

CWM approach in functional trait ecology

R workshop at 63rd IAVS Symposium Vegetation Goes Virtual

David Zelený & Po-Yu Lin

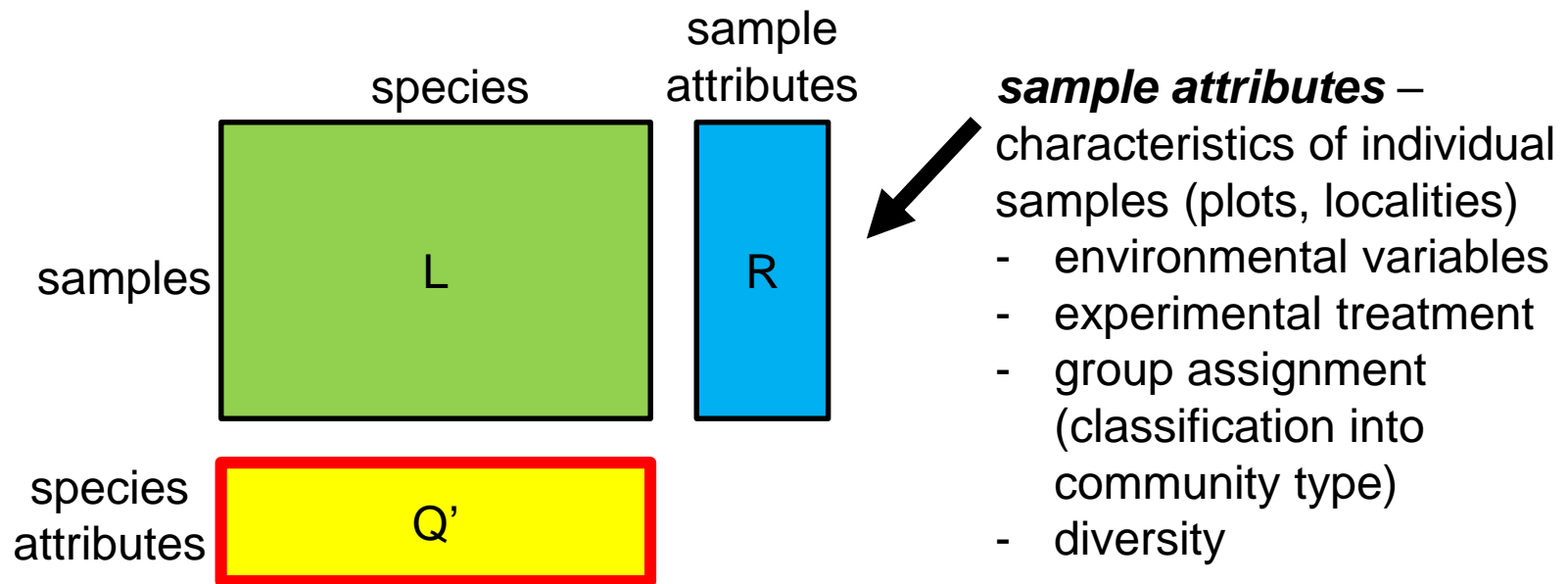
National Taiwan University, Taipei, Taiwan

September 20, 2021



Analysis of species attributes in community ecology

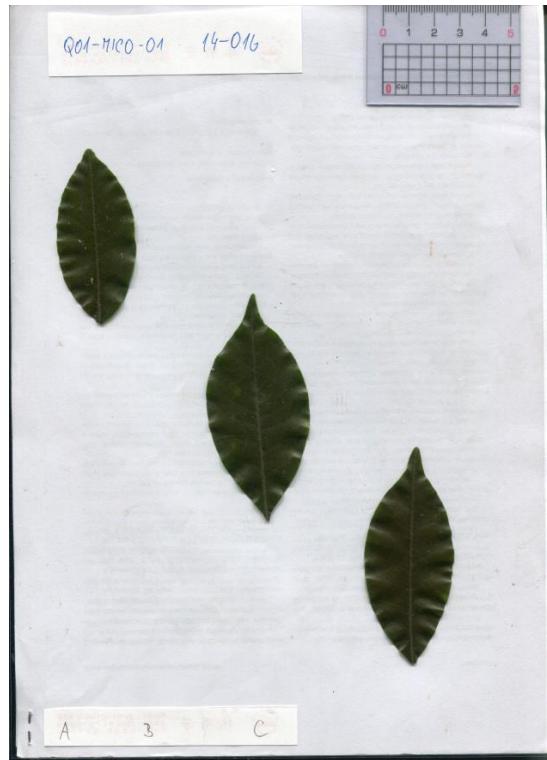
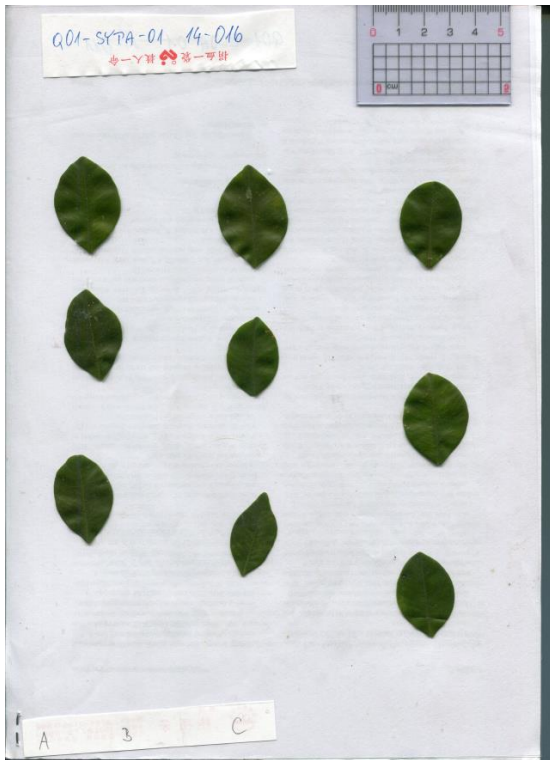
(e.g. traits, species indicator values)



species attributes – characteristics of individual species

- traits
- species indicator values
- species phylogenetic relationship
- species specialization values etc.

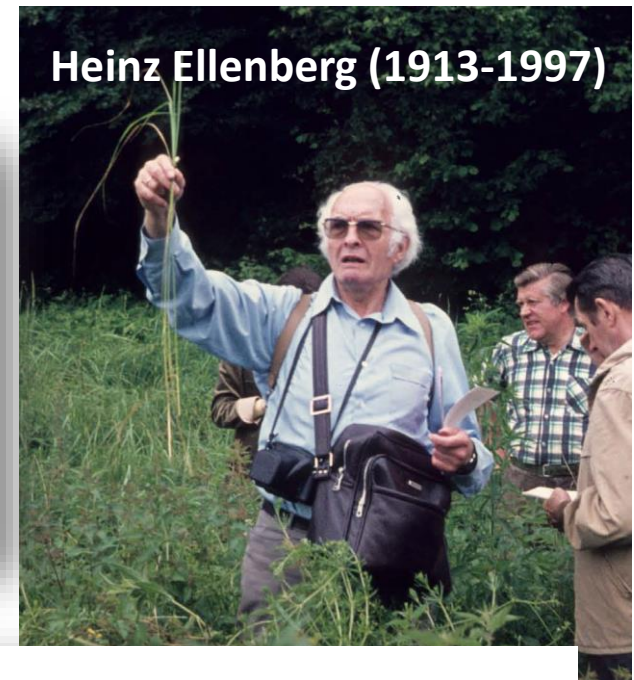
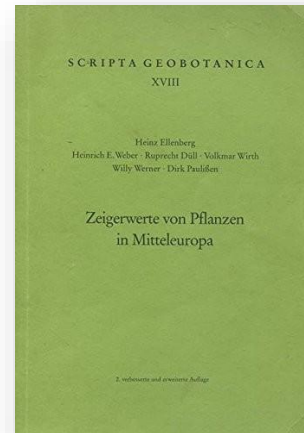
Examples of plant traits: leaf area (LA) and specific leaf area (SLA)



Ellenberg-type indicator values for plant species



System of “indicator values”, describing its species optima along important environmental factors (e.g. temperature, soil pH, moisture)



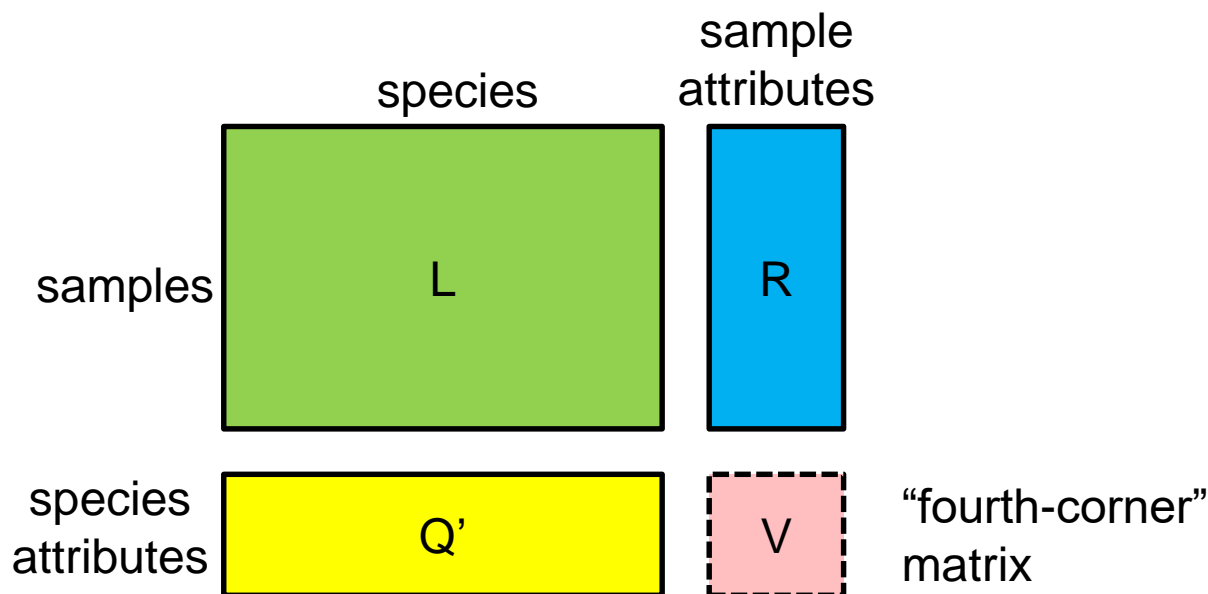
6 27 Zeigerwerte der Pflanzen Mitteleuropas

27.2 Zeigerwerte der Gefäßpflanzen

Entspricht den Angaben in Ellenberg et al. (2001).

Name	L	T	K	F	R	N	S	LF	LF_B
Abies alba	(3)	5	4	x	x	x	0	P	I
Acer campestre	(5)	6	4	5	7	6	0	P	S
Acer monspessulanum	(6)	8	4	3	8	4	0	P	S
Acer negundo	(5)	6	6	6	7	7	0	P	S
Acer opalus agg.	(5)	8	4	4	8	6	0	P	S
Acer platanoides	(4)	6	4	x	x	x	0	P	S
Acer pseudoplatanus	(4)	x	4	6	x	7	0	P	S
Aceras anthropophorum	7	7	2	4~	8	3	0	G	S
Achillea atrata agg.	9	2	4	5	8	3	0	H	W
Achillea cartilaginea	8	6	6	8~	7	6	0	H	S
Achillea clavatae	8	2	5	5	8	3	0	H	W
Achillea clusiana	9	2	4	5	9	3	0	H	W
Achillea macrophylla	6	2	4	6	6	8	0	H	W
Achillea millefolium agg.									
Achillea millefolium collina	9	6	6	2	7	2	0	H	S
Achillea millefolium millefolium	8	x	x	4	x	5	1	H, C	W
Achillea millefolium pannonica	7	7	6	3	6	2	0	H	S
Achillea millefolium roseoalba	8	6	4	5	7	7	0	H, C	W

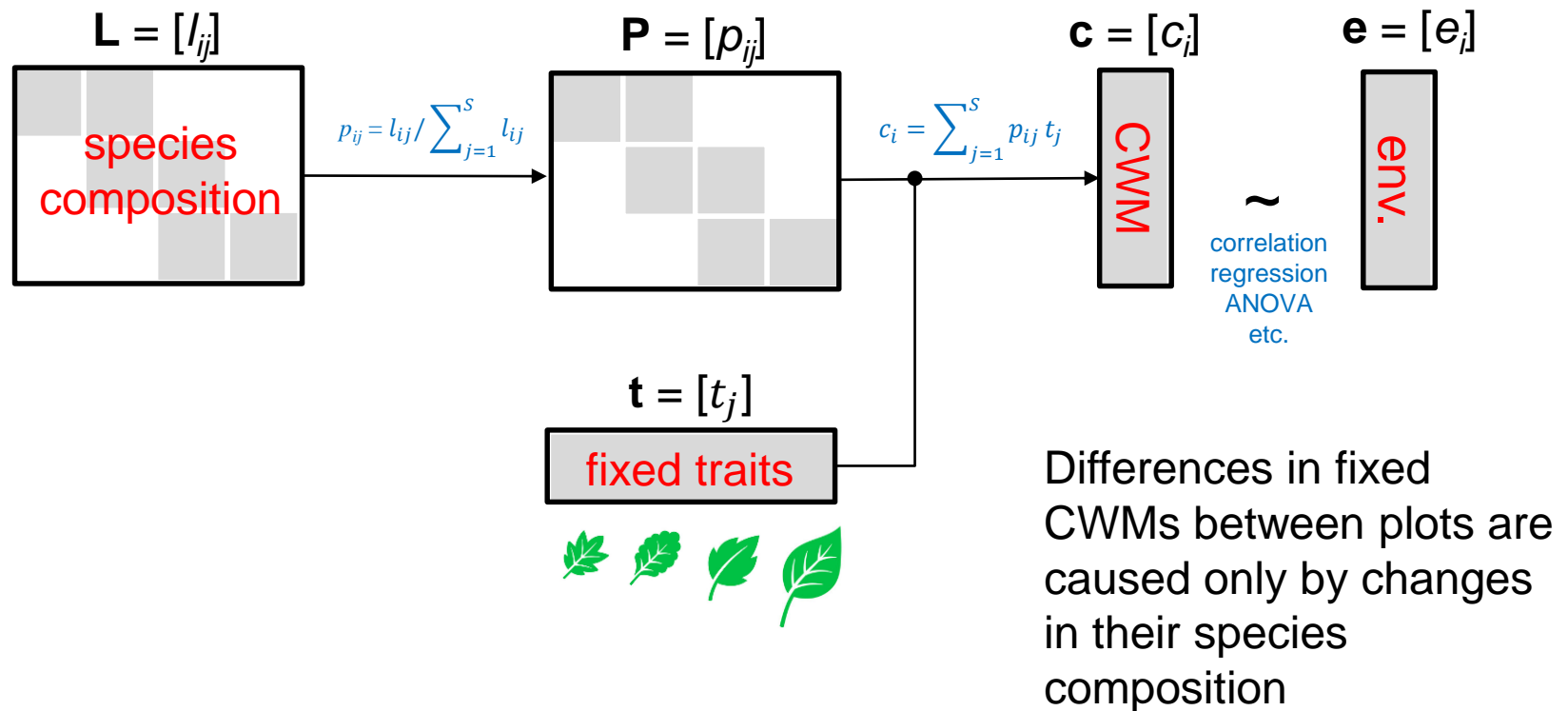
Relationship between sample attributes and species attributes via species composition (R-L-Q)



Three solutions:

- 1) combine **L** & **Q** and relate to **R** - *community-weighted mean* (CWM) approach
- 2) combine **L** & **R** and relate to **Q** - *species niche centroid* (SNC) approach
- 3) relate **R** to **Q** directly via **L** to find **V** - *fourth-corner* approach, *RLQ ordination*

Community weighted mean approach (relating traits to environment on a community level)



Relationship between community weighted mean of functional traits and measured environmental variables

Notes

Ecology, 85(9), 2004, pp. 2630–2637
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PLANT FUNCTIONAL MARKERS CAPTURE ECOSYSTEM PROPERTIES DURING SECONDARY SUCCESSION

ERIC GARNIER,^{1,3} JACQUES CORTEZ,¹ GEORGES BILLÈS,¹ MARIE-LAURE NAVAS,^{1,2} CATHERINE ROUMET,¹
MAX DEBUSSCHE,¹ GÉRARD LAURENT,¹ ALAIN BLANCHARD,¹ DAVID AUBRY,¹ ASTRID BELLMANN,¹
CATHY NEILL,¹ AND JEAN-PATRICK TOUSSAINT¹

¹Centre d'Ecologie Fonctionnelle et Evolutive (C.N.R.S.-U.M.R. 5175) 1919, Route de Mende,
34293 Montpellier Cedex 5, France

²Département des Sciences pour la Protection des Plantes et Ecologie, Ecole Nationale Supérieure Agronomique de
Montpellier, 2, Place Viala, 34060 Montpellier Cedex 1, France

Abstract. Although the structure and composition of plant communities is known to influence the functioning of ecosystems, there is as yet no agreement as to how these should be described from a functional perspective. We tested the biomass ratio hypothesis, which postulates that ecosystem properties should depend on species traits and on species contribution to the total biomass of the community, in a successional sere following vineyard abandonment in the Mediterranean region of France. Ecosystem-specific net primary productivity, litter decomposition rate, and total soil carbon and nitrogen varied significantly with field age, and correlated with community-aggregated (i.e., weighed according to the relative abundance of species) functional leaf traits. The three easily measurable traits tested, specific leaf area, leaf dry matter content, and nitrogen concentration, provide a simple means to scale up from organ to ecosystem functioning in complex plant communities. We propose that they be called “functional markers,” and be used to assess the impacts of community changes on ecosystem properties induced, in particular, by global change drivers.

Key words: biodiversity; ecosystem functioning; functional effect groups; functional leaf traits; litter decomposition; net primary productivity; secondary succession; soil carbon and nitrogen.

Garnier et al. 2004 *Ecology*

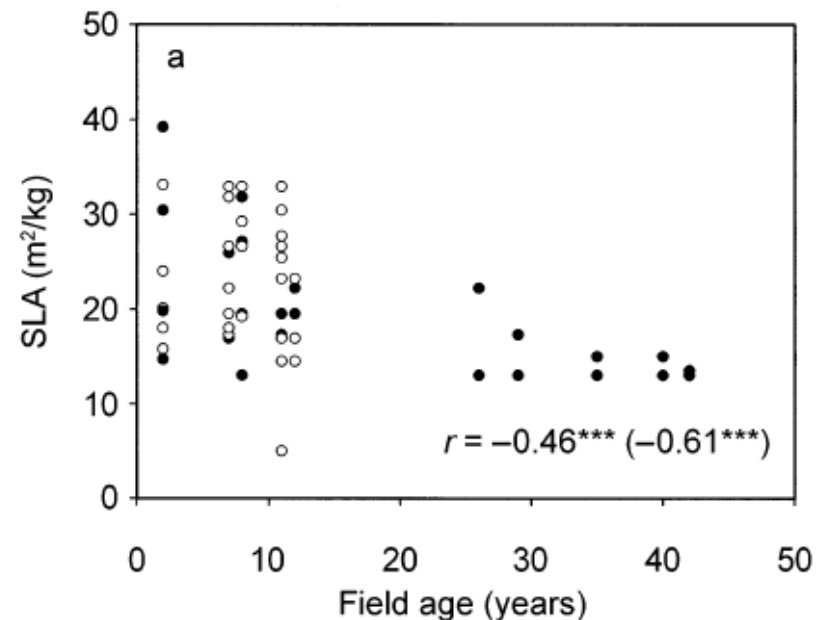


FIG. 1. Relationships between field age and leaf traits of the most abundant species of the communities: (a) SLA, specific leaf area; (b) LDMC, leaf dry matter content; (c) LNC, leaf nitrogen concentration. Pearson correlation coefficients are given in the figures: on each graph, the first value is for all species ($n = 54$), and the values in parentheses are for the two dominant species of the communities ($n = 24$). Solid symbols represent these two dominant species; open symbols represent the other species. Levels of significance: $**P < 0.01$; $***P < 0.001$.

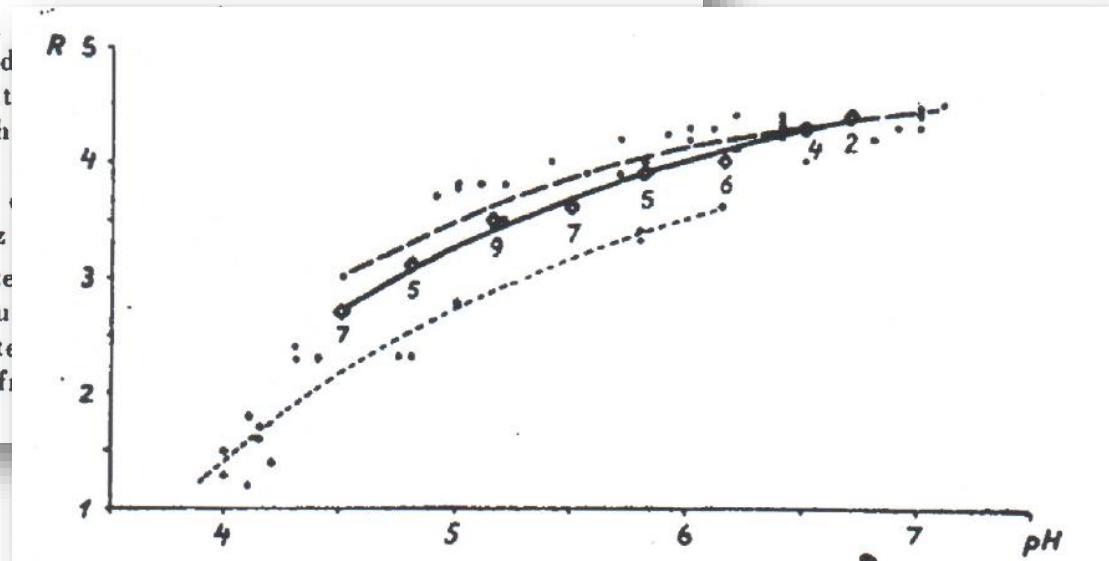
Relationship between mean indicator values and measured environmental variables

UNKRAUTGESELLSCHAFTEN ALS MASS FÜR DEN SÄUREGRAD, DIE VERDICHTUNG UND ANDERE EIGENSCHAFTEN DES ACKERBODENS

Von Dr. H. ELLENBERG, Hohenheim

Zusammenhänge zwischen dem gewissen Eigenschaften ihres Stand Bauern von alters her bekannt. Seit die Wissenschaft mit diesen Bezieh und ihre Ursachen zu ergründen, solchem Studium im Hinblick auf schaft immer wieder neuen Anreiz

1. sind die meisten höheren Pflanze zu erkennen und ihre Verbreitu Falls sie eindeutig auf bestimmte weisen, können sie also die Auf und beschleunigen;



Heinz Ellenberg (1948) *Berichte über Landtechnik*

Relationship between mean indicator values and measured environmental variables tested

SUCCESSION IN A SOUTH SWEDISH DECIDUOUS WOOD: A NUMERICAL APPROACH*

Stefan PERSSON**

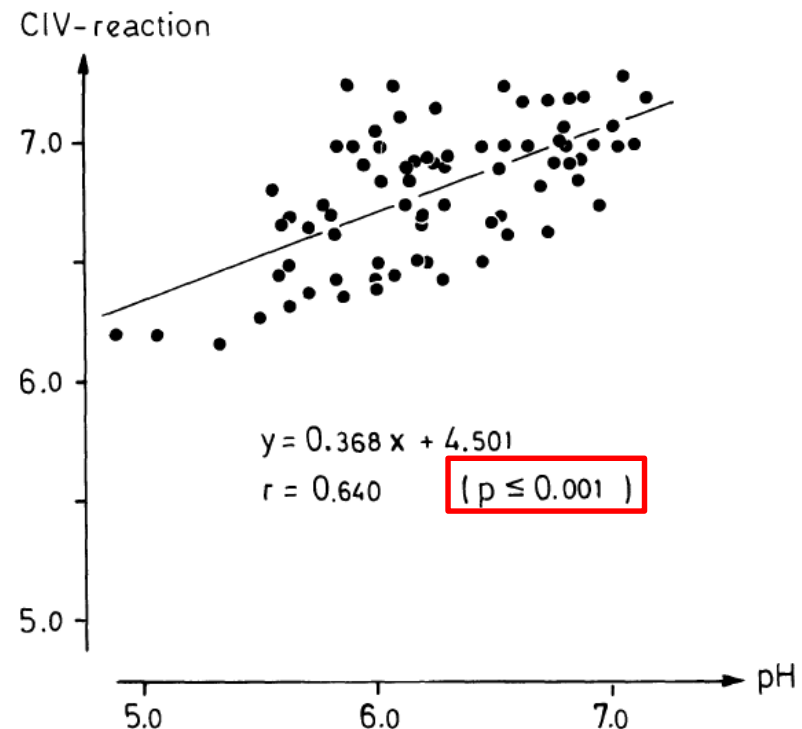
Institute of Plant Ecology, University of Lund, ö Vallgård

Keywords:

Classification, Ordination, Semipermanent plots, Succession

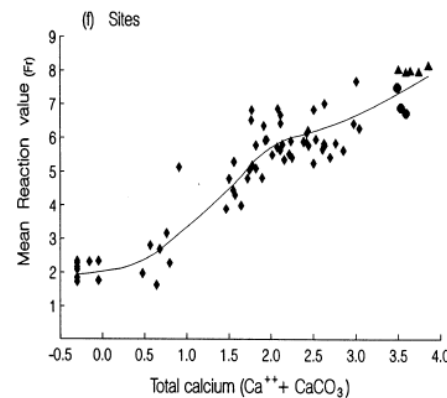
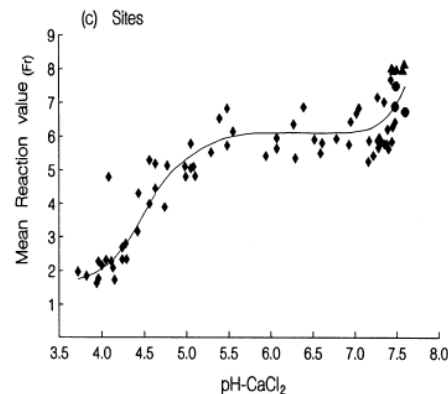
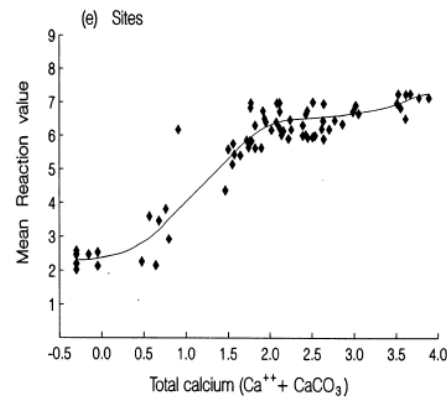
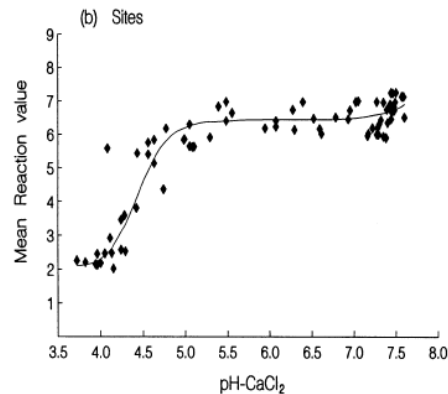
Introduction

Studies of successions in vegetation must, in many cases involve observation periods of considerable length. Especially when successions are dependent on or strongly influenced by developments in tree- and shrub layers, observations must be extended over decades. Very rarely one and the same investigator is in a position to be able to observe his permanent plots for such a long time. An alternative to this dilemma is the possibility of reestablishing, with



Stefan Persson (1980) *Vegetatio*

Relationship between mean indicator values and measured environmental variables tested



Species included		Vascular plants			
Calculation type		Normal		Frequency wt.	
Transformation	<i>n</i>	Pres	Abun	Pres	Abun
Moisture					
Average groundwater	74	0.87	0.87	0.88	0.88
Lowest moisture	74	0.84	0.84	0.87	0.86
Highest pF	74	-0.77	-0.76	-0.77	-0.76
Nitrogen					
Soil C:N ratio	74	-0.54	-0.54	-0.52	-0.50
Soil total N	74	0.61	0.61	0.62	0.61
N-mineralization	74	0.39	0.40	0.41	0.42
Soil mineral N	74	0.50	0.51	0.53	0.54
Soil NO ₃	74	0.68	0.69	0.69	0.69
Nitrification degree	74	0.66	0.67	0.65	0.65
Soil available PO ₄	74	0.51	0.51	0.53	0.52
Soil available K	74	0.59	0.60	0.60	0.59
Tissue N-concentration	72	0.71	0.72	0.69	0.70
N-accumulation	57	0.83	0.85	0.83	0.85
Biomass production	57	0.82	0.85	0.84	0.86

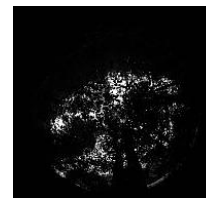
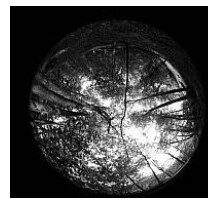
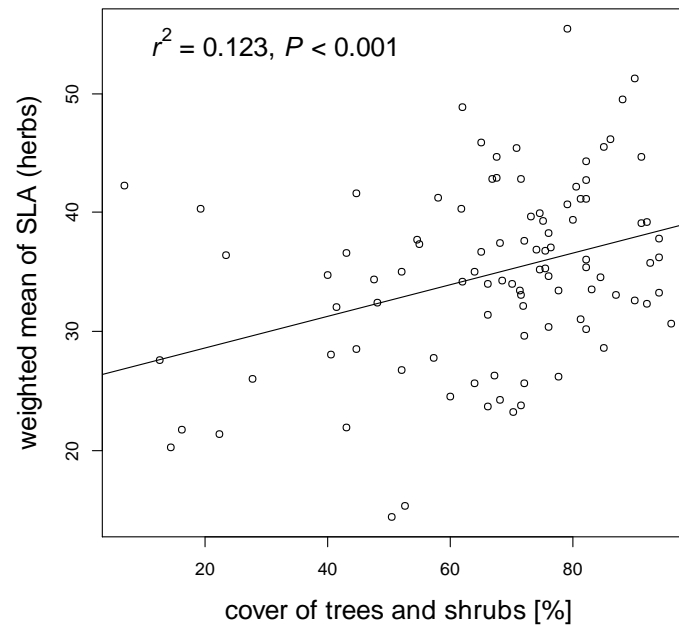
Soil reaction					
pH-CaCl ₂	74	0.79	0.79	0.78	0.78
Base saturation	62	0.94	0.94	0.87	0.86
Ca ²⁺ saturation	62	0.94	0.94	0.88	0.87
Ca ²⁺ amount	73	0.92	0.92	0.90	0.90
Total calcium	73	0.90	0.90	0.86	0.86

<i>Specie</i>					
pH-Ca					14
Base s					10
Ca ²⁺ s					12
Ca ²⁺ a					17
Total calcium	73	0.92	0.91	0.92	
<i>pH > 5.25</i>					
pH-CaCl ₂	45	0.36	0.37	0.32	0.36
Base saturation	37	0.38	0.39	0.31	0.37
Ca ²⁺ saturation	37	0.43	0.45	0.37	0.43
Ca ²⁺ amount	44	ns	ns	ns	ns
Total calcium	44	0.60	0.65	0.60	0.68

* Bryophytes constituted between 0 and 80% of the total number of species with only 14-15%.

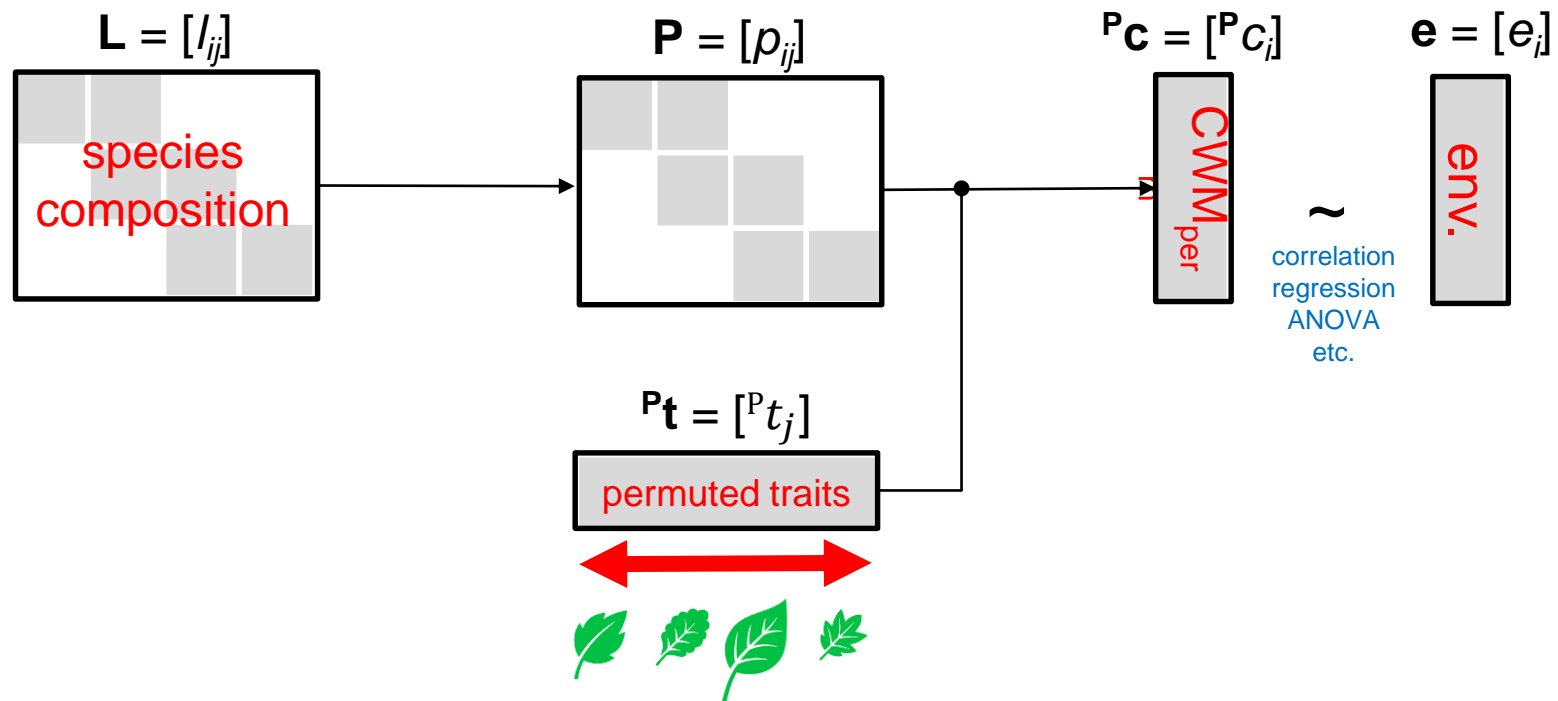
Schaffers & Sýkora (2000) *Journal of Vegetation Science*

Example: CWM of specific leaf area (SLA) for understory herbs related to canopy tree cover

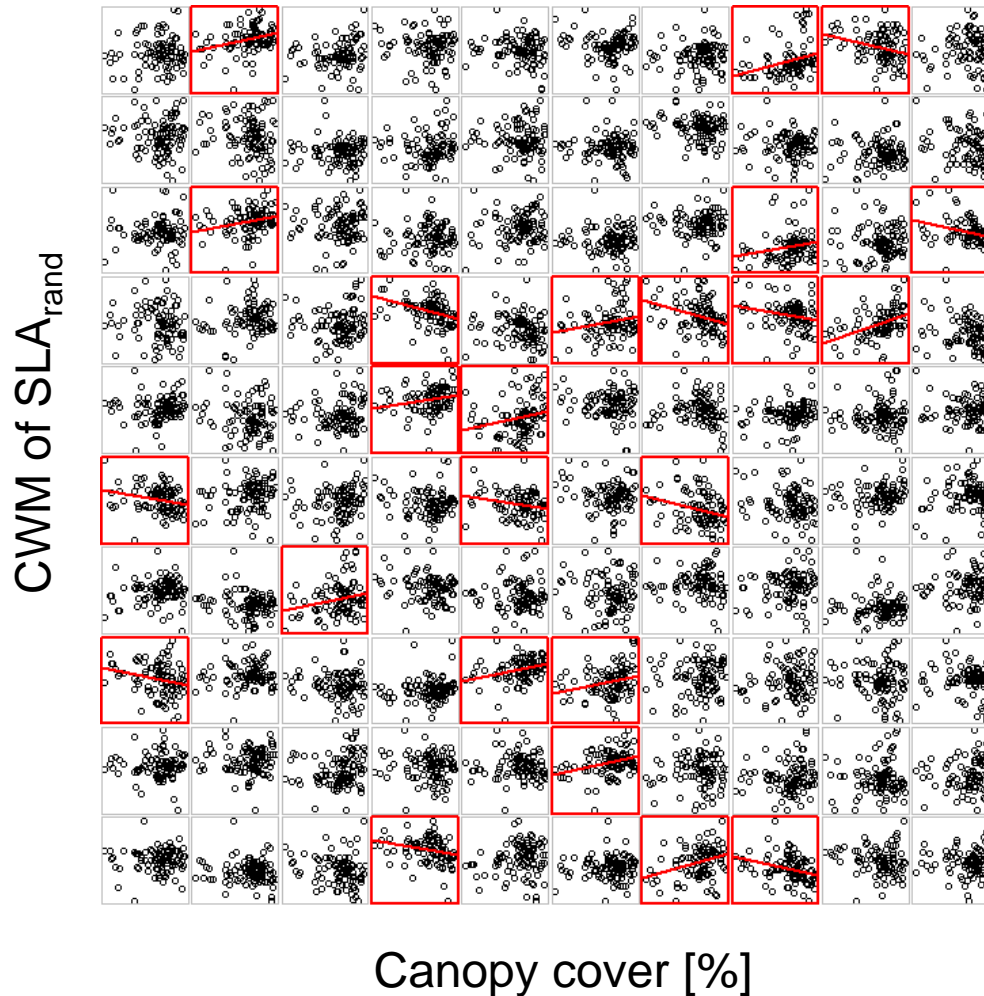


Zelený (*unpubl.*)

Community weighted mean approach (relating traits to environment on a community level)



CWM of SLA calculated from permuted SLA trait values and related to canopy cover (repeated 100 x)

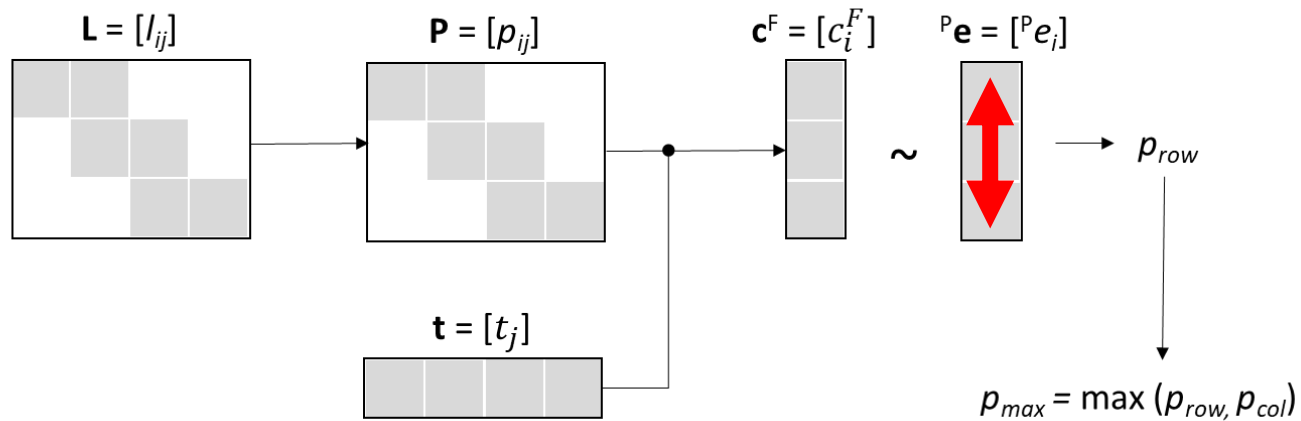


23 out of 100 relationships are **significant ($P < 0.05$)** – but we would expect only 5 out of 100 to be significant ($\alpha = 0.05$)

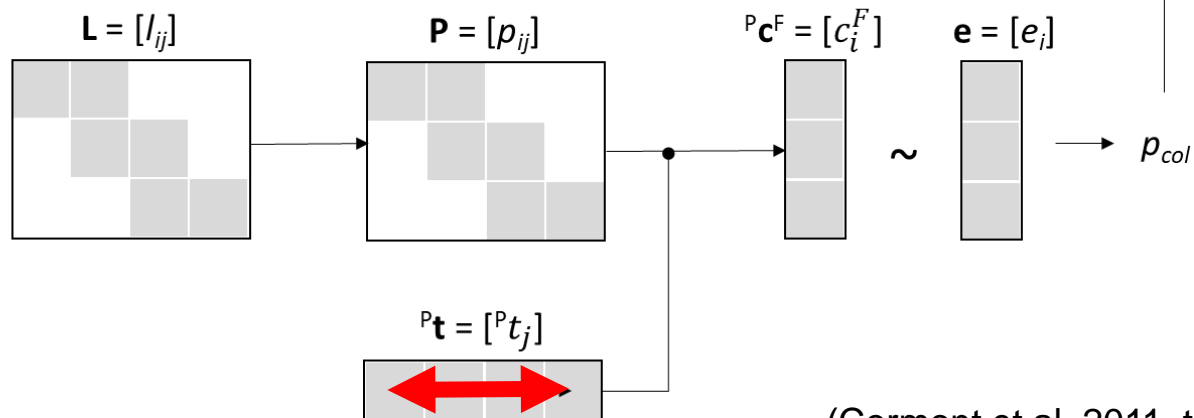
Zelený (*unpubl.*)

Solution to inflated Type I error rate in CWM approach: max permutation test

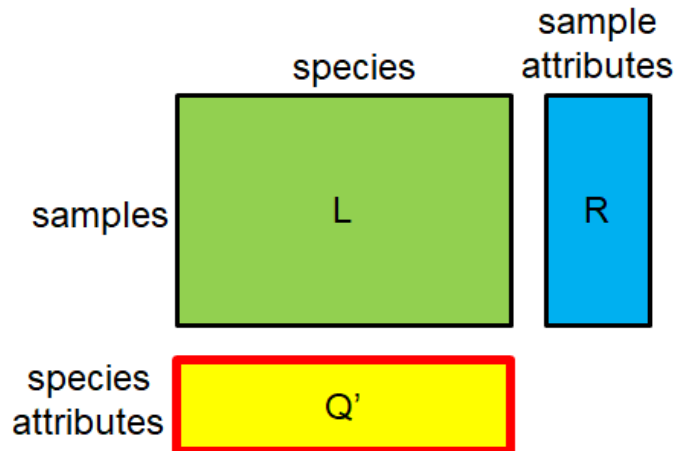
(a) Row-based permutation test



(b) Column-based permutation test



(Cormont et al. 2011, ter Braak et al. 2012)



CWM approach: relating CWM to sample attributes

$$\text{CWM} = f_1(\mathbf{L}, \mathbf{t})$$

extrinsic species attributes:

$$\text{CWM} \sim \text{SA}_{\text{extr}} \text{ or } f_1(\mathbf{L}, \mathbf{t}) \sim \mathbf{e}$$

intrinsic species attributes

$$\text{CWM} \sim \text{SA}_{\text{intr}} \text{ or } f_1(\mathbf{L}, \mathbf{t}) \sim f_2(\mathbf{L})$$

extrinsic sample attributes

measured/estimated environmental variables, experimental treatments

- soil pH (measured),
- canopy cover (estimated)
- temperature (GIS derived)
- fertilized vs control (treatment)

$$\text{SA}_{\text{extr}} = \mathbf{e}$$

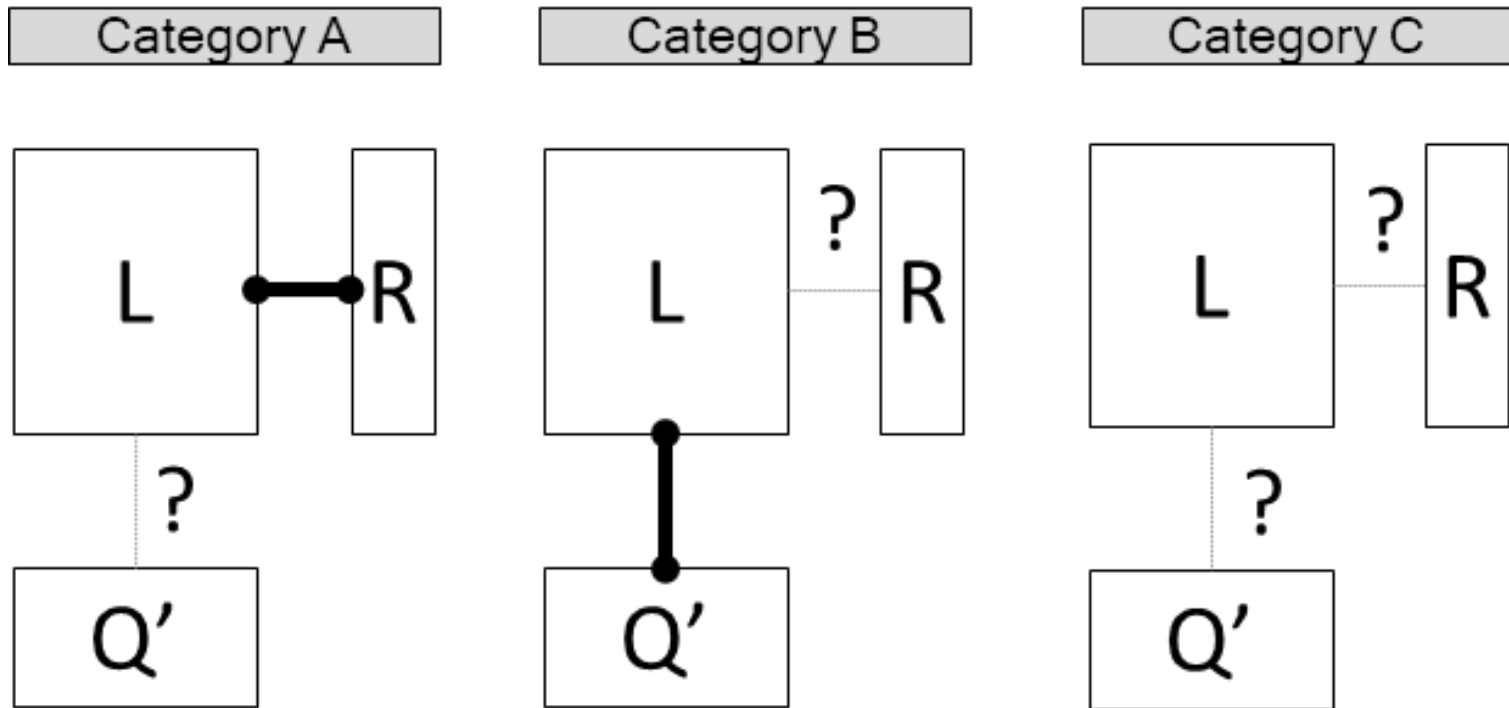
intrinsic sample attributes


calculated from species composition

- sample ordination scores,
- species richness,
- diversity indices,
- assignment of sample into a cluster by numerical classification

$$\text{SA}_{\text{intr}} = f_2(\mathbf{L})$$

Three categories of hypotheses and a test suitable for each of them (extrinsic variables)



Explanation:  = an assumption of the relationship, ? = what is being tested

Category A

- Studies assuming the link of environmental variables to species composition (e.g. we assume that treatment is effective), and evaluating how traits or species indicator values react to it

Standard test has inflated Type I error rate (too good to be true)

Category B

- Studies assuming the link of species attributes to species composition and testing the effect of sample attributes
- e.g. trait studies assuming that measured traits are functional, i.e. they influence species abundance and are linked to species composition, and testing whether environmental variables act as an environmental filter on species abundances.

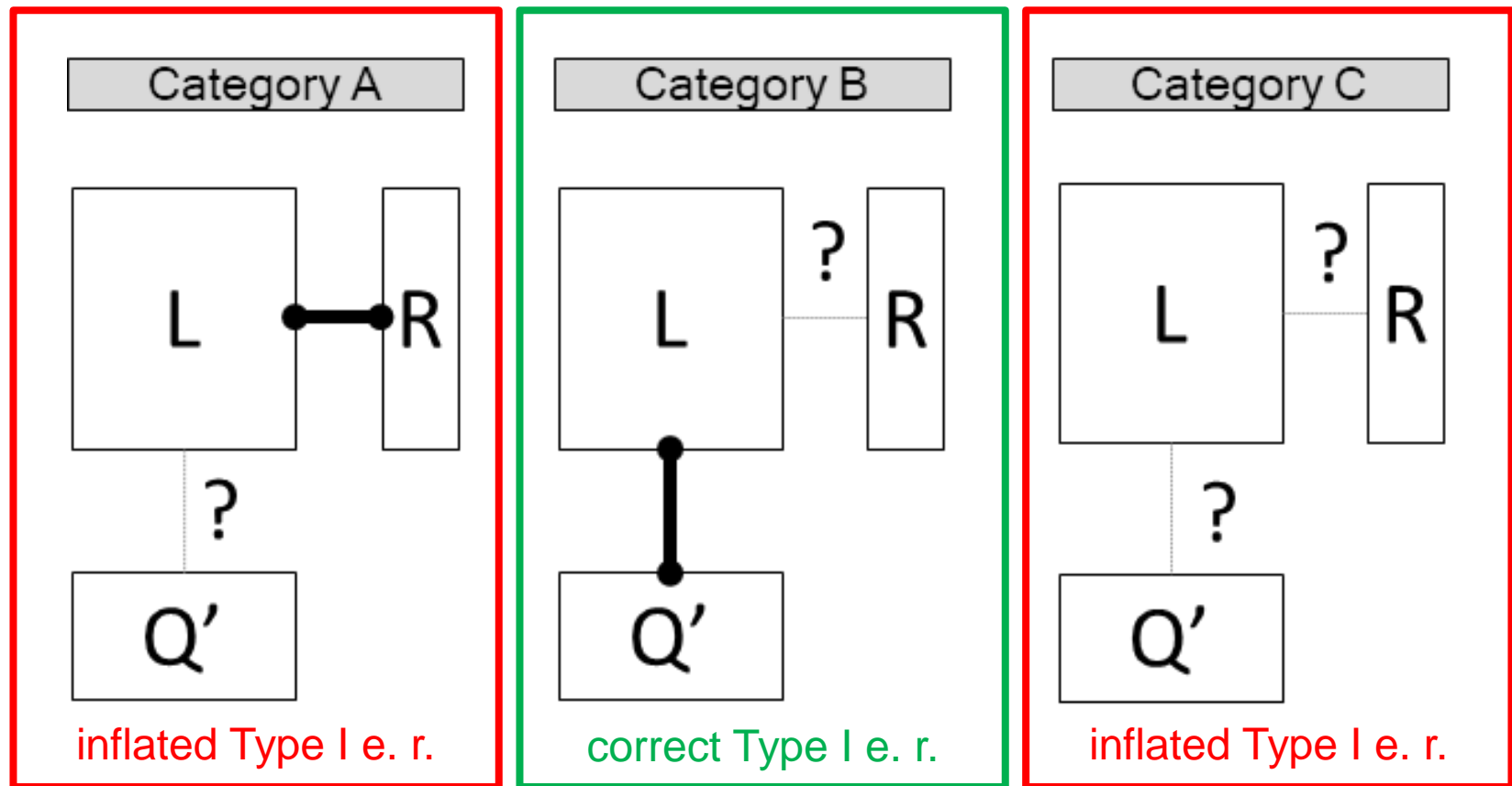
Standard test has correct Type I error rate


Category C

- No explicit assumption
- e.g. relating traits to environment without explicit assumption whether traits are functional or not;
- or relating Ellenberg indicator values to environmental variables to test which environmental variable they most likely represent

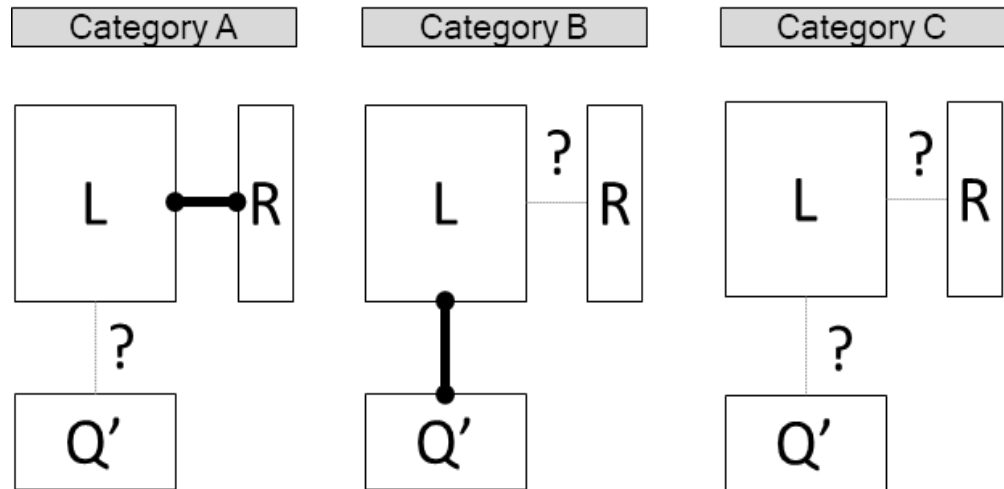
Standard test has inflated Type I error rate (too good to be true)

Three categories of hypotheses and a test suitable for each of them (extrinsic variables)



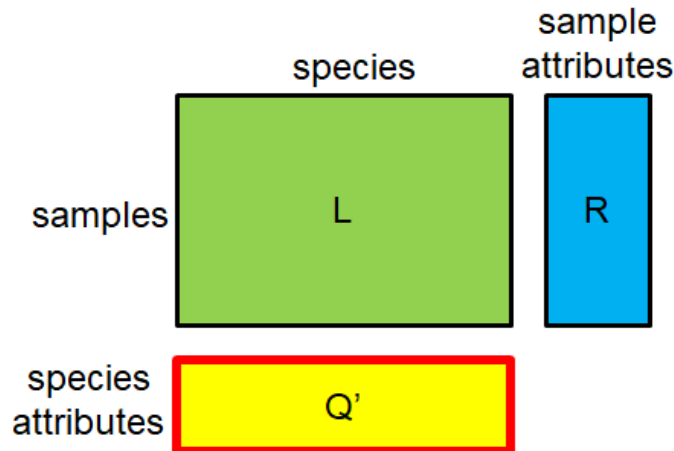
Explanation:  = an assumption of the relationship, ? = what is being tested

Three categories of hypotheses and a test suitable for each of them (extrinsic variables)



Recommended test:

	Category A	Category B	Category C
row-based (standard)	NO	YES	NO
column-based (modified)	YES	NO	NO
row & column-based (max)	YES	YES	YES



CWM approach: relating CWM to sample attributes

$$\text{CWM} = f_1(\mathbf{L}, \mathbf{t})$$

extrinsic species attributes:

$$\text{CWM} \sim \text{SA}_{\text{extr}} \quad \text{or} \quad f_1(\mathbf{L}, \mathbf{t}) \sim \mathbf{e}$$

intrinsic species attributes

$$\text{CWM} \sim \text{SA}_{\text{intr}} \quad \text{or} \quad f_1(\mathbf{L}, \mathbf{t}) \sim f_2(\mathbf{L})$$

extrinsic sample attributes

measured/estimated environmental variables, experimental treatments

- soil pH (measured),
- canopy cover (estimated)
- temperature (GIS derived)
- fertilized vs control (treatment)

$$\text{SA}_{\text{extr}} = \mathbf{e}$$

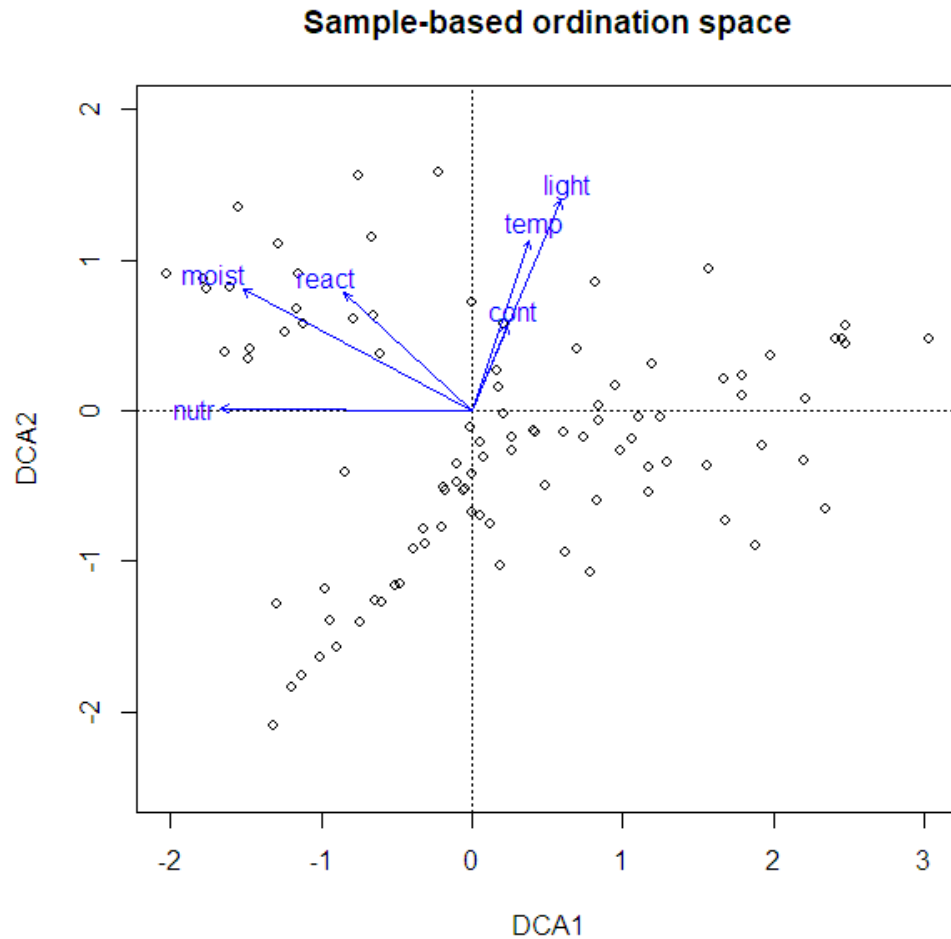
intrinsic sample attributes

calculated from species composition

- sample ordination scores,
- species richness,
- diversity indices,
- assignment of sample into a cluster by numerical classification

$$\text{SA}_{\text{intr}} = f_2(\mathbf{L})$$

Relating mEIV to ordination axes in DCA: standard (row-based) test (using `envfit`)



	r2	Pr(>r)	
light	0.7157	0.001	***
temp	0.4449	0.001	***
cont	0.1170	0.006	**
moist	0.9236	0.001	***
react	0.4176	0.001	***
nutr	0.8706	0.001	***

Package `weimea` - overview

- calculates CWM (and SNC) values while considering missing species attributes
- includes fast permutation tests for correlation, regression or ANOVA analysis between CWM and environmental variables
- includes *modified permutation test* sensu Zelený & Schaffers (2012)
- includes also other trait-env methods, like fourth corner (Legendre et al. 2017) and weighted CWM/SNC regression (ter Braak et al. 2018).

To install, check the Workshop website at
https://github.com/zdealveindy/IAVS2021_weimea_workshop

or scan the QR code on the right ->

