The worldwide leaf economic spectrum

How causal discovery algorithms forced me to re-imagine its generating causes
Some basic notions from evolutionary ecology...

- Evolutionary fitness
- Adaptive value of a trait

Sir Ronald Fisher

Charles Darwin
## Evolutionary fitness

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

<table>
<thead>
<tr>
<th>Age</th>
<th>Average # offspring / survival</th>
<th>Prob of surviving to age i</th>
<th>Expected # offspring</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0.8</td>
<td>0x0.8=0</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0.4</td>
<td>2x0.4=0.8</td>
</tr>
<tr>
<td>...</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>x</td>
<td>3</td>
<td>0.1</td>
<td>3x0.1=0.3</td>
</tr>
</tbody>
</table>

Net reproductive output for this genotype or phenotype:

\[ R_0(x) = \Sigma(\text{average reproduction at age } i)(\text{probability of surviving to age } i) \]

\[ \text{fitness}(x) = R^{\downarrow}0 (x) - R^{\downarrow}0 \]
Adaptive value of a trait (or suite of traits)

Best adapted trait value in environment E

Poorly adapted trait values in environment E

fitness(x)

Trait value (x) of phenotype
Environment

Trait	
  value

fitness

Trait value

Trait value with highest fitness

Environment
Traits often show complicated patterns of covariation

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 transferred 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 transferred 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.

**Measured variables**

**Specific leaf mass (g/cm²)**
- dry mass = allocation to convert energy into sugars
- surface area = amount of photons captured

**A<sub>max</sub>: Maximum net photosynthetic rate (umol/g/s)**

**N<sub>m</sub>: nitrogen content of leaf (mg/g)**
- N is the limiting element for photosynthetic enzymes

**R<sub>m</sub>: 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.
$A_{\text{max}} - \text{LMA} - N_m$

$\text{LL} - \text{LMA} - R_m$

$P_m - \text{LMA} - N_m$

$A_m - \text{LMA} - N_m$
1st principal axis of a PCA explains ~ 80% of variation

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 acquisition

- 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.

\[
g = \frac{\text{total net production of carbon/leaf lifespan}}{t} = \frac{G}{t}
\]

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

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

\[ \int_0^t A(t) dt = [at - \frac{at^2}{2b}] \]

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

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

Solving for \( t \) when \( \frac{dg}{dt} = 0 \)

\[ t_{opt} = \sqrt{\frac{2bC}{a}} \]
Initial causal models


Most leaf nitrogen is in photosynthetic enzymes: more enzymes $\rightarrow$ 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
$\chi^2 = 12.825, \text{ df } = 1, p = 0.0003$

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.

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

Vanishing tetrads (assuming linear relationships & MVN distribution)

\[ \rho_{12} \rho_{34} - \rho_{14} \rho_{23} = 0 \]
\[ \rho_{13} \rho_{24} - \rho_{14} \rho_{23} = 0 \]
\[ \rho_{13} \rho_{24} - \rho_{12} \rho_{34} = 0 \]

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):

\[
\rho \ln(LL), \ln(N\downarrow M) \rho \ln(LMA), \ln(A\downarrow M) - \rho \ln(LL), \ln(LMA) \\
\rho \ln(A\downarrow M), \ln(N\downarrow M) \neq 0
\]

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?

<table>
<thead>
<tr>
<th>Variable 1</th>
<th>Variable 2</th>
<th>All paths linking pair pass through a latent?</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLM</td>
<td>$A_{mass}$</td>
<td>✓</td>
</tr>
<tr>
<td>SLM</td>
<td>LL</td>
<td>✓</td>
</tr>
<tr>
<td>SLM</td>
<td>$N_{mass}$</td>
<td>✓</td>
</tr>
<tr>
<td>$A_{mass}$</td>
<td>$N_{mass}$</td>
<td>✓</td>
</tr>
<tr>
<td>$A_{mass}$</td>
<td>LL</td>
<td>✗</td>
</tr>
<tr>
<td>LL</td>
<td>$N_{mass}$</td>
<td>✓</td>
</tr>
</tbody>
</table>
Where is the latent variable hiding and what might it be?
Where is the latent variable hiding and what might it be?

Chloroplast (where photosynthesis occurs)
Where is the latent variable hiding and what might it be?

- 
  - # chloroplasts $\propto$ volume of cytoplasm
  - photosynthetic rate per chloroplast is very much less variable than the number of chloroplasts per leaf
  - Photosynthetic rate per leaf $\propto$ volume of cytoplasm
  - Nitrogen content per leaf $\propto$ volume of cytoplasm
  - Leaf dry mass is overwhelmingly in the cell walls
  - Leaf dry mass $\propto$ volume of cell walls

\[
\frac{\text{total cytoplasmic volume}}{\text{total cell wall volume}} = \frac{V_{\downarrow c}}{V_{\downarrow w}}
\]
Where is the latent variable hiding and what might it be?

\[
\frac{V_{\downarrow c}}{V_{\downarrow w}} \propto \frac{\text{total}}{\text{dry mass}} \equiv A_{\text{mass}}
\]

\[
\frac{V_{\downarrow c}}{V_{\downarrow w}} \propto \frac{\text{total}}{\text{dry mass}} \equiv N_{\text{mass}}
\]

\[
\frac{V_{\downarrow c}}{V_{\downarrow w}} \propto \frac{1}{\text{dry mass}} \propto \frac{1}{C}
\]

SLM = (tissue density) * thickness

\[
\frac{V_{\downarrow c}}{V_{\downarrow w}} \propto SLM
\]
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?

\[ \chi^2 = 4.080, \text{ df } = 3, P = 0.39 \]

All observed variables In-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