The worldwide leaf economic spectrum

How causal discovery algorithms forced me to re-imagine its generating causes

Laboratoire d'écologie fonctionnelle
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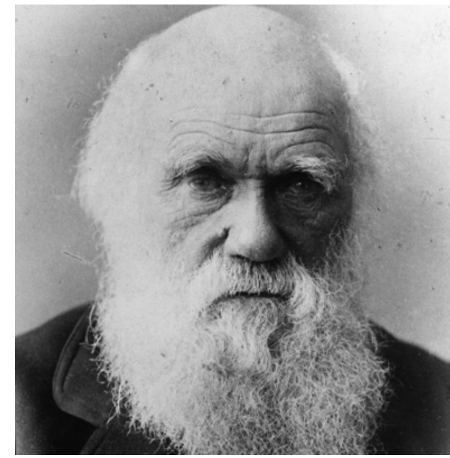
Some basic notions from evolutionary ecology…

Sir Ronald Fisher

- Evolutionary fitness
- Adaptive value of a trait



Charles Darwin

Evolutionary fitness

A cohort of individuals having a trait value « x » in environment E

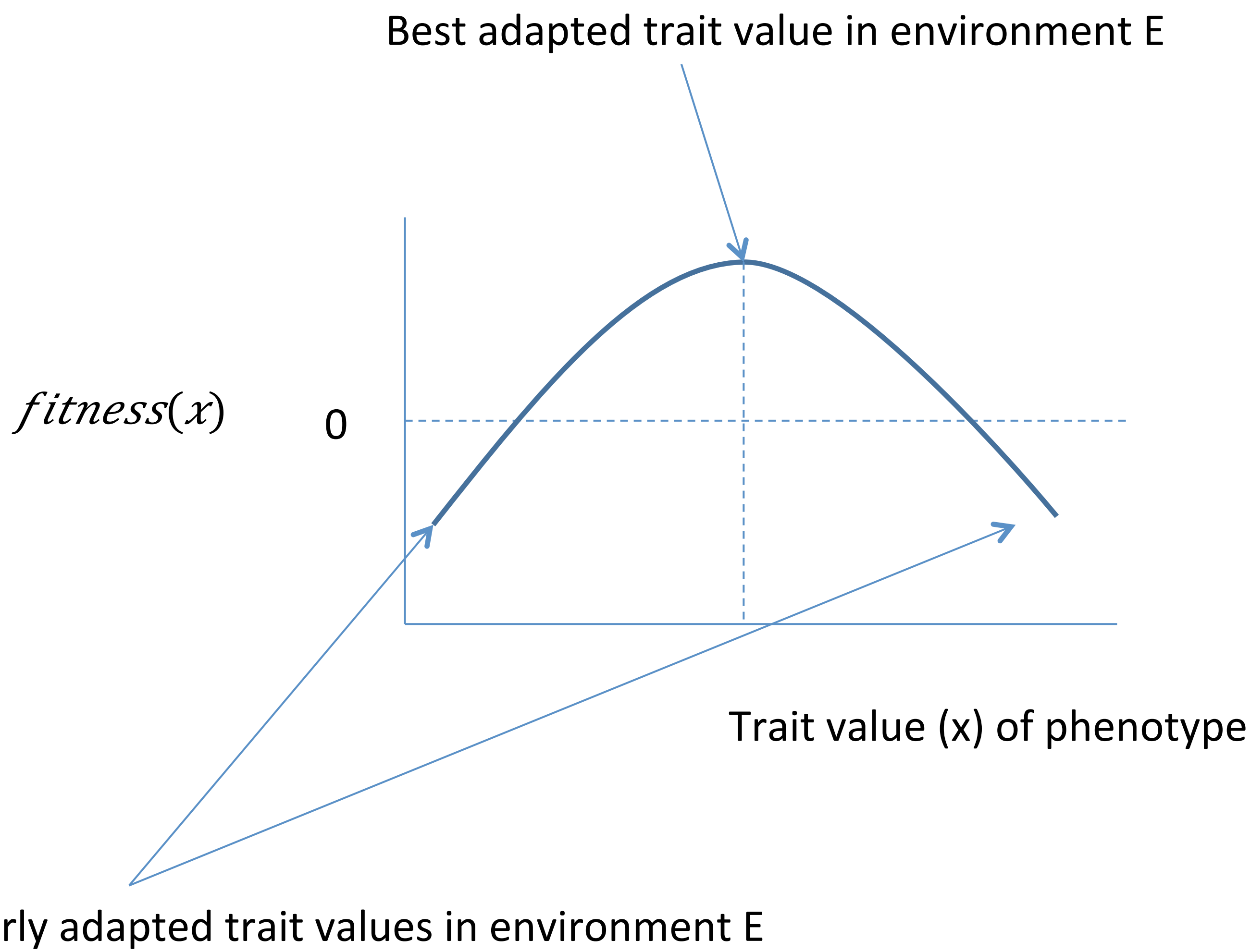
Age	Average # offspring / survival	Prob of surviving to age i	Expected # offspring
1	0	0.8	0x0.8=0
2	2	0.4	2x0.4=0.8
…			
x	3	0.1	3X0.1=0.3

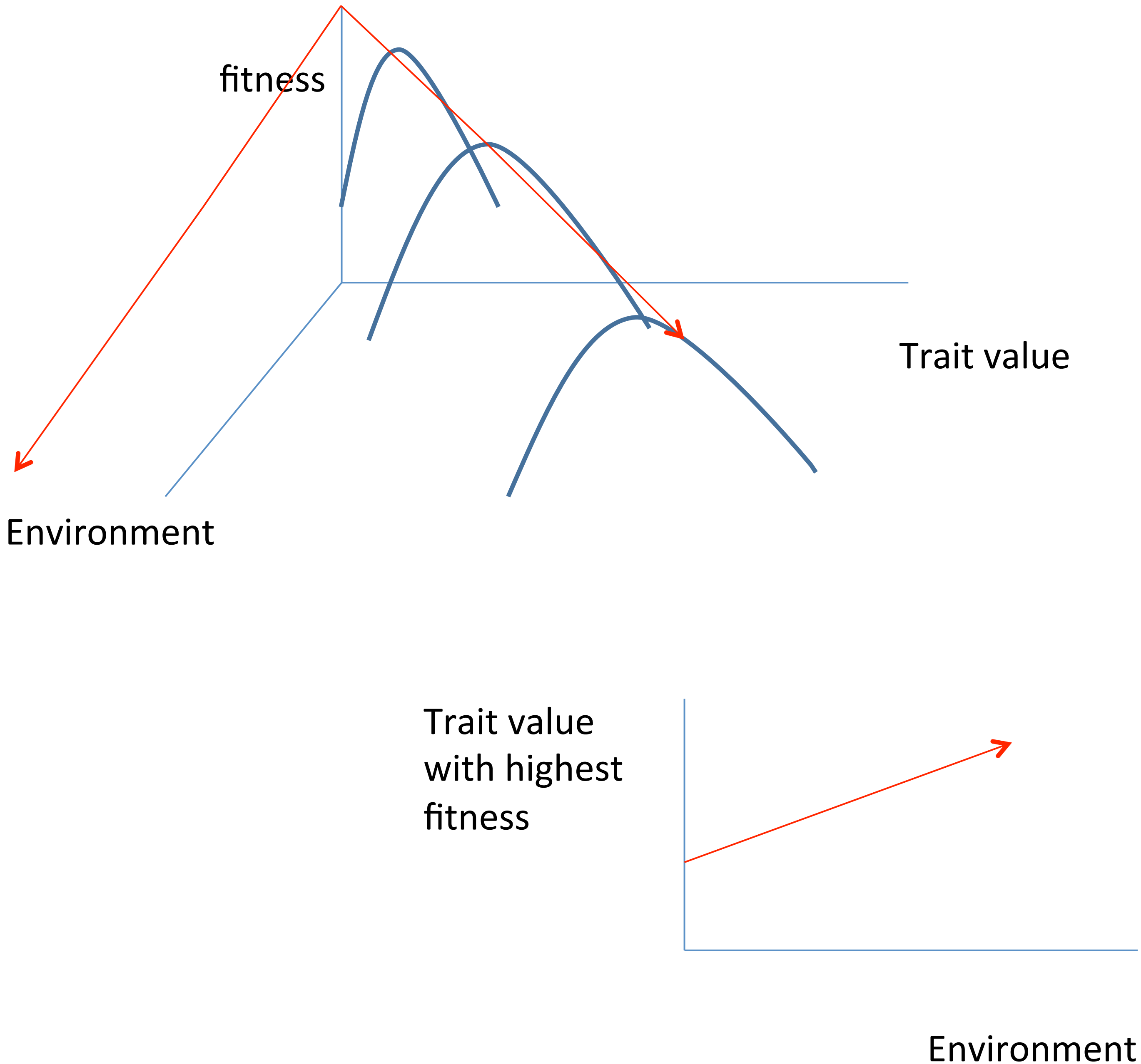
Net reproductive output for this genotype or phenotype:

$R_0(x) = \Sigma$(average reproduction at age i)(probability of surviving to age i)

$$\text{fitness}(x) = R_0(x) - R_0$$

Adaptive value of a trait (or suite of traits)




fitness
Trait value
Environment
Trait value
with highest
fitness
Environment

Traits often show complicated patterns of covariation

traits

traits

[■s↓11↑2 &s↓12 &…&s↓1T @s↓21

[■s↓11↑2 &s↓12 &…&s↓1T @s↓21 &s↓22↑2 &…&s↓2T @…&…&…&…@s↓T1 &s↓

traits

Changing environments

traits

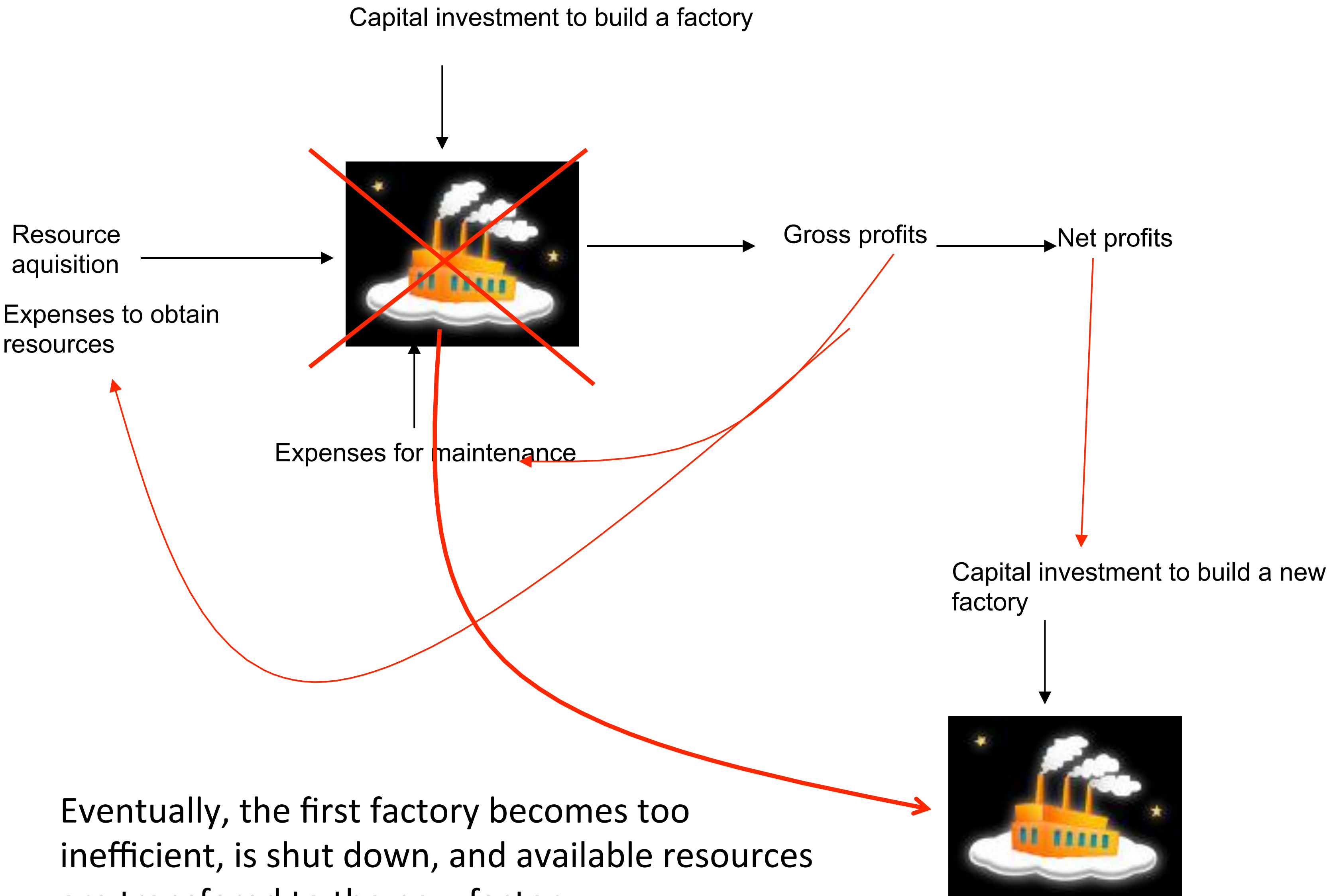
These patterns of covariation can reflect:

- Common selection pressures
- Tradeoffs between traits to maximize fitness
- Physical constraints

What are the causal process generating these patterns of trait covariation?

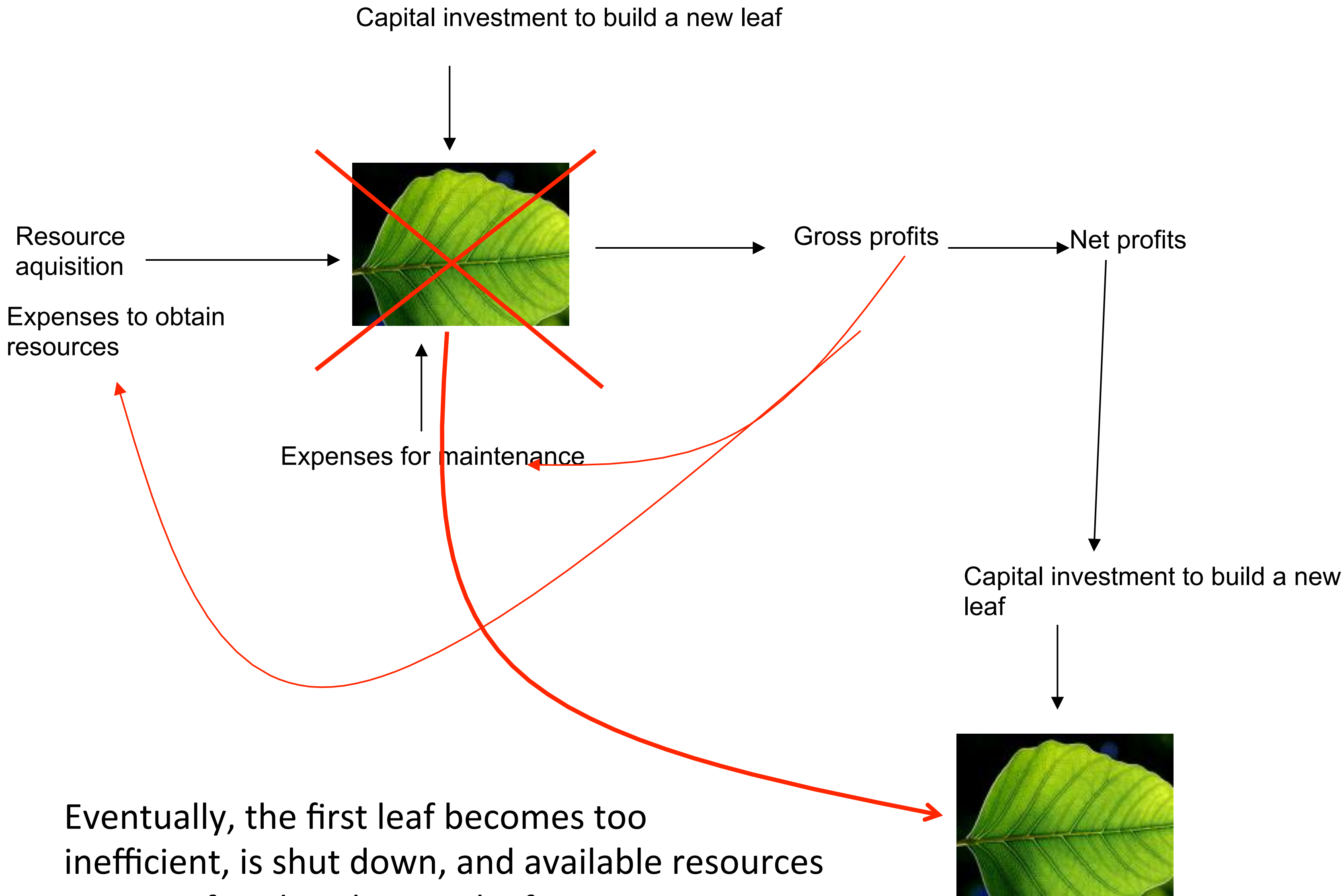
How evolutionary ecologists view co-ordination in leaf traits

An individual plant is a company & an individual leaf is a factory



Eventually, the first factory becomes too inefficient, is shut down, and available resources are transfered to the new factory

An individual plant is a company & an individual leaf is a factory



Eventually, the first leaf becomes too inefficient, is shut down, and available resources are transfered to the new leaf

Abstract

Bringing together leaf trait data spanning 2,548 species and 175 sites we describe, for the first time at global scale, a universal spectrum of leaf economics consisting of key chemical, structural and physiological properties. The spectrum runs from quick to slow return on investments of nutrients and dry mass in leaves, and operates largely independently of growth form, plant functional type or biome. Categories along the spectrum would, in general, describe leaf economic variation at the global scale better than plant functional types, because functional types overlap substantially in their leaf traits. Overall, modulation of leaf traits and trait relationships by climate is surprisingly modest, although some striking and significant patterns can be seen. Reliable quantification of the leaf economics spectrum and its interaction with climate will prove valuable for modelling nutrient fluxes and vegetation boundaries under changing land-use and climate.

[1]Wright, I. et al. (2004). Nature 428: 821-827.

articles

The worldwide leaf economics spectrum

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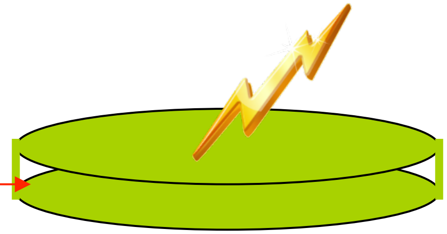
Measured variables

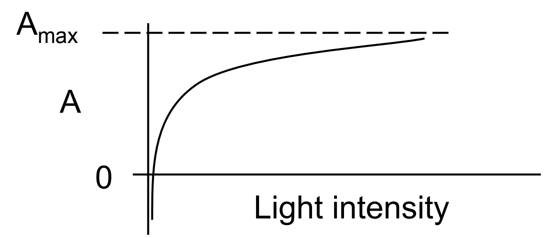


Specific leaf mass (g/cm^2)

dry mass = allocation to convert energy Into sugars

surface area = amount of photons captured

A_{max}: Maximum net photosynthetic rate (umol/g/s)



N_m: nitrogen content of leaf (mg/g)

N is the limiting element for photosynthetic enzymes

R_m: leaf respiration rate (umol/g/s)

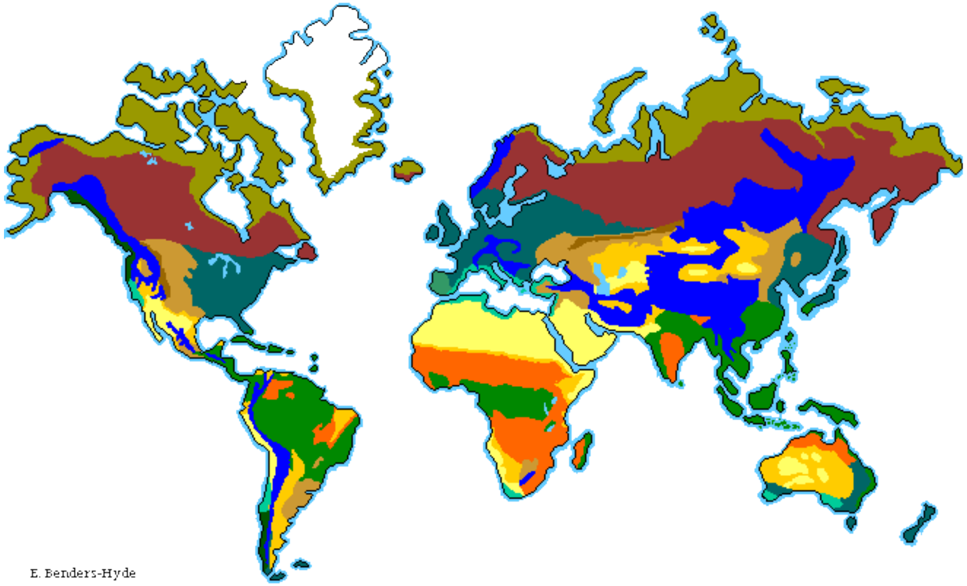
Respiration measures the metabolic activity of the leaf

LL: Leaf lifespan (d)

Average # days until plant allows a leaf to die

The worldwide leaf economic spectrum

2548 species occurring in 175 sites worldwide



Prior expectation: the different environments would select for different patterns of covariation

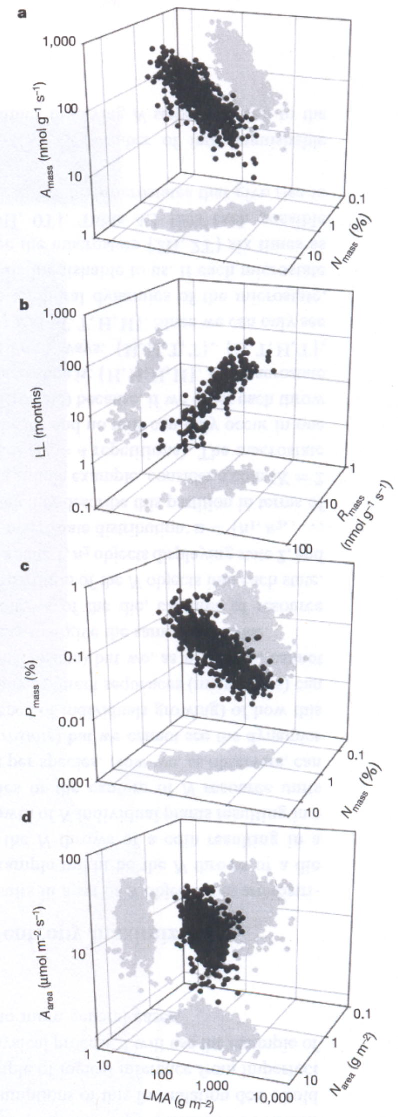
Found: essentially the same relationships between these « economic » variables irrespective of habit or taxonomy.

A_{max} – LMA – N_m

LL – LMA – R_m

P_m – LMA - N_m

A_m – LMA - N_m



gure 2 Three-way trait relationships among the six leaf traits with reference to LMA, e of the key traits in the leaf economics spectrum. The direction of the data cloud in ree-dimensional space can be ascertained from the shadows projected on the floor and alls of the three-dimensional space. Sample sizes for three-way relationships are ecessarily a subset of those for each of the bivariate relationships. **a**, A_{mass}, LMA and $_{mass}$; 706 species. **b**, LL, R_{mass} and LMA; 217 species. **c**, N_{mass}, P_{mass} and LMA; 733 ecies. **d**, A_{area}, LMA and N_{area}; 706 species.

lishing Group NATURE | VOL 428 | 22 APRIL 2004 | www.nature.com/nature

1st principal axis of a PCA explains ~ 80% of variation

→ N_{mass}, A_{mass}, R_{mass}, P_{mass}

← LL, LMA

Resource conservation

- Photosynthetic rate low even under optimal conditions
- Respiration rate low
- Low concentrations of mineral nutrients
- Long lifespan
- Thick, (often small) leaves with cell structure maintained by thick cell walls (dense tissues)

Resource aquisition

- High maximum photosynthetic rate
- High respiration rate
- High concentrations of mineral nutrients
- Short lifespans
- Thin, (often large) leaves with cell structure maintained by water turgour

Generating causes?
What we thought we knew…

Theoretical causes of variation in leaf lifespan

Assumption

Natural selection acts to maximize the cumulative net amount of carbon fixed by the leaf per unit time (g) , and this production is calculated over the lifespan of the leaf.

$$g = total\ net\ production\ of\ carbon / leaf\ lifespan = G/t$$

Construction cost (carbon invested to construct the leaf)

$$g = \frac{1}{t}\left(\int_0^t A(t)dt - C\right)$$

Net instantaneous photosynthetic rate (umol/g/s

$$g = \frac{1}{t}\left(\int_0^t A(t)dt - C\right)$$

$$A(t) = a(1 - \frac{t}{b}) = a\left(\frac{b-t}{b}\right)$$

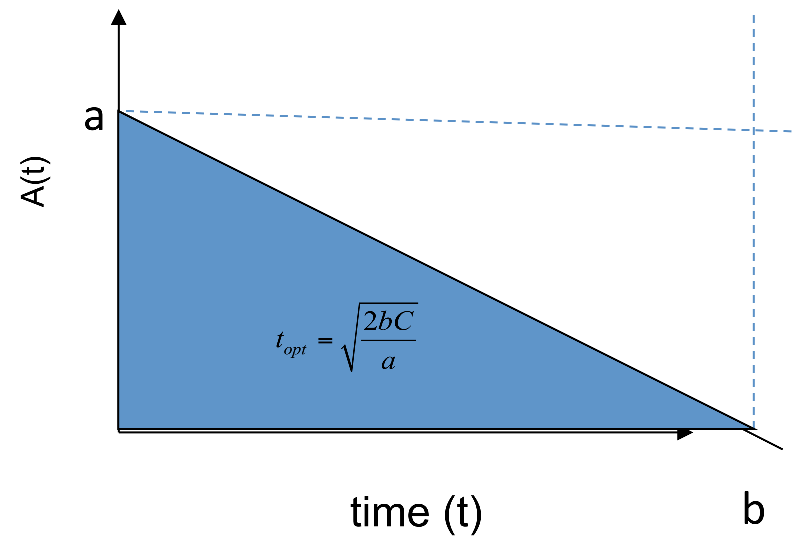
$$\int_0^t A(t)\,dt = [at - at^2/2b]$$

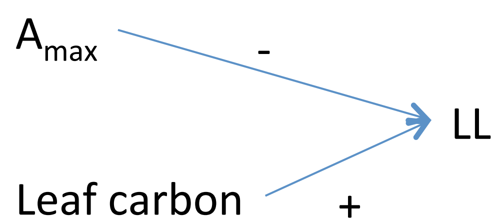
$$g = \frac{1}{t}\left(at - \frac{a}{2b}t^2 - C\right)$$

$$g = \frac{-2bC + 2abt - at^2}{2bt}$$

Solving for t when $dg/dt = 0$

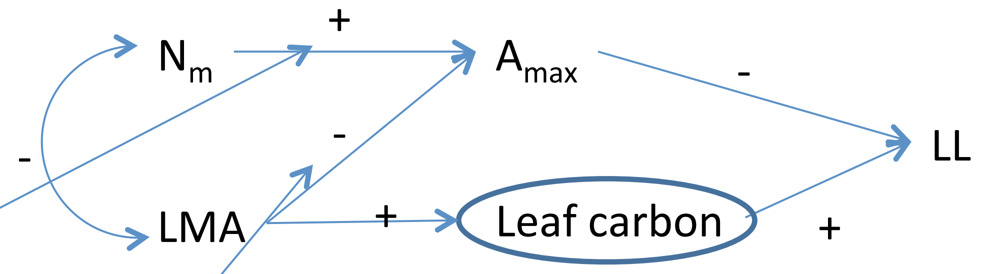
$$t_{opt} = \sqrt{\frac{2bC}{a}}$$





Initial causal models

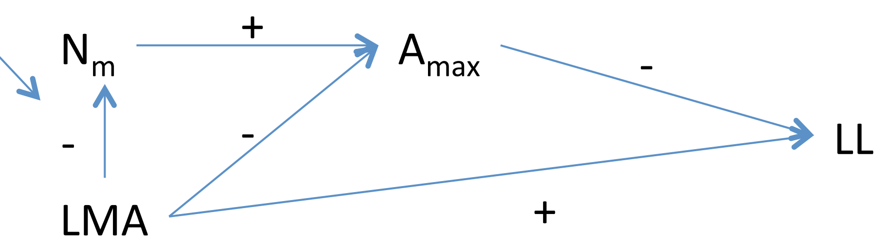
Wright, I. et al. (2004). Nature 428: 821-827.



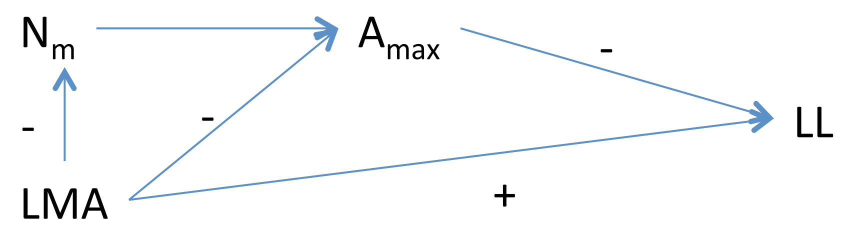
Most leaf nitrogen is in photosynthetic enzymes: more enzymes → more photosynthesis

Cells with thicker cell walls, and structural cells (that have no cytoplasm or enzymes), will increase mass while decreasing total carbon fixation and decreasing total nitrogen

My translation of their explanation



$\chi^2 = 12.825$, df = 1, $p = 0.0003$



Is there any ordering of these four variables that fits the observed patterns of covariation, without requiring common latent causes?

How to answer this:
PC algorithm, testing each equivalent model using a d-sep test of significance[1].

Answer: No.

[1]Shipley, B. 2000. A new inferential test for path models based on directed acyclic graphs. Structural Equation Modeling 7206-218.

Where is the latent variable hiding and what might it be?

Vanishing tetrads (assuming linear relationships & MVN distribution)

$$\rho_{12}\,\rho_{34} - \rho_{14}\,\rho_{23} = 0 \quad \rho_{13}\,\rho_{24} - \rho_{14}\,\rho_{23} = 0 \quad \rho_{13}\,\rho_{24} - \rho_{12}\,\rho_{34} =$$

Vanishing tetrad algorithm

Given a set of 4 observed variables in which no pair of variables are independent conditional on any subset of other variables (including the empty set):

- If the tetrad equation does not equal zero, choose another tetrad equation
- If the tetrad equation does equal zero then there is a latent variable that forms an chokepoint at either (or both) of the pairs of variables not included in the tetrad equation.

Where is the latent variable hiding and what might it be?

Of the three possible tetrad equations involving these four variables, only one is significantly different from zero (i.e. does not vanish):

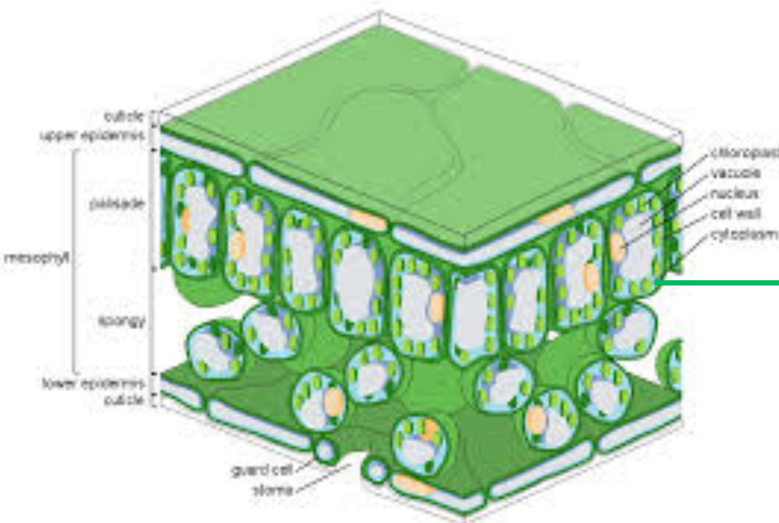
$$\rho_{\ln(LL),\ln(N_M)}\,\rho_{\ln(LMA),\ln(A_M)} - \rho_{\ln(LL),\ln(LMA)}\,\rho_{\ln(A_M),\ln(N_M)} \neq 0$$

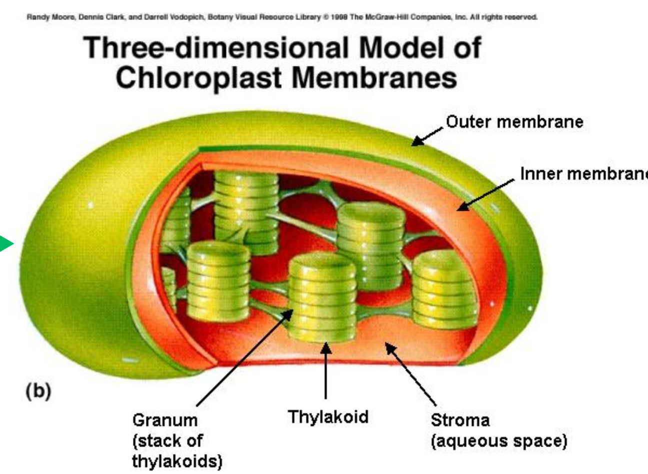
This means that all causal paths linking every pair of variables except for LL and A_M pass through the same latent variable.

Where is the latent variable hiding and what might it be?

Variable 1	Variable 2	All paths linking pair pass through a latent?
SLM	A_{mass}	✓
SLM	LL	✓
SLM	N_{mass}	✓
A_{mass}	N_{mass}	✓
A_{mass}	LL	X
LL	N_{mass}	✓

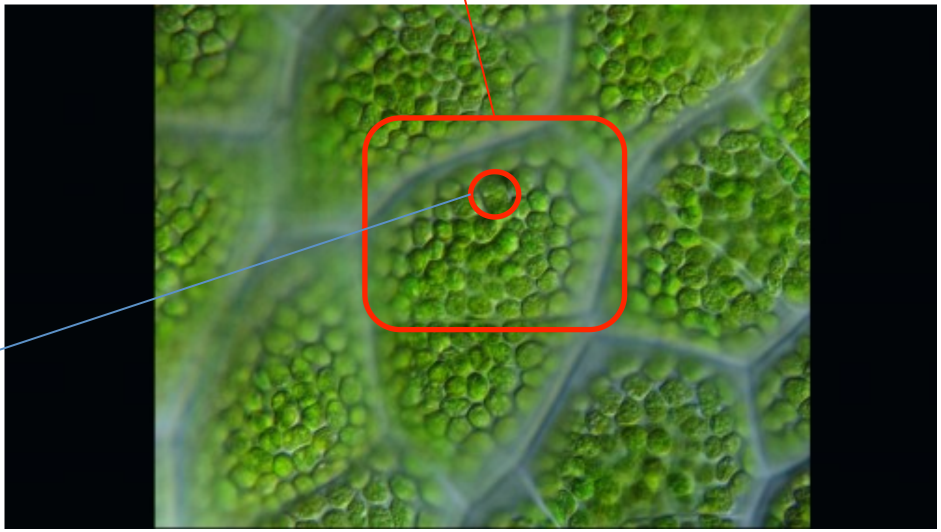
Where is the latent variable hiding and what might it be?





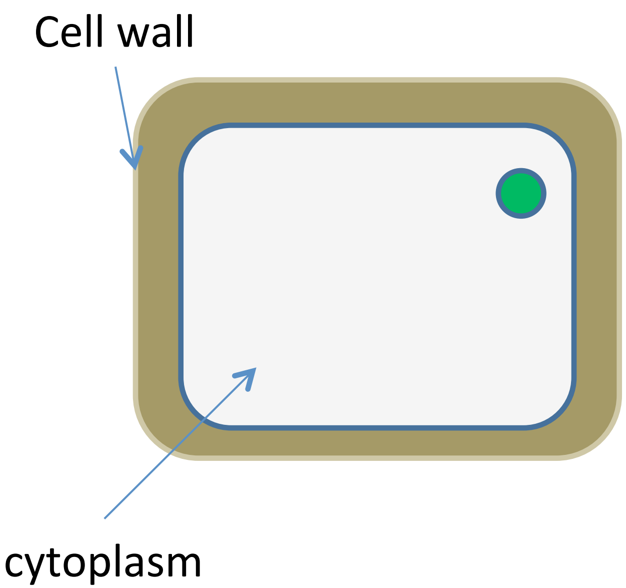
Where is the latent variable hiding and what might it be?

cell



Chloroplast (where photosynthesis occurs)

Where is the latent variable hiding and what might it be?



chloroplasts ∝ volume of cytoplasm

photosynthetic rate per chloroplast is very much less variable than the number of chloroplasts per leaf

Photosynthetic rate per leaf ∝ volume of cytoplasm

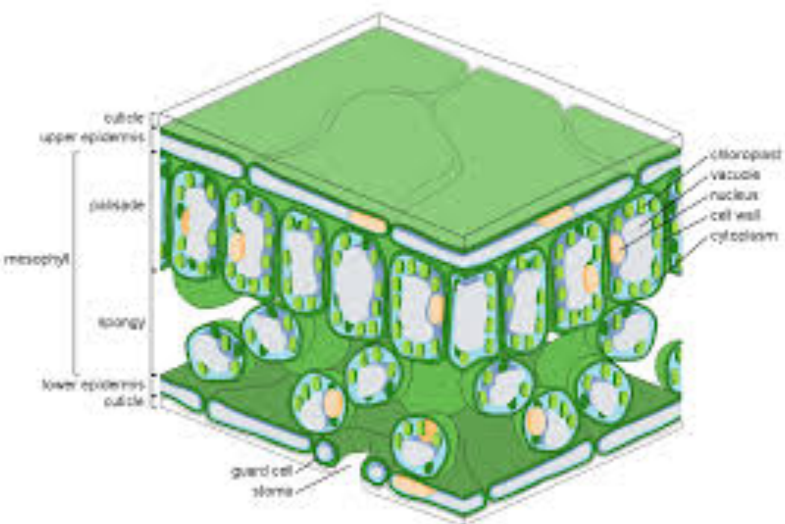
Nitrogen content per leaf ∝ volume of cytoplasm

Leaf dry mass is overwhelmingly in the cell walls

Leaf dry mass ∝ volume of cell walls

total cytoplasmic volume/ total cell wall volume V_c / V_w

Where is the latent variable hiding and what might it be?



$$V_c / V_w \propto A_{total} / dry\ mass = A_{mass}$$

$$V_c / V_w \propto N_{total} / dry\ mass = N_{mass}$$

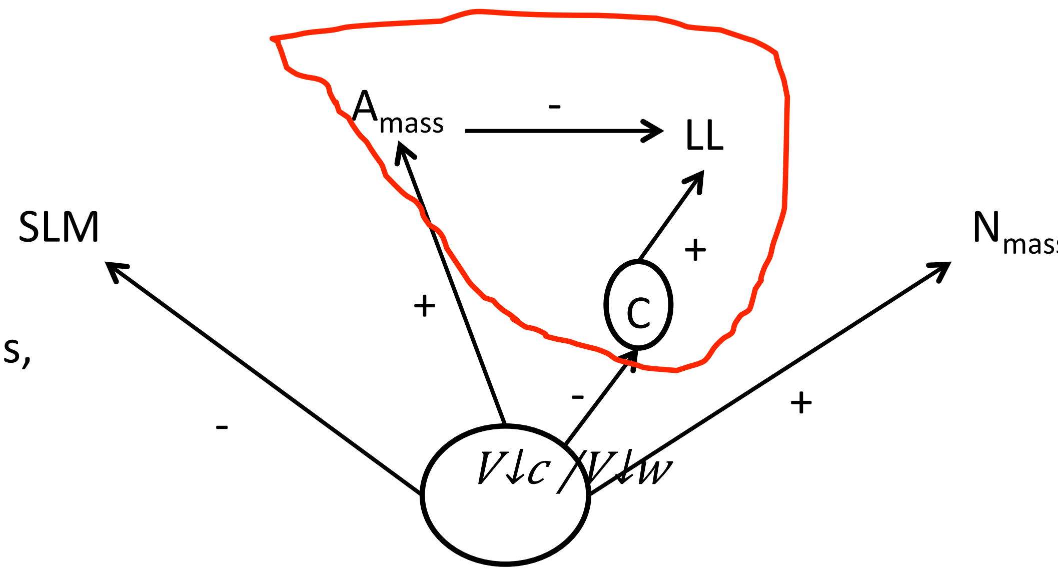
$$V_c / V_w \propto 1/dry\ mass \propto 1/C$$

SLM =(tissue density)*thickness

$$V_c / V_w \propto 1/SLM$$

Where is the latent variable hiding and what might it be?

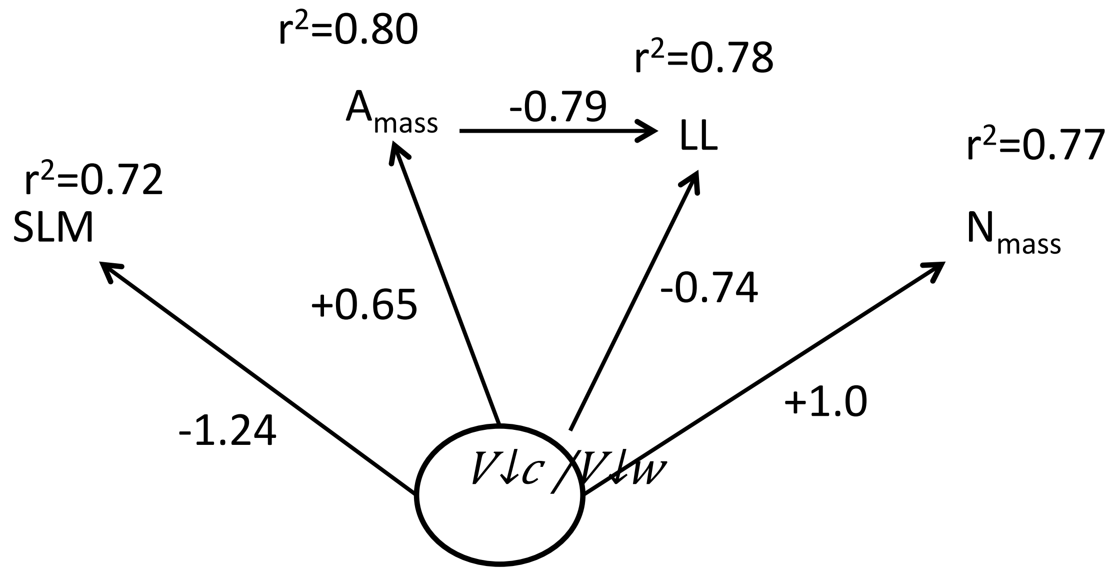
Kikuzawa's model from natural selection
+ detected by non-zero tetrad equation



Agrees with all tetrad equations,
Two vanish, one doesn't

All observed variables ln-transformed

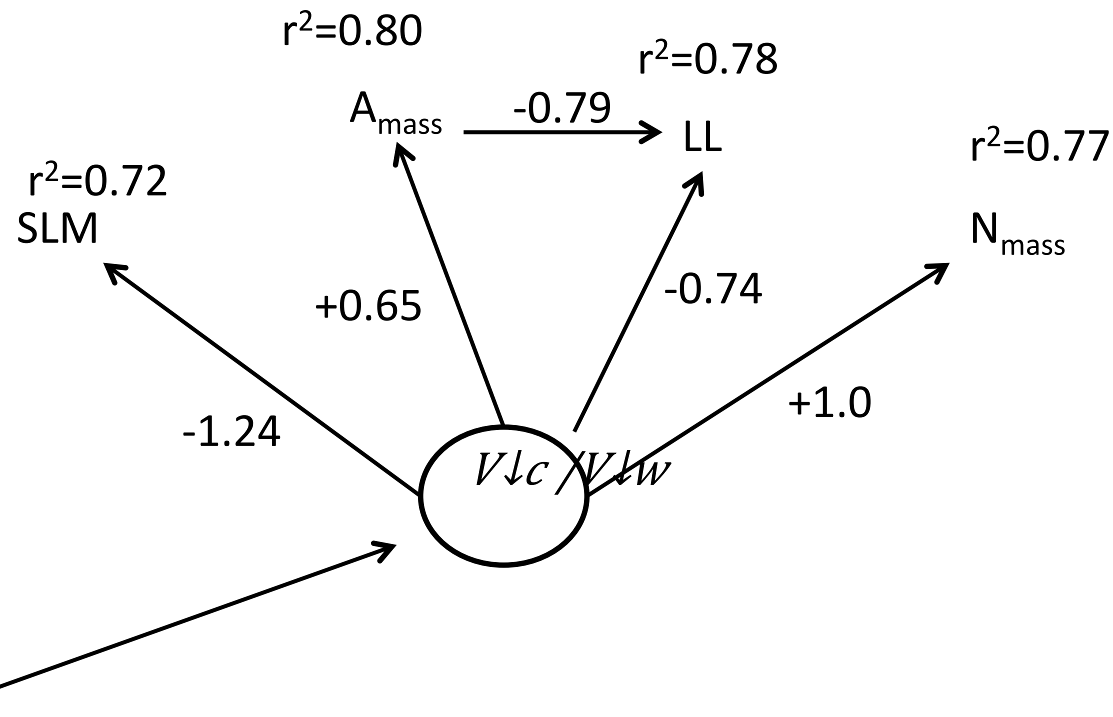
Where is the latent variable hiding and what might it be?



$\chi^2 = 4.080$, df = 3, $P = 0.39$

All observed variables ln-transformed

What’s next?



Next step: this ratio can be estimated (after a lot of work) to provide an independent test of this causal hypothesis