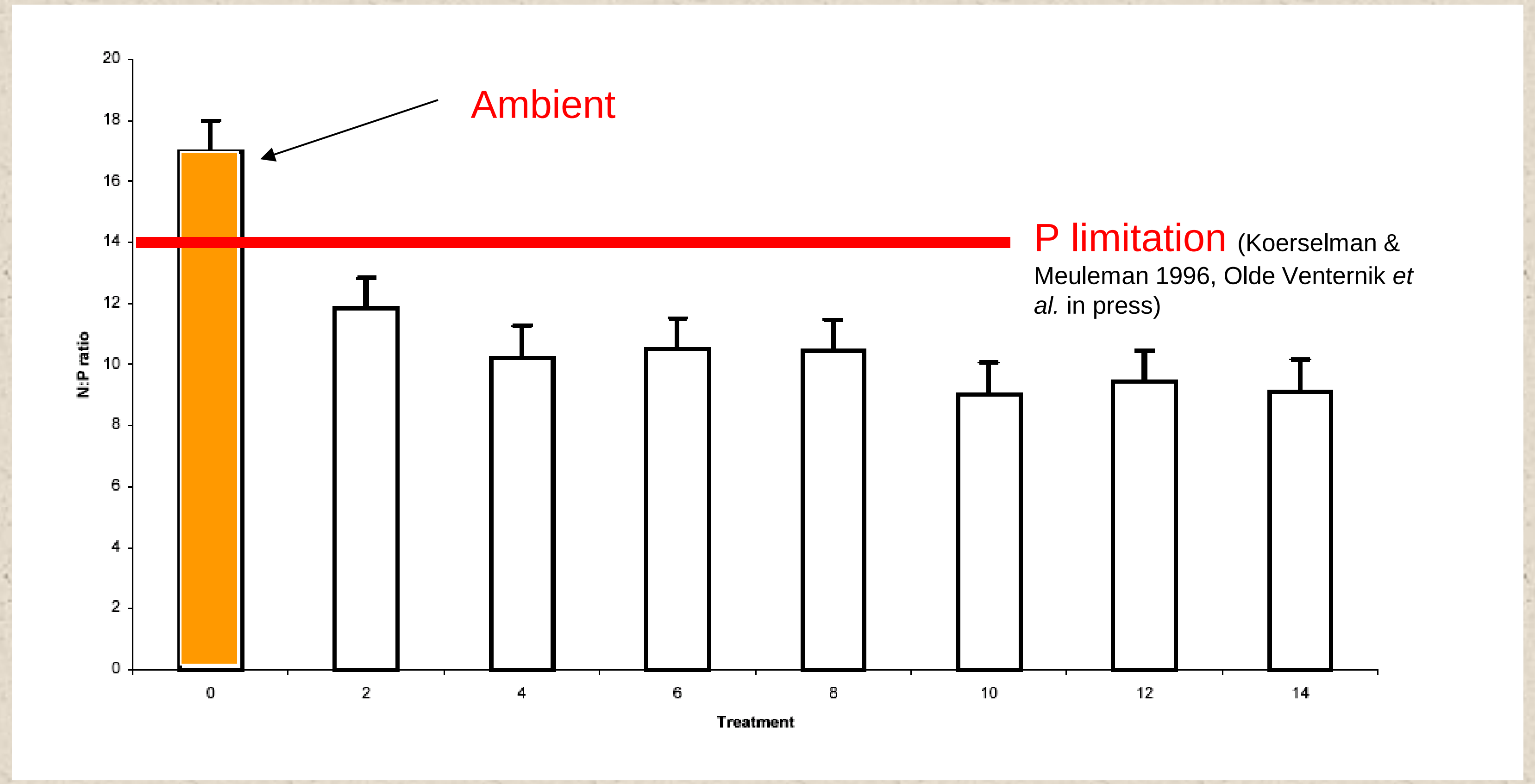
# P uptake increases with food level



# N:P ratio decreases with added food



# Altered N:P ratios suggest P limitation under ambient conditions



# Anthropogenic N additions alter growth and morphology

Increasing
Atmospheric N

# Food additions do not alter growth and morphology

Increasing prey

# Contrasting effects of anthropogenic and natural sources of N

## Anthropogenic N

- Altered N:P ratios
- Morphological shift
- Reduction in prey uptake

## Prey N

- Uptake, storage of N & P
- No morphological shifts
- Continued prey uptake

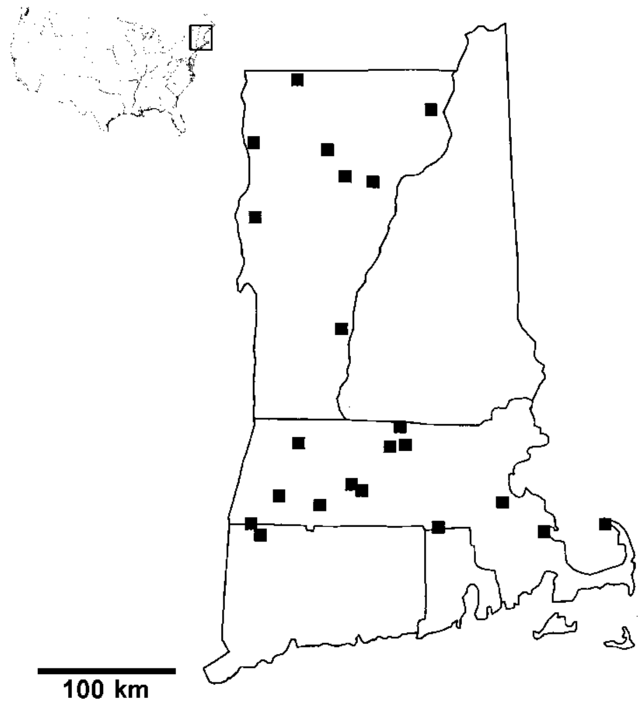
Although *Sarracenia* has evolved adaptations for low N environments, chronic N deposition may have caused populations to be currently limited by P, not N.

# Nitrogen

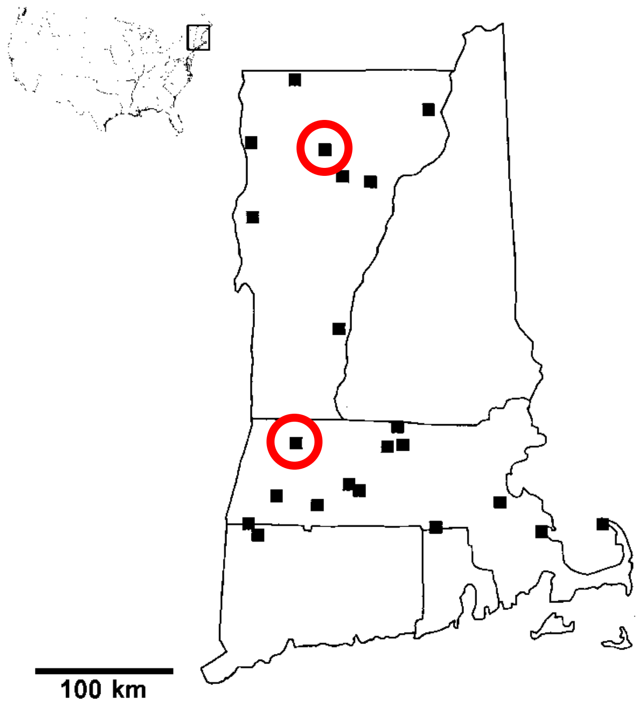
Nitrogen, Phosphorus, other elements, micronutrients

# Effects of N Deposition on Carnivorous Plants

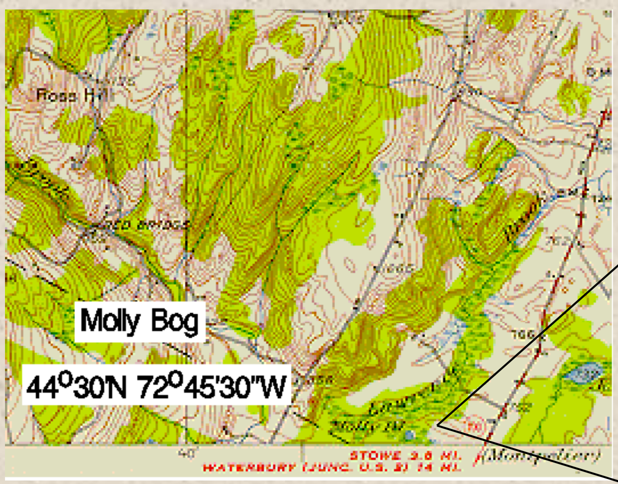
- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

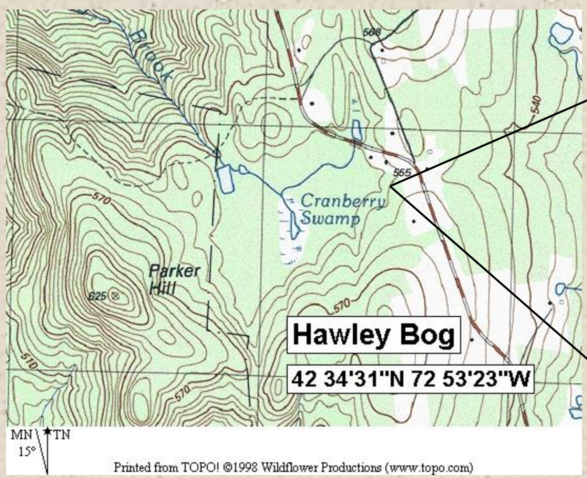

100 km

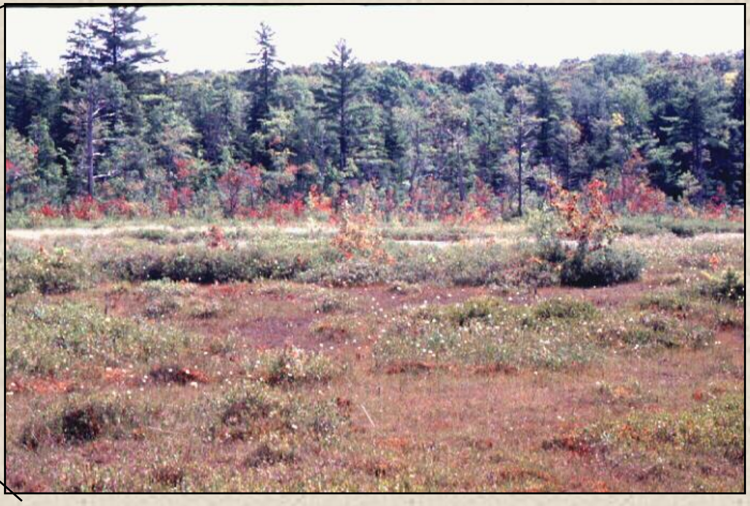
Gotelli & Ellison - Fig. 1



# Study Sites

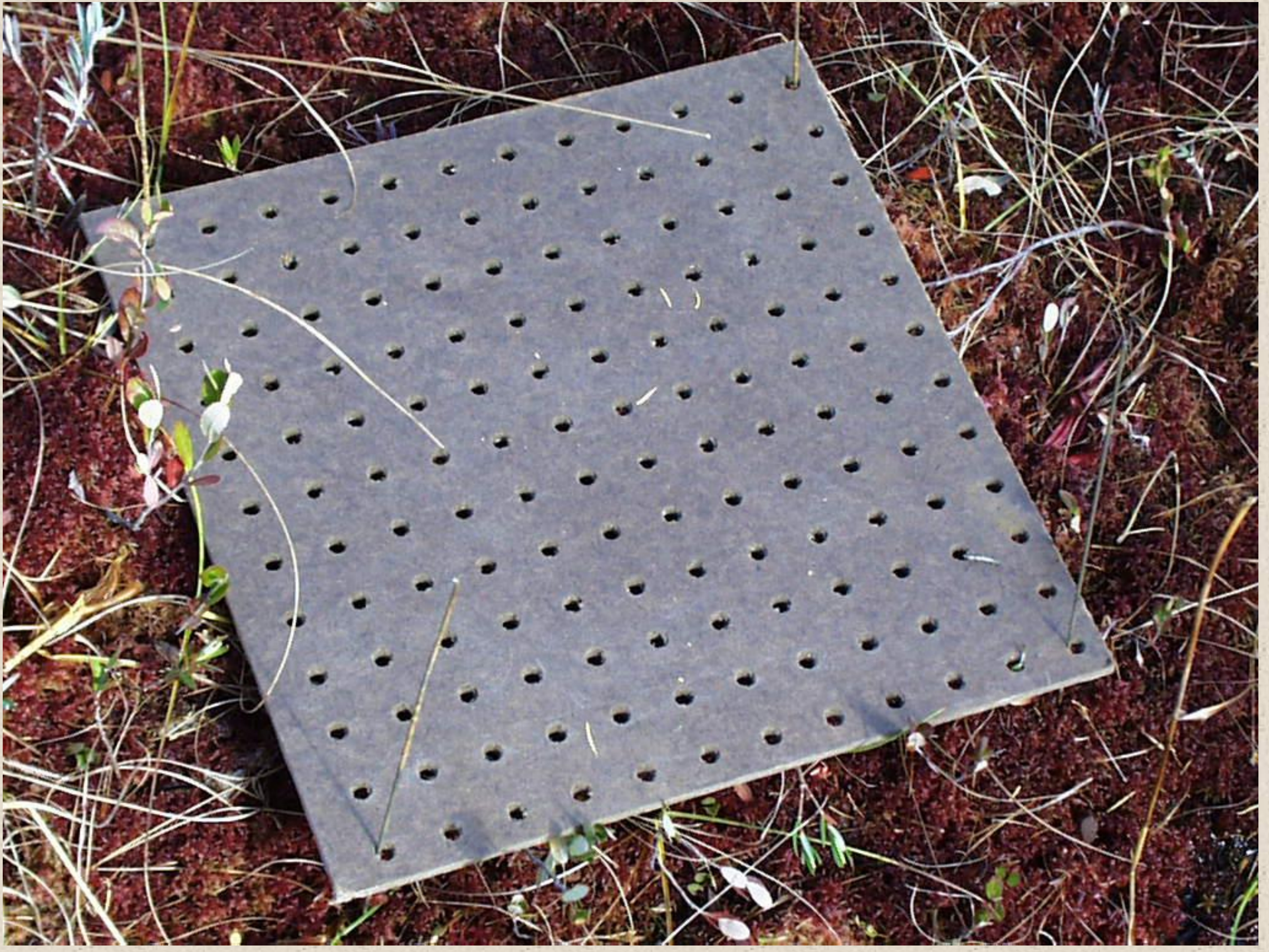

Ross Hill
Molly Bog
44°30'N 72°45'30"W
STOWE 3.8 MI.
WATERBURY (JUNC. U.S. 2) 14 MI.
(Montpelier)

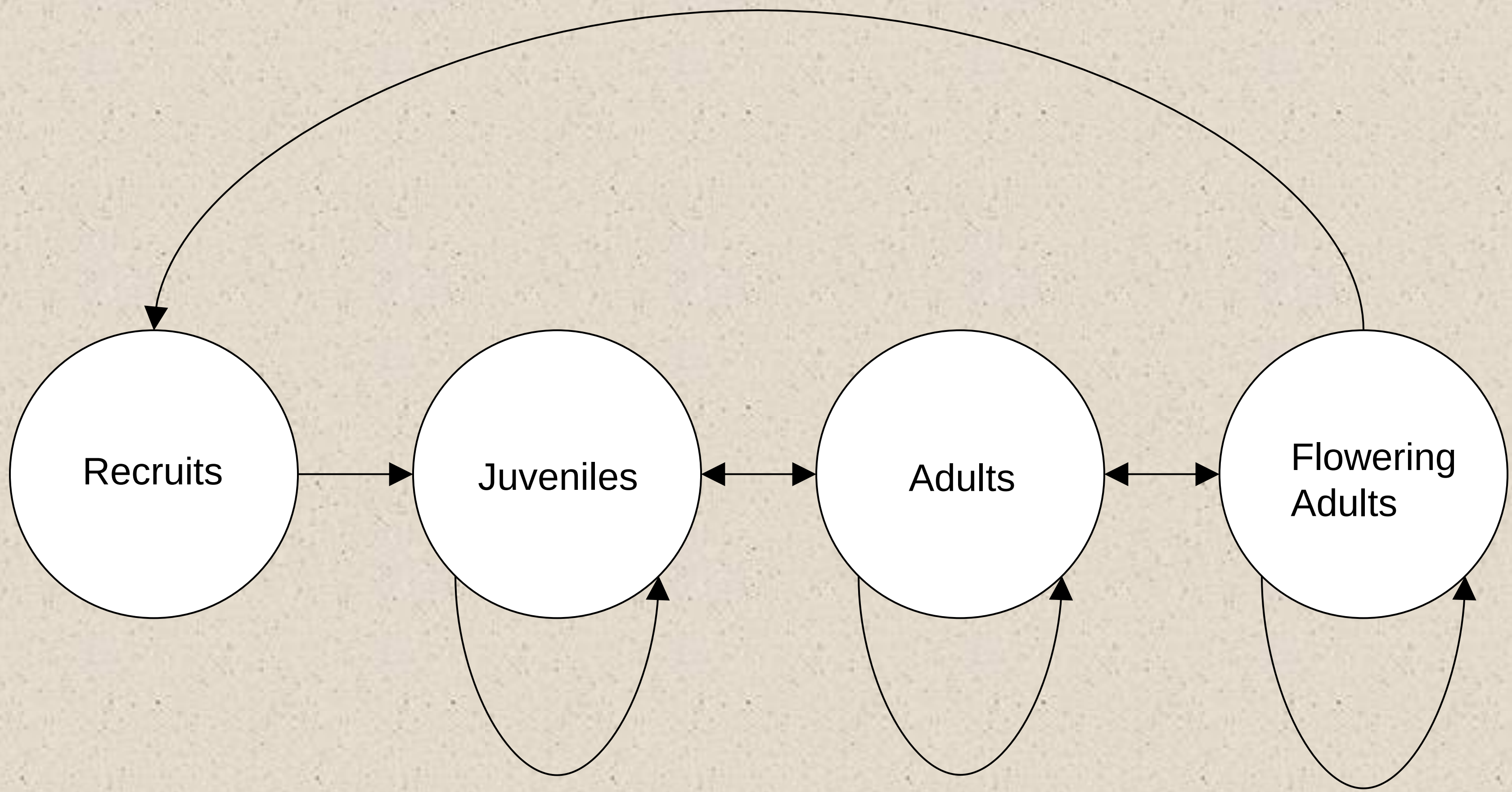

Brook
Cranberry Swamp
Parker Hill
Hawley Bog
42 34'31"N 72 53'23"W
MN TN
15°
Printed from TOPO! ©1998 Wildflower Productions (www.topo.com)



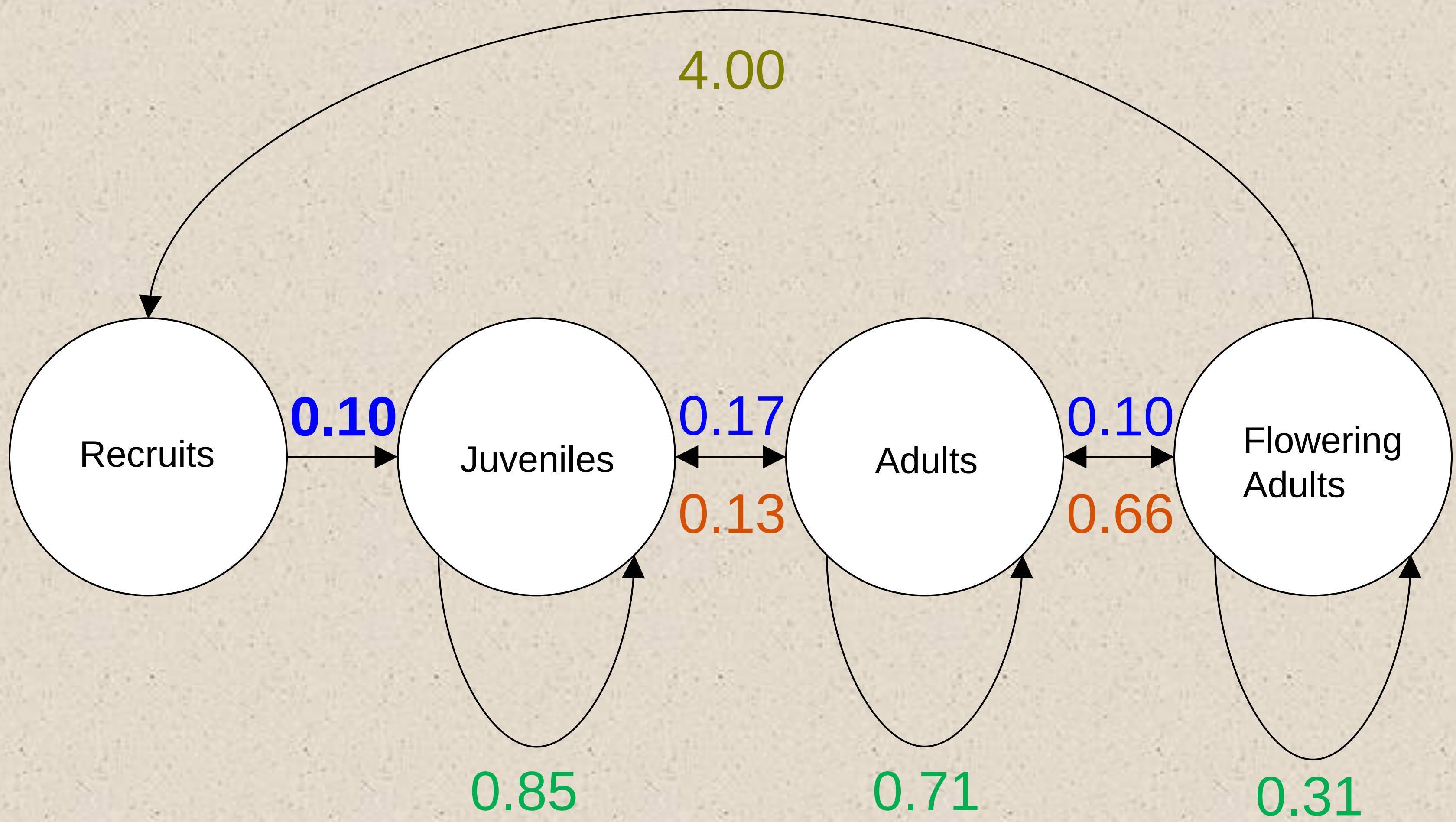
# Demography survey

- 100 adult, juvenile plants tagged at each site
- Plants censused and measured each year
- Seed plantings to estimate recruitment functions






# *Sarracenia* matrix model


4.00
Recruits
0.10
Juveniles
0.17
0.13
Adults
0.10
0.66
Flowering Adults
0.85
0.71
0.31

# Matrix Transition Model

$$n_{t+1} = An_t$$

Population vector at time (t + 1)

Transition matrix

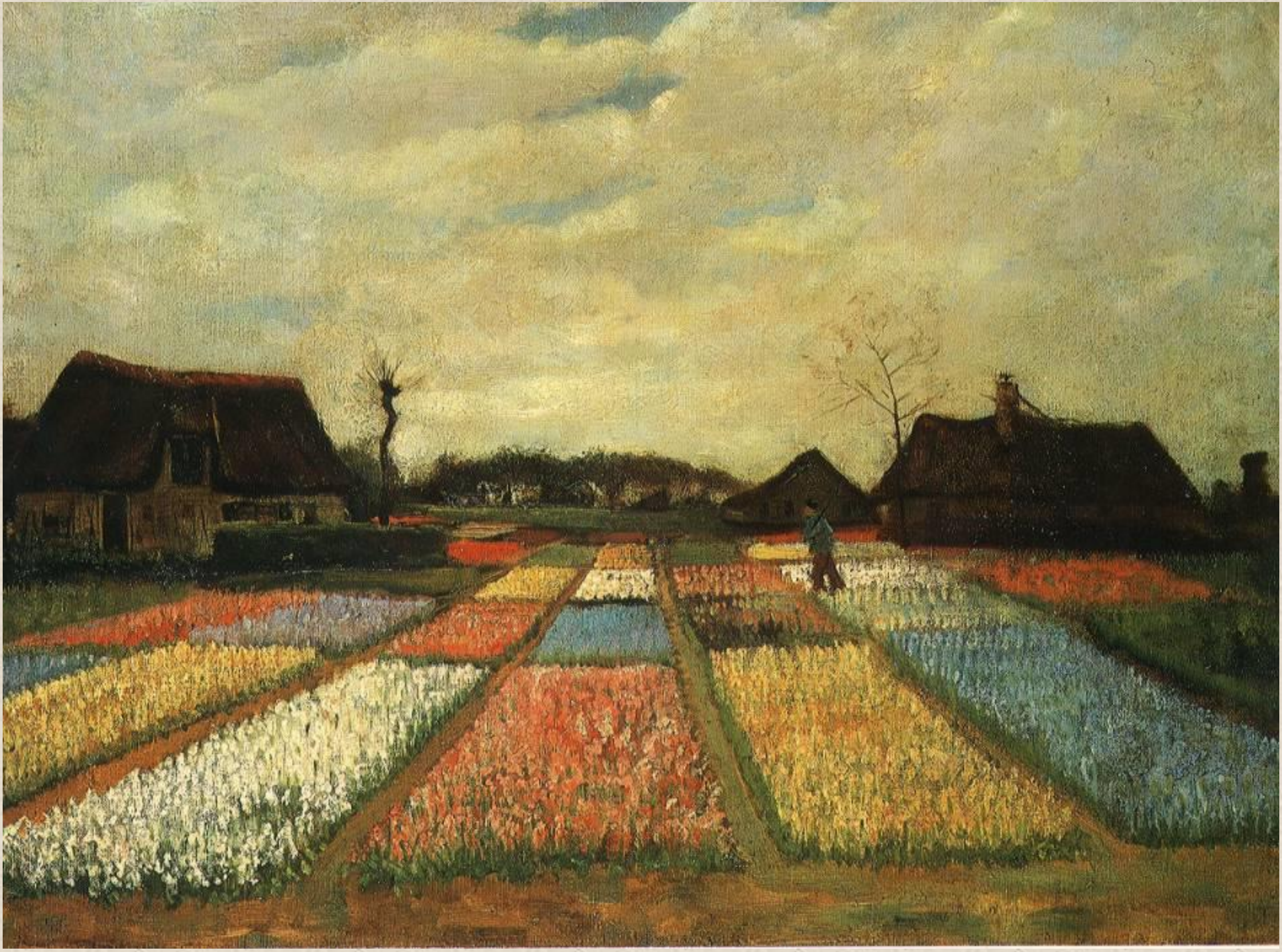
Population vector at time (t)

# Population Projections

| Site | r individuals/individual•year | Doubling Time |
|---|---|---|
| **Hawley Bog** | 0.00456 | 152 y |
| **Molly Bog** | 0.00554 | 125 y |

Global human population 0.0138 ~ 50 y

# How do N and P concentrations affect population growth of *Sarracenia*?



# Nutrient Addition Experiment

- 10 juveniles, 10 adults/treatment
- Nutrients added to leaves twice/month
- Nutrient concentrations bracket observed field values
- Nutrient treatments maintained 1998, 1999
- "Press" experiment

# Nutrient Treatments

- Distilled $H_20$
- Micronutrients
- Low N (0.1 mg/L)
- High N (1.0 mg/L)
- Low P (0.025 mg/L)
- High P (0.25 mg/L)

- N:P(1) Low N + Low P
- N:P(2) Low N + High P
- N:P(3) High N + Low P

*Nutrient Source:*

*Micronutrients: Hoaglands*

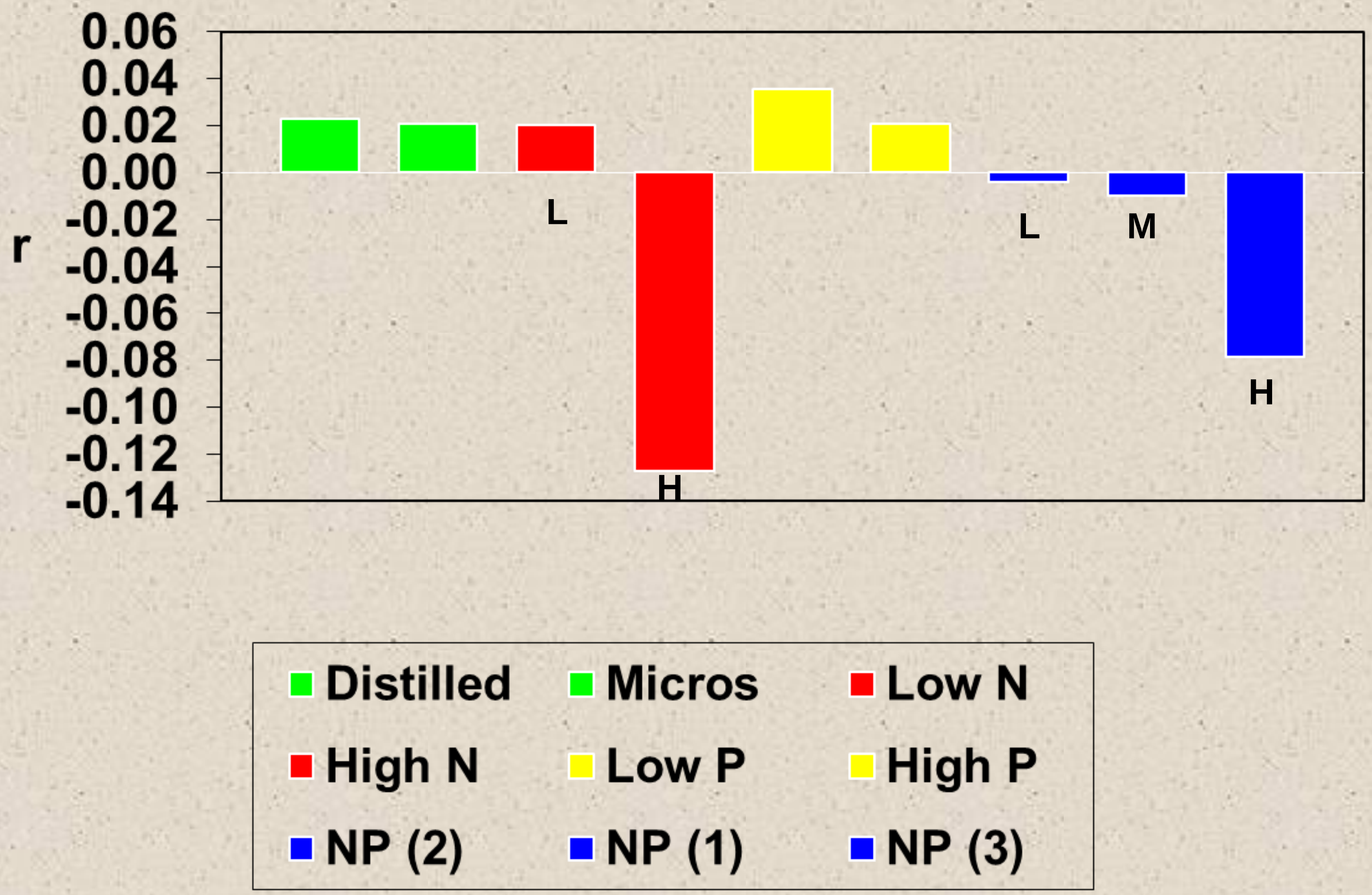
*N: $NH_4Cl$*

*P: $NaH_2PO_4$*

# Effects of N additions

- Increased production of phyllodia
- Increased probability of flowering
- Decreased juvenile survivorship

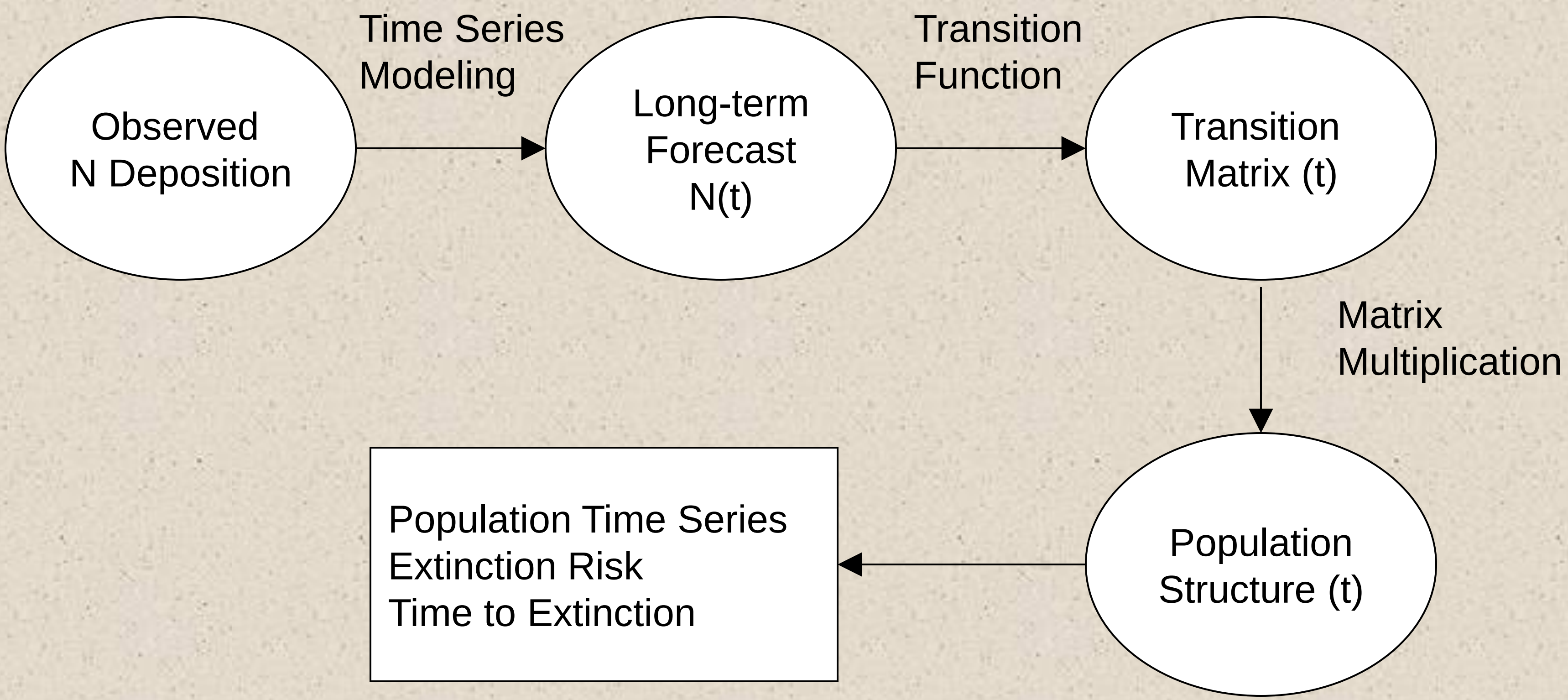
# Population Growth Rate



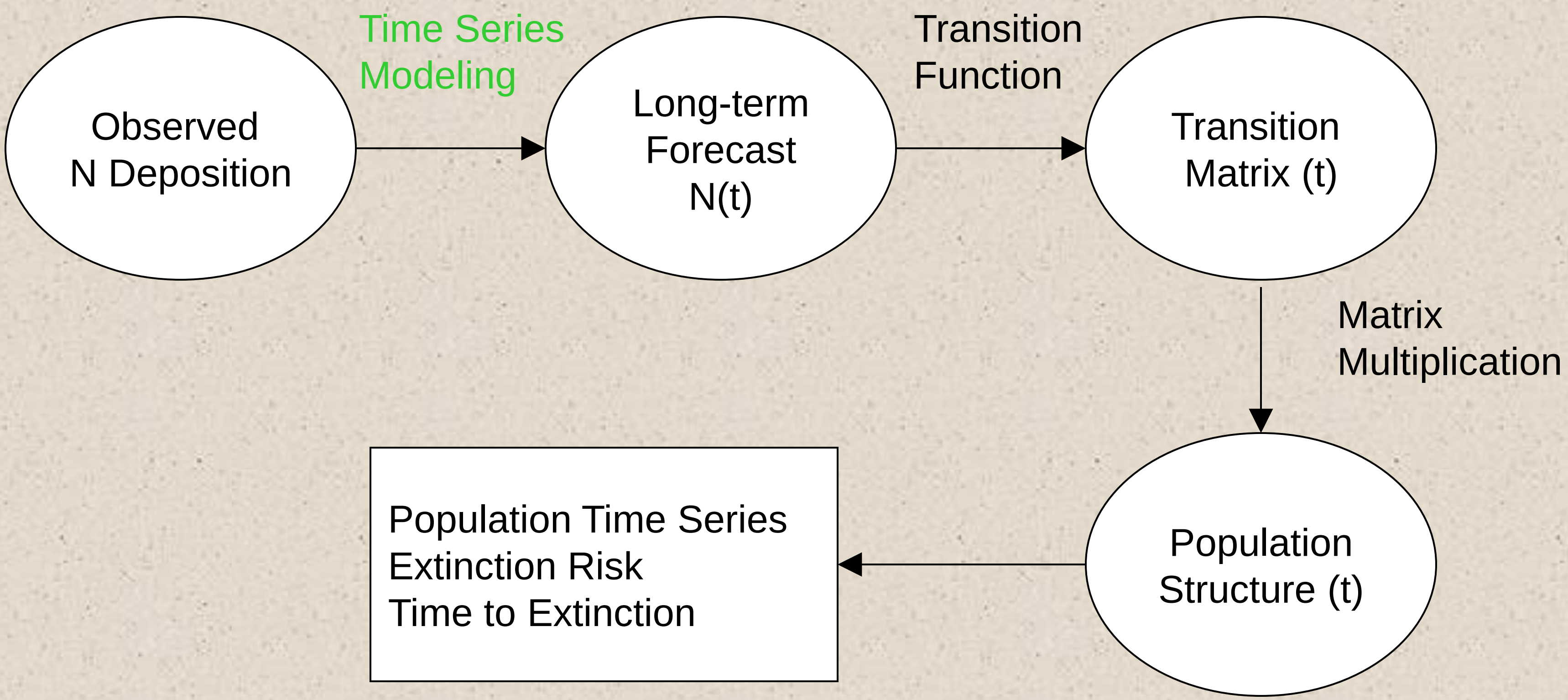
# Effects of Nitrogen on Demography: Results

- Population growth rates respond to different N and P regimes
- Population growth rate decreases in response to increasing N
- Population growth rate decreases in responses to increasing N:P

# Modeling Long-term Environmental Change



# Modeling Long-term Environmental Change



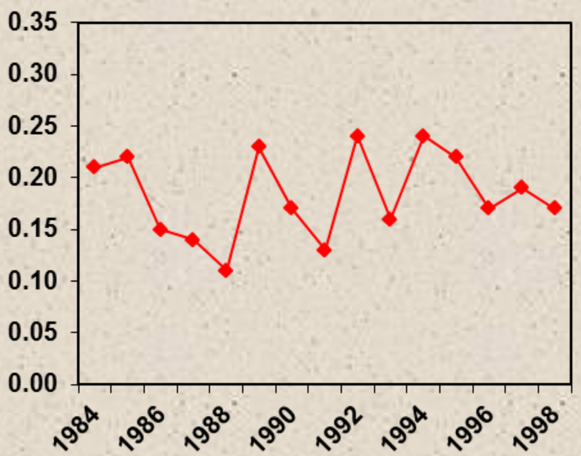
# N monitoring

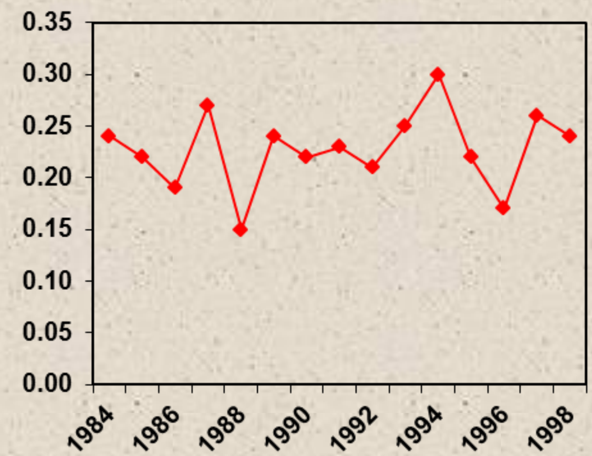
- National Atmospheric Deposition Program
- $NH_4$, $NO_3$ measured as mg/l/yr
- Annual data 1984-1998
- Monitoring sites
  - Shelburne, VT
  - Quabbin, MA

Quabbin, MA

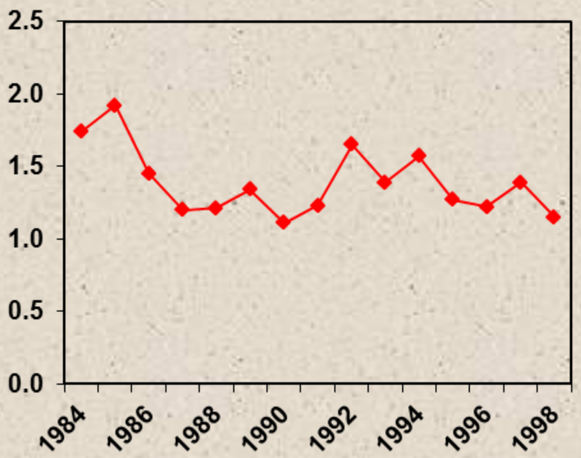
Shelburne, VT

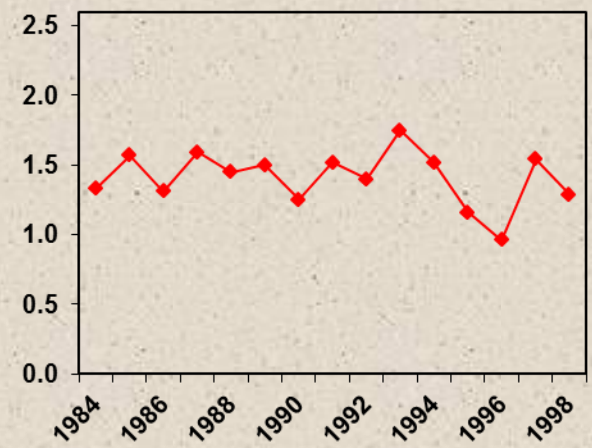
$NH_4$




$N0_3$



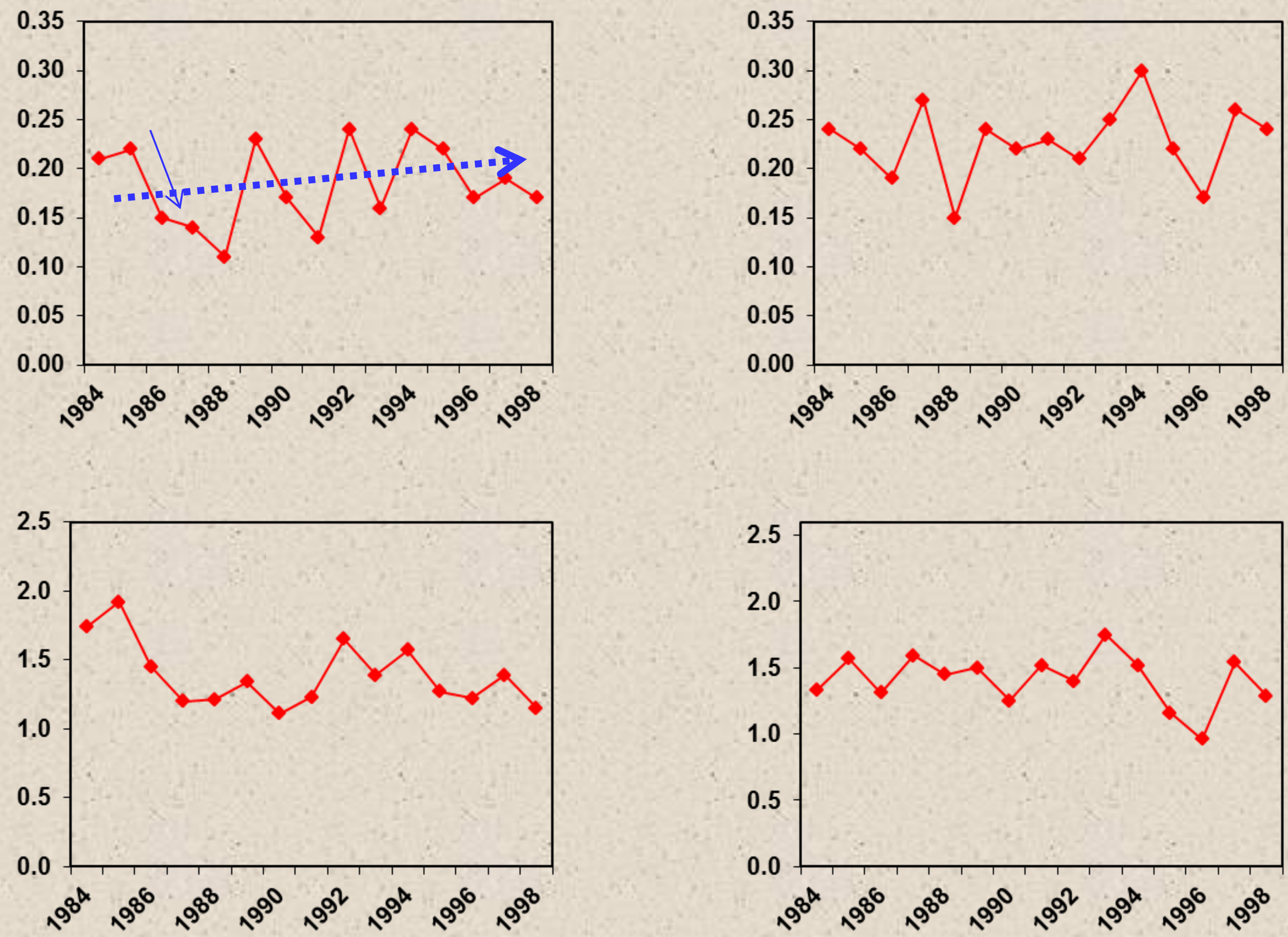



Quabbin, MA

Shelburne, VT

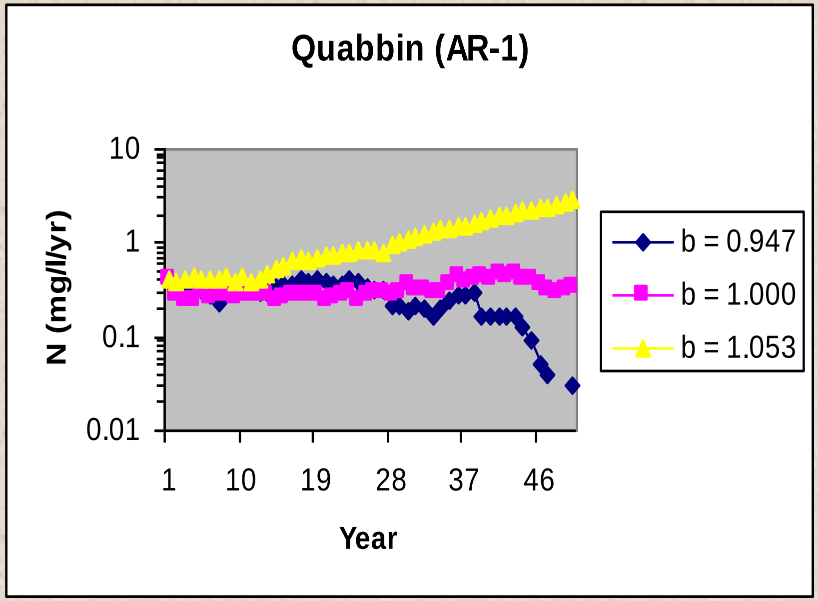
$NH_4$

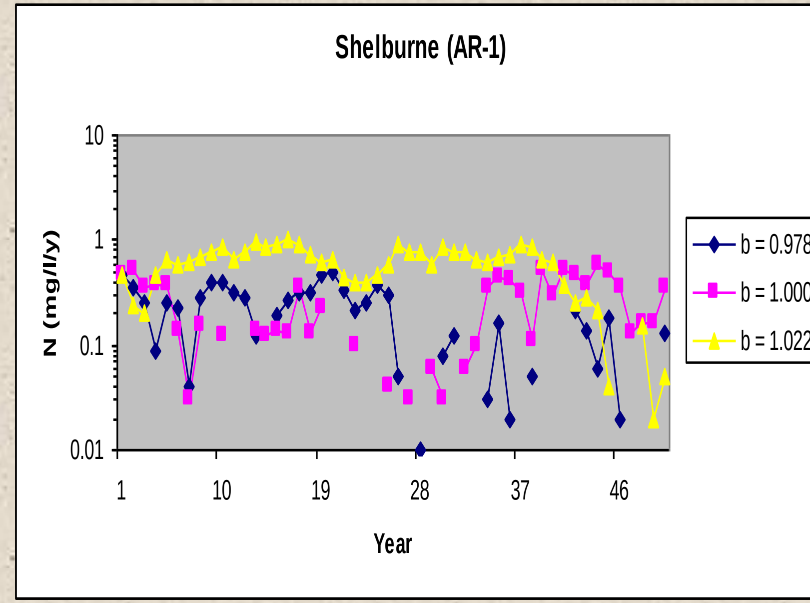
$N0_3$

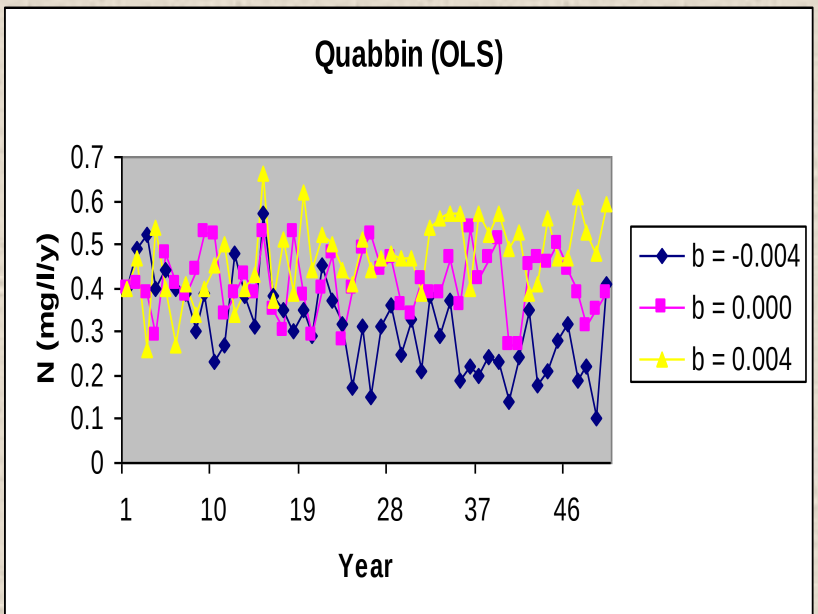


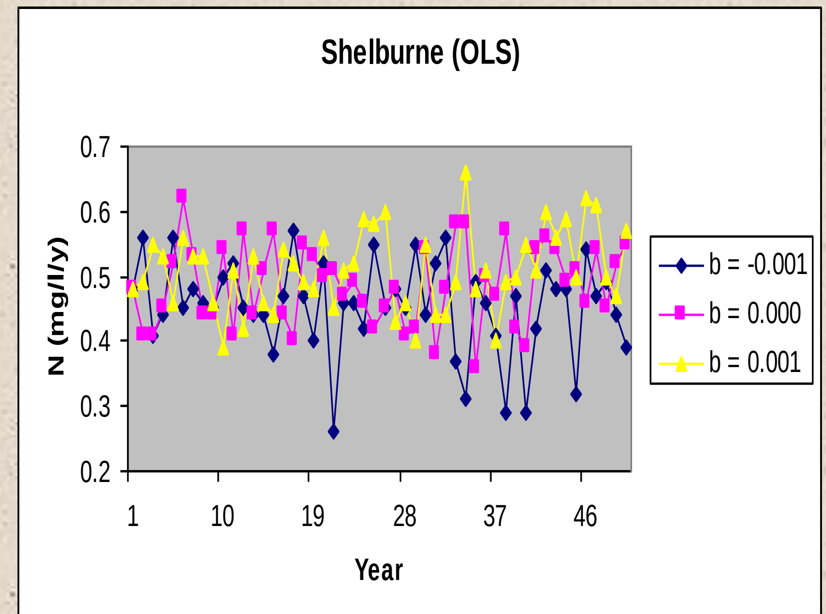
# Regression Models

| | |
|---|---|
| Ordinary Least Squares (OLS) | $N_t = a + bt + e$ |
| First-order auto-regressive (AR-1) | $N_t = a + bN_{t-1} + e$ |

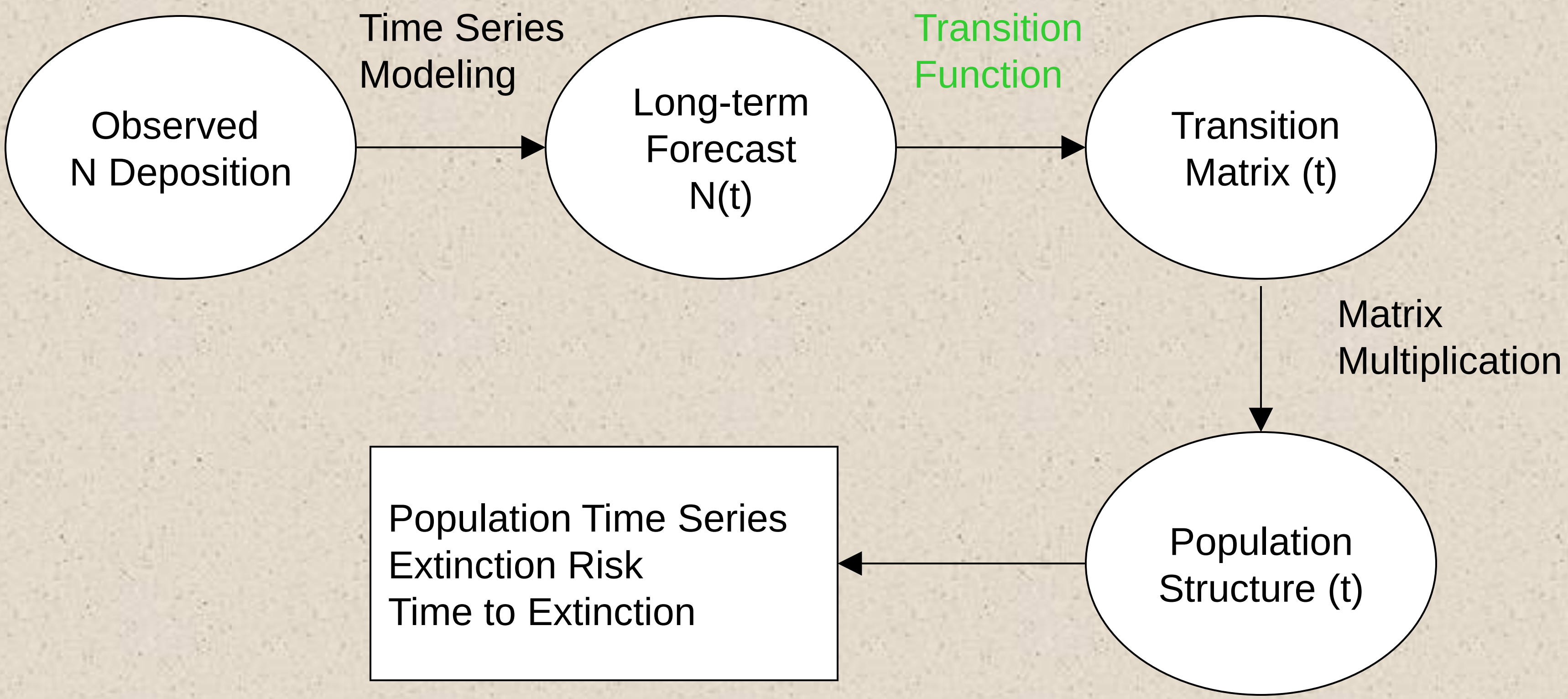

Quabbin (AR-1)
N (mg/l/yr)
10
1
0.1
0.01
1
10
19
28
37
46
Year
b = 0.947
b = 1.000
b = 1.053


Shelburne (AR-1)
N (mg/l/y)
10
1
0.1
0.01
1
10
19
28
37
46
Year
b = 0.978
b = 1.000
b = 1.022

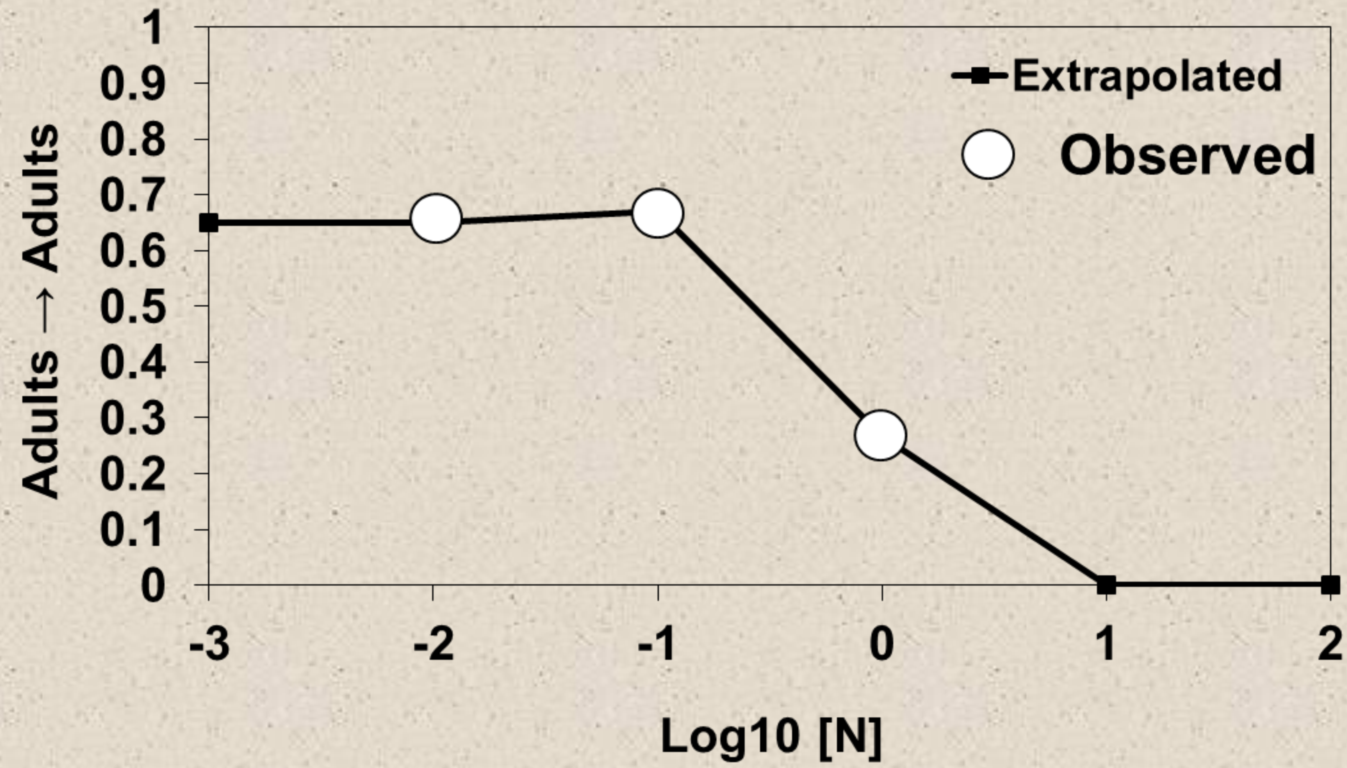

Quabbin (OLS)
N (mg/l/y)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1
10
19
28
37
46
Year
b = -0.004
b = 0.000
b = 0.004


Shelburne (OLS)
N (mg/l/y)
0.7
0.6
0.5
0.4
0.3
0.2
1
10
19
28
37
46
Year
b = -0.001
b = 0.000
b = 0.001

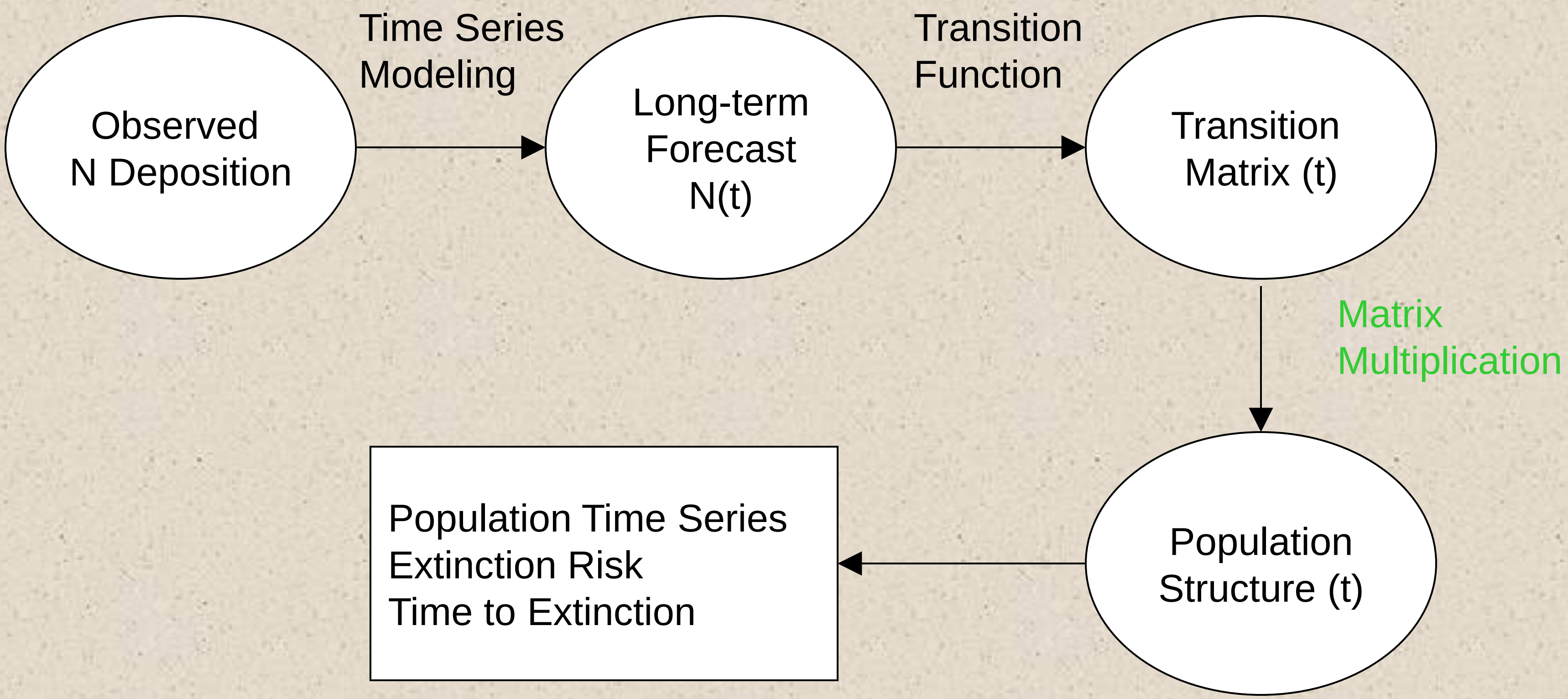
# Modeling Long-term Environmental Change



# Modeling Demographic Transitions as a Function of Nitrogen



# Modeling Long-term Environmental Change



# Matrix Transition Model (changing environment)

$$n_{t+1} = A_t n_t$$

Population vector at time (t + 1)

Sequentially changing transition matrix at time (t)

Population vector at time (t)

# Estimated population size

| **Stage** | **Number of individuals** |
|---|---|
| Recruits | 1500 |
| Juveniles | 23,500 |
| Non-flowering Adults | 1400 |
| Flowering Adults | 500 |

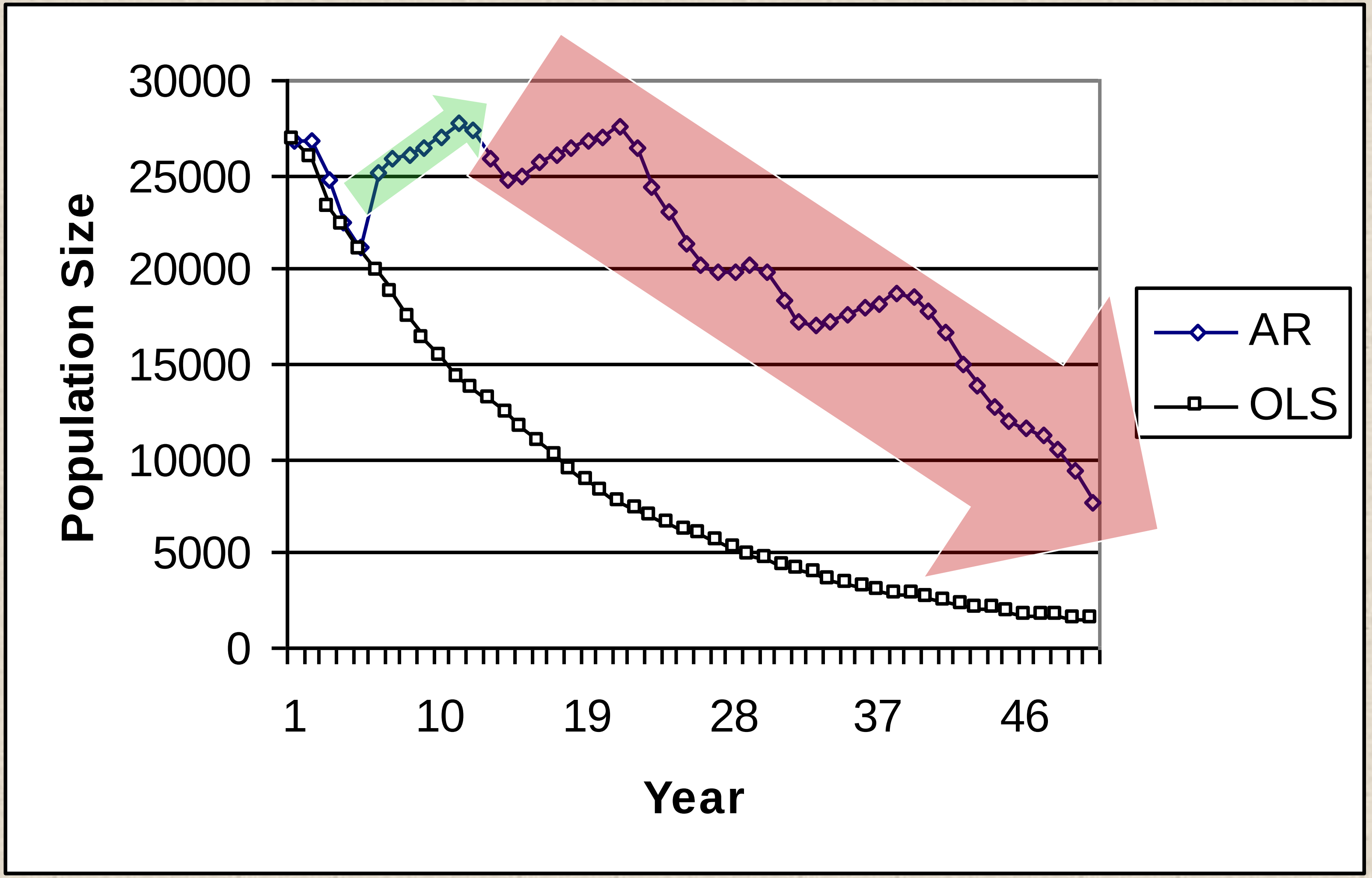
# Massachusetts Forecast

| Scenario | Annual % Change | P (ext) at 100 y | Time to ext (p = 0.95) |
|---|---|---|---|
| Best case | -4.7% | 0.00 | > 10,000 y |
| No change | 0.0% | 0.038 | 650 y |
| Small increase | 1% | 0.378 | 290 y |
| Worst case | 4.7% | 0.996 | 70 y |

# Vermont Forecast

| Scenario | Annual % Change | P (ext) at 100 y | Time to ext (p = 0.95) |
|---|---|---|---|
| Best case | -2.2% | 0.158 | > 10,000 y |
| No change | 0.0% | 0.510 | 230 y |
| Small increase | 1.0% | 0.694 | 200 y |
| Worst case | 2.2% | 0.838 | 140 y |

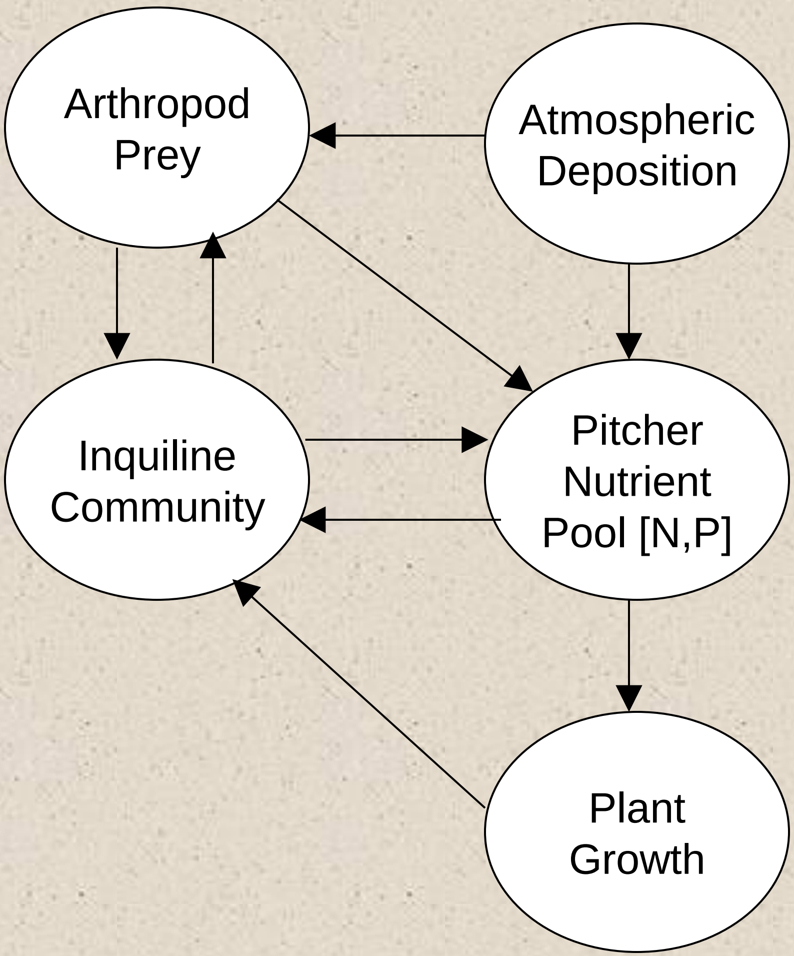
# Projected Population Dynamics



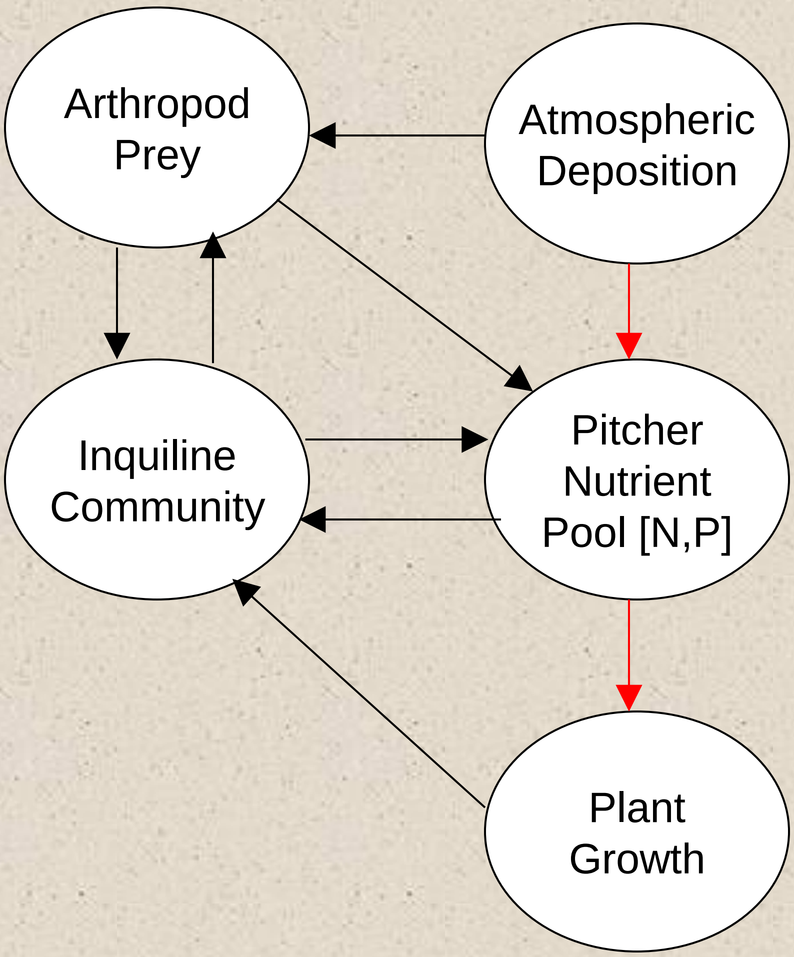
# Effects of N Deposition on Carnivorous Plants

- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

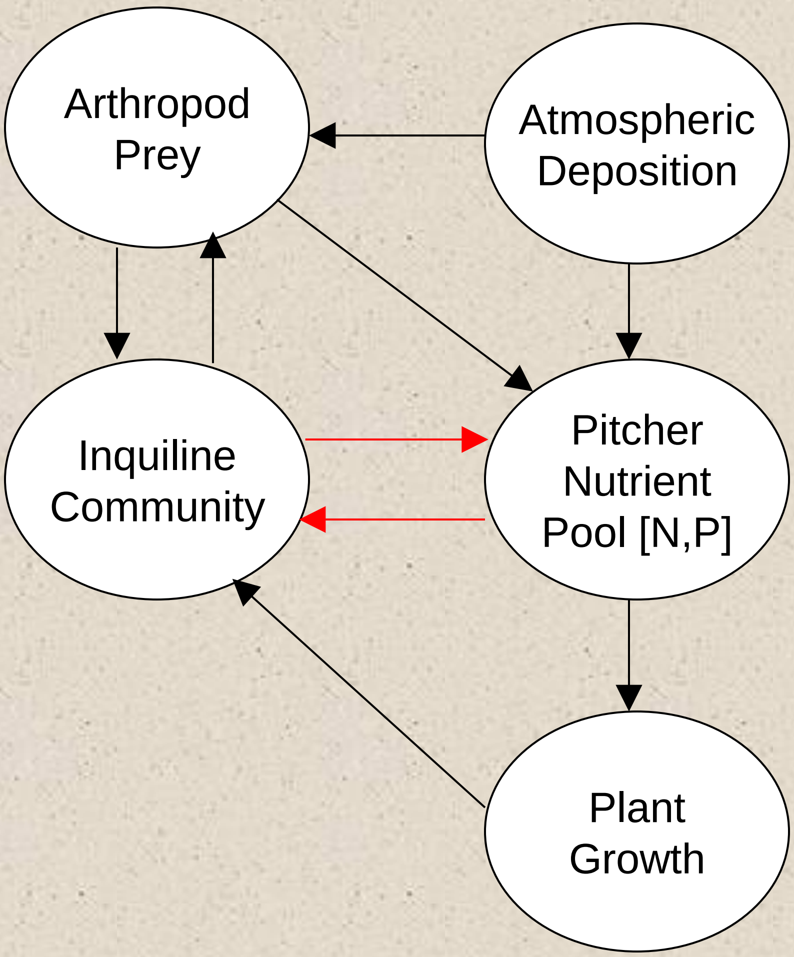
# *Sarracenia* Nutrient Feedback Loop



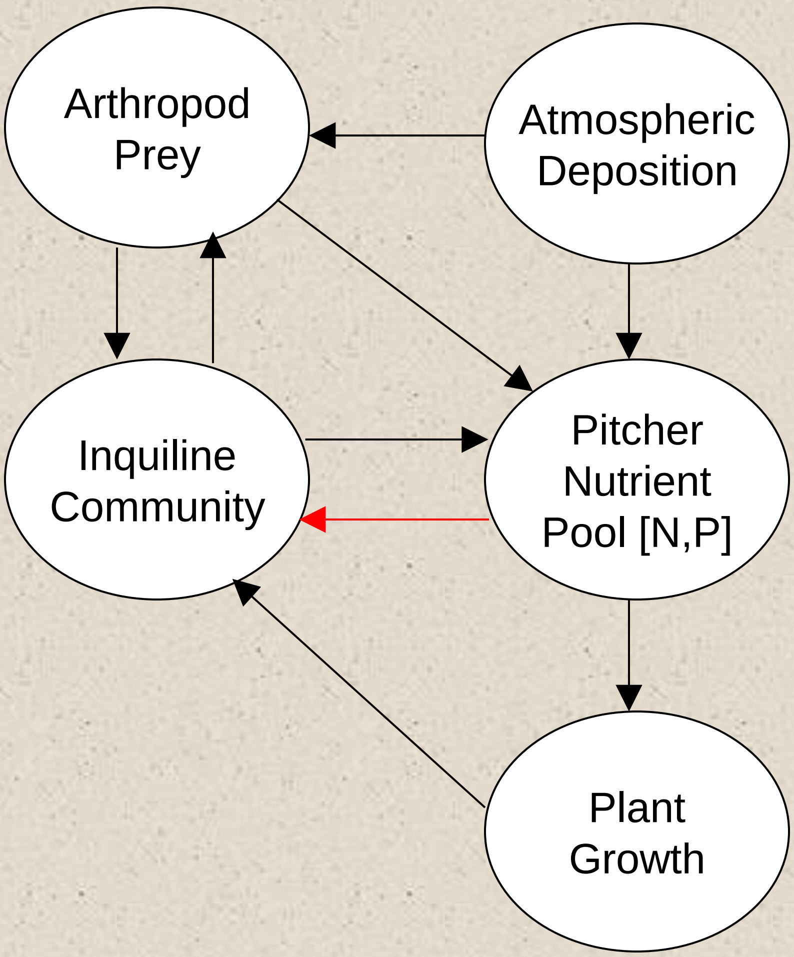
# *Sarracenia* Nutrient Feedback Loop



# *Sarracenia* Nutrient Feedback Loop



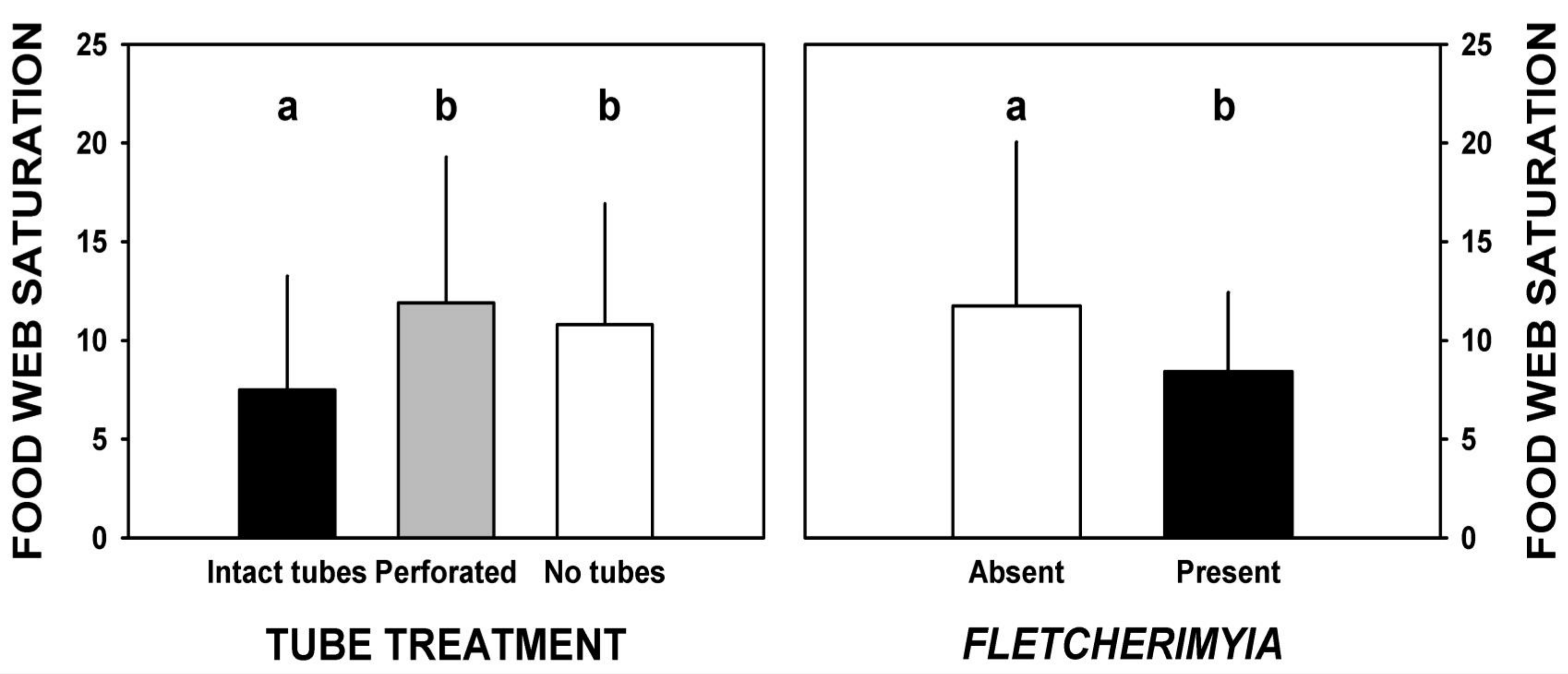
# *Sarracenia* Nutrient Feedback Loop



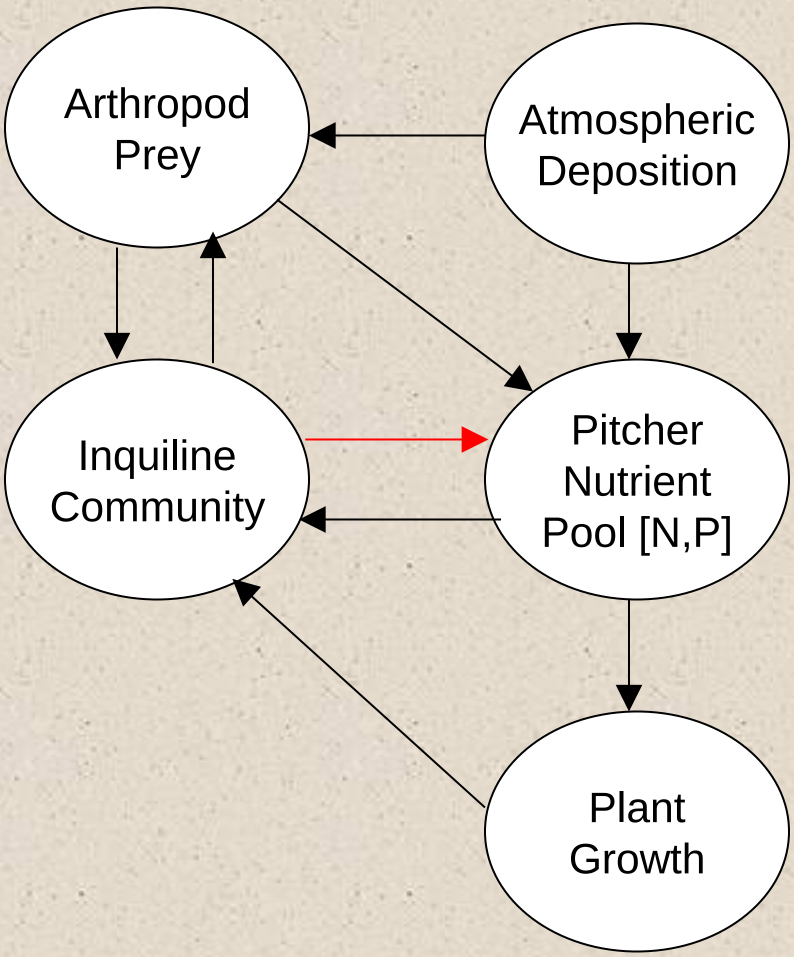
# Four-level Multi-Factorial Experiment

- Atmospheric N (8 levels)
- Prey supplement (yes,no)
- Top predator removal (yes,no)
- Nutrient exchange with plant (unmanipulated, isolated, control)

# Nutrient exchange with the plant and top predators affect food web structure



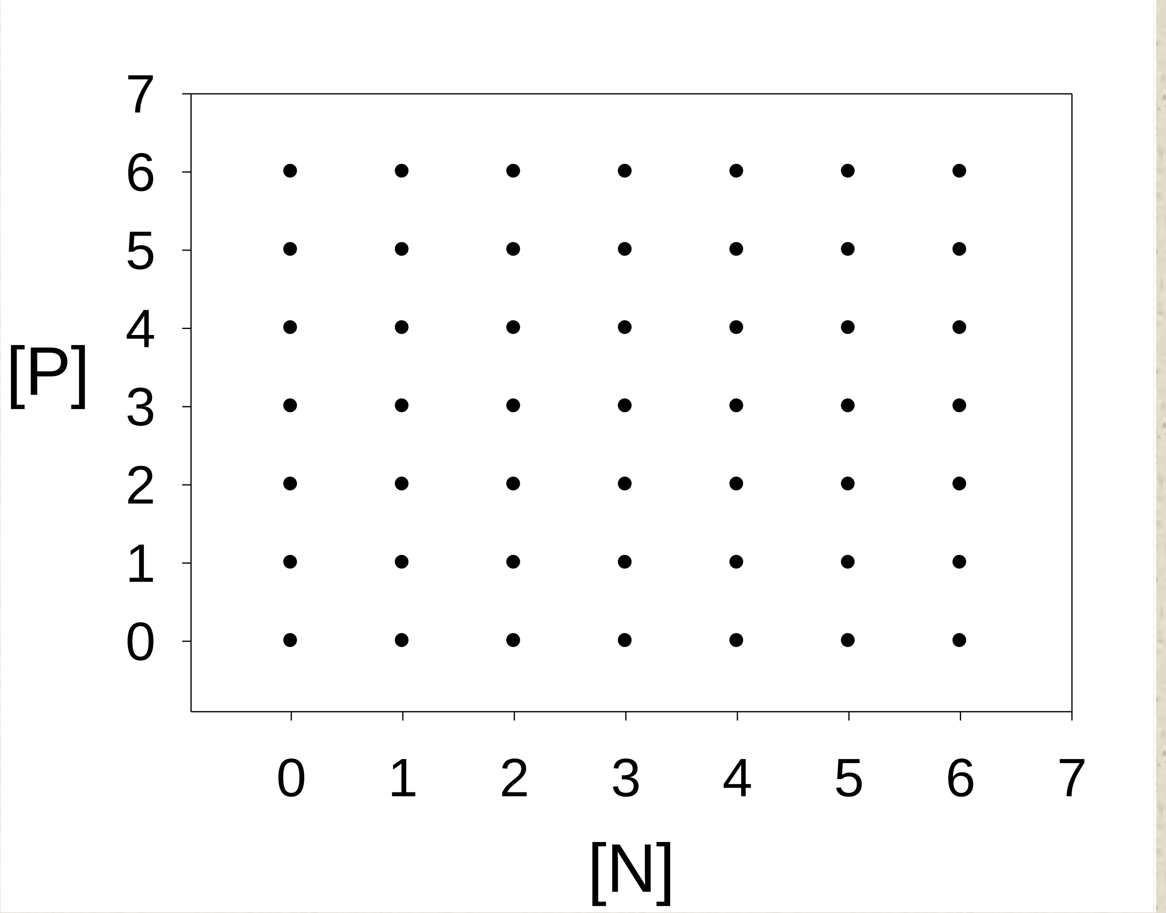
# *Sarracenia* Nutrient Feedback Loop



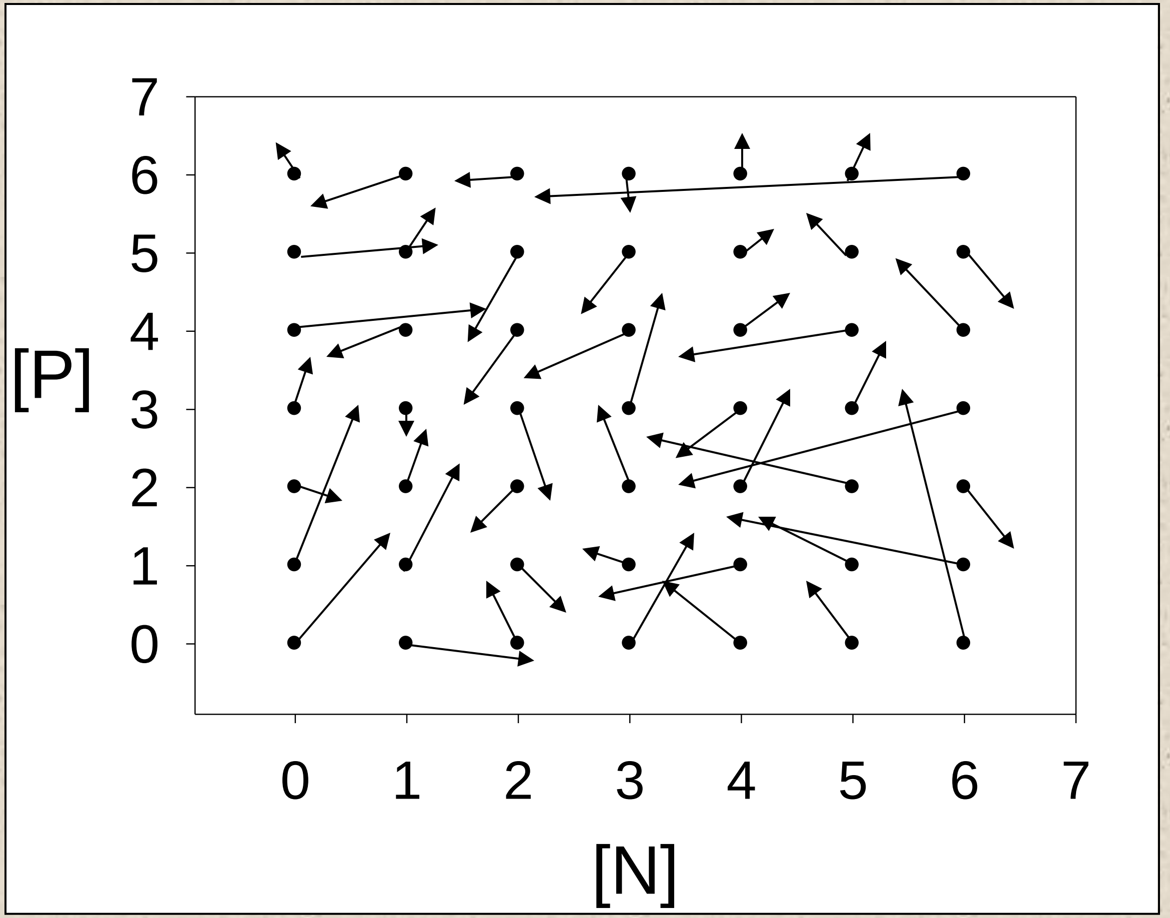
# Inquilines → Nutrients

- Manipulate [N], [P] in leaves
- Orthogonal “regression” design
- Establish initial [] in a “pulse” experiment

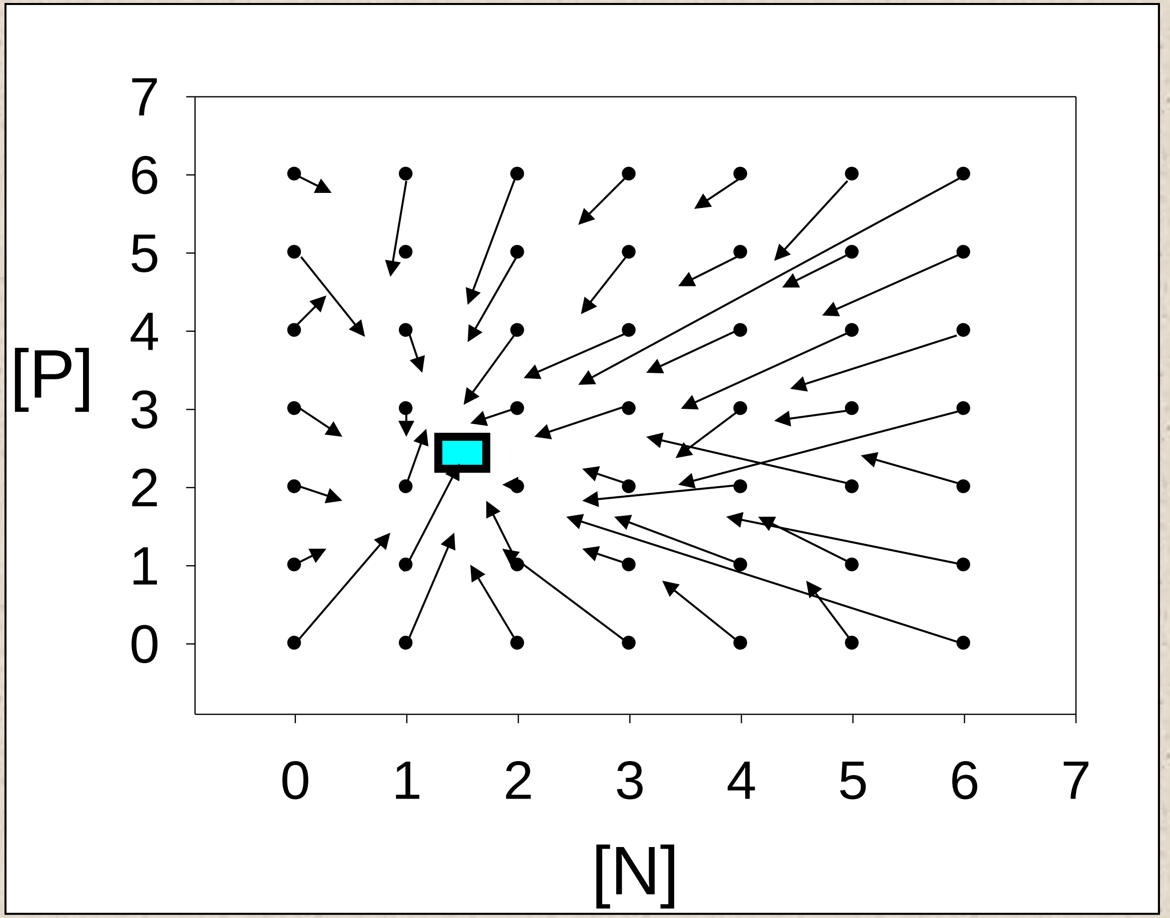
# Response Surface Experimental Design

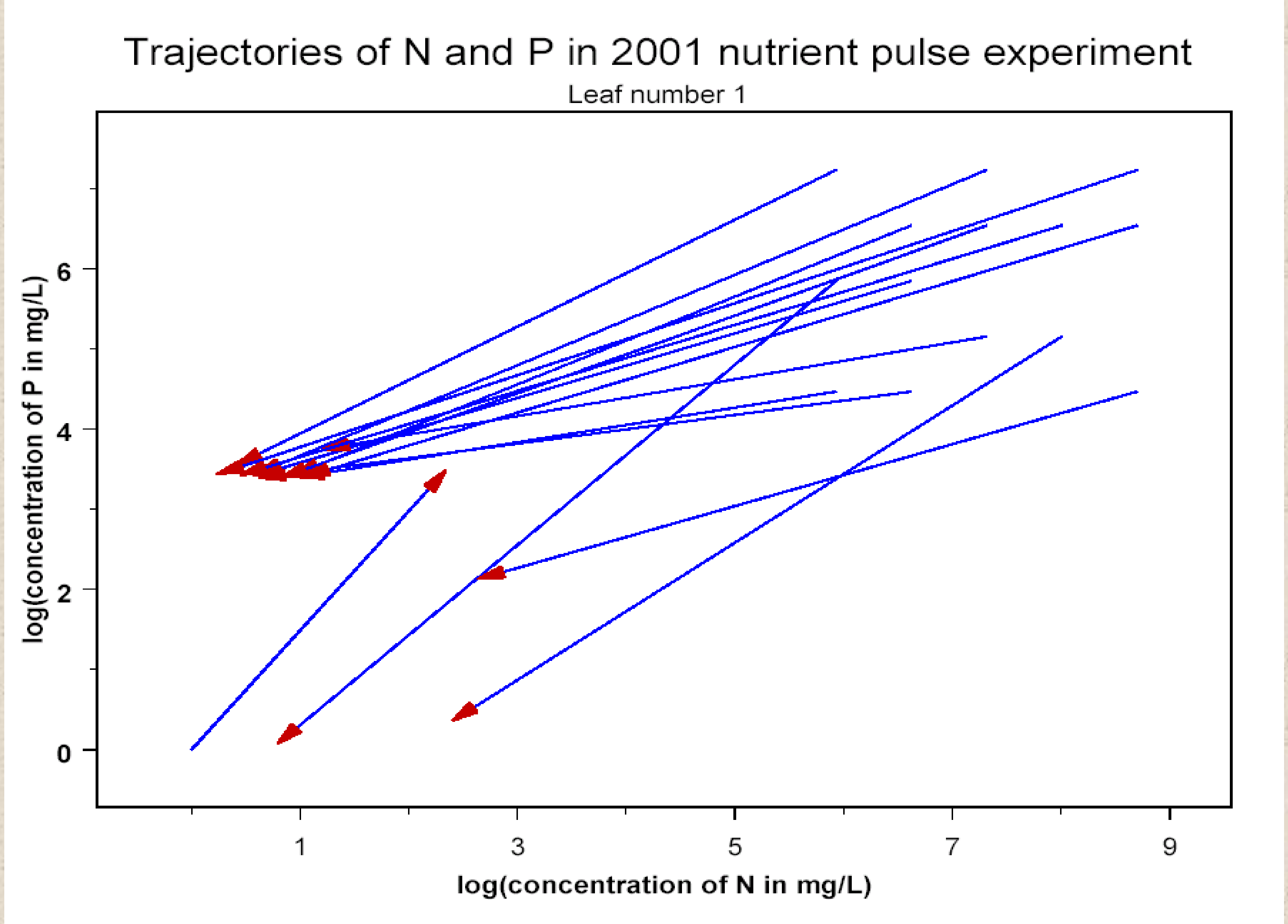


# Null Hypothesis

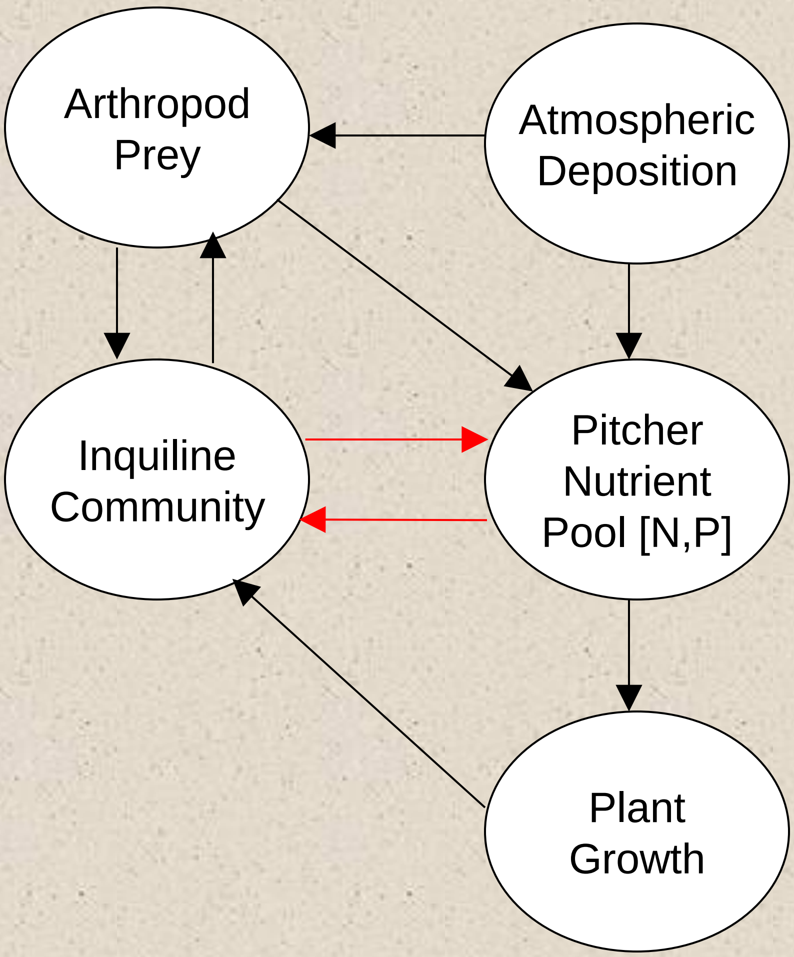


# Community Regulation of Nutrients




Trajectories of N and P in 2001 nutrient pulse experiment
Leaf number 1
log(concentration of P in mg/L)
0
2
4
6
1
3
5
7
9
log(concentration of N in mg/L)

# *Sarracenia* Nutrient Feedback Loop



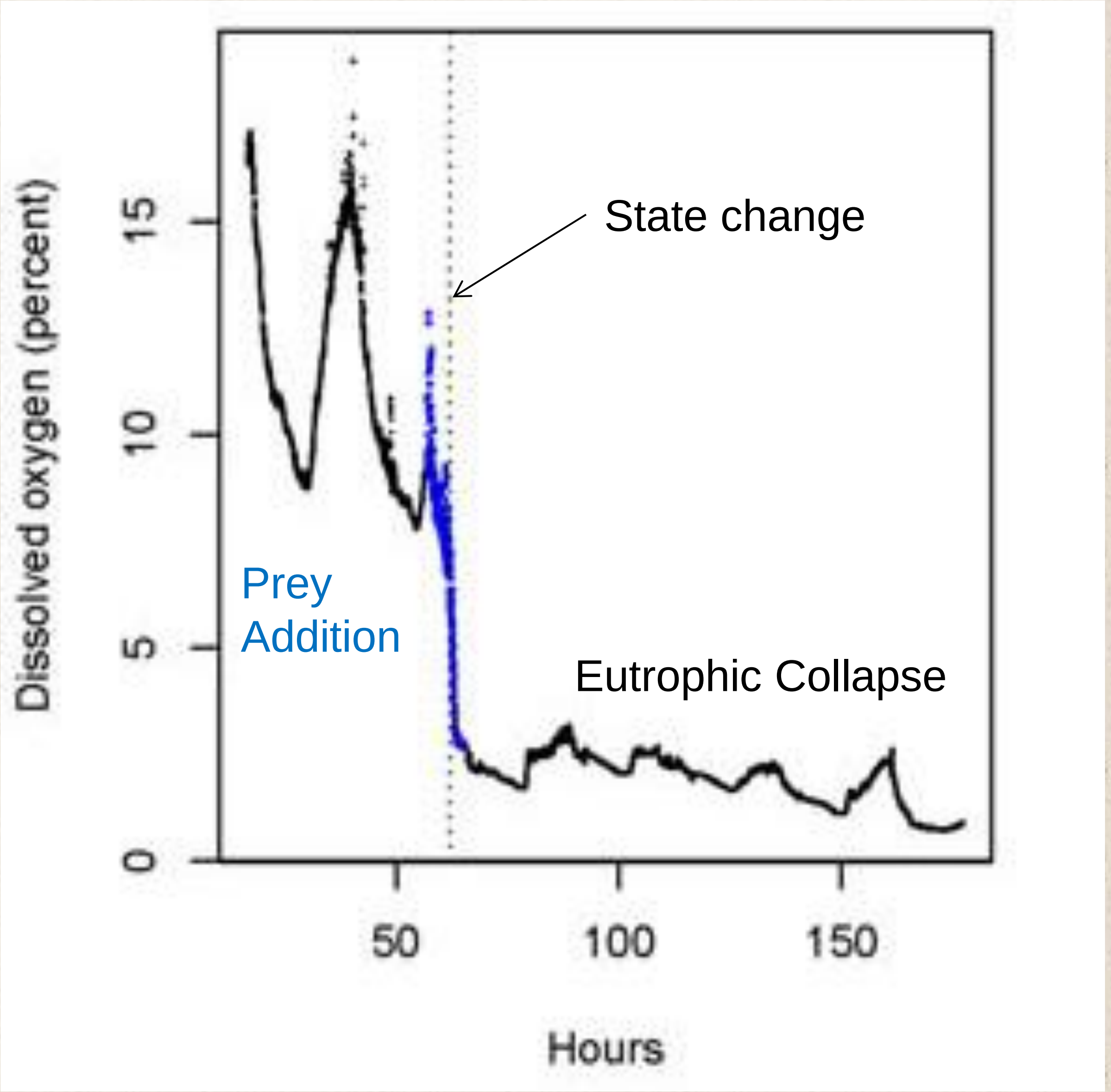
# Nutrients ↔ Inquilines

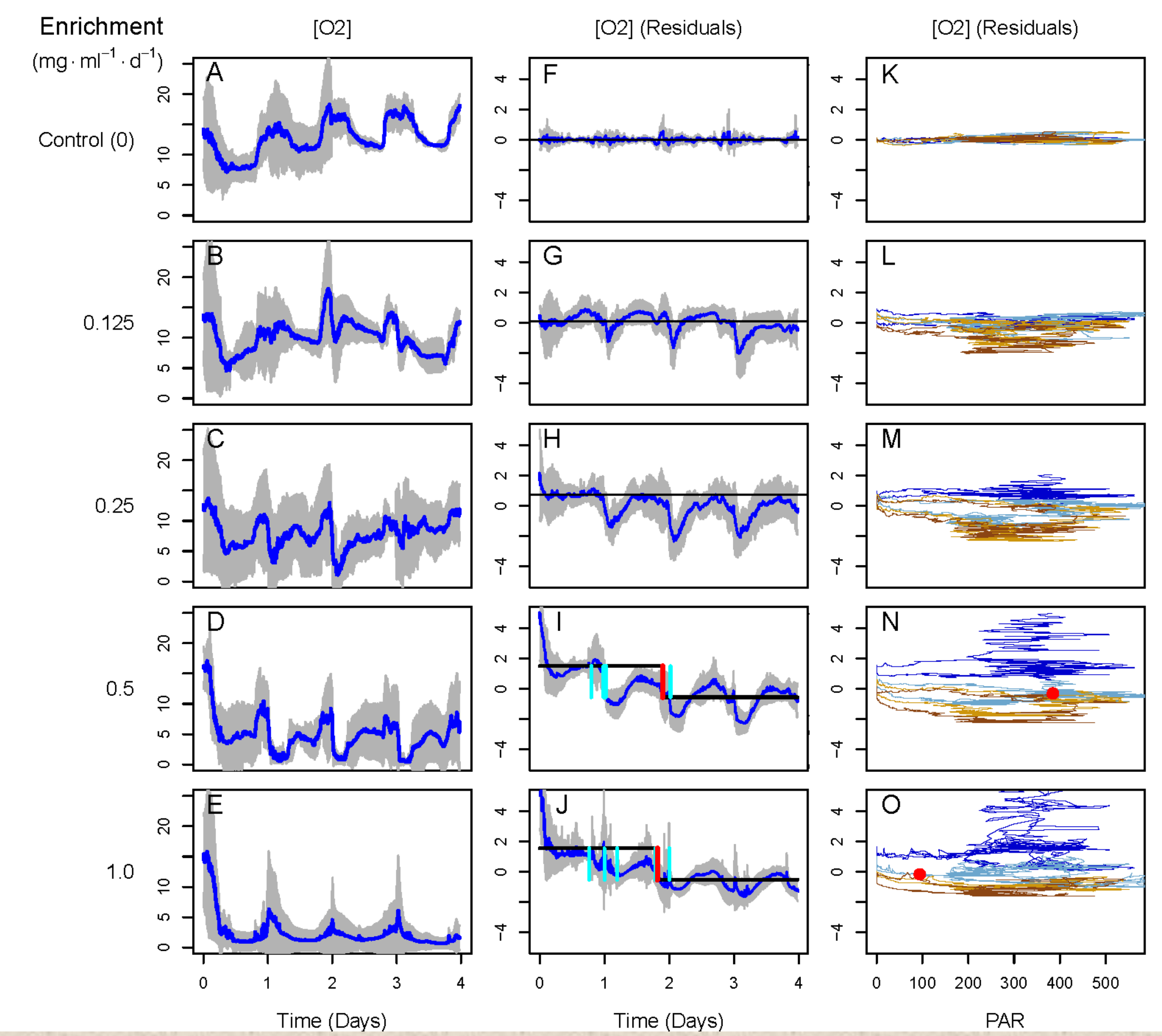
$$\frac{dN}{dt} = f(N, I, t)$$

$$\frac{dI}{dt} = g(I, N, t)$$

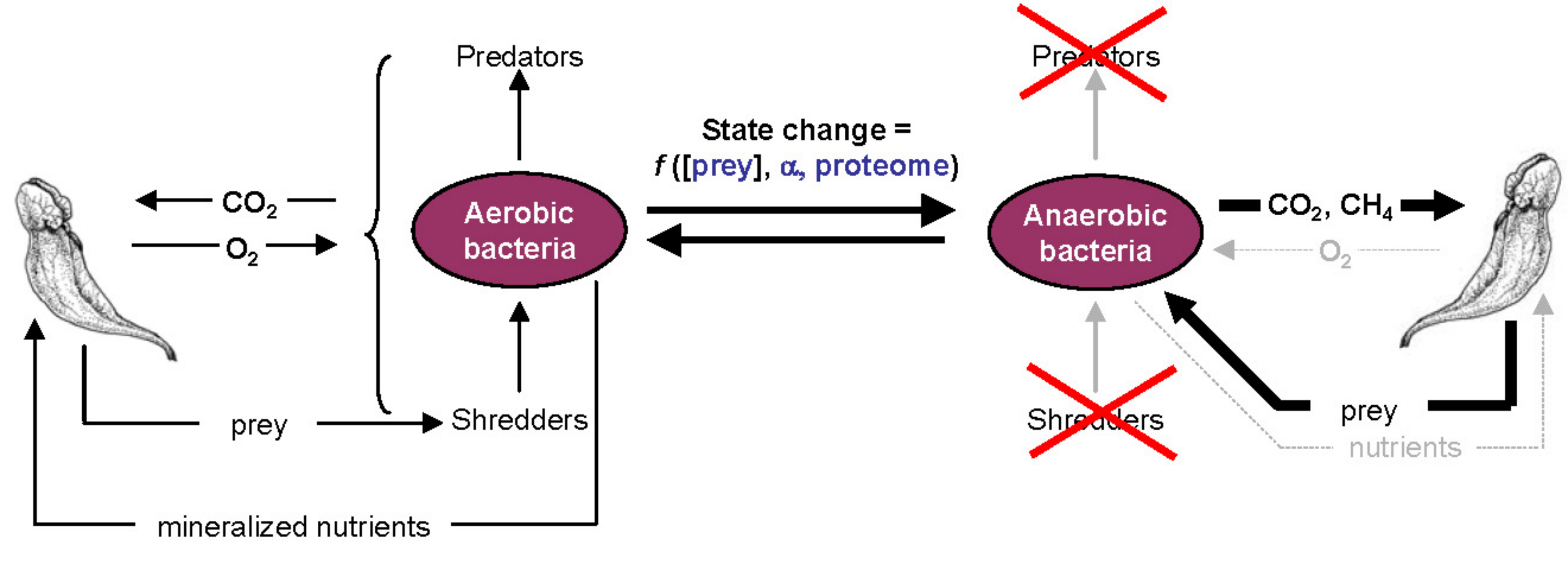
# *Sarracenia* as a model system for studying eutrophication

# Experimental enrichment and ecosystem collapse

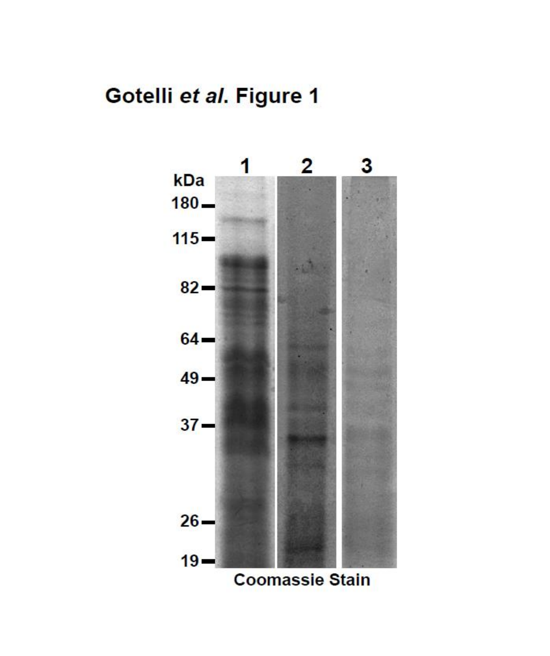




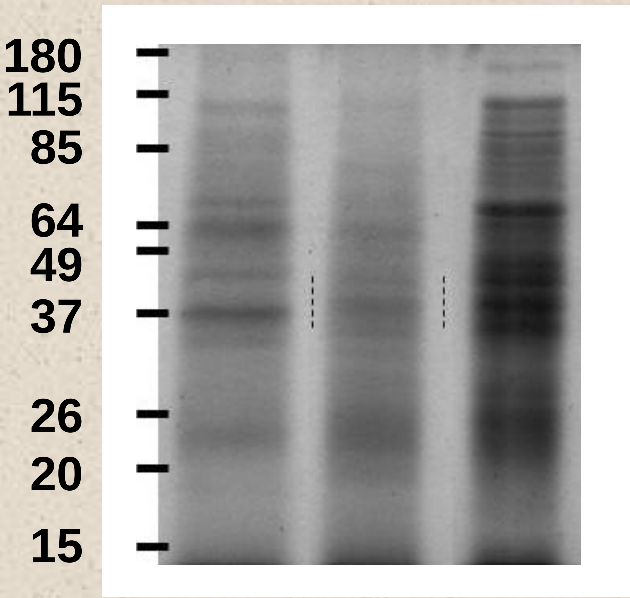
Enrichment
(mg · ml⁻¹ · d⁻¹)
[O2]
[O2] (Residuals)
[O2] (Residuals)
Control (0)
0.125
0.25
0.5
1.0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Time (Days)
Time (Days)
PAR



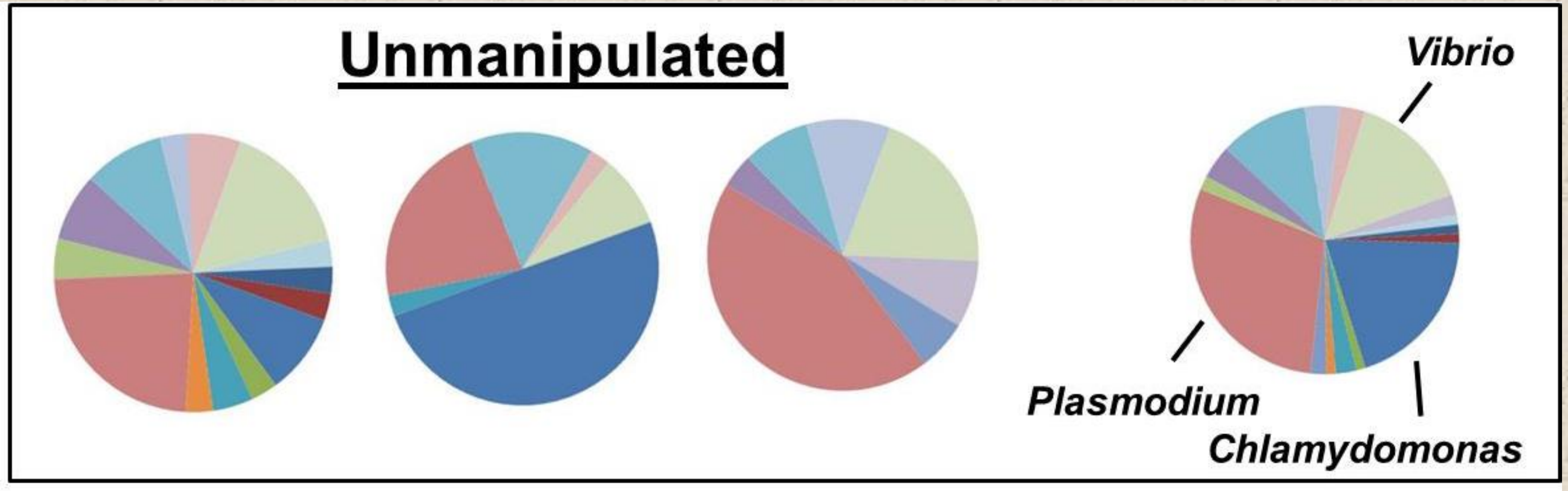

# Proteomic biomarkers as early warning indicators of state changes



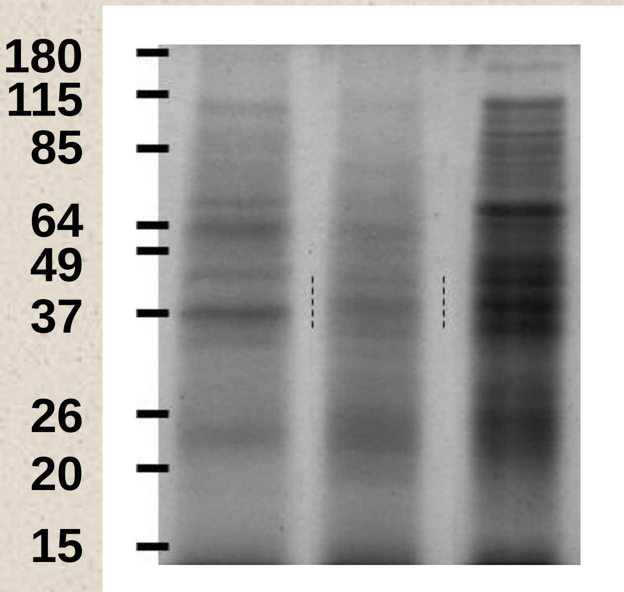
# Species Profiles of Top 30 Identified Proteins when Searching NRP NCBI Indexed Database



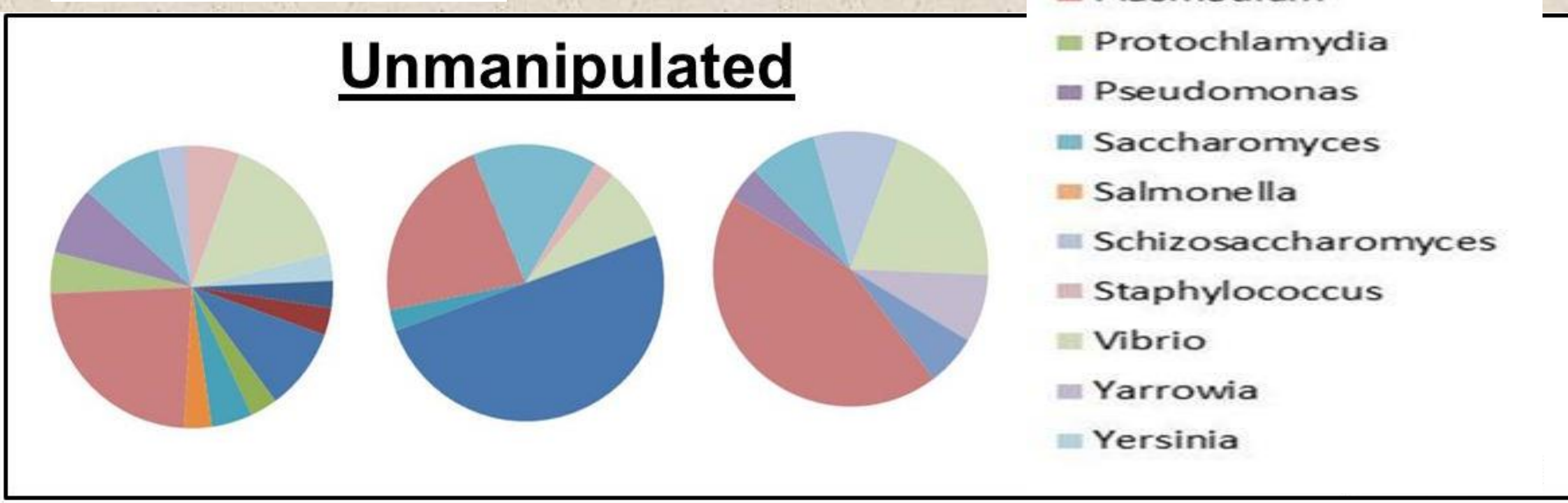

## Unmanipulated Controls



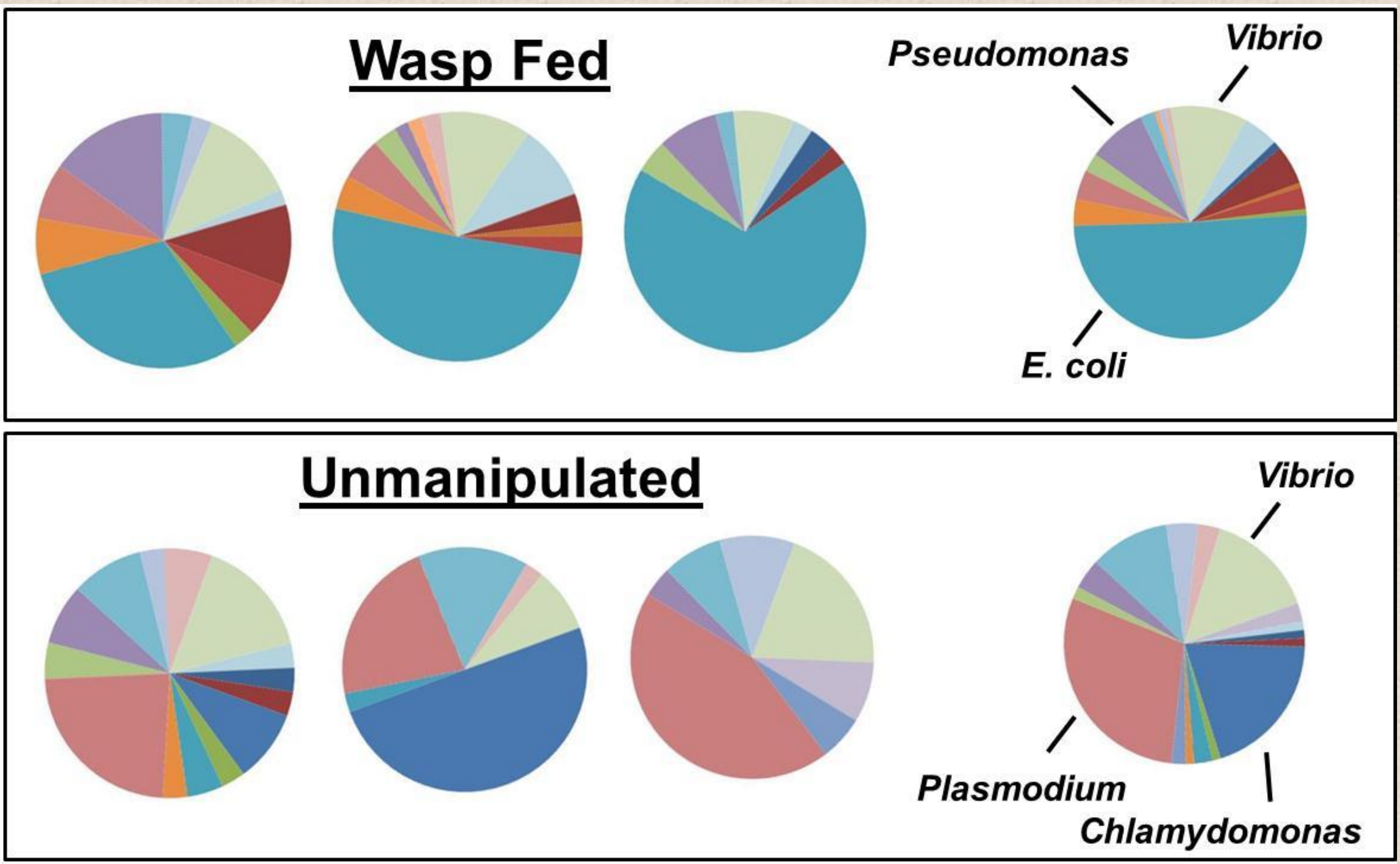
# Species Profiles of Top 30 Identified Proteins when Searching NRP NCBI Indexed Database




Unmanipulated C



# Species Profiles of Top 30 Identified Proteins when Searching NRP NCBI Indexed Database

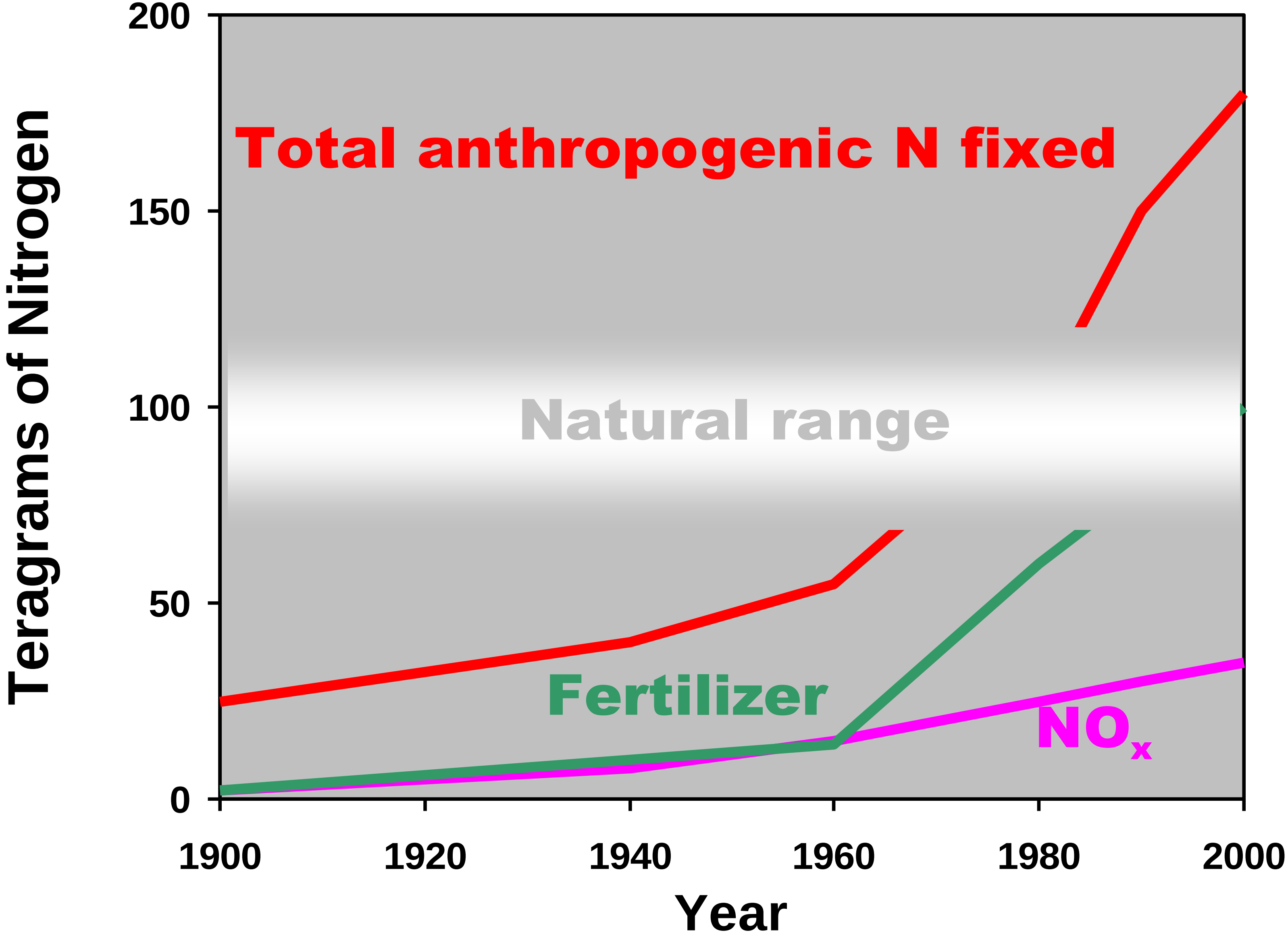


# Effects of N Deposition on Carnivorous Plants

- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists

Burning of Fossil Fuels

Use of Synthetic Fertilizers



Total anthropogenic N fixed
Natural range
Fertilizer
$NO_x$
Teragrams of Nitrogen
0
50
100
150
200
1900
1920
1940
1960
1980
2000
Year

Ecology

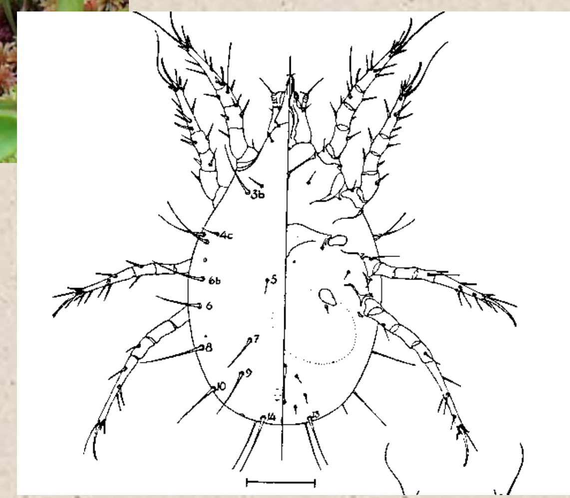
≠

Environmental Science

# Reasons for Studying Ecology

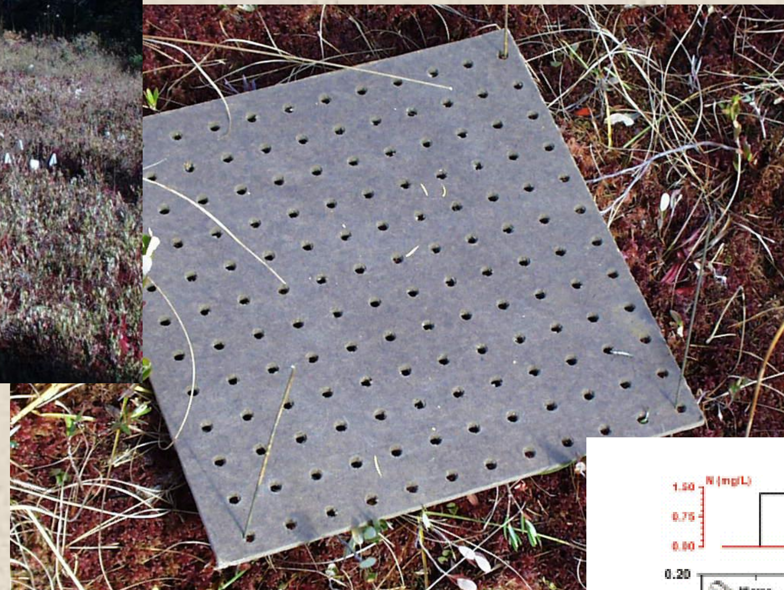
# Reasons for Studying Ecology

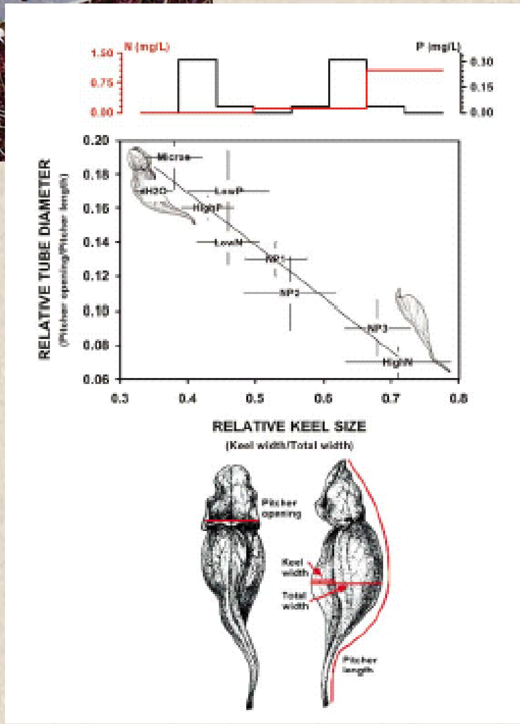
- Natural History



# Reasons for Studying Ecology

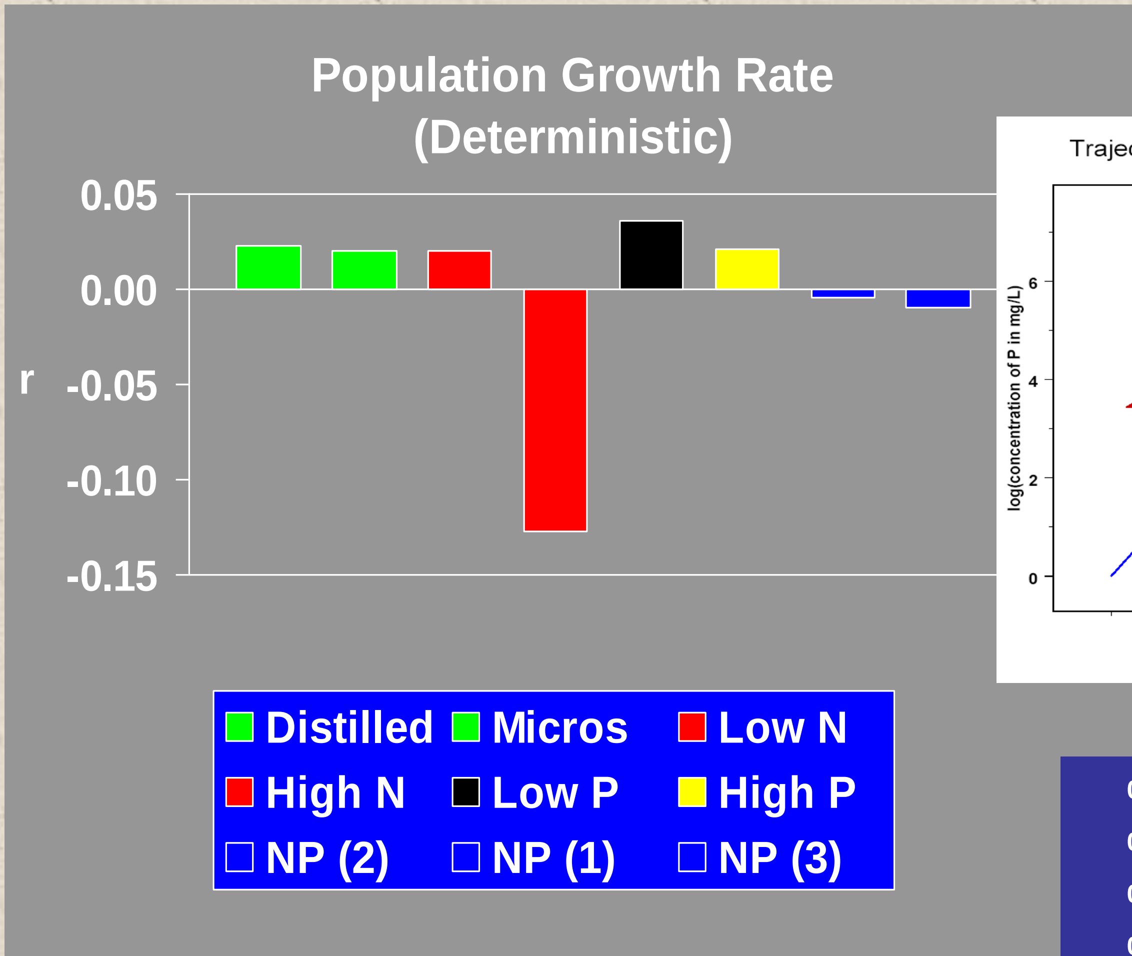
- Natural History
- Field Studies & Experiments

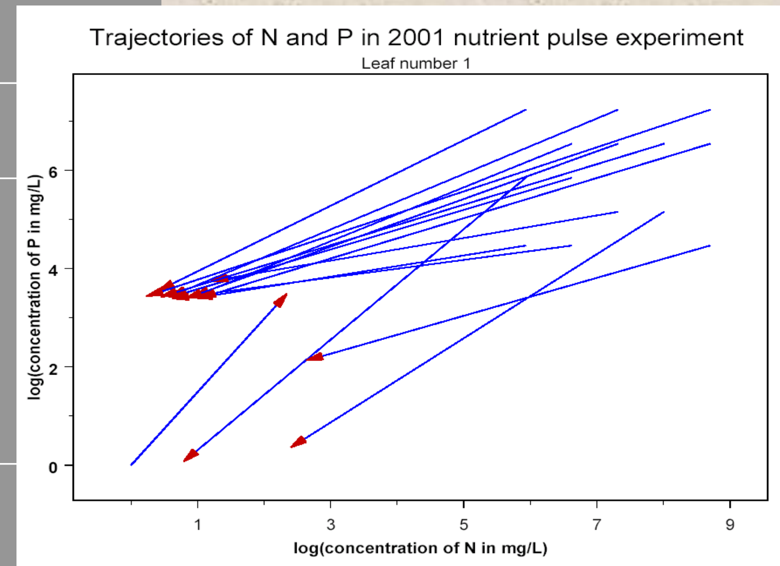


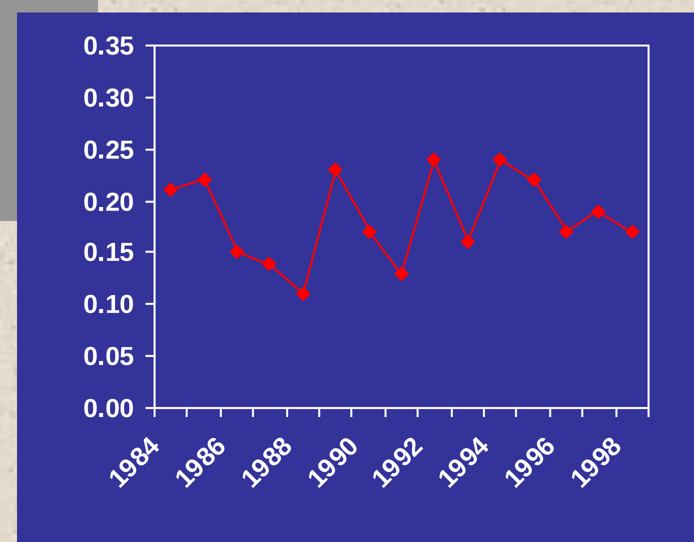

N (mg/L)
P (mg/L)
1.50
0.75
0.00
RELATIVE TUBE DIAMETER
(Pitcher opening/Pitcher length)
Micrse
dH2O
LowP
HighP
LowN
NP1
NP2
NP3
HighN
RELATIVE KEEL SIZE
(Keel width/Total width)
Pitcher opening
Keel width
Total width
Pitcher length

# Reasons for Studying Ecology

- Natural History
- Field Studies & Experiments
- Statistics & Data Analysis


Population Growth Rate
(Deterministic)
r
0.05
0.00
-0.05
-0.10
-0.15
Distilled
Micros
Low N
High N
Low P
High P
NP (2)
NP (1)
NP (3)


Trajectories of N and P in 2001 nutrient pulse experiment
Leaf number 1
log(concentration of P in mg/L)
log(concentration of N in mg/L)
0
2
4
6
1
3
5
7
9

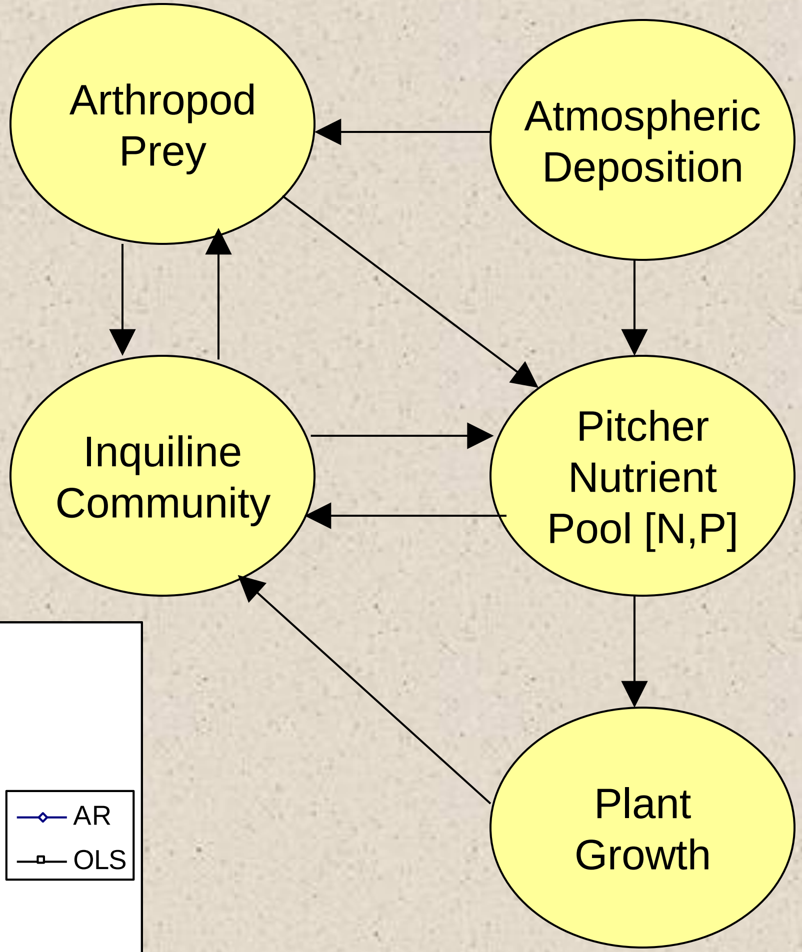

0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1984
1986
1988
1990
1992
1994
1996
1998

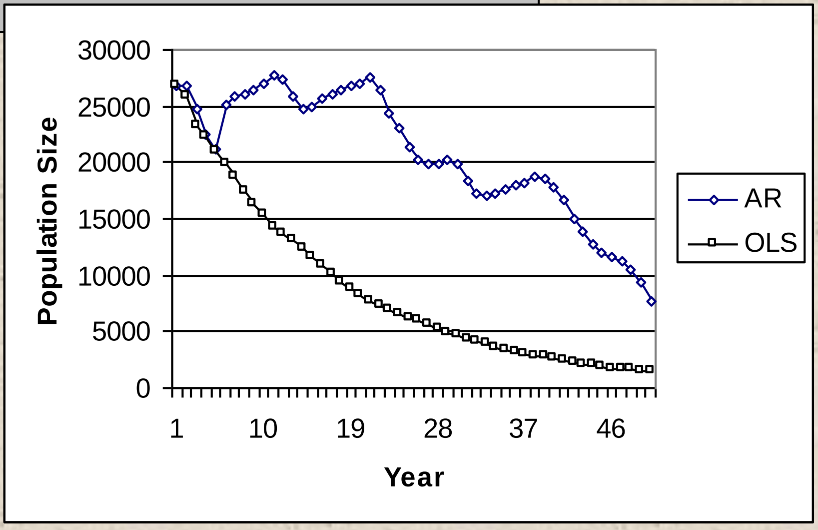
# Reasons for Studying Ecology

- Natural History
- Field Studies & Experiments
- Statistics & Data Analysis
- Modeling

$$\frac{dN}{dt} = f(N, I, t)$$

$$\frac{dI}{dt} = g(I, N, t)$$



# Reasons for Studying Ecology

- Natural History
- Field Studies & Experiments
- Statistics & Data Analysis
- Modeling
- Collaboration

Aaron M. Ellison

Harvard Forest

# Conclusions

- Anthropogenic deposition of N is a major ecological challenge

# Conclusions

- Anthropogenic deposition of N is a major ecological challenge
- Carnivorous plants in ombrotrophic bogs are a model system

# Conclusions

- Anthropogenic deposition of N is a major ecological challenge
- Carnivorous plants in ombrotrophic bogs are a model system
- Individual response
  - plants alter morphology and growth in response to N:P ratios

# Conclusions

- Anthropogenic deposition of N is a major ecological challenge
- Carnivorous plants in ombrotrophic bogs are a model system
- Individual response
  - plants alter morphology and growth in response to N:P ratios
- Population response
  - N and P environments affect population growth rate

# Conclusions

- Anthropogenic deposition of N is a major ecological challenge
- Carnivorous plants in ombrotrophic bogs are a model system
- Individual response
  - plants alter morphology and growth in response to N:P ratios
- Population response
  - N and P environments affect population growth rate
- Community response
  - Further study of nutrient ↔ inquiline feedback loop