Design and analysis of experiments testing for biodiversity

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Theoretical advances in experimental design
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Ongoing joint work with Julia Reiss and Daniel Perkins

Abstract

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We also fit a nested family of plausible models to the data.
Our results suggest that the underlying model is not diversity at all. One of my crucial inputs has been the use of Hasse diagrams as a way of understanding a complicated family of plausible models for the expectation of the response.

Biodiversity experiments

This seems to be the received wisdom.

Treatments:	random sets of species
Measured response Y:	some eco-desirable outcome
Conclusion:	the greater the number of different species, the better the outcome.

A more carefully controlled experiment

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Put 12 shrimps in a jar containing stream water and alder leaf litter.
Measure how much leaf litter is eaten after 28 days.

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Actually 42 jars, because untreated jars were included,
but their data was so obviously different that it was excluded from further modelling.

Initial model fitting

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This model for the response Y is

$$\mathbb{E}(Y) = \begin{cases} \alpha_1 & \text{on monocultures A, \ldots, F} \\ \alpha_2 & \text{on duocultures AB, \ldots, EF} \\ \alpha_3 & \text{on tricultures ABC, \ldots, DEF} \end{cases}$$

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The data did not give any evidence against the null hypothesis that

$$\alpha_1 = \alpha_2 = \alpha_3 :$$

this is the ‘Constant’ model, or null model.

Call in a statistician

		Assemblage identity	R	$x1$	$x2$	$x3$	$x4$	$x5$	$x6$
1	A	12 of type A	1	12	0	0	0	0	0
⋮			⋮						
6	F	12 of type F	1	0	0	0	0	0	12
7	AB	6 of A, 6 of B	2	6	6	0	0	0	0
⋮			⋮						
21	EF	6 of E, 6 of F	2	0	0	0	0	6	6
22	ABC	4 of A, 4 of B, 4 of C	3	4	4	4	0	0	0
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$$\mathbb{E}(Y) = \sum_{i=1}^{6} \beta_i x_i$$

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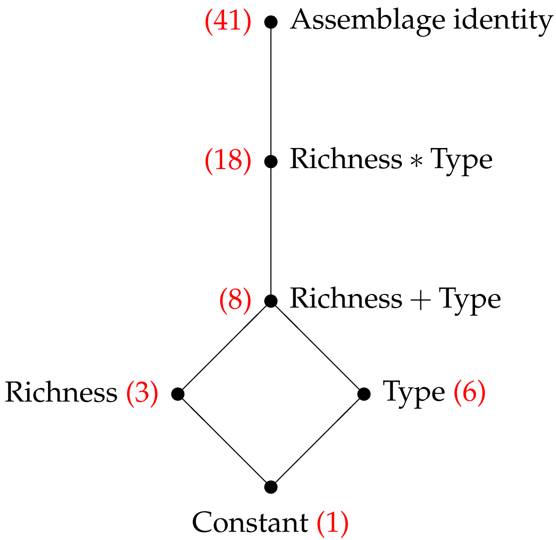
Family of expectation models (subspaces): dimensions shown in red



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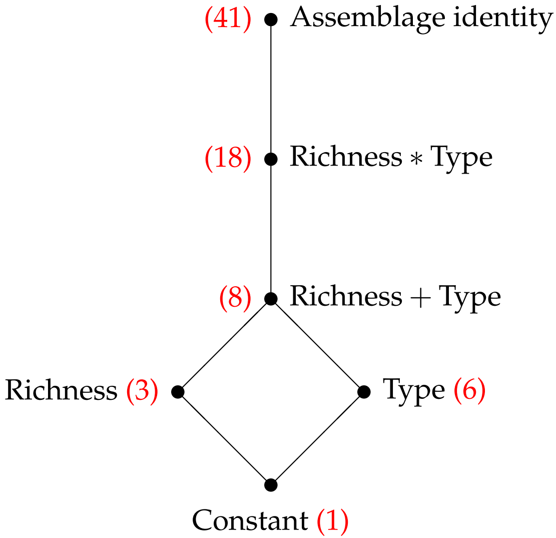
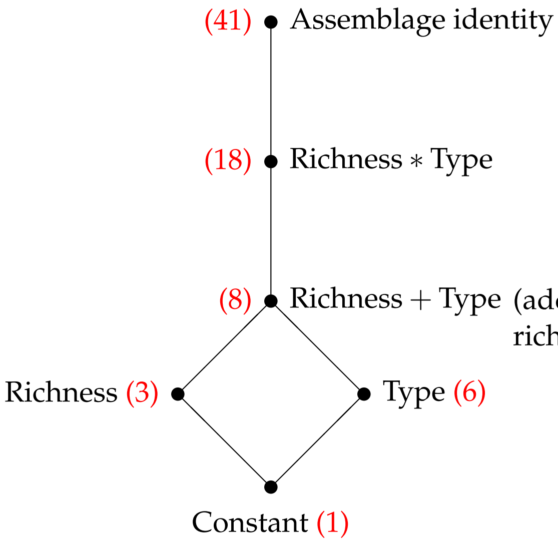


The subspace at the bottom of a line is contained in the subspace at the top of it



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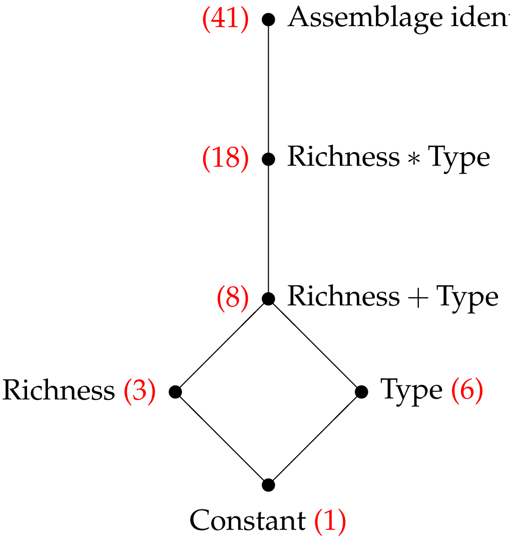
Richness + Type (add a different constant for each level of richness)



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Richness ∗ Type: (β_i can change with each level of richness but does not depend on what else is present)

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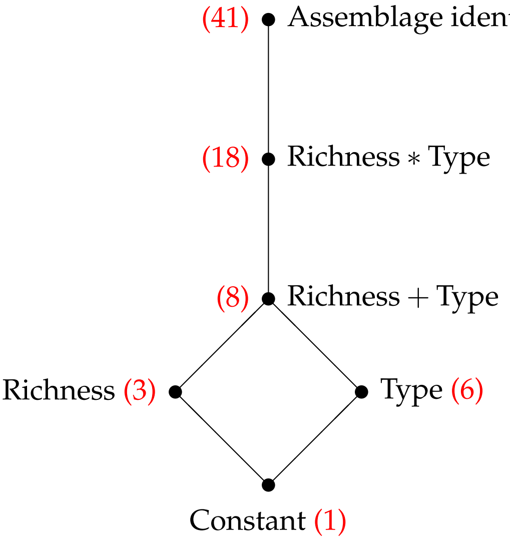

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Success: an ecology journal published

- Hasse diagram of family of models
- statement that each row of an ANOVA table is for a difference between models.

Analysis of Variance (ANOVA) table

Source	df	SS	MS	F	P
Richness	2	0.000009	0.000005	0.49	n.s.
Type	5	0.003859	0.000772	81.37	< 0.0005
Richness $*$ Type	10	0.000127	0.000013	1.34	n.s.
Assemblage Identity	23	0.000105	0.000005	0.48	n.s.
Block	3	0.000067	0.000022		
Error	120	0.001138	0.000009		
Total	163	0.005306			

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Verbatim from *Journal of Animal Ecology*

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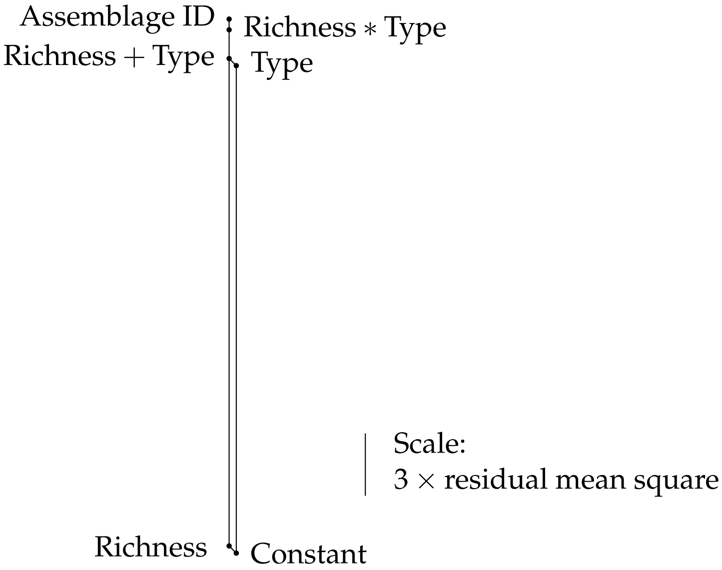
Scale the Hasse diagram so that each edge has length proportional to the relevant mean square,
and show the residual mean square to give a scale.

What the data showed: mean squares



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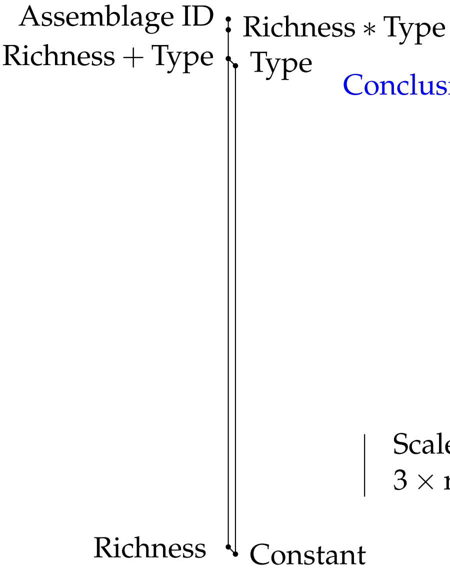

Conclusions:

Scale:
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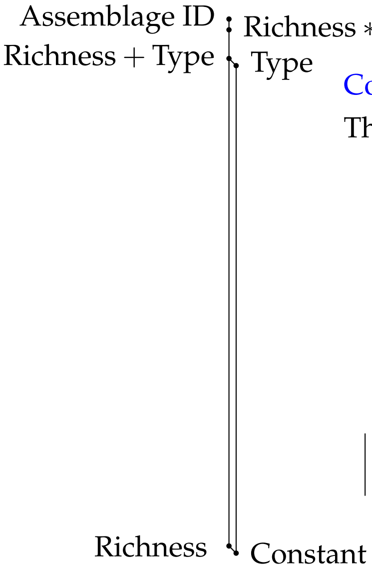

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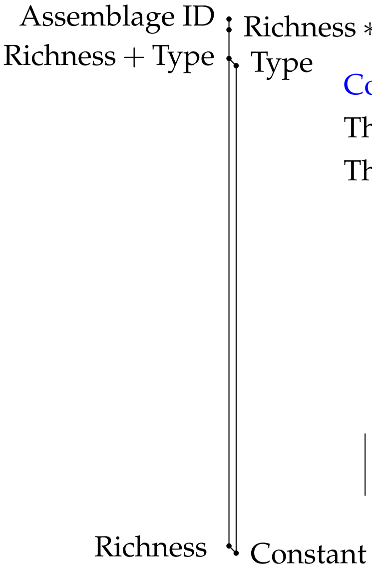

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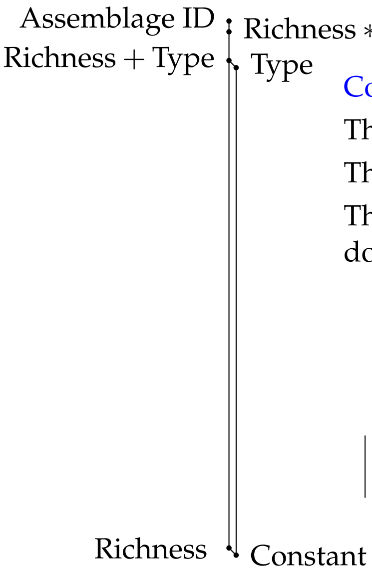

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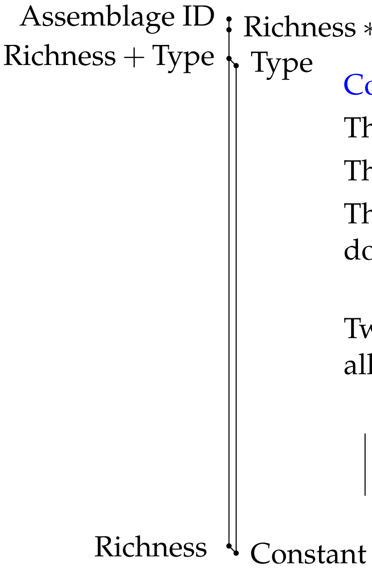

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Two experiments, with two responses each, all led to similar conclusions.

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Similarly, they find the scaled Hasse diagram
easier to understand than the anova table.

A new experiment on a different ecosystem (7 types)

Assemblage identity			Richness Level
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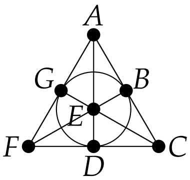

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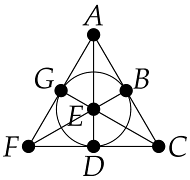

Another success: *Advances in Ecological Research* published this picture of the Fano plane.

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- To estimate the parameters (response per individual for each type) for the model Type?
  - If so, we should not include any polycultures.

How should we choose which subsets to include?

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For a given level k of richness,
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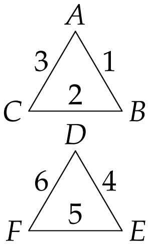
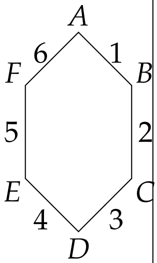
- adopt some other strategy?

6 subsets of size 2, from 6 types

design		
		
		

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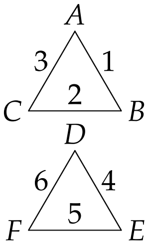		
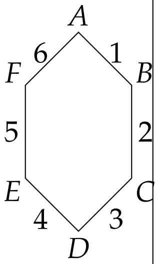		

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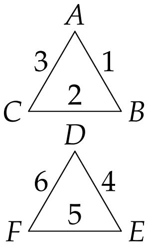
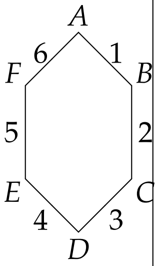
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$	
		

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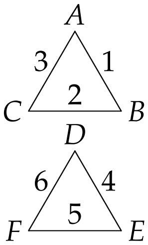
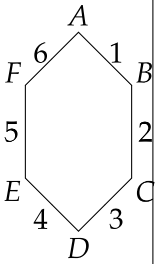
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_B) = \frac{4\sigma^2}{3}$	
		

6 subsets of size 2, from 6 types

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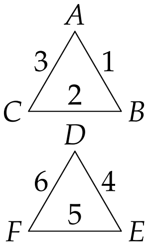
<tr><td>
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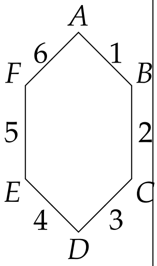
<tr><td>
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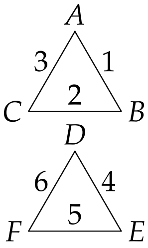
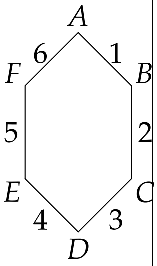
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_B) = \dfrac{4\sigma^2}{3}$ $\tau_A - \tau_D$ is not estimable	
		

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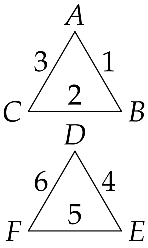
<tr><td>
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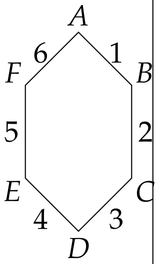
<tr><td>
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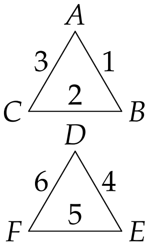
<tr><td></td><td>$$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$$
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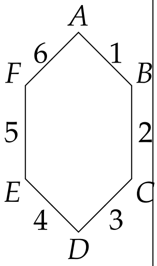
<tr><td></td><td></td><td></td></tr>
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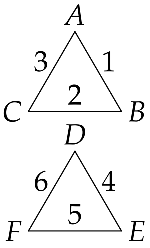
<tr><td>
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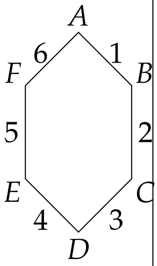
<tr><td>
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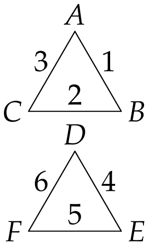
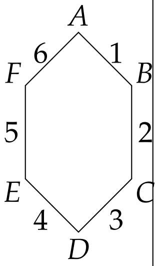
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_B) = \frac{4\sigma^2}{3}$ $\tau_A - \tau_D$ is not estimable	$\mathbb{E}(Y_1) = n(\beta_A + \beta_B)$ $\hat{\beta}_A = \frac{Y_1 + Y_3 - Y_2}{2n}$ $\mathrm{Var}(\hat{\beta}_A) = \frac{3\sigma^2}{4n^2}$ $\sum_i \mathrm{Var}(\hat{\beta}_i)$ is minimized
		

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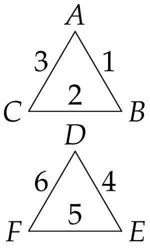
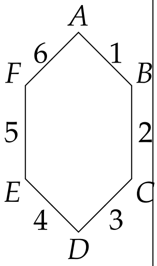
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_B) = \frac{4\sigma^2}{3}$ $\tau_A - \tau_D$ is not estimable	$\mathbb{E}(Y_1) = n(\beta_A + \beta_B)$ $\hat{\beta}_A = \frac{Y_1 + Y_3 - Y_2}{2n}$ $\mathrm{Var}(\hat{\beta}_A) = \frac{3\sigma^2}{4n^2}$ $\sum_i \mathrm{Var}(\hat{\beta}_i)$ is minimized
	$\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_D) = 3\sigma^2$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_C) = \frac{8\sigma^2}{3}$ $\mathrm{Var}(\hat{\tau}_A - \hat{\tau}_B) = \frac{5\sigma^2}{3}$	

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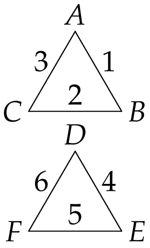
<td></td>
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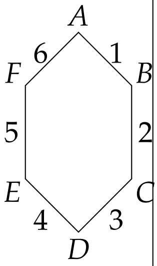
<td></td>
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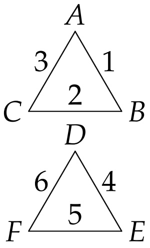
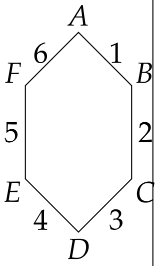
	$\mathbb{E}(Y_{1A}) = \tau_A + \delta_1$ $\mathrm{Var}(\hat\tau_A - \hat\tau_B) = \frac{4\sigma^2}{3}$ $\tau_A - \tau_D$ is not estimable	$\mathbb{E}(Y_1) = n(\beta_A + \beta_B)$ $\hat\beta_A = \frac{Y_1 + Y_3 - Y_2}{2n}$ $\mathrm{Var}(\hat\beta_A) = \frac{3\sigma^2}{4n^2}$ $\sum_i \mathrm{Var}(\hat\beta_i)$ is minimized
	$\mathrm{Var}(\hat\tau_A - \hat\tau_D) = 3\sigma^2$ $\mathrm{Var}(\hat\tau_A - \hat\tau_C) = \frac{8\sigma^2}{3}$ $\mathrm{Var}(\hat\tau_A - \hat\tau_B) = \frac{5\sigma^2}{3}$ $\sum_{i \neq j} \mathrm{Var}(\hat\tau_i - \hat\tau_j)$ is minimized	β_A is not estimable

A non-intuitive result

Consider incomplete-block designs for t treatments in b blocks of size k.

Usual model	expected response on any unit with treatment i in block B is $\tau_i + \delta_B$
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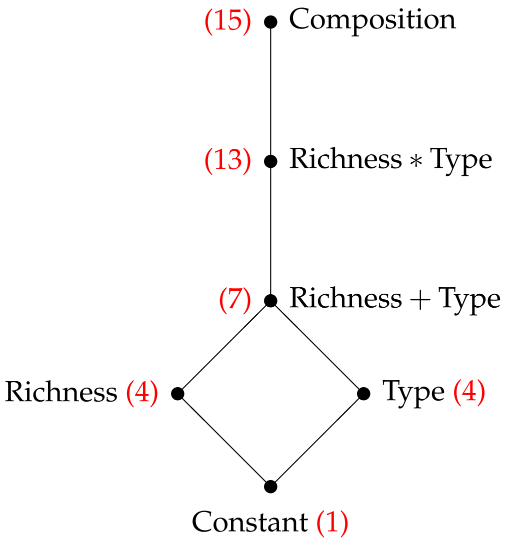
If there is no balanced incomplete-block design for t treatments in b blocks of size k then a design which is best for one situation may be worst for the other.

One aspect of a third biodiversity experiment: 4 types of "shrimp"

	Composition		Richness	$x1$	$x2$	$x3$	$x4$
1	A	12 of type A	1	12	0	0	0
2	B	12 of type B	1	0	12	0	0
3	C	12 of type C	1	0	0	12	0
4	D	12 of type D	1	0	0	0	12
5	AB	6 of A, 6 of B	2	6	6	0	0
6	AC	6 of A, 6 of C	2	6	0	6	0
7	AD	6 of A, 6 of D	2	6	0	0	6
8	BC	6 of B, 6 of C	2	0	6	6	0
9	BD	6 of B, 6 of D	2	0	6	0	6
10	CD	6 of C, 6 of D	2	0	0	6	6
11	ABC	4 of A, 4 of B, 4 of C	3	4	4	4	0
12	ABD	4 of A, 4 of B, 4 of D	3	4	4	0	4
13	ACD	4 of A, 4 of C, 4 of D	3	4	0	4	4
14	BCD	4 of B, 4 of C, 4 of D	3	0	4	4	4
15	$ABCD$	3 each of A, B, C and D	4	3	3	3	3

Family of expectation models (so far)



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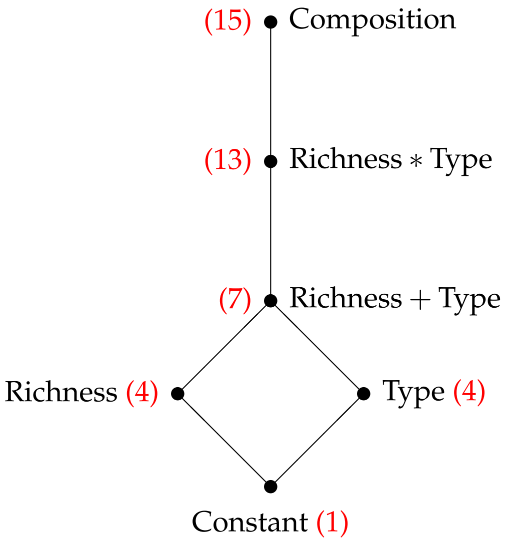

Five responses were measured. For every response, the sum of squares of fitted values for Composition was hardly any bigger than the sum of squares of fitted values for the model Richness ∗ Type, so we decided to omit Richness ∗ Type.

Other details of the third experiment

Each of the 15 compositions was combined with three temperatures: 5^o C, 10^o C and 15^oC.

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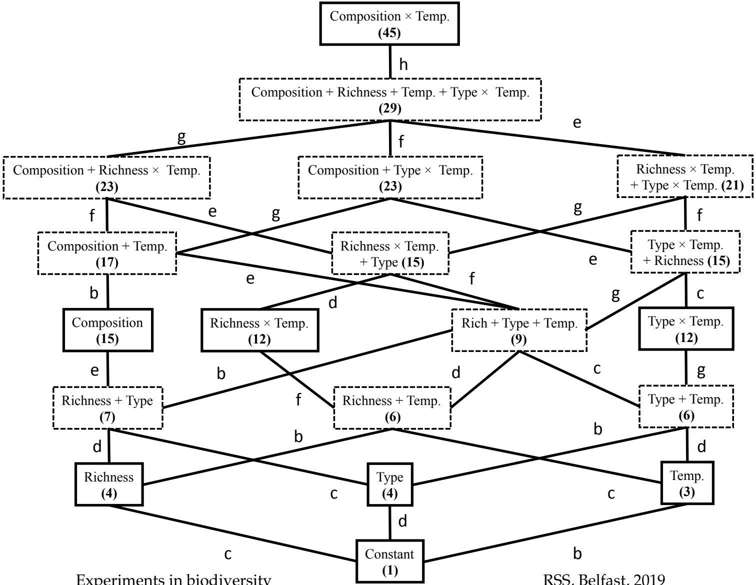
Three temperature-controlled rooms in a lab were used.
Each room had a single temperature and two of each composition.
Therefore there was no appropriate residual mean square to compare the main effect of Temperature with, but all other effects could be assessed.

Diagram from a paper in *Global Change Biology*



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Note that this is a simple consequence of the model

$$\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4$$

if the rankings of β_1, β_2, β_3 and β_4 are different over the five types of response.

One aspect of a fourth biodiversity experiment

A, B, C— types of freshwater "shrimp".
Put 12 shrimps in a jar with stream water and alder leaf litter.
Measure how much leaf litter is eaten after 28 days.

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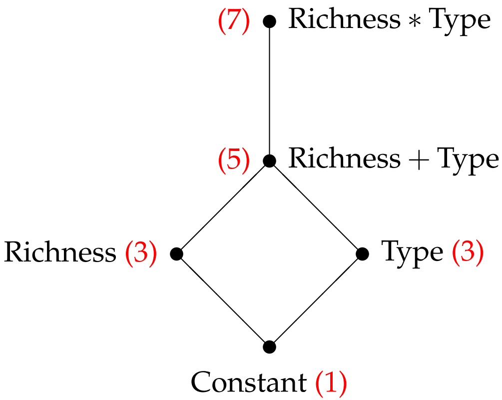

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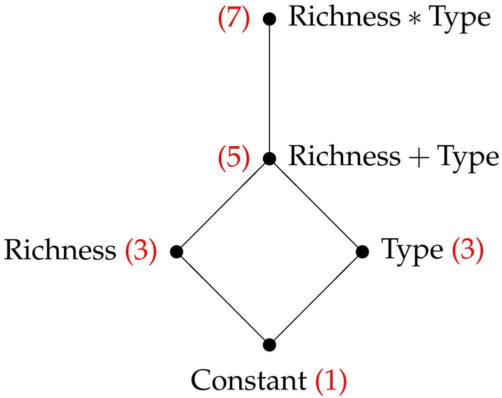

For these numbers, Assemblage identity = Richness ∗ Type.

The other aspect of the biodiversity experiment

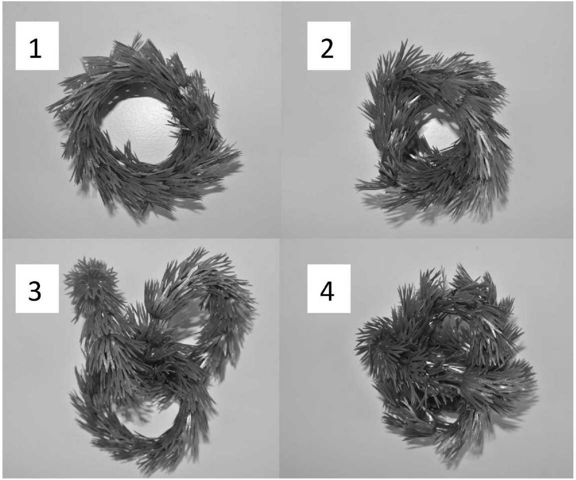

Fig 1. Photographs of the structures used to create habitat complexity in microcosms with 'structure present'. The basic unit of each structure was a plastic plant strip (mimicking *Ceratophyllum* spp.), joined up as a ring (~ 8cm in diameter) and four levels of fractal dimension were created with them: 1) level 1 consisted of two rings aligned, with a fractal dimension (D) of 1.77; 2) level 2 consisted of two rings twisted into each other (D = 1.80); 3) level 3 consisted of three rings locked together (D = 1.81) and 4) level four was a ball made from 3 rings together (D = 1.83). This design therefore also gave two levels of 'amount of structure' - 3 g for complexity level 1 and 2 and 4.5 g for complexity level 3 and 4.

Hasse diagram for enviromental model subspaces

(5) Fractal dimension (how twiddly were the extra bits?)

(3) Number of plastic rings (0 or 2 or 3)

(2) Plastic rings or not

(1) Constant

The experiment: 3 blocks, each with 35 jars

Environment Complexity	Assemblage identity						
	A	*B*	*C*	*AB*	*AC*	*BC*	*ABC*
0	×	×	×	×	×	×	×
1	×	×	×	×	×	×	×
2	×	×	×	×	×	×	×
3	×	×	×	×	×	×	×
4	×	×	×	×	×	×	×

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Environment Complexity	Assemblage identity						
	A	B	C	AB	AC	BC	ABC
0	×	×	×	×	×	×	×
1	×	×	×	×	×	×	×
2	×	×	×	×	×	×	×
3	×	×	×	×	×	×	×
4	×	×	×	×	×	×	×

Spanish PhD student Lorea Flores visited the University of Roehampton for three months;
gathered the “shrimps” from ponds on the campus;
put the combinations of leaves, shrimps and plastic rings into jars;
put one jar of each type onto each of three shelves in a temperature-controlled room;
measured various responses on each jar (some daily, some at the end).

Models and data analysis

The models consist of all interactions and sums of those shown in the two previous diagrams
(the gentle reader can draw her own Hasse diagram!).

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Solution! Summer student Justin Thong dug into the statistical software R to find a short sequence of commands that gives precisely the right output
(not straightforward, because R makes some stupid assumptions).

Hooray!

PLOS | ONE

RESEARCH ARTICLE

Habitat Complexity in Aquatic Microcosms Affects Processes Driven by Detritivores

Lorea Flores[1]*, R. A. Bailey[2,3], Arturo Elosegi[4], Aitor Larrañaga[4], Julia Reiss[5]*

1 INRA, UMR 1224, Ecologie Comportementale et Biologie des Populations de Poissons, Aquapôle, quartier Ibarron, 64310 Saint-Pée sur Nivelle, France, **2** School of Mathematical Sciences, Queen Mary University of London, London E1 4 NS, United Kingdom, **3** School of Mathematics and Statistics, University of St Andrews, St Andrews, Fife, KY16 9SS, United Kingdom, **4** Laboratory of Stream Ecology, Dept. of Plant Biology and Ecology, Fac. of Science and Technology, University of the Basque Country, UPV/EHU PO Box 644; 48080 Bilbao, Spain, **5** Department of Life Sciences, Whitelands College, University of Roehampton, London SW15 4JD, United Kingdom

* lorea.flores@st-pee.inra.fr (LF); julia.reiss@roehampton.ac.uk (JR)

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click for updates

Abstract

So what affected the three measured responses?

Individual species numbers;
Plastic rings or not;
Number of plastic rings.

Nothing more complicated, so
not Richness,
not Fractal dimension,
no interactions.