Design and analysis of experiments testing for diversity in ecology



Joint work with Julia Reiss, University of Roehampton

3rd International Conference on Design of Experiments, Memphis, USA, May 2011 It is now widely believed that biological diversity is good for the environment. One way that ecologists test this is to place random collections of species in mini-environments and then measure some outcome. I have been working with a group of fresh-water ecologists to improve this in two ways. The first is that our subsets of species are carefully chosen, not random. The second is that we fit a nested family of plausible models. Our results suggest that the underlying model is not diversity at all. This seems to be the received wisdom.

Treatments:random sets of speciesMeasured response Y:some eco-desirable outcomeConclusion:the greater the number of different species,<br/>the better the outcome.

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Experimental unit = jar.

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RichnessTreatmentLevelA, ..., Fmonoculture12 of type A1AB, ..., EFduoculture6 of A, 6 of B2ABC, ..., DEFtriculture4 of A, 4 of B, 4 of C3

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				Richness
	Treatment			Level
6	$A, \ldots, F$	monoculture	12 of type A	1
15	$AB, \ldots, EF$	duoculture	6 of A, 6 of B	2
20	$ABC, \ldots, DEF$	triculture	4 of A, 4 of B, 4 of C	3
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The experiment was carried out in 4 blocks of 41 jars.

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The biologist fitted the model 'Richness' with 3 parameters, one for each level of richness,

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I suggested the model 'Type' with 6 parameters  $\alpha_A, \ldots, \alpha_F$ :



In other words, if there are  $x_i$  shrimps of type *i* then

$$\mathbb{E}(Y) = \sum_{i=1}^{6} a_i x_i \qquad \text{where } 12a_i = \alpha_i$$

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

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Treatment Richness \* Type Type Scale:  $3 \times$  residual mean square Richness <ロト</p>
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Treatment Fichnes	s * Type
Richness + Type	Conclusions: The model Richness does not explain the data. The model Type explains the data well.
	Scale:
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Richness + Type	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.
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Treatment	Richness	s * Type
Richness + Type	▶ Type	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 × residual mean square
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			Richness
Treatment			Level
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	Treatment			Level
7	A,, G	monoculture	12 of type A	1
21	$AB, \ldots, FG$	duoculture	6 of A, 6 of B	2
35	ABC,, EFG	triculture	4 of A, 4 of B, 4 of C	3

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	Treatment			Level
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"Do I really need all 35 tricultures?"

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

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Another achievement: an ecology journal published a picture of the Fano plane.

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- To discriminate between the (incomparable) models Richness and Type?

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- To discriminate between the (incomparable) models Richness and Type?
- ► To discriminate between the model Type and the more general model which allows the response of each type to depend on what other types are present?

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- To discriminate between the model Type and the more general model which allows the response of each type to depend on what other types are present?
- To estimate the parameters (response per individual for each type) for the model Type?
  - If so, we should not include any polycultures.

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Suppose that there are *t* types in all.

For a given level *k* of richness,

each treatment consists of equal numbers of each type in some subset of *k* types.

Suppose that we can include *b* such treatments.

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Should we

- choose subsets at random (traditional for ecologists)?
- choose the subsets that would be best for an incomplete-block design with the usual linear model (e.g. the Fano plane)?
- adopt some other strategy?





design	usual model 12 responses	
$C \frac{3 1}{D} B$ $C \frac{3}{2} B$ $C \frac{3}{2} B$ $C \frac{3}{2} B$	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	
$ \begin{array}{c}                                     $		・ロト (四ト (ミト ミン ミンののの) 11/13

design	usual model 12 responses	
$C \xrightarrow{\begin{array}{c} A \\ 3 \\ 2 \\ D \\ \end{array}}^{A} B$	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$ $\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{3}$	
$\frac{6 4}{5 E}$		
$\begin{array}{c c} F & 6 & 1 \\ F & 5 & 2 \\ \end{array}$		
E $4$ $3$ $C$ $D$ $C$		
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design	usual model	
	12 responses	
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{3}$	
$\frac{6}{5}$ 4 E $E$	$\alpha_A - \alpha_D$ is not estimable	
$F \stackrel{A}{\frown} B$		
5 2		
$E \xrightarrow{4} 3 C$		
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design	usual model	duoculture
	12 responses	6 responses
A $3 \land 1$	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{3}$	
$\frac{6}{5}$ 4 E $E$	$\alpha_A - \alpha_D$ is not estimable	
$F \stackrel{6}{\frown} 1 B$		
5 2		
E 4 3 C		
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design	usual model	duoculture
	12 responses	6 responses
A $3 \land 1$	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{3}$	
$\frac{6}{5} \frac{4}{E}$	$\alpha_A - \alpha_D$ is not estimable	
$F \stackrel{6}{\frown} 1 B$		
5 2		
$E \xrightarrow{4} 3 C$		
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A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{3}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$
$\frac{6}{5}$ $E$	$\alpha_A - \alpha_D$ is not estimable	
$F \stackrel{6}{\frown} 1 B$		
5 2		
$E \xrightarrow{4} 3 C$		
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	12 responses	6 responses
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \xrightarrow{2} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{2}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$
$6 \wedge 4$	3	$\operatorname{Var}(\alpha_A) = 3\sigma^2$
$F \xrightarrow{5} E$	$\alpha_A - \alpha_D$ is not estimable	
$\stackrel{A}{}$		
$F \stackrel{6}{\frown} 1 B$		
5 2		
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	12 responses	6 responses
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \xrightarrow{2} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{2}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$
$\stackrel{D}{\wedge}$	$(a_1(a_A a_B) 3$	$\operatorname{Var}(\hat{\alpha}_A) = 3\sigma^2$
$E \xrightarrow{6} 4$	$\alpha_A - \alpha_D$ is not estimable	$\sum_{i} \operatorname{Var}(\hat{\alpha}_{i}) \text{ is minimized}$
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$F \stackrel{6}{\frown} 1 B$		
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	12 responses	6 responses
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{lpha}_{A}-\hat{lpha}_{B})=rac{4\sigma^{2}}{2}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$
D	3	$\operatorname{Var}(\alpha_A) = 3\sigma^2$
$F \xrightarrow{6} 5 \\ E$	$\alpha_A - \alpha_D$ is not estimable	$\sum_{i} \operatorname{Var}(\hat{\alpha}_{i}) \text{ is minimized}$
A	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_D) = 3\sigma^2$	
	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_C) = \frac{8\sigma^2}{3}$	
$\begin{bmatrix} 5\\ E \end{bmatrix} \begin{bmatrix} 2\\ C \end{bmatrix}$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{5\sigma^2}{2}$	
$E \xrightarrow{4} 3$	3	
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design	usual model	duoculture
	12 responses	6 responses
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \xrightarrow{\frac{3}{2}} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{\sigma^2}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$
$\stackrel{D}{\wedge}$	$(\alpha_A \circ \alpha_B) = 3$	$\operatorname{Var}(\hat{\alpha}_A) = 3\sigma^2$
$F \xrightarrow{6} 5 \\ E$	$\alpha_A - \alpha_D$ is not estimable	$\sum_{i} \operatorname{Var}(\hat{\alpha}_{i}) \text{ is minimized}$
A	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_D) = 3\sigma^2$	
F	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_C) = \frac{8\sigma^2}{2}$	
5 2	$5\sigma^2$	
E	$\operatorname{Var}(\alpha_A - \alpha_B) = -\frac{1}{3}$	
$\overset{4}{D}$	$\sum_{i \in \mathcal{A}} \operatorname{Var}(\hat{\alpha}_i - \hat{\alpha}_j) \text{ is minimized}$	
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design	usual model	duoculture
	12 responses	6 responses
A	$\mathbb{E}(Y_{1A}) = \alpha_A + \beta_B$	$\mathbb{E}(Y_1) = \frac{\alpha_A + \alpha_B}{2}$
$C \frac{2}{D} B$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{4\sigma^2}{2}$	$\hat{\alpha}_A = Y_1 + Y_3 - Y_2$ $V_{\text{or}}(\hat{\alpha}_L) = 2\sigma^2$
$\epsilon \wedge \epsilon$	3	$\operatorname{var}(\alpha_A) = 50^{-1}$
$F \xrightarrow{6} 5 \xrightarrow{4} E$	$\alpha_A - \alpha_D$ is not estimable	$\sum_{i} \operatorname{Var}(\hat{\alpha}_{i}) \text{ is minimized}$
A	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_D) = 3\sigma^2$	
F $B$ $C$ $B$ $C$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_C) = \frac{8\sigma^2}{3}$	$\alpha_{\rm L}$ is not estimable
E $C$	$\operatorname{Var}(\hat{\alpha}_A - \hat{\alpha}_B) = \frac{5\sigma^2}{3}$	0 <sub>A</sub> is not estimatic
$4 \bigvee 3$	$\sum_{i,j} \operatorname{Var}(\hat{\alpha}_i - \hat{\alpha}_j) \text{ is minimized}$	
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Consider incomplete-block designs for t treatments in b blocks of size k.

Usual model	expected response on any unit with treatment <i>i</i> in block <i>B</i> is $\alpha_i + \beta_B$
Polyculture model	expected response on any unit whose treatment is an equal mixture of the species in subset <i>B</i> is $\sum_{i \in B} \alpha_i / k$

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Usual model expected response on any unit with treatment *i* in block *B* is  $\alpha_i + \beta_B$ 

Polyculture model expected response on any unit whose treatment is an equal mixture of the species in subset *B* is  $\sum_{i \in B} \alpha_i / k$ 

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.

- 1. 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.
- 2. 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*, 2011, in press.