Functional groups revisited

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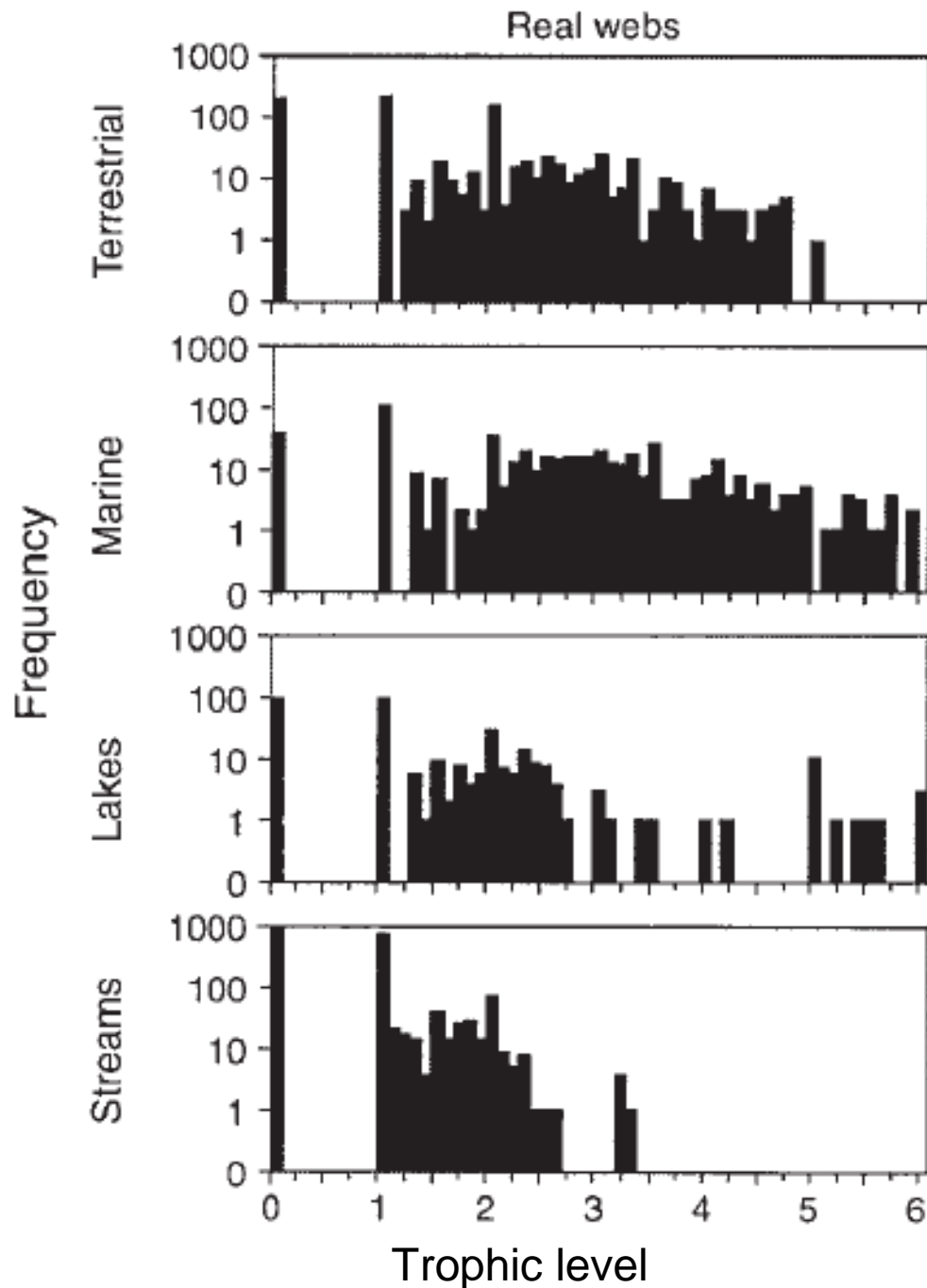
Groups versus continuous

- Groups easy, natural, but
- There may be overlap within groups
- Continuous data better for models/statistics

Some groups may be real

- Herbivore feeding groups: chewing versus sucking
- C3, C4 and CAM photosynthesis
- Web-building, ambush, hunting spiders

Trophic levels

Examination of food webs indicates that trophic levels 0 (plants) and 1 (herbivores) are discrete, but all higher levels are continuous.

Thompson et al. 2007, Ecology 88:612-617.

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Practical issue

- "Soft" or categorical traits are often much easier to get.
- Fertilization synthesis group used categories (N-fixing or not, C3 vs. C4, short vs. tall, etc.) because we couldn't get continuous traits for a large number of species.
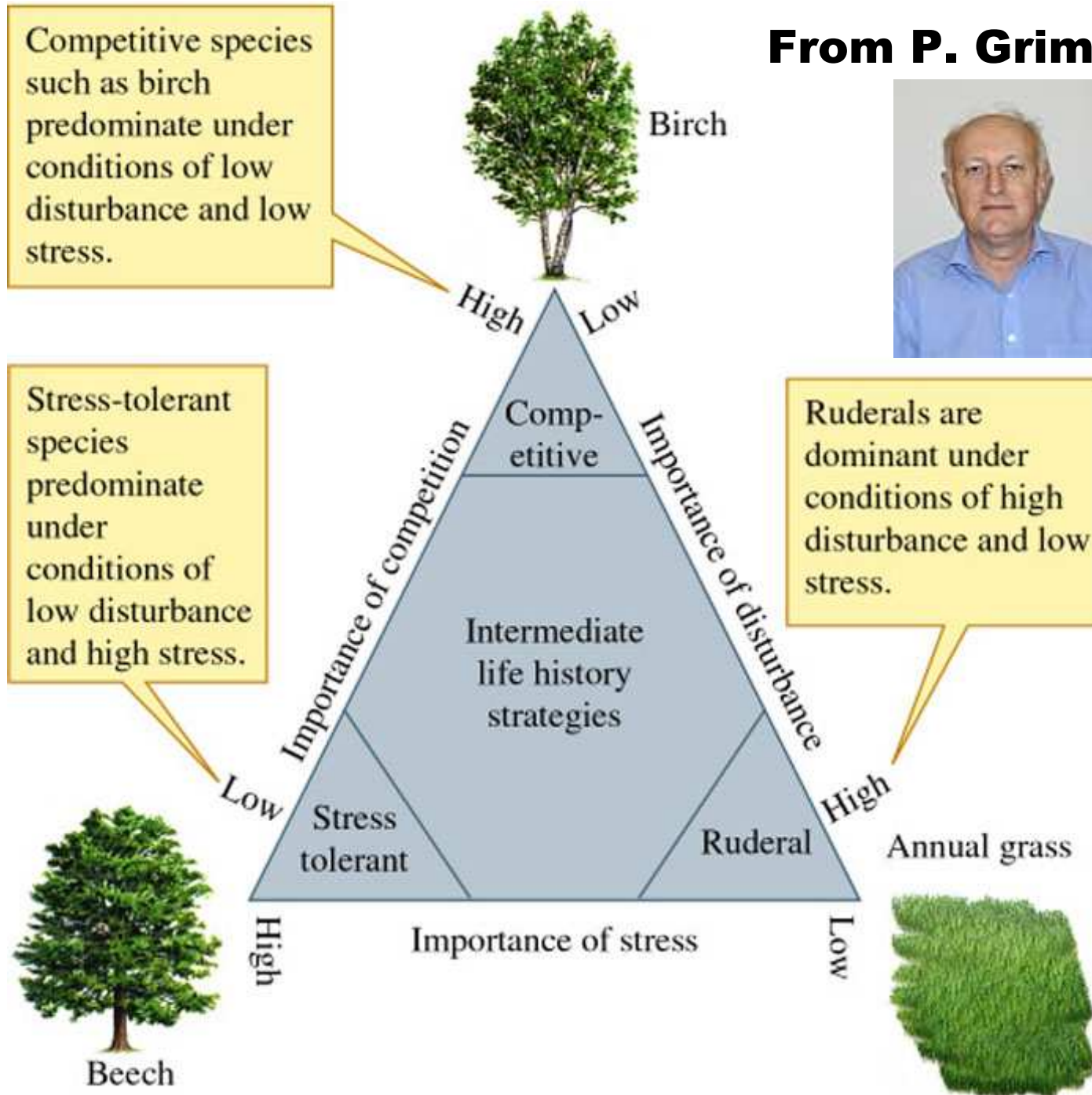- We are now talking about measuring one or two continuous traits.

Three approaches

- 1) Concept-driven
- 2) Natural groupings
- 3) Testing relationships

1) Concept-driven

- Based on theory/model, measure traits that should matter

From P. Grime 1979

Competitive species such as birch predominate under conditions of low disturbance and low stress.

Stress-tolerant species predominate under conditions of low disturbance and high stress.

Ruderals are dominant under conditions of high disturbance and low stress.

Birch

High   Low

Competitive

Importance of competition

Importance of disturbance

Intermediate life history strategies

Low   High

Stress tolerant

Ruderal

High   Importance of stress   Low

Annual grass

Beech

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Plant Apparency Theory--Paul Feeny

TABLE 11.2 Some correlates of apparent and unapparent plants.

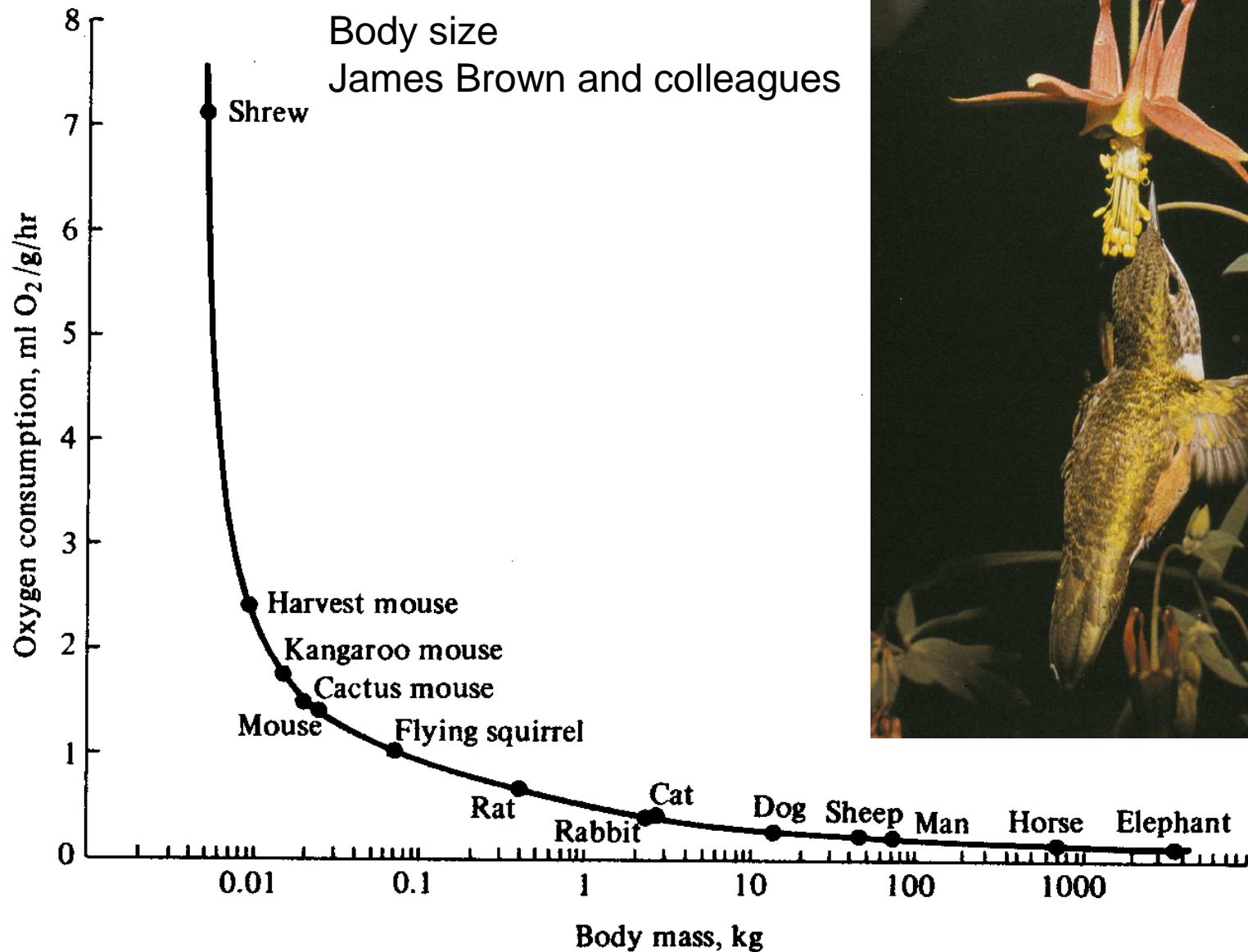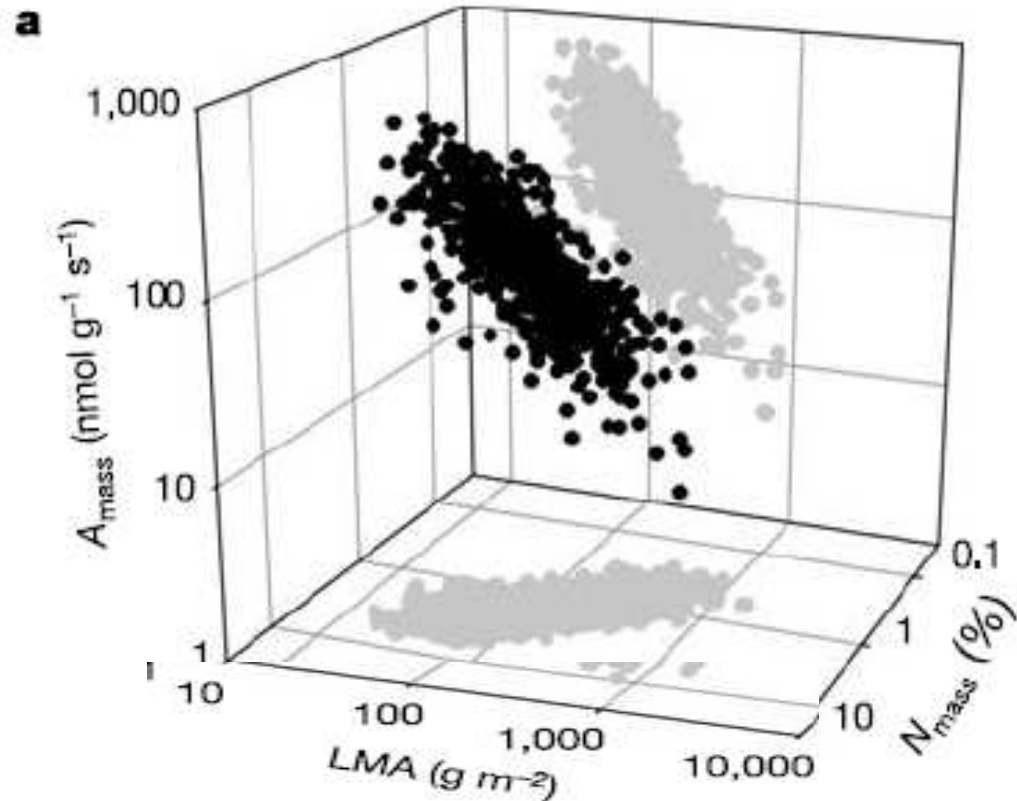| Apparent Plants	Unapparent Plants
1. Often in monocultures	1. Often in polycultures (patches of mixed species)
2. Large	2. Small
3. Long lived	3. Short lived
4. Chemical defenses against generalist and specialist herbivores	4. Chemical defenses against generalist herbivores that may happen upon the plant
5. Quantitative defenses, such as tannins, often > 1% of the fresh weight of a leaf	5. Qualitative defenses, such as toxins, often < 1% of the fresh weight of a leaf
6. Late successional (e.g., trees)	6. Early successional (e.g., weeds and annuals)

Body size
James Brown and colleagues

FIGURE 4.4 Semilogarithmic plot of rates of oxygen consumption per unit body mass for a wide variety of mammals plotted against body mass. [From Schmidt-Nielsen (1975).]

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2) Natural groupings

- Natural groupings can be identified by "obvious differences", tree-based methods, or correlation-based methods.

- It is reasonable to expect traits to correlate with each other if there are trade-offs.

- It is reasonable to expect traits to fall into discrete groups if only some combinations of traits function effectively.

Leaf traits

Photosynthesis on a per gram basis is correlated with leaf mass per unit area (LMA) and leaf nitrogen (per gram). 2,548 species and 175 sites. Single "leaf economic spectrum" running from quick return (high nutrient and A, short leaf life) to slow return (low nutrient and A, long leaf life) on investments in leaves. Functional groups show substantial overlap along the spectrum. Wright et al. 2004 Nature 428:821-827.
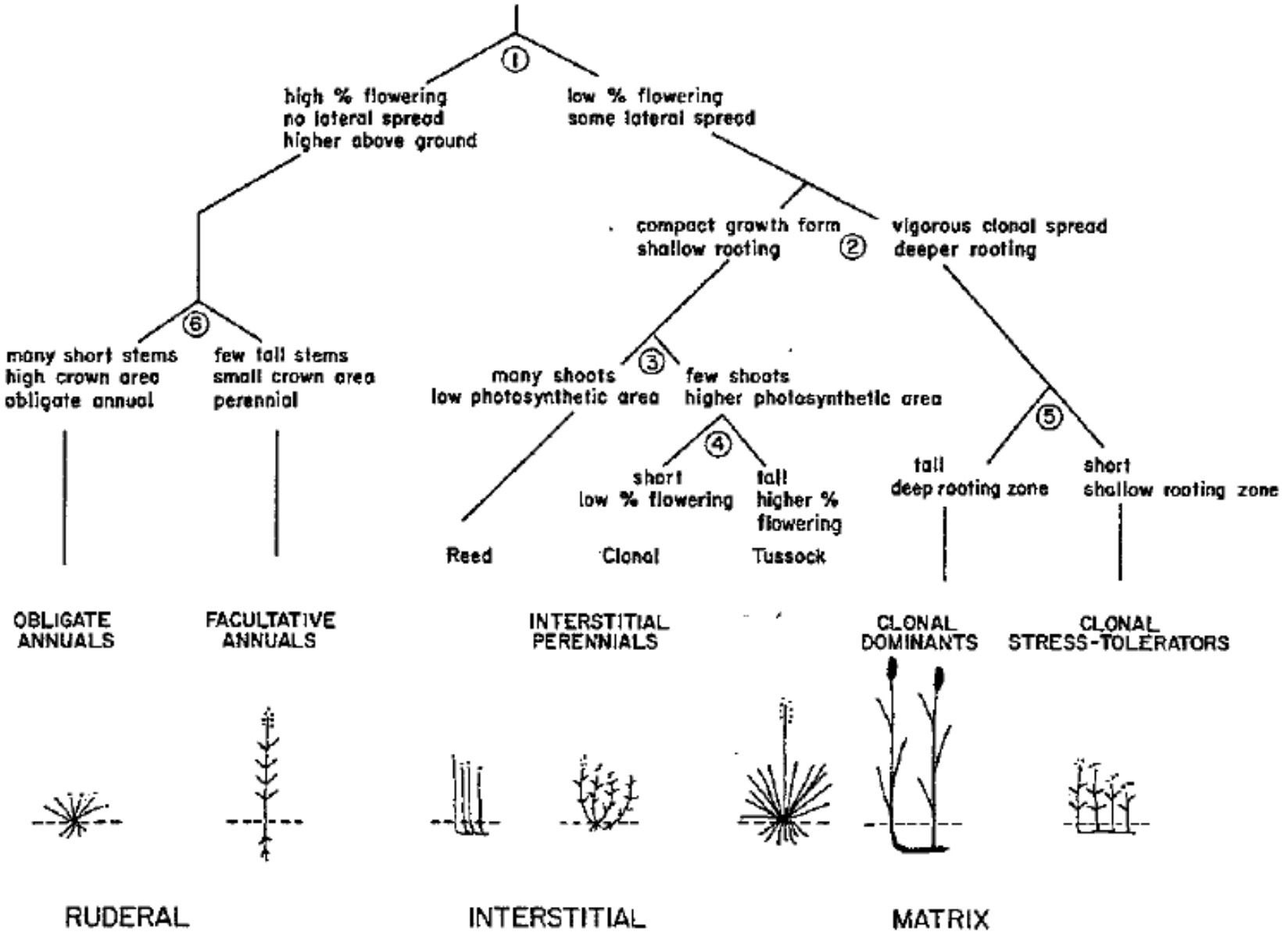

Because many leaf traits are correlated with each other, you don't need to measure them all.

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Leaf traits and plant functional groups

- Leaf traits differ on average among common plant functional groups (deciduous, evergreen, herb, etc.), but there is a lot of overlap. Continuous index is better than groups.
- Continuous variables provide better link to ecosystems ecology because currencies are leaf nutrients and turnover times.
- Reich et al. 1992, Ecol Mongr 62:365-392
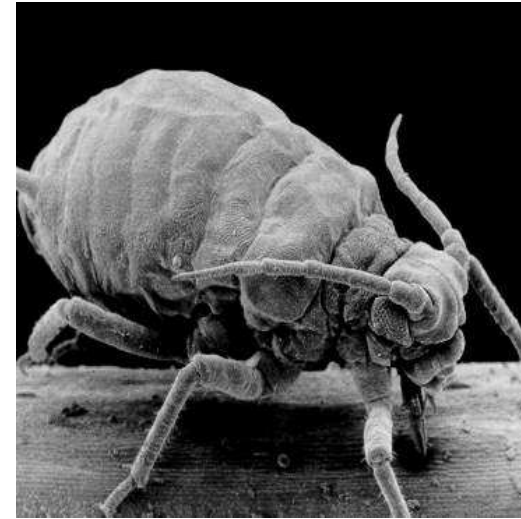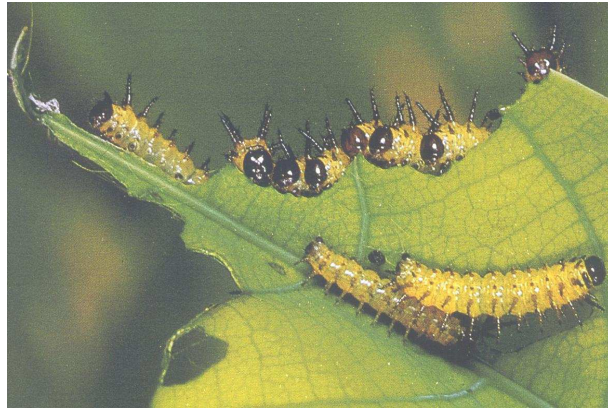- Reich et al. 1997, PNAS 94:13730-13734

Plant traits using cluster analysis

- Boutin and Keddy 1993 Journal of Vegetation Science 4:591-600
- 27 traits on 43 species of wetland plants
- cluster analysis to group plants

high % flowering
no lateral spread
higher above ground

low % flowering
some lateral spread

compact growth form
shallow rooting ②

vigorous clonal spread
deeper rooting

⑥

many short stems
high crown area
obligate annual

few tall stems
small crown area
perennial

③

many shoots
low photosynthetic area

few shoots
higher photosynthetic area

④

short
low % flowering

tall
higher %
flowering

⑤

tall
deep rooting zone

short
shallow rooting zone

Reed   Clonal   Tussock

OBLIGATE
ANNUALS

FACULTATIVE
ANNUALS

INTERSTITIAL
PERENNIALS

CLONAL
DOMINANTS

CLONAL
STRESS-TOLERATORS

RUDERAL   INTERSTITIAL   MATRIX

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Herbivore feeding guilds

- Chewing
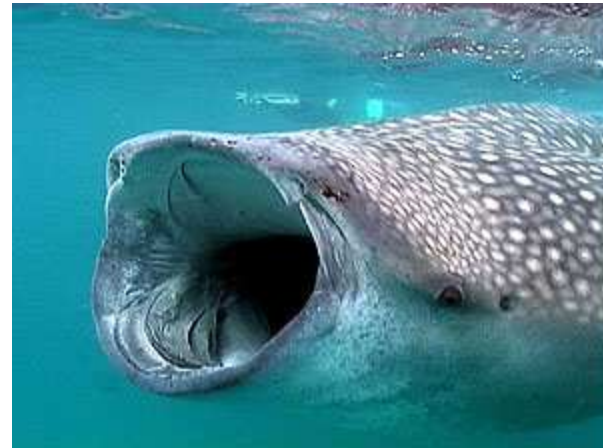- Sucking
- Mining
- Galling
- Boring

Caterpillar feeding guilds

- Caterpillar families form guilds
- Saturniids: cut leaves into large pieces, short simple mandibles, eat old, tough leaves with tannins
- Sphingids: tear and crush leaves into small pieces, long, toothed mandibles, eat young, soft leaves with toxins
- Bernays and Janzen 1988, Ecology 69:1153-1160

Predatory fish feeding guilds

- Suction (bass, grouper)
- Ram (filter feeder)
- Bite (great white shark)
- Because these methods require fundamentally different musculature, they probably are discrete categories

Algal functional groups

Steneck and Watling 1982, Marine Biology 65:299-319, proposed that algae fall into seven functional groups that were increasingly harder for herbivores to graze. Argued for a match between algal group and herbivore feeding mode leading to specialization.

1) Microalgae like diatoms

2) Filamentous algae

3) Foliose algae with thin blades like *Ulva*

4) Corticated algae with fine branching structure

5) Leathery algae with thick, tough blades, like kelps

6) Articulated calcareous algae

7) Crustose coralline algae

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Danger

- Natural groups may not be relevant to your question

- Humans: height and mass correlated, differ among groups (sex).

- But diabetes predicted by mass:height ratio, not their positive relationship and not by sex.

3) Testing relationships

- Solution: test whether traits explain natural processes?

- Effects and responses

- Testing can both refine existing classification schemes and suggest new approaches in an iterative fashion
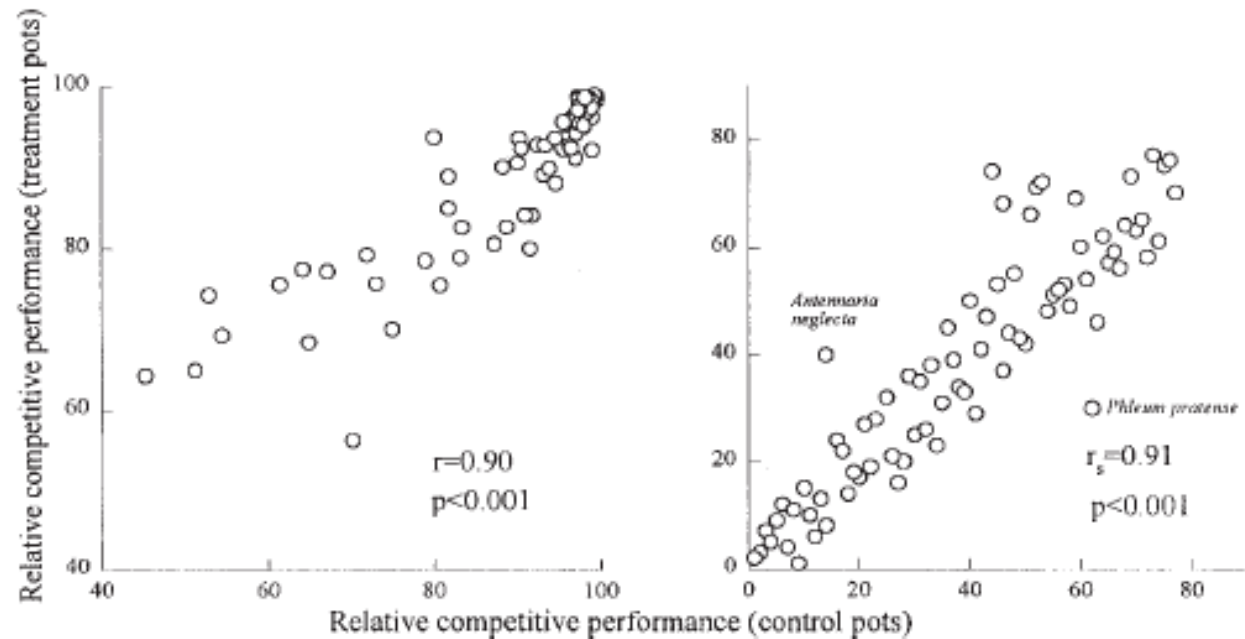
Effect: Population traits

Leaf traits are not only correlated with each other, but also predict population-level traits such as growth rate and survival. At a single site, traits varied 3-15 fold among species (53 rain forest tree species in Bolivia). Species with short-lived high A leaves had high growth rates but low survival. Poorter and Bongers 2006. Ecology 87:1733-1743.

Effect: Competition

Fig. 1. Scatter plots of competitive performance in the stress treatment pots versus competitive performance in the control pots ($n = 77$). The left-hand figure shows competitive performance measured as percent reduction in phytometer and the right-hand figure shows only rank order (position in competitive hierarchy).
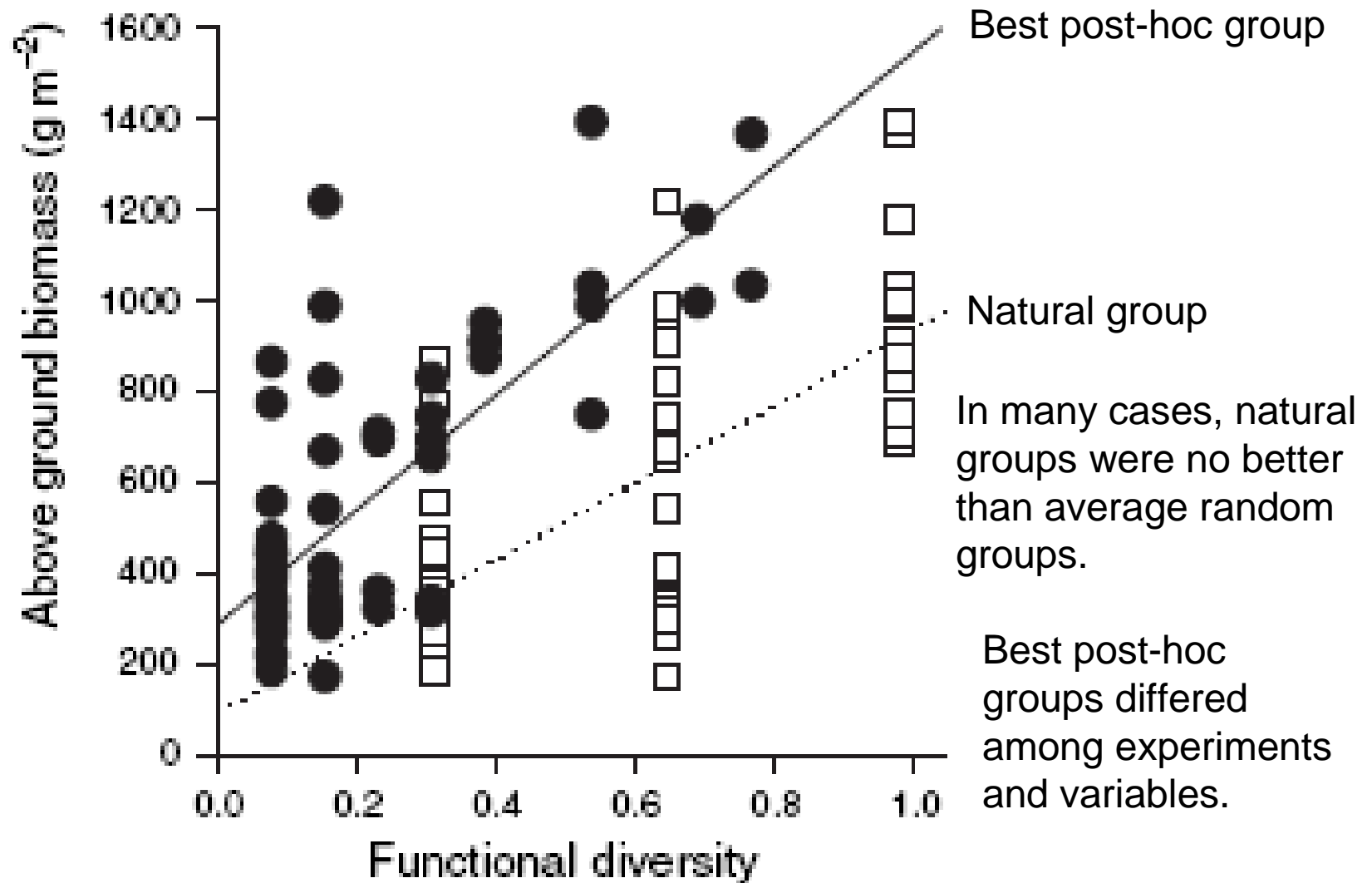
Competitive ability (competitive effect on a common "phytometer") in two pot sizes was correlated, and could be predicted based on traits related to plant size and leaf shape (Keddy et al. 2002, J. Veg. Sci. 13:5-16). Earlier study with wetland plants also found that competitive effect was related to size and leaf shape (Gaudet and Keddy 1988, Nature 334:242-243).
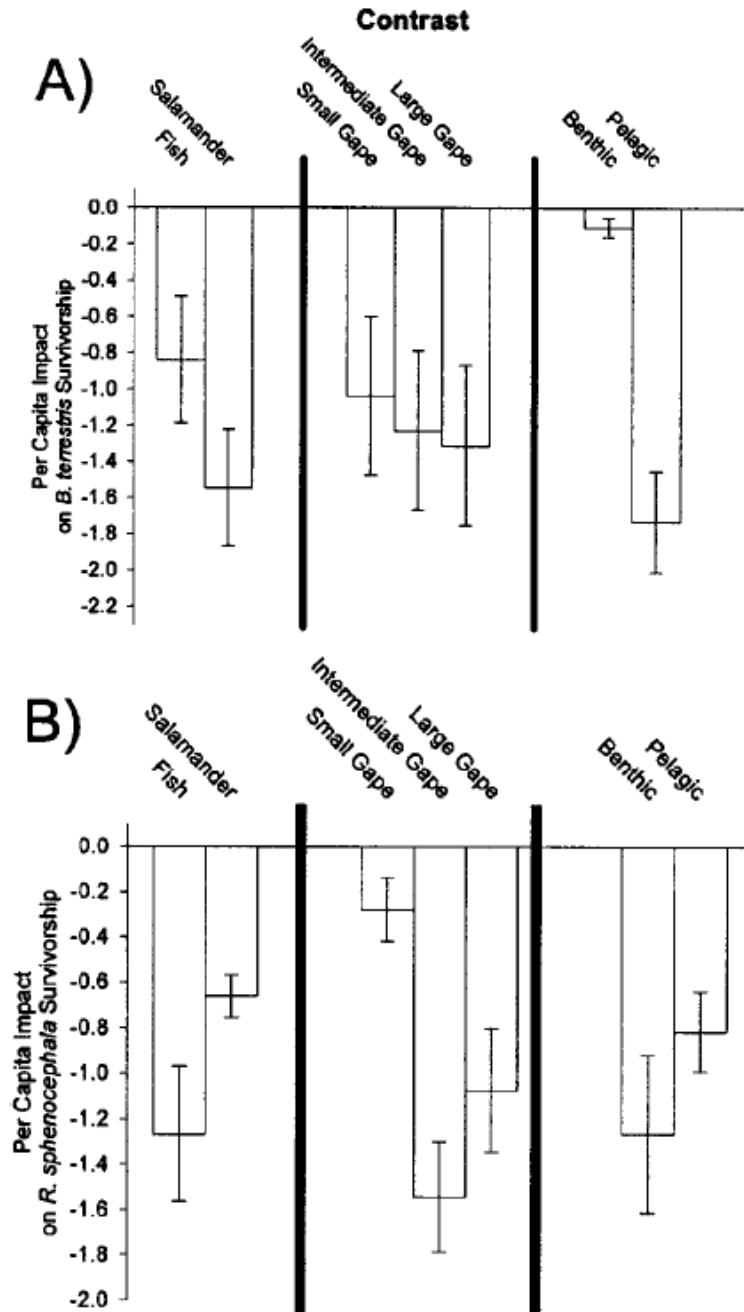
Effect: Diversity

- Many studies of diversity use "natural" groups of grass, forb, legume

- Some also divide grasses into C3 and C4

- Wright et al. 2006, Ecology letters 9:111-120 tested whether natural groups better than random in 10 experiments from the literature.

(d)

Best post-hoc group

Natural group

In many cases, natural groups were no better than average random groups.

Best post-hoc groups differed among experiments and variables.
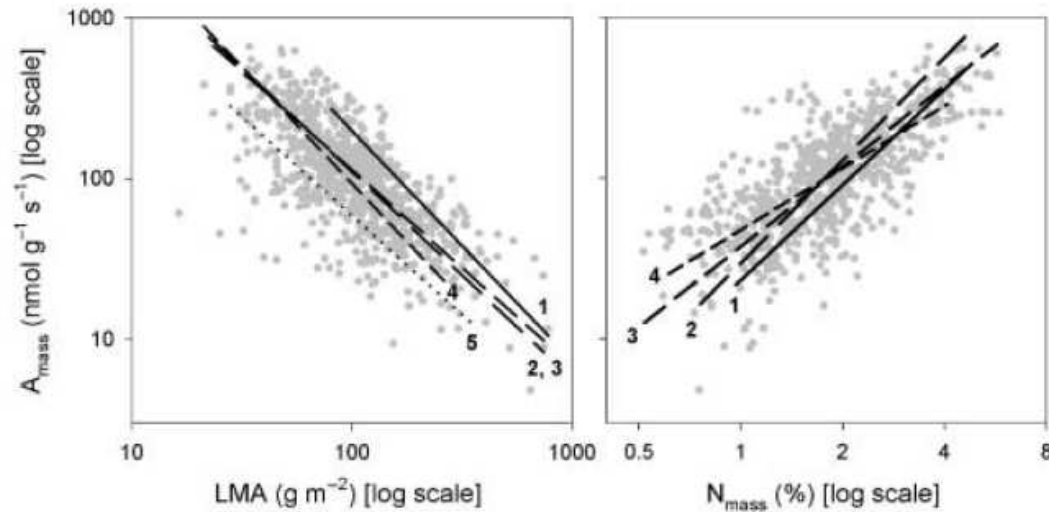
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Effect: Predation

Effects of six aquatic predators (fish and salamanders) on larval amphibians could be predicted by traits, but different traits predicted effects on different species. Overall, similarity among predators in traits did not predict similarity in effects. In order to use traits to predict effects, you need to know which traits matter for which effect.

Response: plant stress

- Koricheva et al. 1998, Annu Rev Ecol Syst 43:195-216, reviewed studies on how plant stress affected herbivores

- Stress benefitted boring and sucking insects

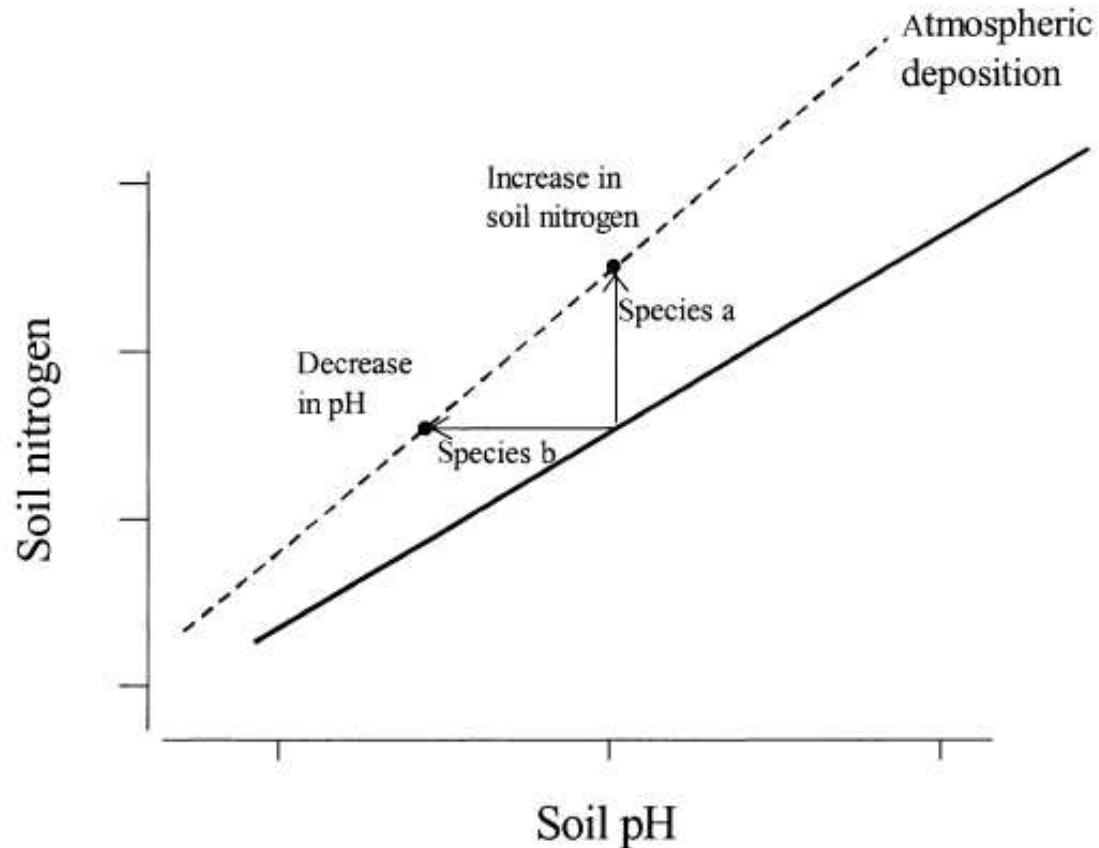- Stress negatively affected galling and chewing insects

Response: Climate

Figure 4 Modulation of A_{mass}–LMA and A_{mass}–N_{mass} relationships by climate. Climate classes and associated statistics are given in Tables 4 and 5. (a) A_{mass} vs. LMA, with individual SMA slopes shown for species pooled into rainfall classes. (b) A_{mass} vs. N_{mass}, with individual SMA slopes shown for species pooled into MAT classes.

Photosynthetic rate (A) is negatively correlated with leaf mass per unit area (LMA) and positively correlated with leaf nitrogen content (N). A is higher at drier (left graph) and hotter (right graph) sites. 18% of variation in traits was driven by climate. Wright et al. 2005. Global Ecology and Biogeography 14:411-421.
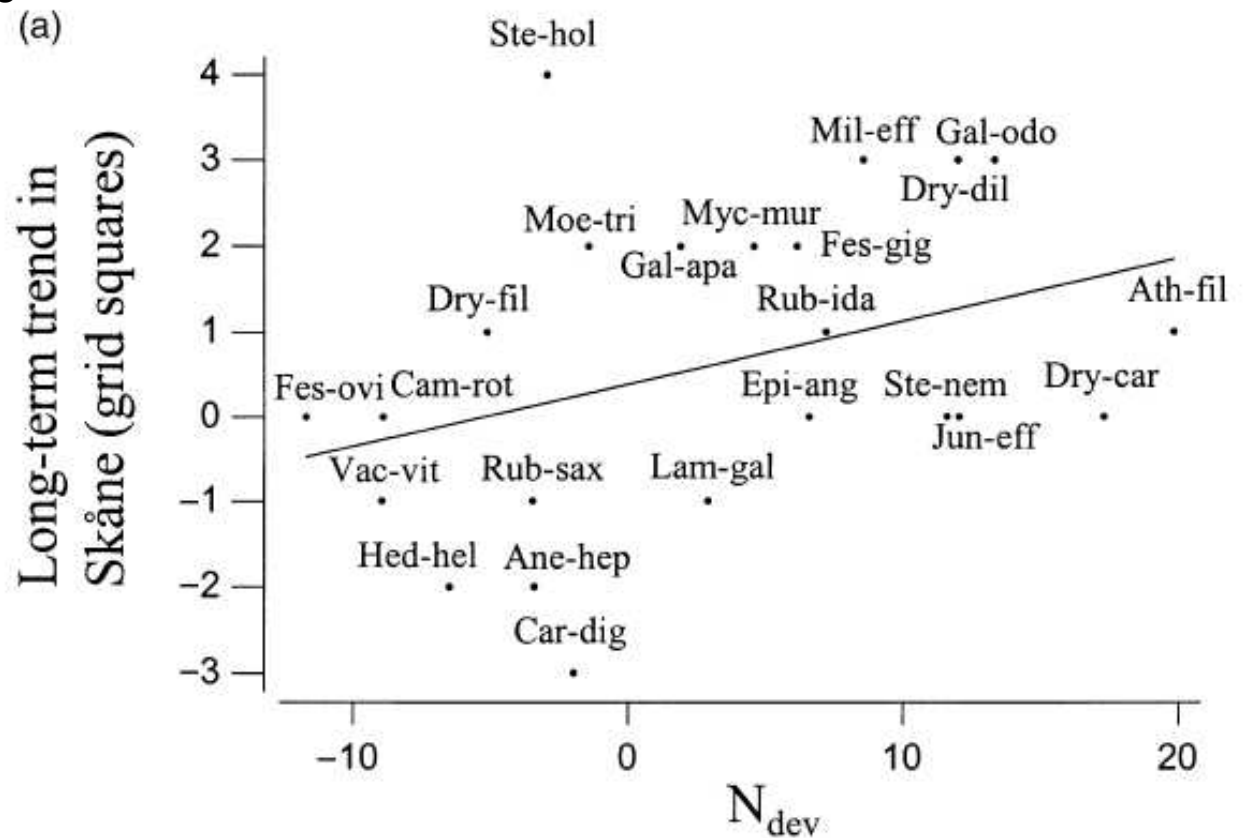
Response: N deposition

The solid line is the normal relationship. Some species lie above this line and some below it. Atmospheric deposition should favor species like a or b that occur at a relatively high level of soil N for a given pH (or can tolerate acidification at a given N level). These have a positive Ndev value.
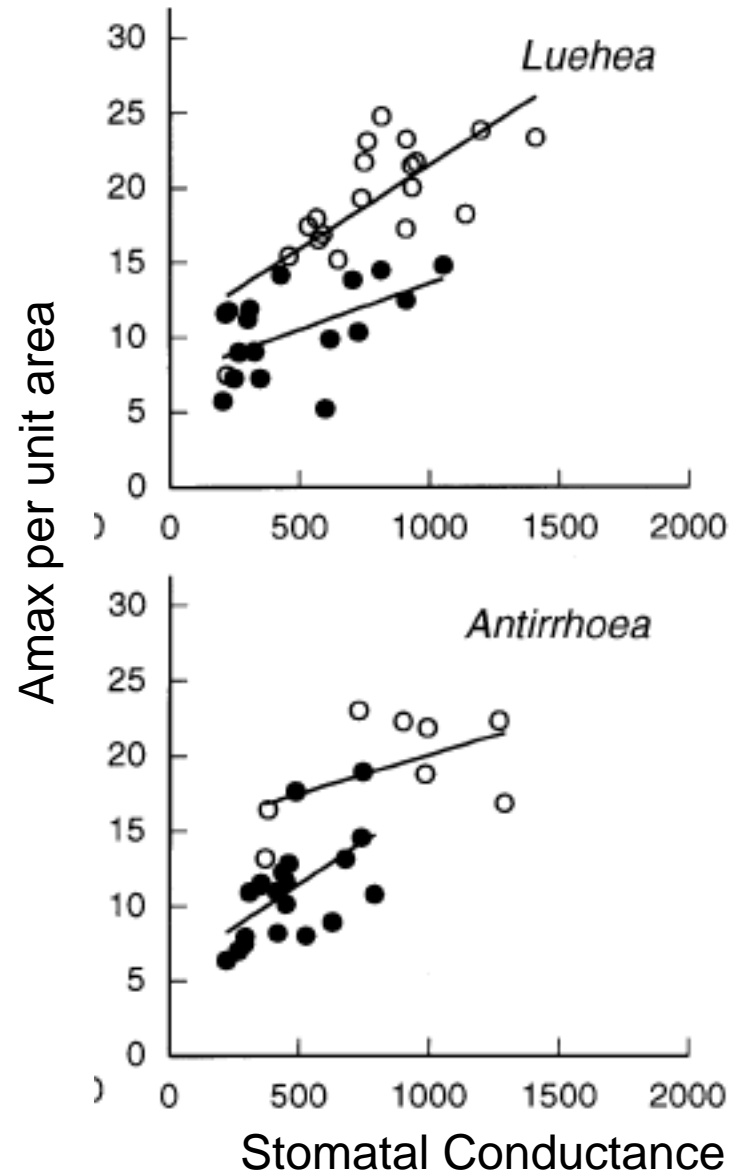
Response: N deposition

An index of local soil nitrogen availability (Ndev) for each species predicted its long-term response to increasing nitrogen availability in Sweden (positive values mean soil N is higher than expected based on soil pH). Other traits (height, growth rate, leaf N, phenology, etc.) also predicted long-term trends, but not as well. Diekmann and Falkengren-Grerup 2002. J Ecol 90:108-120.
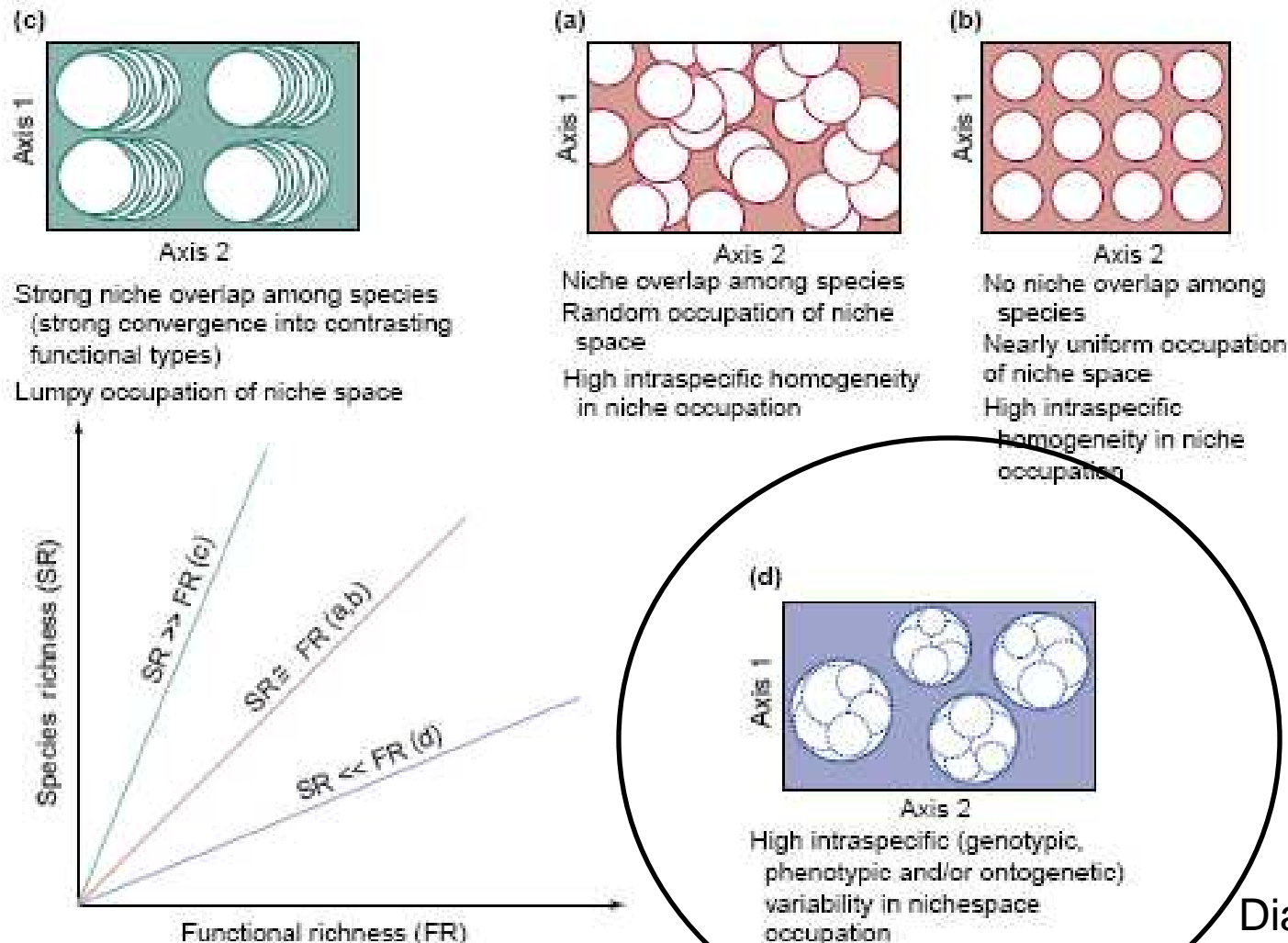
Response: seasonality

In a seasonal forest in Panama, dry season leaves (open circles) had more mass per unit area, higher maximum photosynthetic rates (Amax) per unit area and higher water-use efficiency than wet season leaves (closed circles). Kitajima et al. 1997. Oecologia 109:490-498.
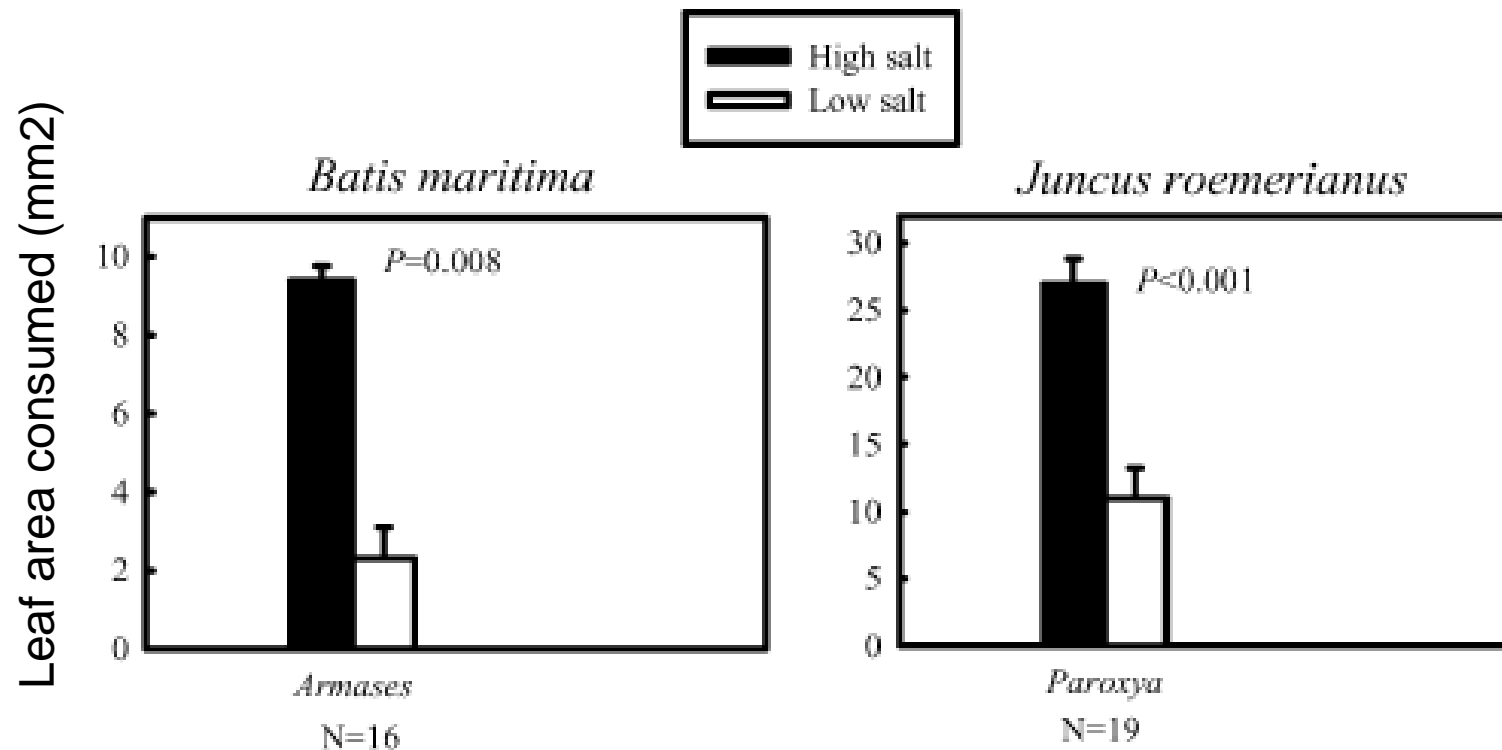
Phenotypic plasticity

(c)

Axis 1 / Axis 2

Strong niche overlap among species (strong convergence into contrasting functional types)

Lumpy occupation of niche space

(a)

Axis 1 / Axis 2

Niche overlap among species
Random occupation of niche space
High intraspecific homogeneity in niche occupation

(b)

Axis 1 / Axis 2

No niche overlap among species
Nearly uniform occupation of niche space
High intraspecific homogeneity in niche occupation

Species richness (SR) / Functional richness (FR)

SR >> FR (c)
SR = FR (a,b)
SR << FR (d)

(d)

Axis 1 / Axis 2

High intraspecific (genotypic, phenotypic and/or ontogenetic) variability in nichespace occupation

Diaz and Cabido 2001
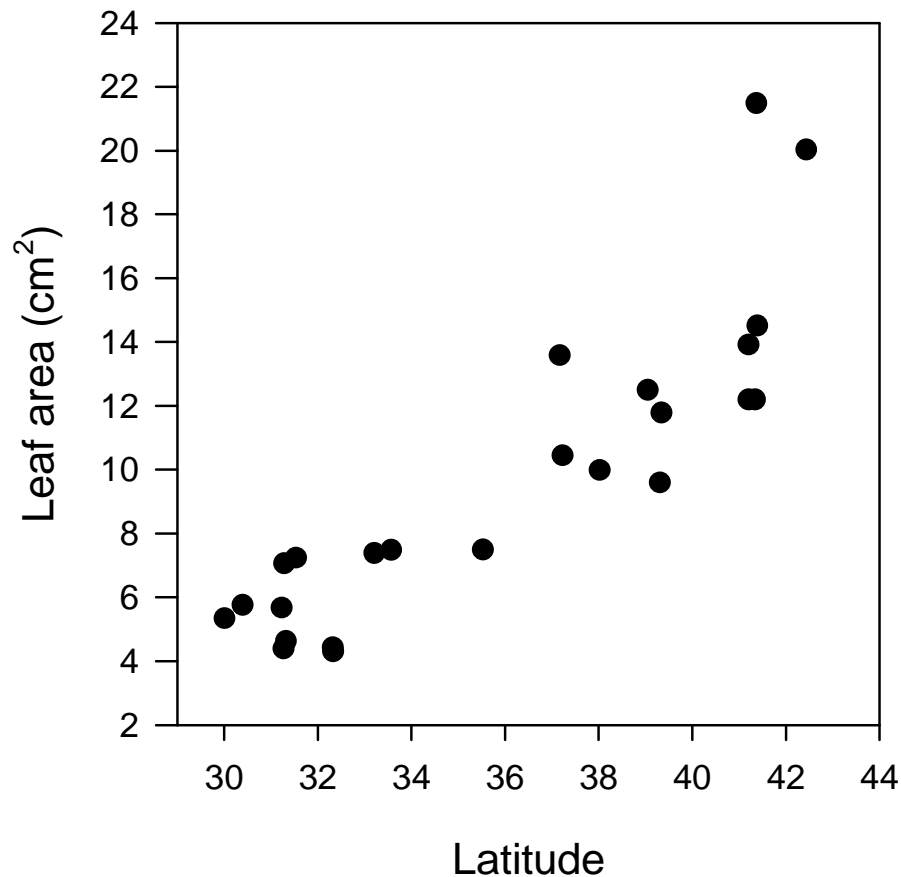
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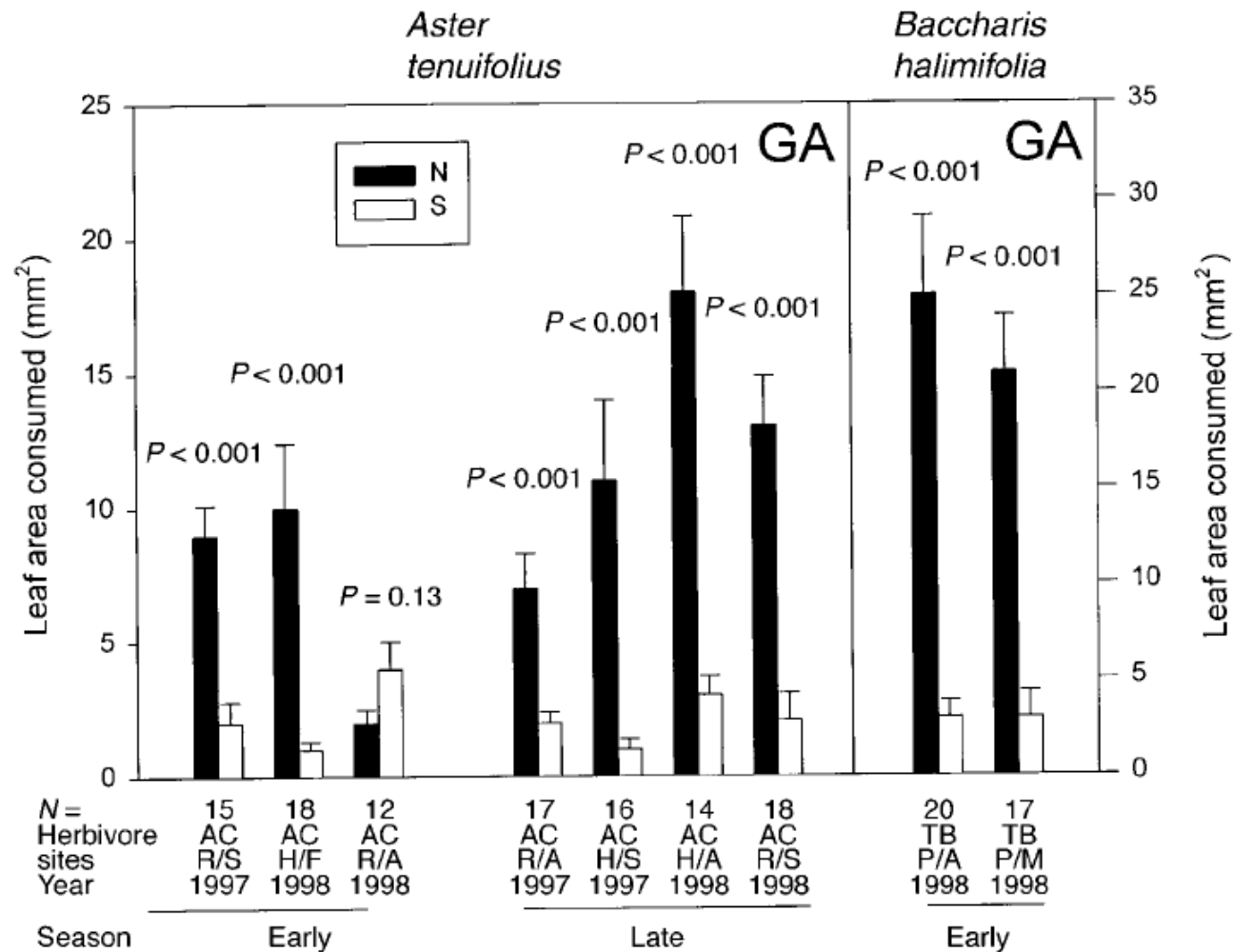
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Stress gradients

Salt marshes have strong gradients in salinity and waterlogging, which affect plant height and other traits. Example: plants from saltier areas of the marsh were more palatable to herbivores than conspecifics from less-salty areas of the marsh. Goranson et al. 2004, Oecologia 140:591-600.

Latitudinal gradients 1

Leaves of *Iva frutescens* are 4 times larger at high than low latitudes. Pennings unpublished.
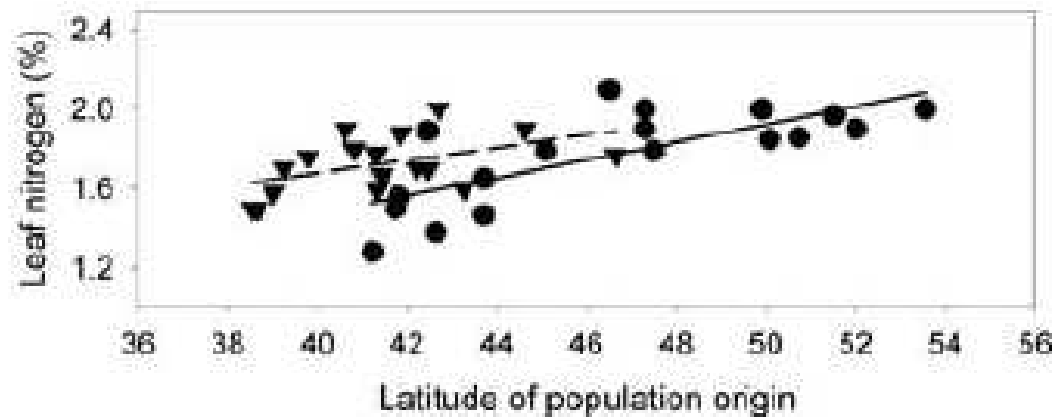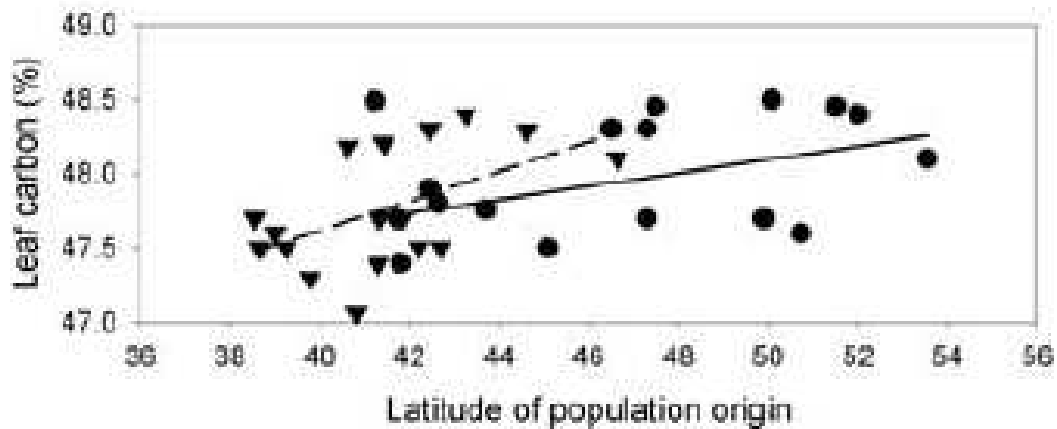
Latitudinal gradients 2

Pennings et al. 2001, Ecology 85:1344-1359

Latitudinal gradients 3

In a common garden study, leaf N and C of St. John's Wort varied across latitude in plants from both native and introduced populations. Maron et al. 2007. Evolution 61:1912-1924.

For more on latitudinal variation in leaf N and P, see Reich and Oleksyn 2004, PNAS 101:11001-11006.

Lessons learned

- Continuous traits better than categories
- But easier to get data for categories
- Different traits may matter for different processes
- Be careful about intraspecific variation if environment is variable

- Further reading: Petchey and Gaston 2006, Ecology Letters 9:741-758