Response vs. Effect functional traits

1. Overview and Definitions
2. Goal: to understand how different kinds of environmental change, or environmental drivers, can cause changes in biodiversity that in turn affect ecosystem functioning at landscape levels
3. How can this be done beyond confirming that functional diversity plays an important role in ecosystem functioning i.e. predictive? What mechanisms can be elucidated? Can we apply this approach at broad scales?

Environmental Driver:
N deposition
P enrichment
Atmospheric CO2
Temperature
Precipitation

↔

Response Trait:
Life form
Seed mass
Rooting depth
Root type
Fire tolerance

???

↔

Effect Trait:
Leaf CNP concentration
Litter CNP concentration
Nutrient efficiency

Ecosystem Function:
P availability
Soil CO2 flux
N mineralization
ANPP

How can the role of plant diversity in ecosystem resource dynamics be explained?

Two main mechanisms:

1. Selection effect- the higher the species richness in a community, the higher the probability of the presence of a species with a particularly important trait i.e. stresses the presence of certain key trait values

2. Niche complementarity effect or complementarity of resource use-at higher diversity, a greater range of functional traits will be represented, providing opportunities for more sufficient resource use in a spatially or temporally variable environment i.e. stresses the presence of a range of different traits

Diaz and Cabido, 2001

Definitions

Diaz and Cabido 2001:

Plant functional types - sets of species showing similar responses to the environment and similar effects on ecosystem functioning; groupings are based on common attributes, not phylogenetics

Functional response types – groups of plant species that respond to the abiotic and biotic environment (resource availability, climatic conditions, disturbance) in similar ways i.e. xerophytic vs. mesophytic, gap vs. understory, fire-tolerant vs. fire-intolerant

Functional effect types – groups of plant that have similar effects on the dominant ecosystem processes (NPP, nutrient cycling, trophic transfer) i.e. nitrogen fixers, ecosystem engineers, nurse species, fire-promoting species

Response and effect types often coincide, particularly in the case of resource use i.e. traits that confer high resistance to environmental stress and herbivory (response) also determine slow decomposition and nutrient cycling (effect)

Some important implications of evaluating response and effect relationships and role in ecosystem functioning (Diaz and Cabido 2001)

1. Functional redundancy – the disappearance of one species within a functional effect group has no effect on ecosystem function

2. Functional insurance – the greater the variation of different response traits of species belonging to the same functional effect group enable the maintenance of long-term ecosystem functioning

Empirical evidence:

- Different degrees of grazing resistance among species within a functional effect group found to buffer C and N cycling (Walker et al 1999)
- Species belonging to the same effect type showed variation in response to experimental warming (Chapin et al 1996)
- Drought tolerance among pairs of species showing similar resource dynamics within growth forms (Buckland et al 1997)

Also suggests that minor species present in a functional effect group could have an important role in maintaining ecosystem function if these species were favored with climatic changes or disturbance events

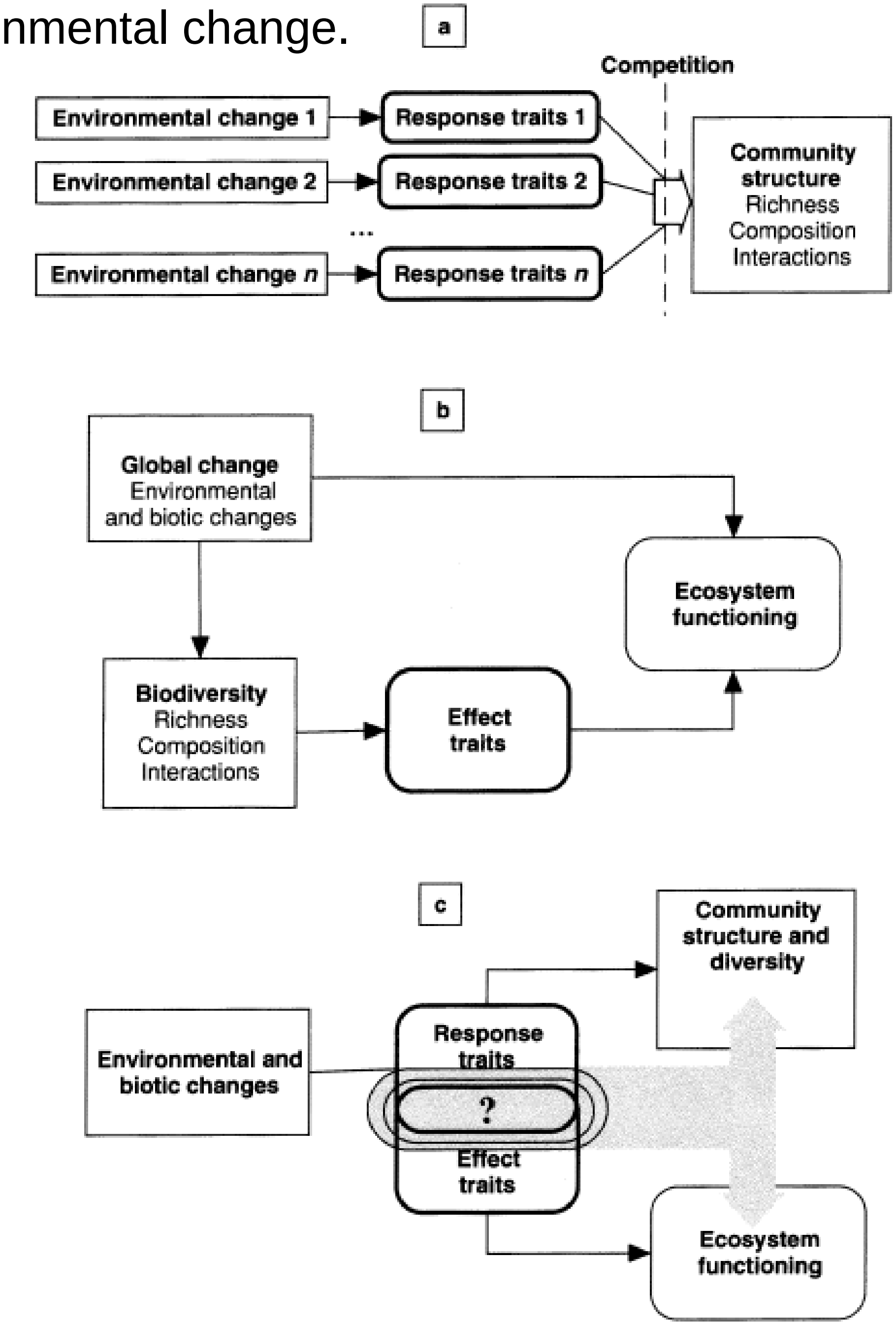
Conceptual framework to effects of environmental change.

A. RESPONSE APPROACH: Filter theory – response of community structure to environmental conditions is the result of species response traits (Keddy 1992, Woodward and Diament 1991). Plant communities can be seen as the result of a hierarchy of abiotic and biotic filters that successively constrain which species and traits (from the regional pool) can persist at a site.

B. EFFECT APPROACH: Framework predicting the ecosystem consequences of environmental changes via species effect traits (Chapin et al. 2000).

C. RESPONSE AND EFFECT APPROACH: Framework that articulates environmental response and ecosystem effects through varying degrees of overlap of relevant traits

Lavorel and Garnier 2002



Three key tenets of conceptual framework (Lavorel and Garnier 2002):

1. Traits can simultaneously explain responses to biotic and abiotic factors and effects on ecosystems

2. Ecosystem function is predictable from composition if those traits involved in the response to environmental filters can be used to estimate ecosystem processes → focus on traits that represent changes in intensity of those processes (continuous traits)

3. Functional linkages and trade-offs among traits that relate to one or more processes determine whether filtering by different factors holds up and can be used to deduce ecosystem effects, but can be largely contextual (scale, environmental conditions, and evolution)

A framework for *broad-scale* biodiversity and ecosystem function research (Naeem and Wright 2003)

Identifying links between community properties of biodiversity and the magnitude and dynamics of ecosystem function

What governs the response of an ecosystem to changes in biodiversity?

1. Species composition
2. Abundance of each species
3. Functional traits each species possesses
4. The biotic interactions among species that regulate magnitude and variability of expression of the function under investigation

A framework (suggested approaches and algorithms to predict at each level of inquiry):

1. Identify species composition across sites
2. Determine abundance
3. Determine functional traits
4. Determine ecosystem function

A trait-based response and effect framework for scaling from individuals to ecosystems (*Suding et al. 2008, GCB*)

Involves an integration of:

1. How a community responds to change
2. How that changed community affects ecosystem processes

Key aspects:

1. Similarly distinguishes functional response groups and functional effect groups
2. But, scales processes from individuals to ecosystems through the community level to predict effects of environmental change
3. Furthers the framework presented by Naeem and Wright (2003) by developing a basic formulation

Important factors to predict how environmental change influences ecosystem function through community dynamics:

1. Species abundance responses as related by response functional traits
2. The relationship between response and effect traits
3. Resulting altered representation of effect traits

$$Y_2 = \sum_{j=1}^{S} f(n_{j1} * R_j, E_j)$$

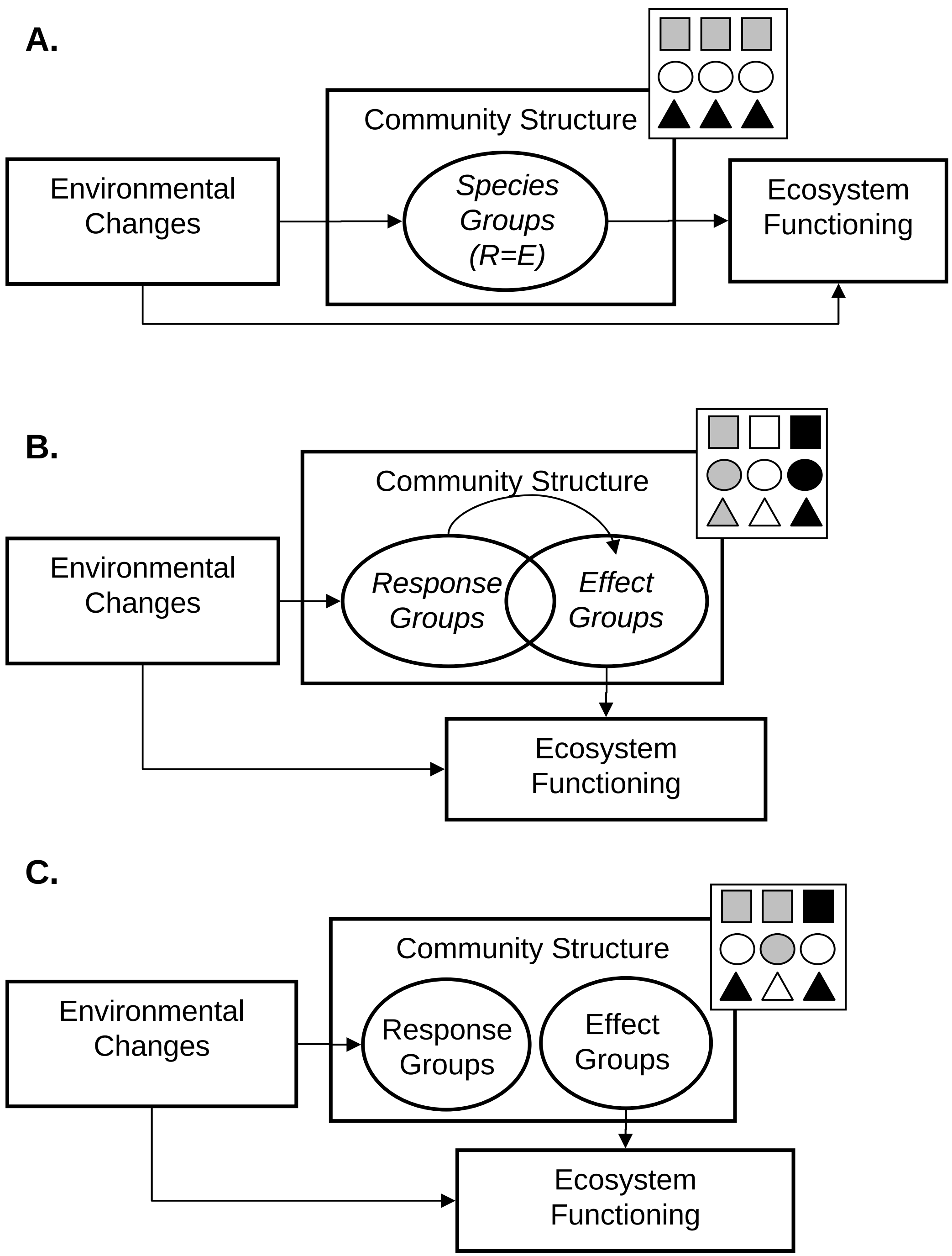
The contribution of a given species to future aggregate ecosystem function can be assumed to be a function of the effect of a species on Y (ecosystem function) and its predicted abundance

A trait-based response and effect framework for scaling from individuals to ecosystems (*Suding et al. 2008, GCB*)

A. Response and effect groups completely overlap, likely most useful for linkages, exhibit strongest plant-soil feedbacks, and lead to non-linear effects

B. Effect groups represented by all response groups with potential functional redundancy and resilience (threshold?) to effects of environmental change on ecosystem function

C. Effect groups random with respect to effect, system would be more resilient based on responses



In terrestrial systems with strong plant-soil feedbacks, are there scenarios in which environmental change might affect soils at similar or greater rates than plants?

1. Indirect effect of functional response: factors in which soil conditions will be directly modified (i.e. microbial effect) and plants respond to these conditions (i.e. increased nutrient availability), and thus feedback on soil conditions i.e. nutrient enrichment

2. Direct effect of functional response: factors in which plants are modified and thus affect soil or other ecosystem conditions i.e. drawdown or nutrient enrichment effects in submersed aquatic macrophytes (Engelhardt 2006)

In either case of direct or indirect effects of response on ecosystem function, plant-ecosystem relationships would be strong, but if they are indirect, how can functional response and ecosystem function via functional effect be directly linked i.e. mechanisms elucidated?

Possible scenarios:

(1) functional response may not be linked with functional effect

(2) some environmental factors may modify soil conditions making it difficult to directly link response traits and ecosystem function

How can we resolve these issues?

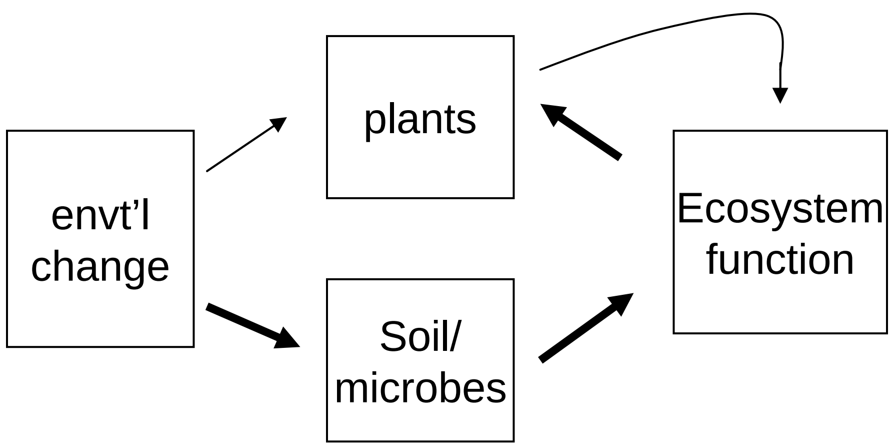
(1) screening for effect classifications not based on traditional morphotype classifications would improve the ability to link response and effect *(Suding et al. 2008, GCB)*

(2) determine common functional responses (to environmental change) that overlap functional effects expected to have an influence on ecosystem processes i.e. involved in biogeochemical cycling (Lavorel and Garnier 2002)

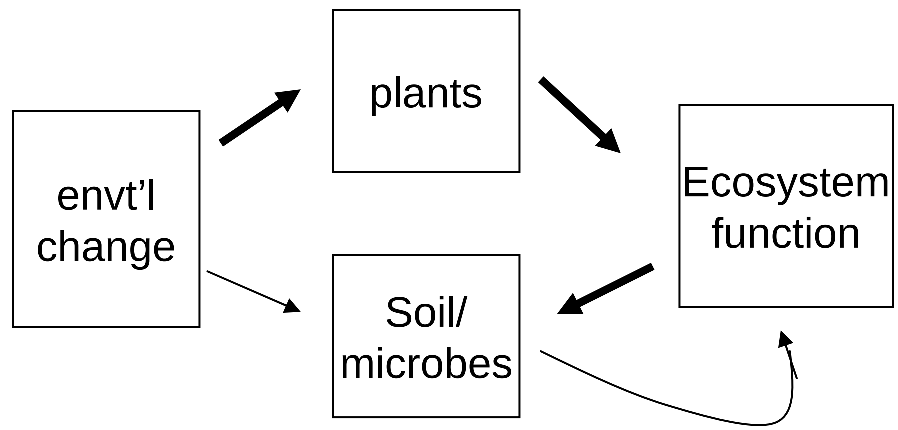
(3) Initiate experiments that utilize the functional effect traits as the treatment – employ combinatorial designs to predict synergistic effects of future environmental change. This approach would also help to elucidate links between response and effect that we may not expect. Robust assessments might employ multiple ecosystem types.

Important distinction if relating back to changes in functional composition and diversity, especially in elucidating mechanisms for how the response causes changes in ecosystem function

Indirect effect of response/effect trait



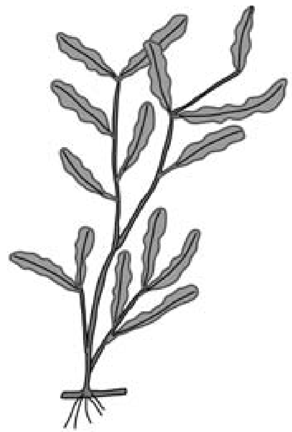
Direct effect of response/effect trait



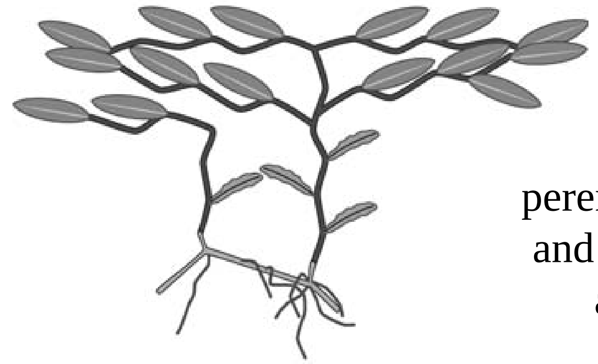
Other biotic aspects of the ecosystem may be influenced by environmental change at similar or greater rates when linking functional response to ecosystem process

RELATING EFFECT AND RESPONSE TRAITS IN SUBMERSED AQUATIC MACROPHYTES (Engelhardt 2006)

perennial, broad, submersed leaves, affinity for bicarbonate



Potamogeton crispus

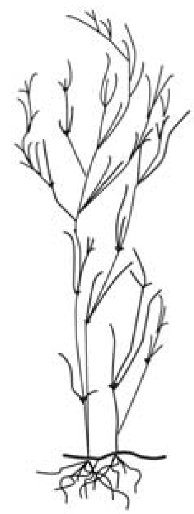


Potamogeton nodosus

perennial, broad, submersed and floating leaves, tubers, atmospheric carbon

perennial, filiform leaves with high SA:V, tubers, affinity for bicarbonate

Stuckenia pectinata



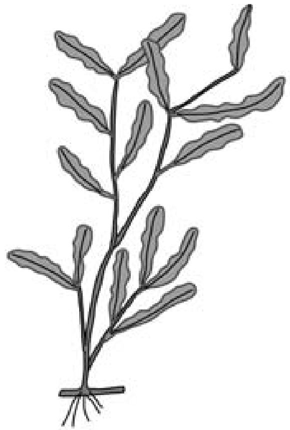
Zannichellia palustris

Annual, filiform leaves with high SA:V

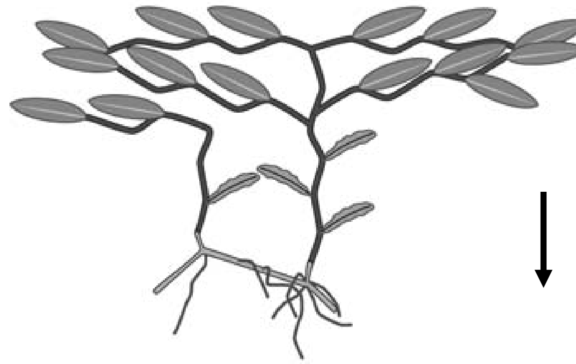
RELATING EFFECT AND RESPONSE TRAITS IN SUBMERSED AQUATIC MACROPHYTES (Engelhardt 2006)

↓ Water PAR, Alk, CO_2
Soil Temp, Algae

↑ Water pH, O_2



Potamogeton crispus



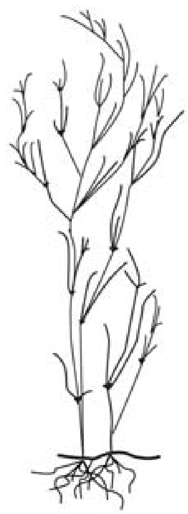
Potamogeton nodosus

↓ Water TP, PAR, Alk
Soil Temp

↓ Water Alk, CO_2
Soil Temp, Algae

↑ Water pH

Stuckenia pectinata



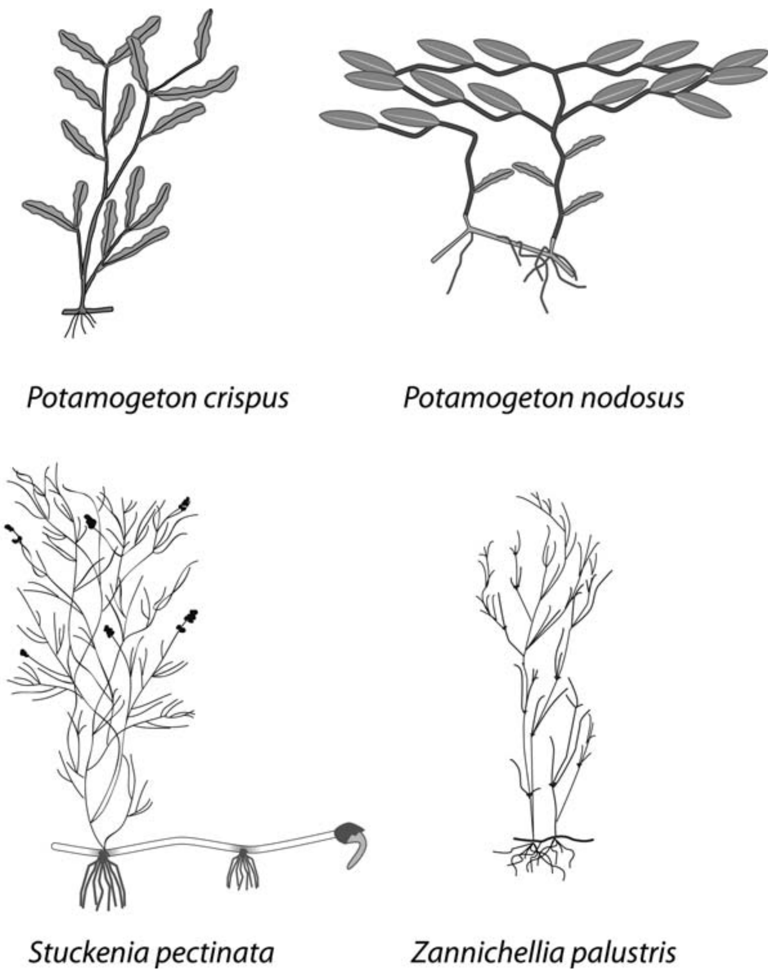
Zannichellia palustris

↓ Water Alk, CO_2
Soil Temp, Algae

↑ Water pH

Negative correlations between root growth and sediment phosphorus

Negative correlations between shoot growth and water column phosphorus, PAR and alkalinity



Changes in ecosystem properties after environmental change (water draw-down)

1. *P. nodosus* increased TP concentration of outflowing water

2. Associated with 3 of 4 species, pH decreased

3. *P. crispus* increased DIN supply in sediments (absorbed on ion exchange membranes

4. *Z. palustris* increased SRP availability in sediments (porewater concentration)

Summary of conclusions

- Some effect traits were common to several species (a function of the presence of a plant) with different response traits – functional redundancy or experimental artifact?

- Some response and effect traits were correlated, but mechanisms linking inorganic nutrient supply and availability (ecosystem function) with response traits not clearly identified

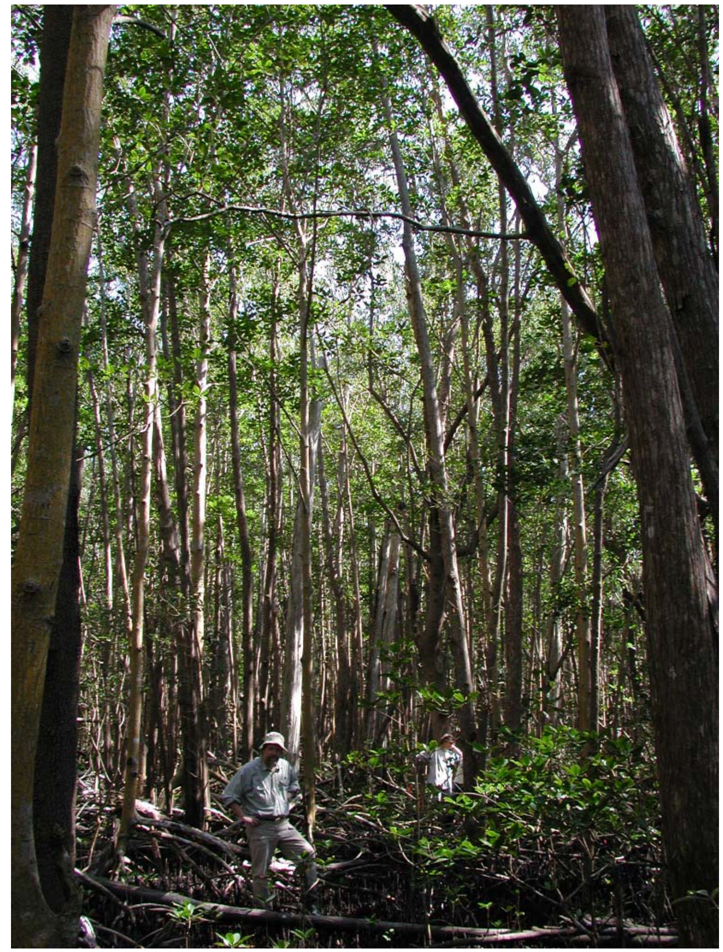
- Root growth and presence of tubers conferred highest resistance following disturbance

- Author illustrates the importance of evaluating response and effect traits before and after an environmental change

Potential implications: 1) Identifiable linkages in single vs. mixed species in field setting? 2) link between response and effect may not be as easily observable in terrestrial systems as nutrient acquisition is mostly from the soil environment

Wetlands are typically ecosystems that exhibit strong plant-soil relationships, but also exhibit relatively fast responses to environmental changes

Low soil phosphorus



High soil phosphorus

In assemblages that are dominated by one species, links between environmental change and ecosystem function, via response and effect traits, are robust.

Response and effect traits often completely overlap, but often with little variation in key traits, as in this mangrove forest dominated by *R. mangle*

Low soil phosphorus, **low** aboveground biomass, **high** belowground biomass, **low** tissue P concentration

High soil phosphorus, **high** aboveground biomass, **low** belowground biomass, **high** leaf tissue P concentration

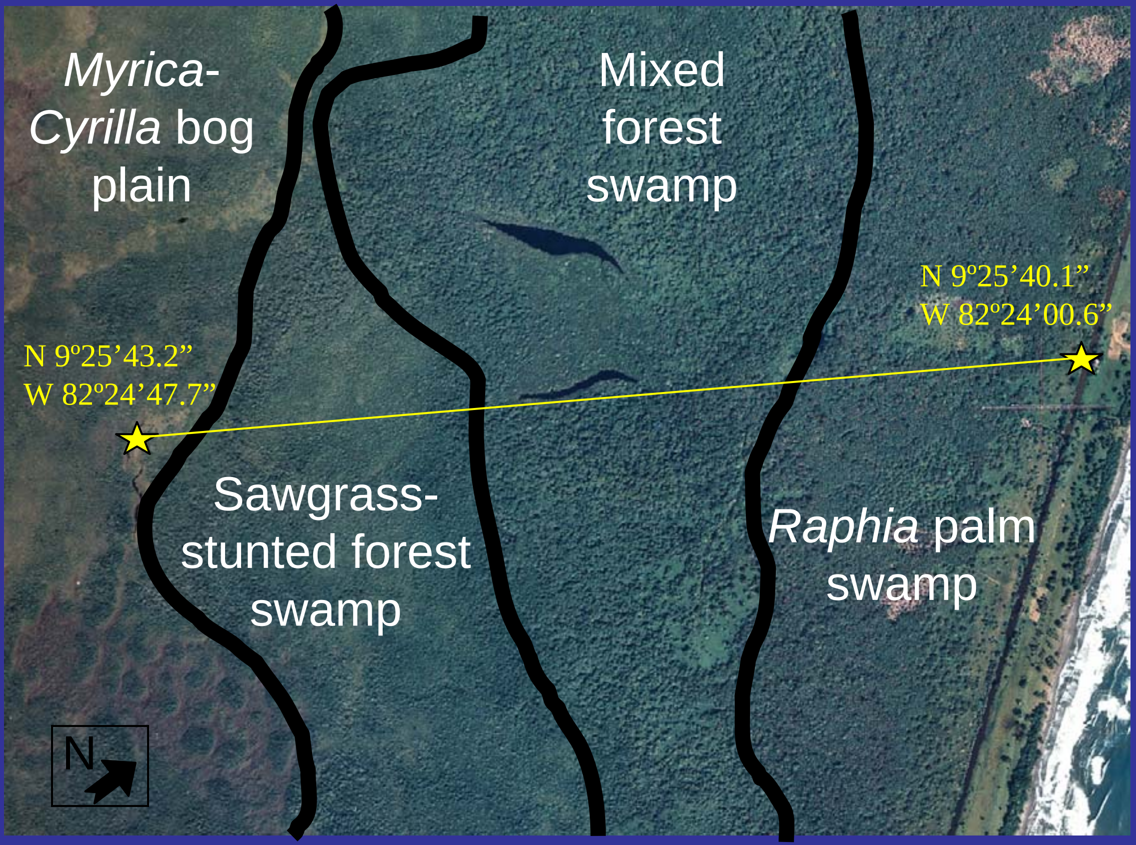
Mixed species assemblages, however, may be very useful in elucidating relationships between response and effect traits, and predictions of ecosystem function with environmental change

Raphia palm forest at 0.3 km

Campnosperma panamensis forest at 1.5 km

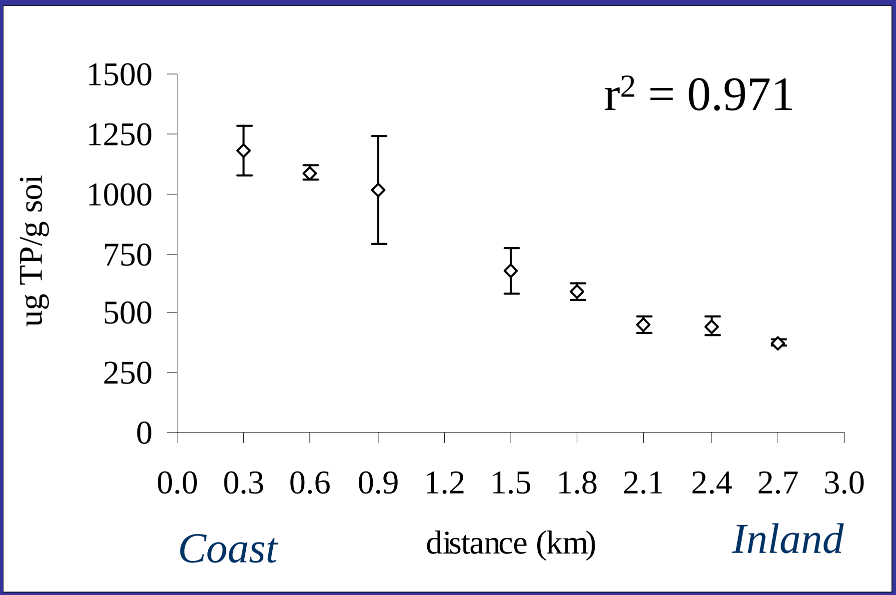
Myrica-cyrilla bog at 2.4 km

Vegetation types (Phillips et al 1997)



Variation in soil nutrients with distance along peat development gradient

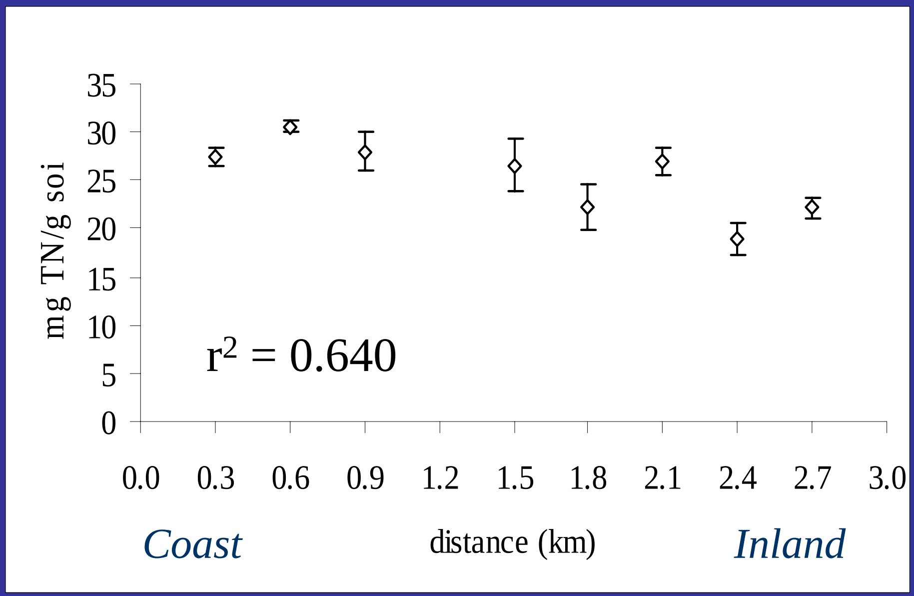
Soil Phosphorus



$y = -362.48x + 1284.14$

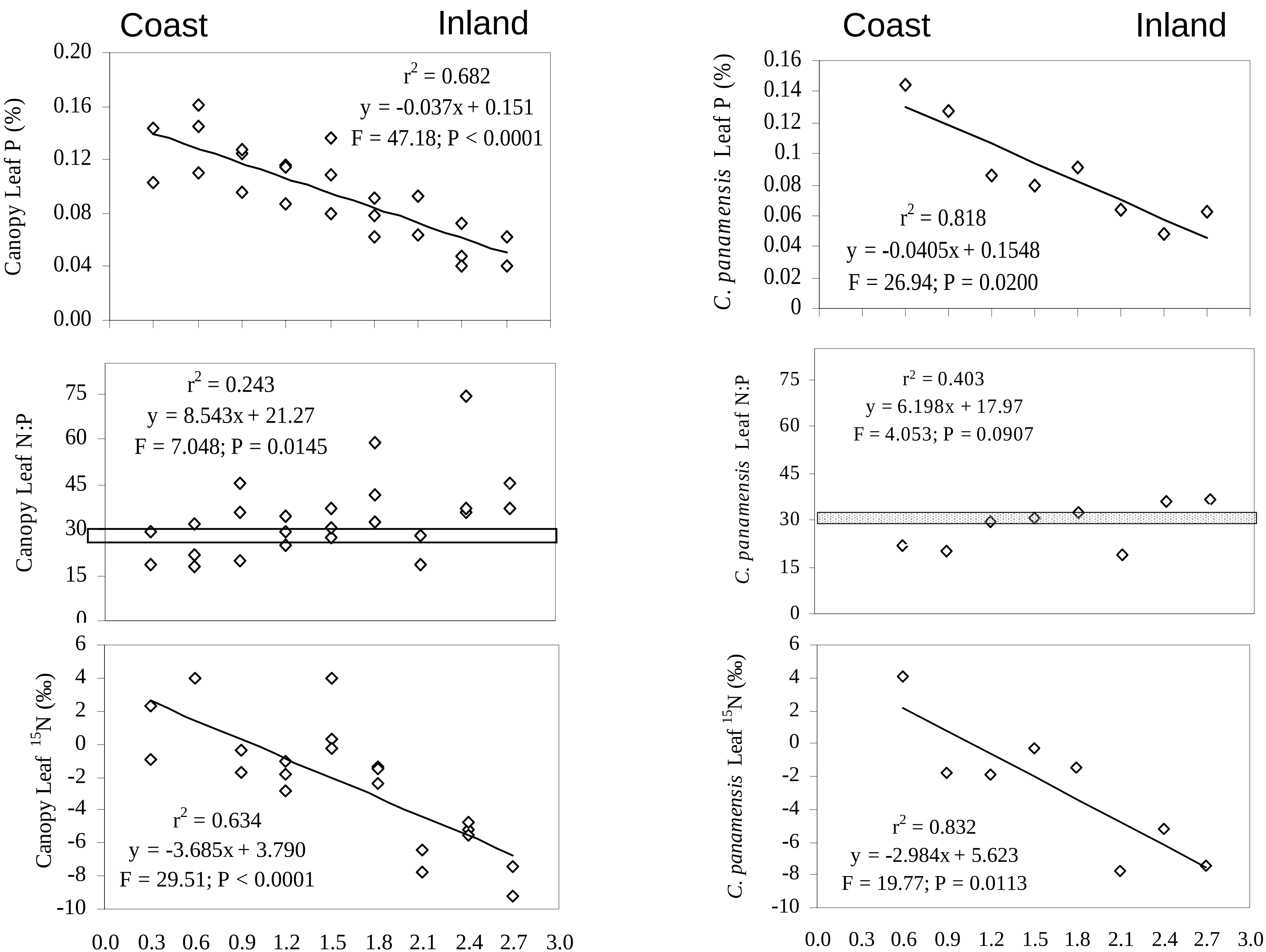
$F = 200.94$; $p < 0.0001$

Soil Nitrogen



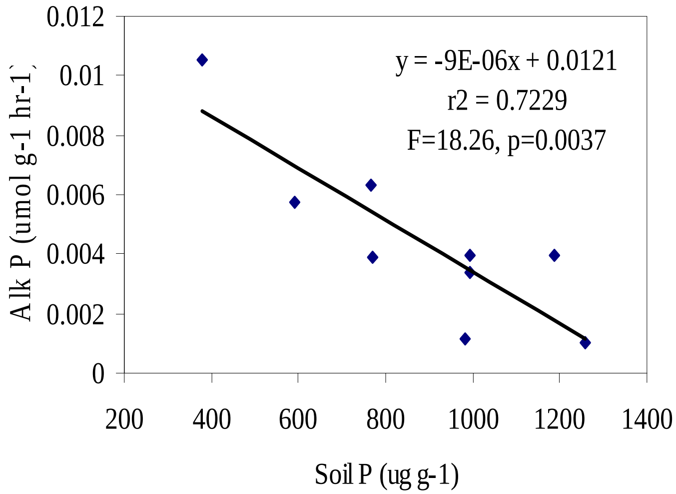
$y = -3.66x + 30.58$

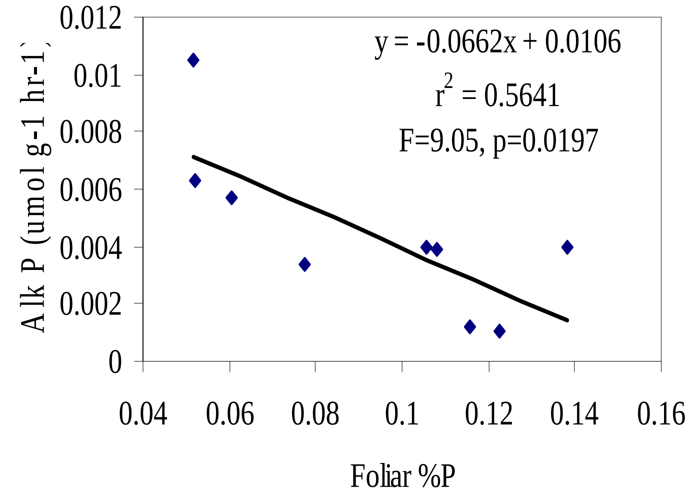
$F = 10.651$; $p = 0.0172$

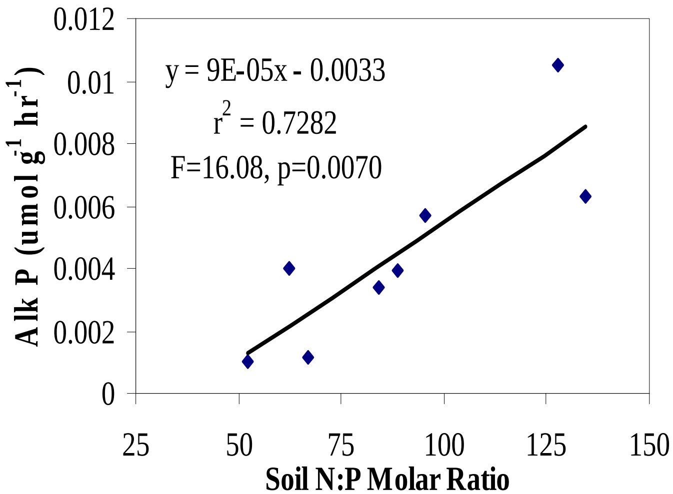


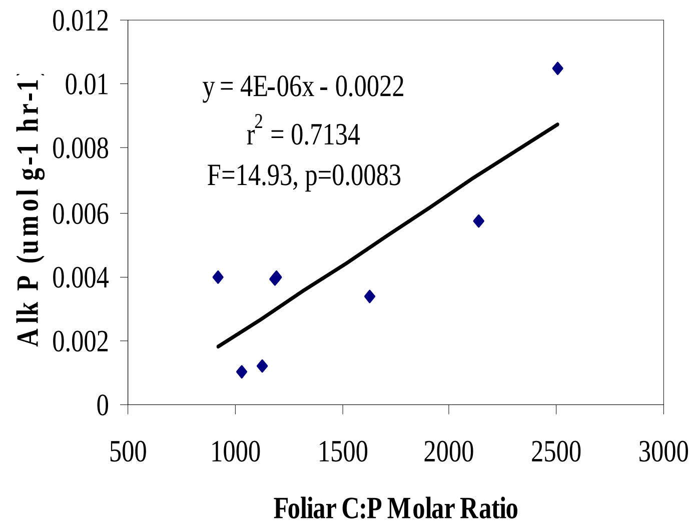
Coast
Inland
Canopy Leaf P (%)
r2 = 0.682
y = -0.037x + 0.151
F = 47.18; P < 0.0001
Canopy Leaf N:P
r2 = 0.243
y = 8.543x + 21.27
F = 7.048; P = 0.0145
Canopy Leaf 15N (‰)
r2 = 0.634
y = -3.685x + 3.790
F = 29.51; P < 0.0001
C. panamensis Leaf P (%)
r2 = 0.818
y = -0.0405x + 0.1548
F = 26.94; P = 0.0200
C. panamensis Leaf N:P
r2 = 0.403
y = 6.198x + 17.97
F = 4.053; P = 0.0907
C. panamensis Leaf 15N (‰)
r2 = 0.832
y = -2.984x + 5.623
F = 19.77; P = 0.0113
0.0 0.3 0.6 0.9 1.2 1.5 1.8 2.1 2.4 2.7 3.0

Relationships between alkaline phosphatase activity & nutrient status









Soil P and foliar %P of canopy species were negatively related to alkaline phosphatase activity whereas soil N:P and foliar C:P were positively related to AlkP.

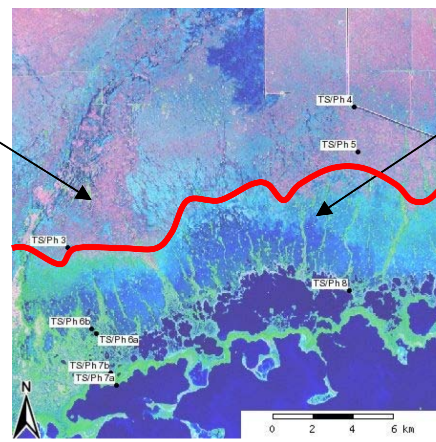
Can we use variation in response and effect traits along natural nutrient gradients to predict ecosystem function as a result of environmental change?

How will relationships between response and effect traits vary with type and magnitude of environmental change with consequent effect on ecosystem function?

Natural nutrient gradient

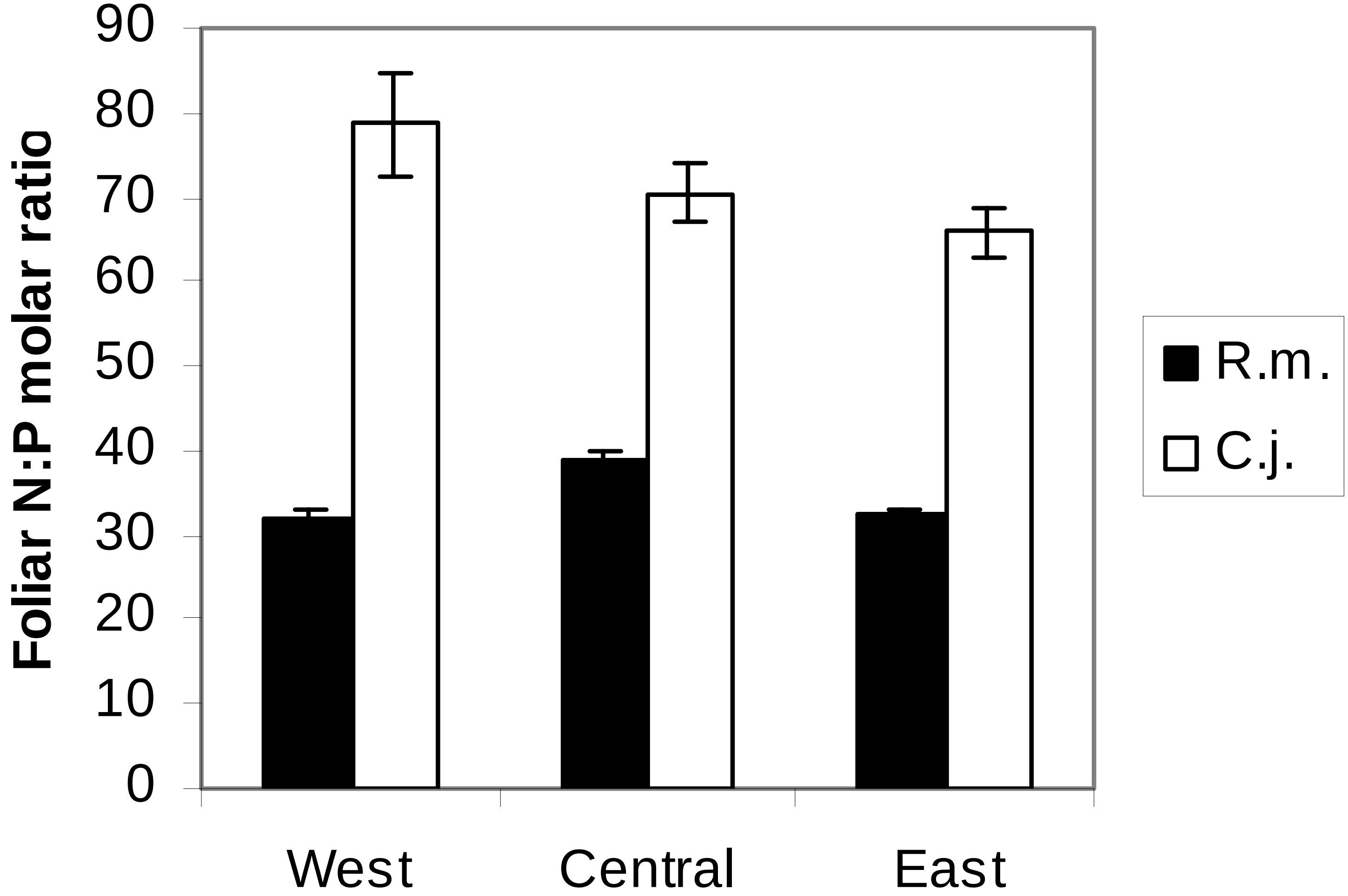
Phosphorus loading effect

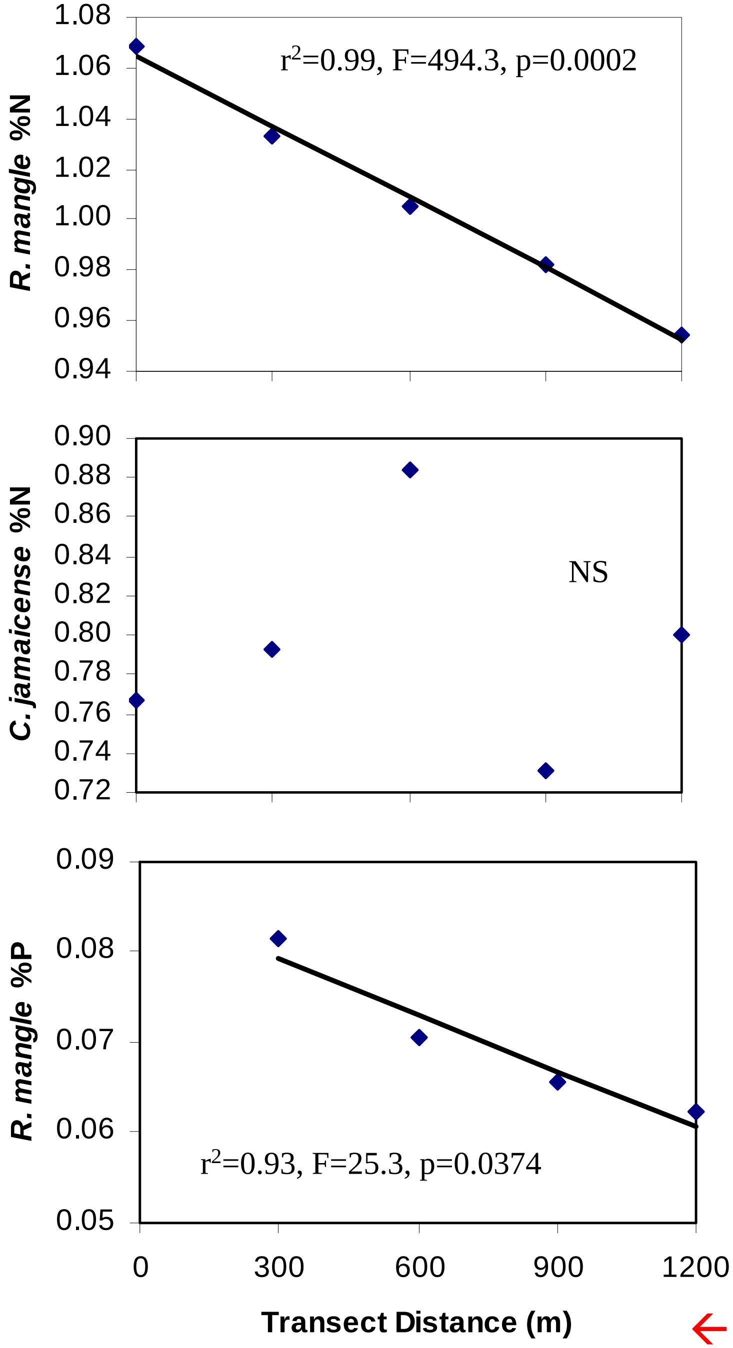
More complicated patterns appear to emerge with more recent environmental changes and/or pulsed disturbance events



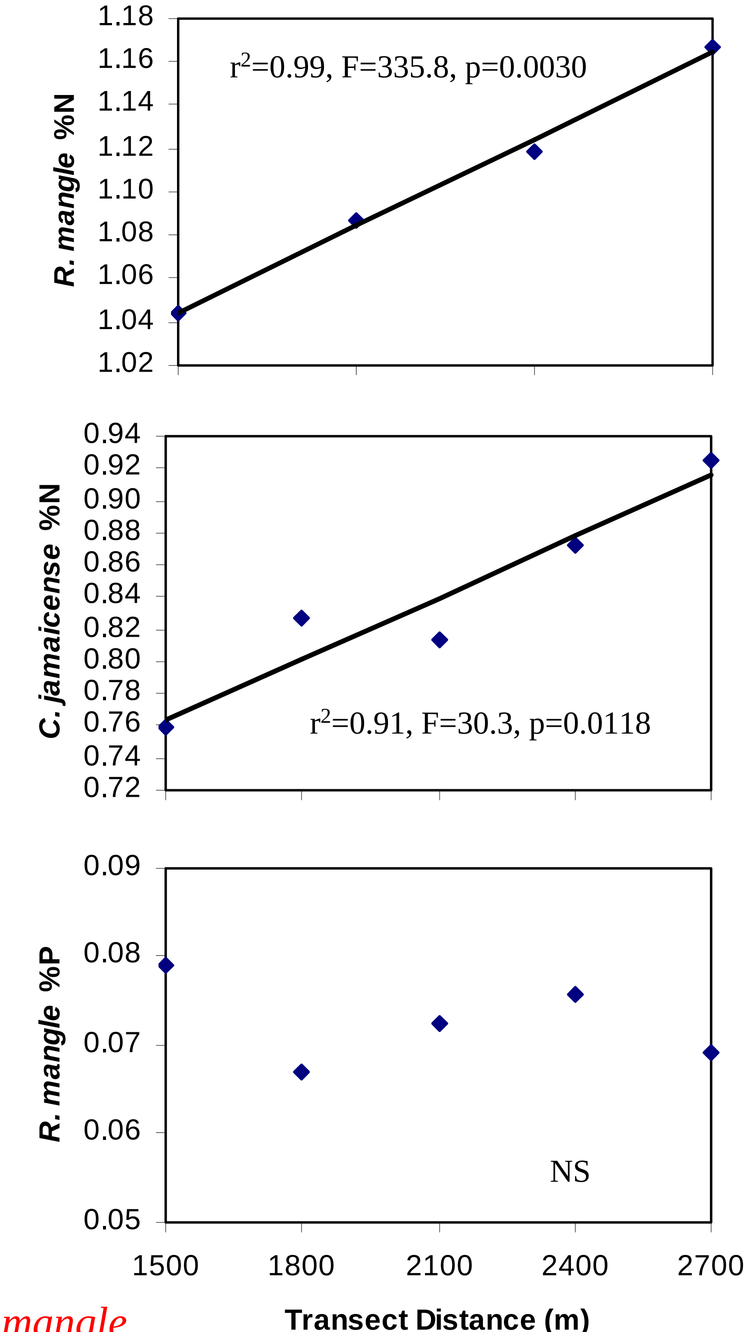
Mangrove encroachment into freshwater marshes along the coastal Everglades ecotone resulting from sea-level rise and reductions in freshwater flow from upstream water diversions and drainage

- *Single species replacement*
- *Hypothesis: large difference in potential effect traits and consequent ecosystem functions i.e. water quality, C accumulation, P mineralization, salinization and faciliatory effects*





No apparent relationship with soil nutrient patterns - and the response (increased density of woody species) and effect traits (tissue N) do not appear to be related, but some other underlying environmental gradient does seem to be present



← Encroachment of *R. mangle*

Low *R. mangle* density

High *R. mangle* density

Summary

- Recent progress suggests linking environmental change and ecosystem function through community dynamics would be a powerful predictive tool

- In some scenarios, likely difficult to explicitly link response and effect traits

- Traits and change-response-effect-process linkages are likely to be largely contingent upon time since disturbance, and would vary along natural gradients as opposed to those imposed as a result of some more recent environmental change of varying magnitude

- Future change may be one that cannot be predicted under future disturbance scenarios because of non-linear responses and synergistic effects.

- Identifying effect classifications that link environmental change and response (involved in biogeochemical cycling) would provide the tightest response-effect linkages

- Integrating these research approaches experimentally may provide a range of potential responses, effects and links to predict ecosystem function based on environmental change, and help to elucidate mechanisms.

- For example, litter decomposition experiments using litter of altered quality (effect trait) across environmental gradients with imposed experimental disturbances