Design and Analysis of Biodiversity Experiments

R. A. Bailey
University of St Andrews

Network Analysis Methods in Statistical Ecology
University of St Andrews, 4 June 2024

Outline

Network = Graph

Outline

Network = Graph

A Hasse diagram is a special kind of graph
(do not worry if you have not seen these before).

Outline

Network = Graph

A Hasse diagram is a special kind of graph
(do not worry if you have not seen these before).

A Hasse diagram can be used to show a family of expectation models
(this is useful if your collaborators do not like equations).

Outline

Network = Graph

A Hasse diagram is a special kind of graph
(do not worry if you have not seen these before).

A Hasse diagram can be used to show a family of expectation models
(this is useful if your collaborators do not like equations).

Then a scaled version of the Hasse diagram can be used to summarize the relevant ANOVA
(this is useful if your collaborators jump straight to P-values).

Biodiversity experiments

When my ecology colleagues and I started, this seemed 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

A, B, C, D, E, F — six types of freshwater "shrimp".

Put 12 shrimps in a jar containing stream water and alder leaf litter.

Measure how much leaf litter is eaten after 28 days.

A more carefully controlled experiment

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

Experimental unit = jar.

A more carefully controlled experiment

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

Experimental unit = jar.

Assemblage identity			Richness Level
A, ..., F	monoculture	12 of type A	1
AB, ..., EF	duoculture	6 of A, 6 of B	2
ABC, ..., DEF	triculture	4 of A, 4 of B, 4 of C	3

A more carefully controlled experiment

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

Experimental unit = jar.

	Assemblage identity			Richness Level
6	A, . . . , F	monoculture	12 of type A	1
15	AB, . . . , EF	duoculture	6 of A, 6 of B	2
20	ABC, . . . , DEF	triculture	4 of A, 4 of B, 4 of C	3
41				

A more carefully controlled experiment

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

Experimental unit = jar.

	Assemblage identity			Richness Level
6	A, ..., F	monoculture	12 of type A	1
15	AB, ..., EF	duoculture	6 of A, 6 of B	2
20	ABC, ..., DEF	triculture	4 of A, 4 of B, 4 of C	3
41				

The experiment was carried out in 4 blocks of 41 jars.

A more carefully controlled experiment

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

Experimental unit = jar.

	Assemblage identity			Richness Level
6	A, ..., F	monoculture	12 of type A	1
15	AB, ..., EF	duoculture	6 of A, 6 of B	2
20	ABC, ..., DEF	triculture	4 of A, 4 of B, 4 of C	3
41				

The experiment was carried out in 4 blocks of 41 jars.
Actually 42 jars, because untreated jars were included, but their data were so obviously different that they were excluded from further modelling.

Initial model fitting

A biologist fitted the model 'Richness' with 3 parameters,
one for each level of richness,
and found no evidence of any differences between the levels.

Initial model fitting

A biologist fitted the model ‘Richness’ with 3 parameters,
one for each level of richness,
and found no evidence of any differences between the levels.

This model for the response Y is

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

Initial model fitting

A biologist fitted the model 'Richness' with 3 parameters,
one for each level of richness,
and found no evidence of any differences between the levels.

This model for the response Y is

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

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
⋮			⋮						
41	DEF	4 of D, 4 of E, 4 of F	3	0	0	0	4	4	4

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
⋮			⋮						
41	DEF	4 of D, 4 of E, 4 of F	3	0	0	0	4	4	4

I suggested the model ‘Type’ with 6 parameters $\beta_1, \ldots, \beta_6$:

$$\mathbb{E}(Y) = \sum_{i=1}^{6} \beta_i x_i$$

($\sum x_i = 12$ always, so no need for intercept.)

Showing the family of models on a Hasse diagram

Suppose that the number of observational units is N.
Then the expectation part of any linear model is the subspace W of $\mathbb{R}^N$ consisting of all possible vectors of fitted values.

Showing the family of models on a Hasse diagram

Suppose that the number of observational units is N.
Then the expectation part of any linear model is the subspace W of $\mathbb{R}^N$ consisting of all possible vectors of fitted values.

In the Hasse diagram, put a dot for each expectation subspace.
Put its name and dimension beside it.

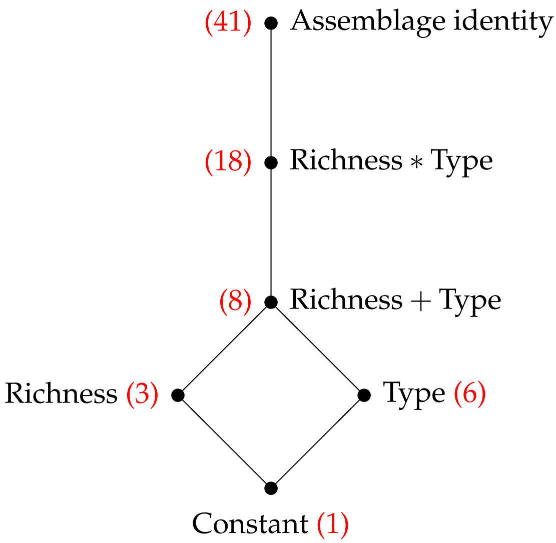
Showing the family of models on a Hasse diagram

Suppose that the number of observational units is N.
Then the expectation part of any linear model is the subspace W of $\mathbb{R}^N$ consisting of all possible vectors of fitted values.

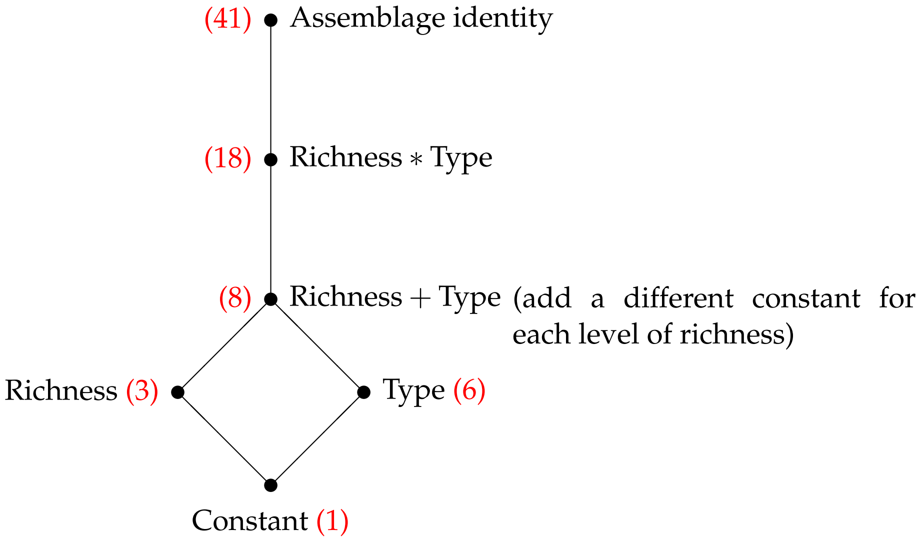
In the Hasse diagram, put a dot for each expectation subspace.
Put its name and dimension beside it.

If W_1 is a subspace of W_2, then
put the dot for W_1 lower in the diagram than the dot for W_2,
and join W_1 to W_2 by a sequence of upwards lines
(which may be a single direct line, or may go through other dots).

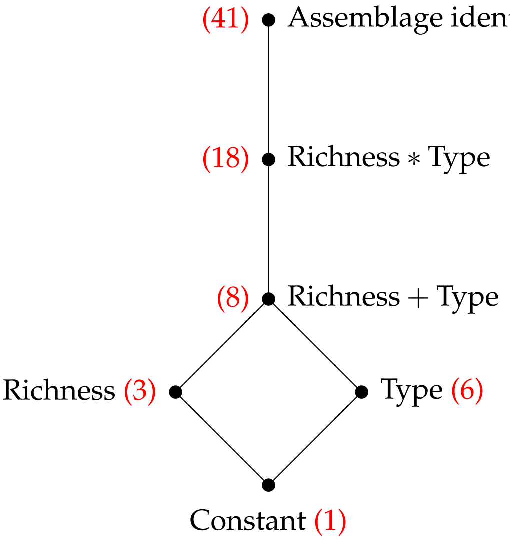
Family of expectation models (subspaces)



Family of expectation models (subspaces)



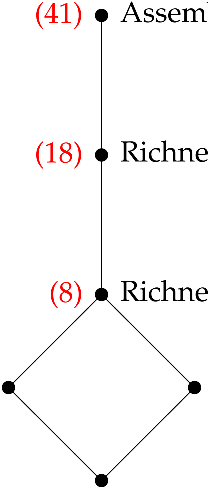
Family of expectation models (subspaces)



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

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

Family of expectation models (subspaces)



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

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

Success: an ecology journal published

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

Scaled Hasse diagram

Once the data have been obtained, make the ANOVA table.

Scaled Hasse diagram

Once the data have been obtained, make the ANOVA table.

Each line in this corresponds to
a difference between two expectation models.

Scaled Hasse diagram

Once the data have been obtained, make the ANOVA table.

Each line in this corresponds to
a difference between two expectation models.

Scale the edges of the Hasse diagram so that the length of each edge is proportional to the corresponding mean square.

Scaled Hasse diagram

Once the data have been obtained, make the ANOVA table.

Each line in this corresponds to
a difference between two expectation models.

Scale the edges of the Hasse diagram so that the length of each edge is proportional to the corresponding mean square.

To give a visual comparison with the error mean square,
show this on a line using the same scale.

Scaled Hasse diagram

Once the data have been obtained, make the ANOVA table.

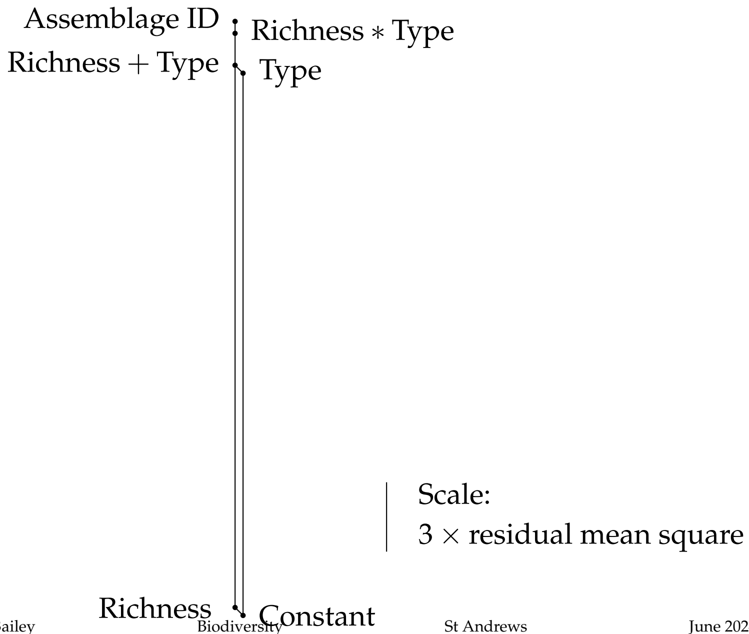
Each line in this corresponds to
a difference between two expectation models.

Scale the edges of the Hasse diagram so that the length of each edge is proportional to the corresponding mean square.

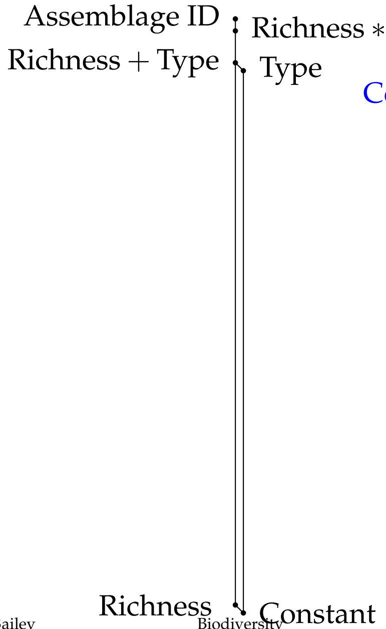
To give a visual comparison with the error mean square, show this on a line using the same scale.

If there is more than one relevant mean square
(as in a split-plot design)
use different types of lines (straight, dashed, dotted, …) which match the type of line used for the relevant error mean square.

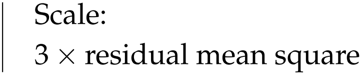
What the data showed: mean squares



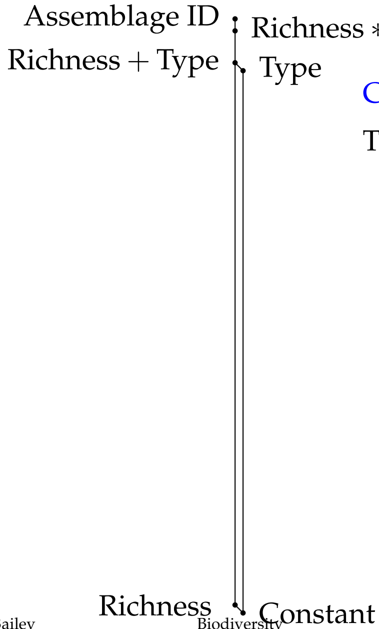
What the data showed: mean squares



Conclusions:



What the data showed: mean squares

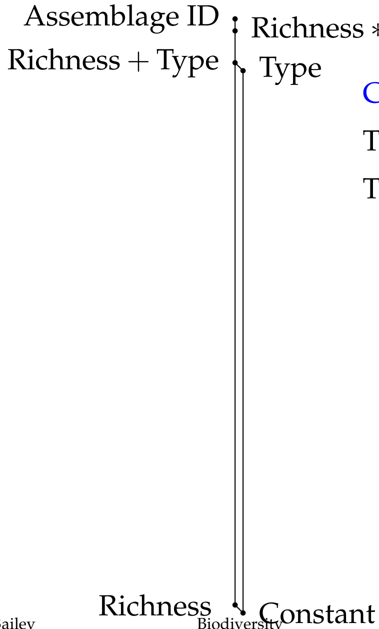


Conclusions:

The model Richness does not explain the data.

Scale:
3 × residual mean square

What the data showed: mean squares



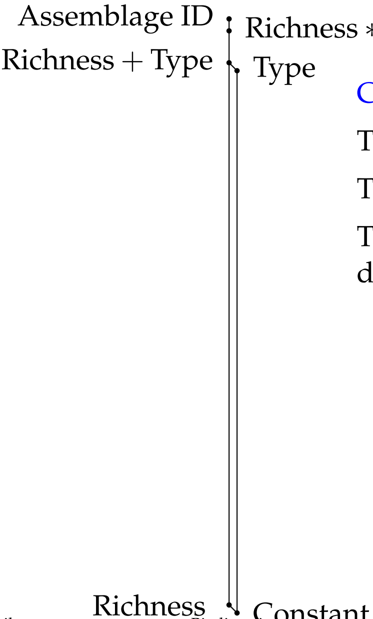
Conclusions:

The model Richness does not explain the data.

The model Type explains the data well.

Scale:
$3 \times$ residual mean square

What the data showed: mean squares



Conclusions:

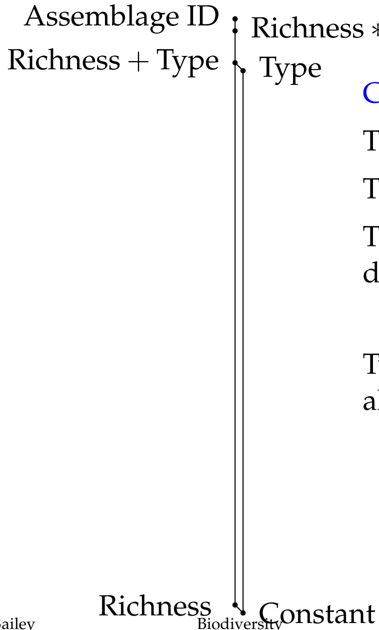
The model Richness does not explain the data.

The model Type explains the data well.

There is no evidence that any larger model does any better.

Scale:
3 × residual mean square

What the data showed: mean squares



Conclusions:

The model Richness does not explain the data.

The model Type explains the data well.

There is no evidence that any larger model does any better.

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

Scale:
$3 \times$ residual mean square

A new experiment on a different ecosystem (7 types)

Assemblage identity			Richness Level
A, ..., G	monoculture	12 of type A	1
AB, ..., FG	duoculture	6 of A, 6 of B	2
ABC, ..., EFG	triculture	4 of A, 4 of B, 4 of C	3

A new experiment on a different ecosystem (7 types)

	Assemblage identity			Richness Level
7	A, . . . , G	monoculture	12 of type A	1
21	AB, . . . , FG	duoculture	6 of A, 6 of B	2
35	ABC, . . . , EFG	triculture	4 of A, 4 of B, 4 of C	3
63				

A new experiment on a different ecosystem (7 types)

	Assemblage identity			Richness Level
7	A, . . . , G	monoculture	12 of type A	1
21	AB, . . . , FG	duoculture	6 of A, 6 of B	2
35	ABC, . . . , EFG	triculture	4 of A, 4 of B, 4 of C	3
63				

"Do I really need all 35 tricultures?"

A new experiment on a different ecosystem (7 types)

	Assemblage identity			Richness Level
7	A, . . . , G	monoculture	12 of type A	1
21	AB, . . . , FG	duoculture	6 of A, 6 of B	2
35	ABC, . . . , EFG	triculture	4 of A, 4 of B, 4 of C	3
63				

"Do I really need all 35 tricultures?"

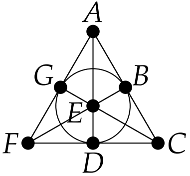
"Use 7 tricultures making a balanced incomplete-block design."

A new experiment on a different ecosystem (7 types)

	Assemblage identity			Richness Level
7	A, . . . , G	monoculture	12 of type A	1
21	AB, . . . , FG	duoculture	6 of A, 6 of B	2
35	ABC, . . . , EFG	triculture	4 of A, 4 of B, 4 of C	3
63				

"Do I really need all 35 tricultures?"

"Use 7 tricultures making a balanced incomplete-block design."

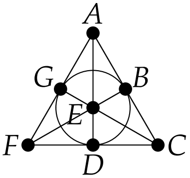


A new experiment on a different ecosystem (7 types)

	Assemblage identity			Richness Level
7	A, ..., G	monoculture	12 of type A	1
21	AB, ..., FG	duoculture	6 of A, 6 of B	2
35	ABC, ..., EFG	triculture	4 of A, 4 of B, 4 of C	3
63				

"Do I really need all 35 tricultures?"

"Use 7 tricultures making a balanced incomplete-block design."



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

One aspect of a third biodiversity experiment

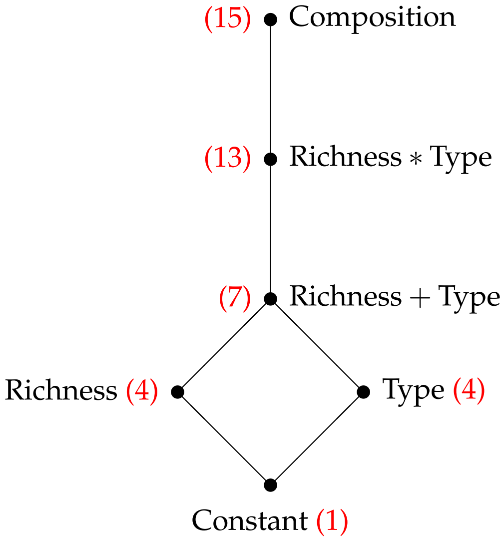
A, B, C, D—types of freshwater "shrimp".

One aspect of a third biodiversity experiment

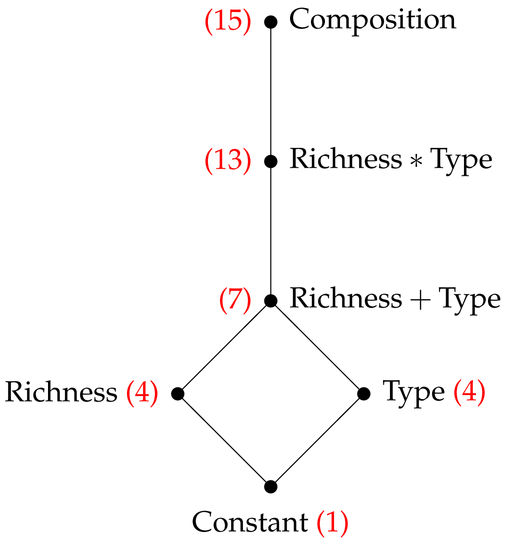
A, B, C, D—types of freshwater "shrimp".

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)

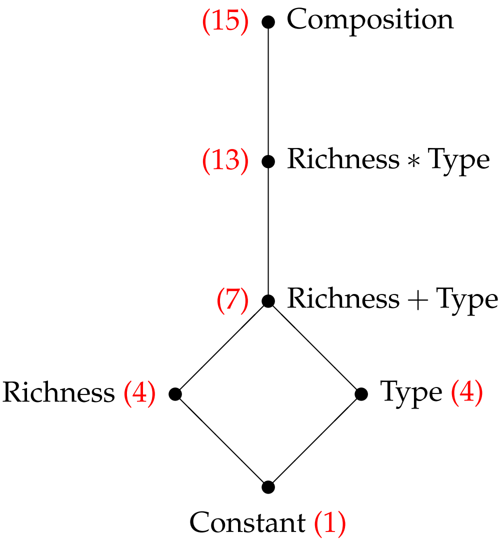


Family of expectation models (so far)



Because there is only one possible combination of 4 types, the dimension of Richness ∗ Type is $3 \times 4 + 1$.

Family of expectation models (so far)



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.

Because there is only one possible combination of 4 types, the dimension of Richness ∗ Type is $3 \times 4 + 1$.

Other details of the third experiment

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

Other details of the third experiment

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

Each of the 45 combinations was replicated twice.

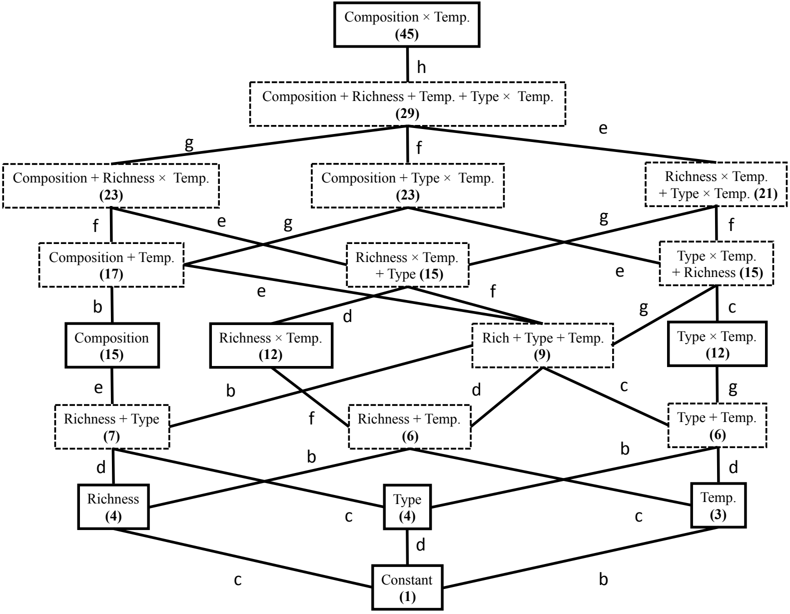
Other details of the third experiment

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

Each of the 45 combinations was replicated twice.

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*



Brief results from the third biodiversity experiment

For each single type of response,
Type $*$ Temperature explained the data well,
with no need for further terms.

Brief results from the third biodiversity experiment

For each single type of response,
Type $*$ Temperature explained the data well,
with no need for further terms.

For multifunctionality, for each of the five types of response,
the mean of the three best outcomes was calculated.

Brief results from the third biodiversity experiment

For each single type of response,
Type $*$ Temperature explained the data well,
with no need for further terms.

For multifunctionality, for each of the five types of response,
the mean of the three best outcomes was calculated.
For each of the 45 treatment combinations,
we recorded the number of types of response on which the mean outcome exceeded 25% of this “best score”.
On this measure, compositions with high levels of Richness scored well.

Brief results from the third biodiversity experiment

For each single type of response,
Type $*$ Temperature explained the data well,
with no need for further terms.

For multifunctionality, for each of the five types of response,
the mean of the three best outcomes was calculated.
For each of the 45 treatment combinations,
we recorded the number of types of response on which the mean outcome exceeded 25% of this "best score".
On this measure, compositions with high levels of Richness scored well.

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.

Some references

- Julia Reiss, R. A. Bailey, Fernanda Cássio, Guy Woodward and Cláudia Pascoal: Assessing the contribution of micro-organisms and macrofauna to biodiversity-ecosystem functioning relationships in freshwater microcosms.
  Advances in Ecological Research **43** (2010), 151–176.
- Julia Reiss, R. A. Bailey, Daniel M. Perkins, Angela Pluchinotta and Guy Woodward: Testing effects of consumer richness, evenness and body size on ecosystem functioning.
  Journal of Animal Ecology **80** (2011), 1145–1154.
- R. A. Bailey and Julia Reiss: Design and analysis of experiments testing for biodiversity effects in ecology.
  Journal of Statistical Planning and Inference, **144** (2014), 69–80.

Some more references

- Daniel M. Perkins, R. A. Bailey, Matteo Dossena, Lars Gamfeldt, Julia Reiss, Mark Trimmer and Guy Woodward: Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. *Global Change Biology*, **21** (2015), 396–406.
- R. A. Bailey: Hasse diagrams as a visual aid for linear models and analysis of variance. *Communications in Statistics: Theory and Methods*, **50** (2021), 5034–5067.