

Application of mixed models & multivariate hypothesis testing to repeated measures of tropical tree assemblages from a BACI experiment

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Overview

- A. Diversity of **sources of variation** in community trajectories of degraded tropical forests
- B. Statistical **applications to account for variability** (spatial & temporal)
 - (1) **Univariate mixed models** (~ type of fit)
 - of total plot measures
 - of subsets of species with similar responses
 - (2) **Multivariate hypothesis testing**



Mature complex tropical forest
dynamics (100s tree species/ha)
... large permanent plots helped

BUT: NONE in *Mha* degraded
regrowth!

Potential sources of variation

(e.g. ecosystem engineers)

~ meter- versus km-scales

Spatial – intrinsic:
Soil/microsites

Spatial – extrinsic:

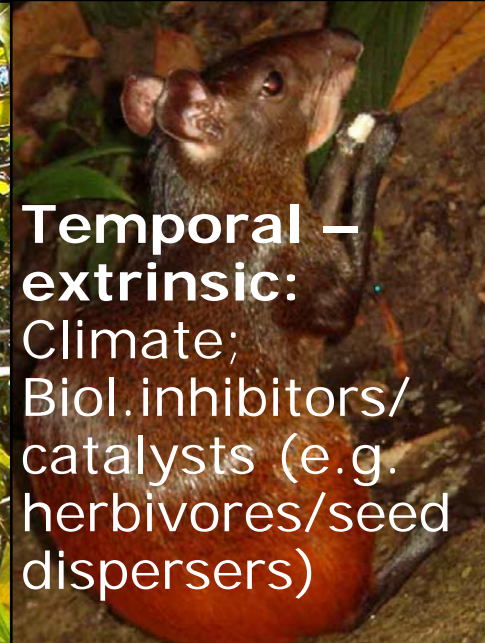
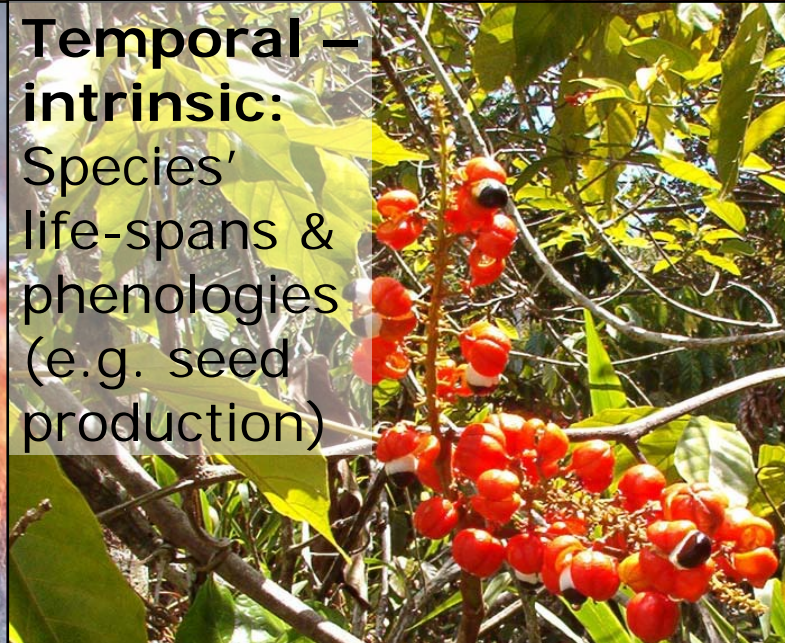
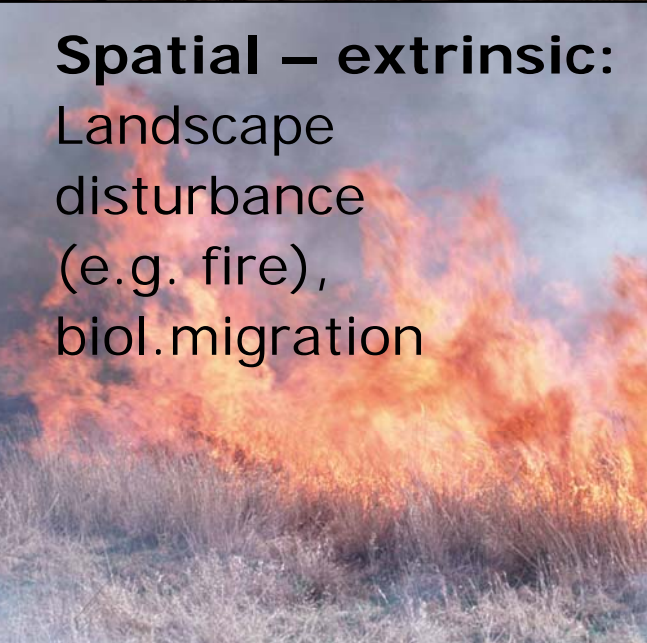
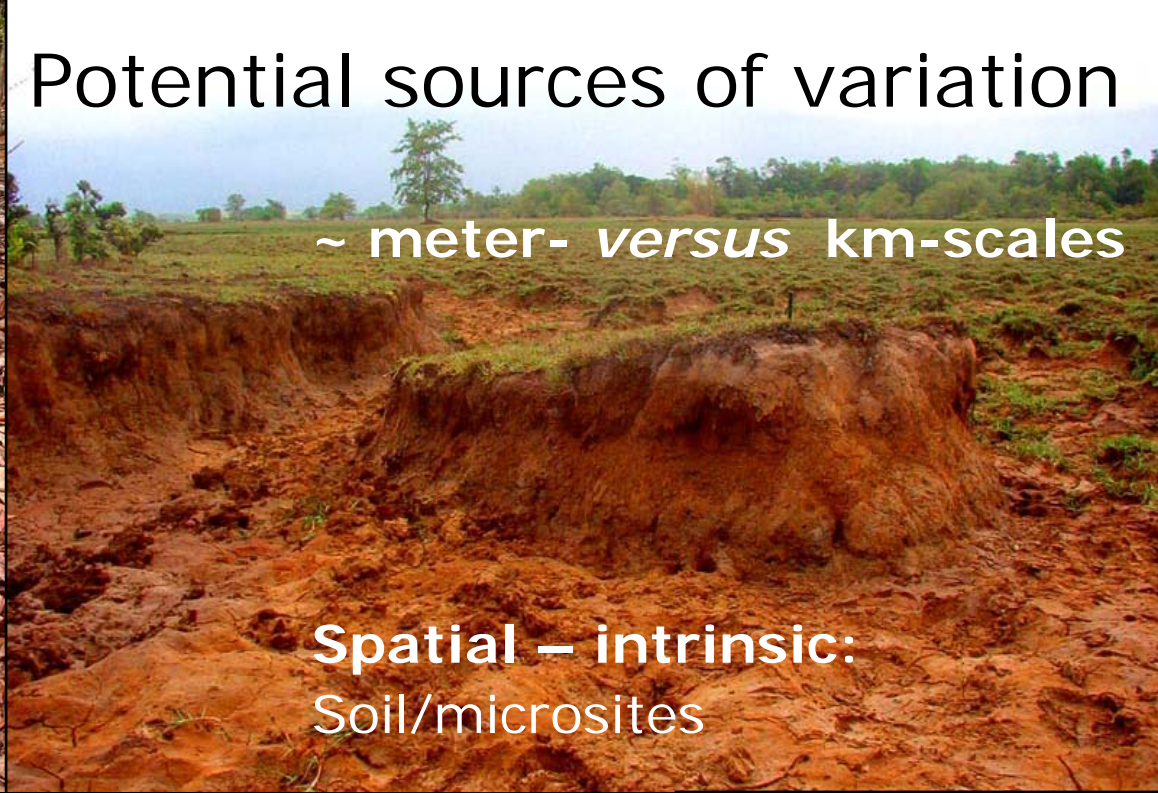
Landscape disturbance
(e.g. fire),
biol.migration

Temporal – intrinsic:

Species' life-spans & phenologies
(e.g. seed production)

Temporal – extrinsic:

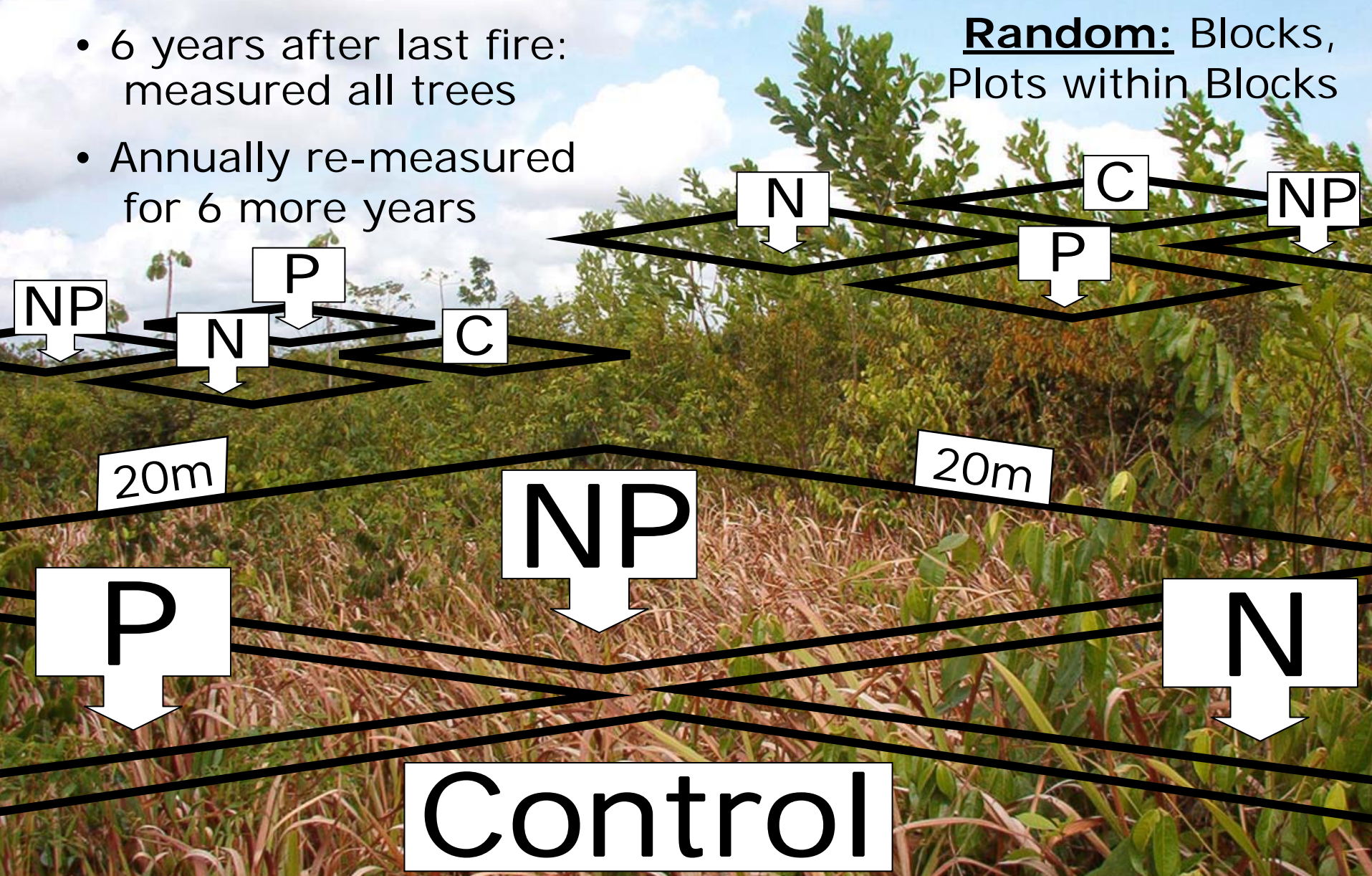
Climate;
Biol.inhibitors/
catalysts (e.g.
herbivores/seed
dispersers)



Aim: How can we detect experimental effects despite high background variability?

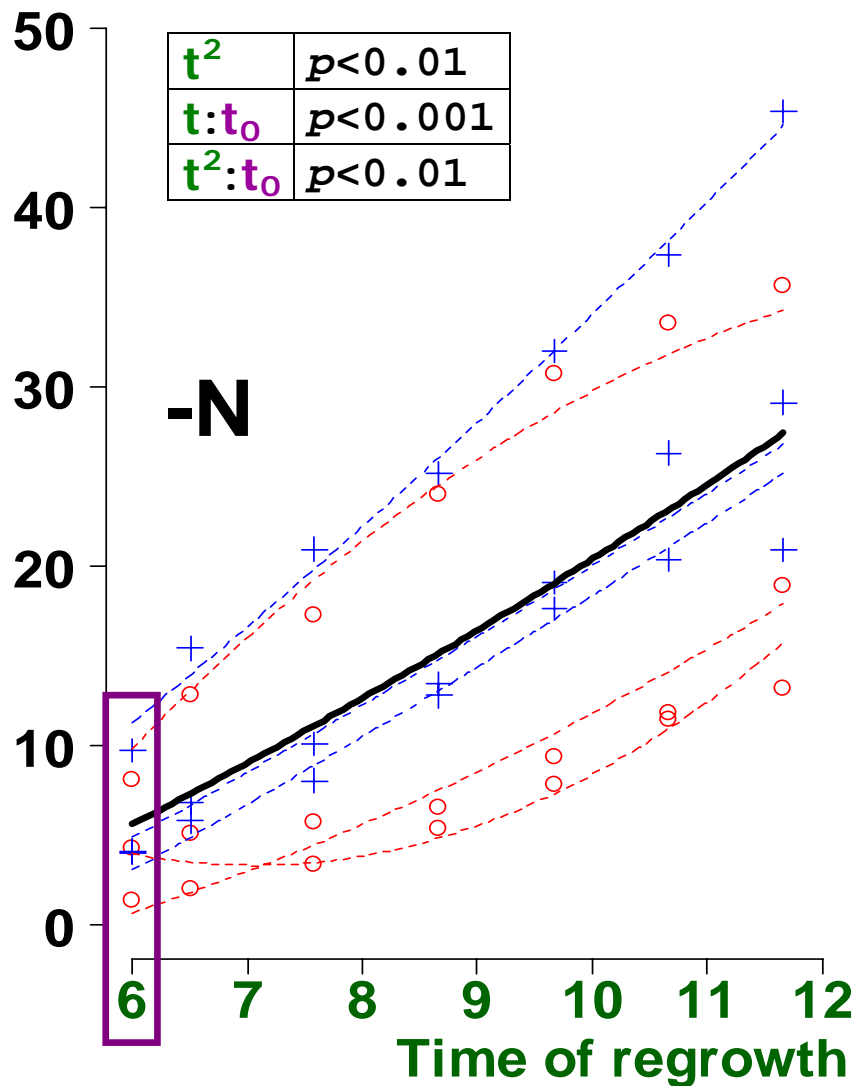
- 6 years after last fire: measured all trees
- Annually re-measured for 6 more years

Random: Blocks, Plots within Blocks

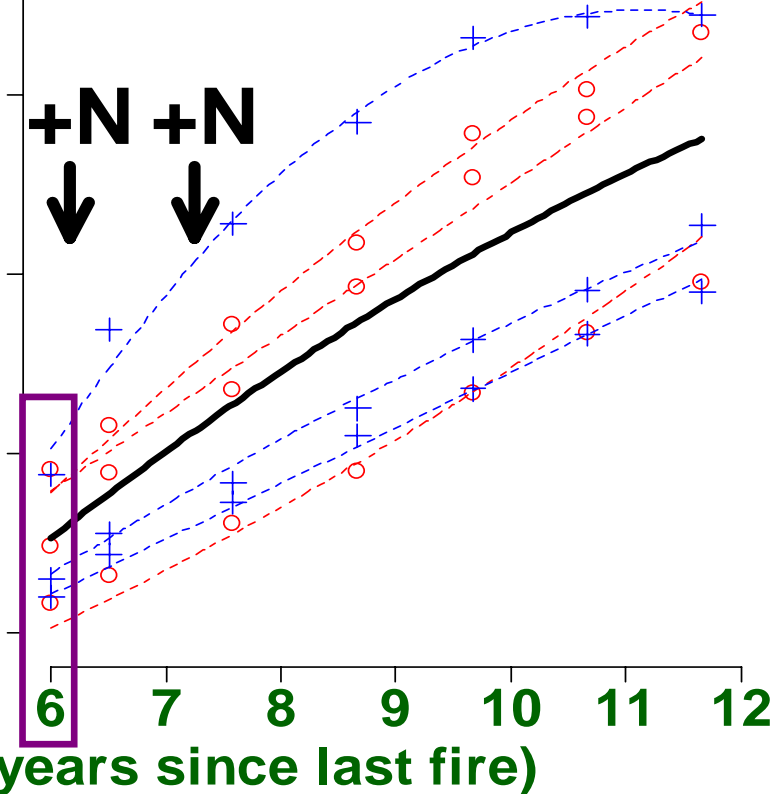


2nd order polynomial fit (REML; Random: Blocks, Plots within Blocks)

Total woody biomass of all tree species (Mg/ha)



+N:t	$p < 0.05$
+P:t	$p < 0.05$
+P:t:t ₀	$p < 0.05$
+P:t ² :t ₀	$p < 0.05$
+N:+P:t:t ₀	$p < 0.05$
+N:+P:t ² :t ₀	$p < 0.05$



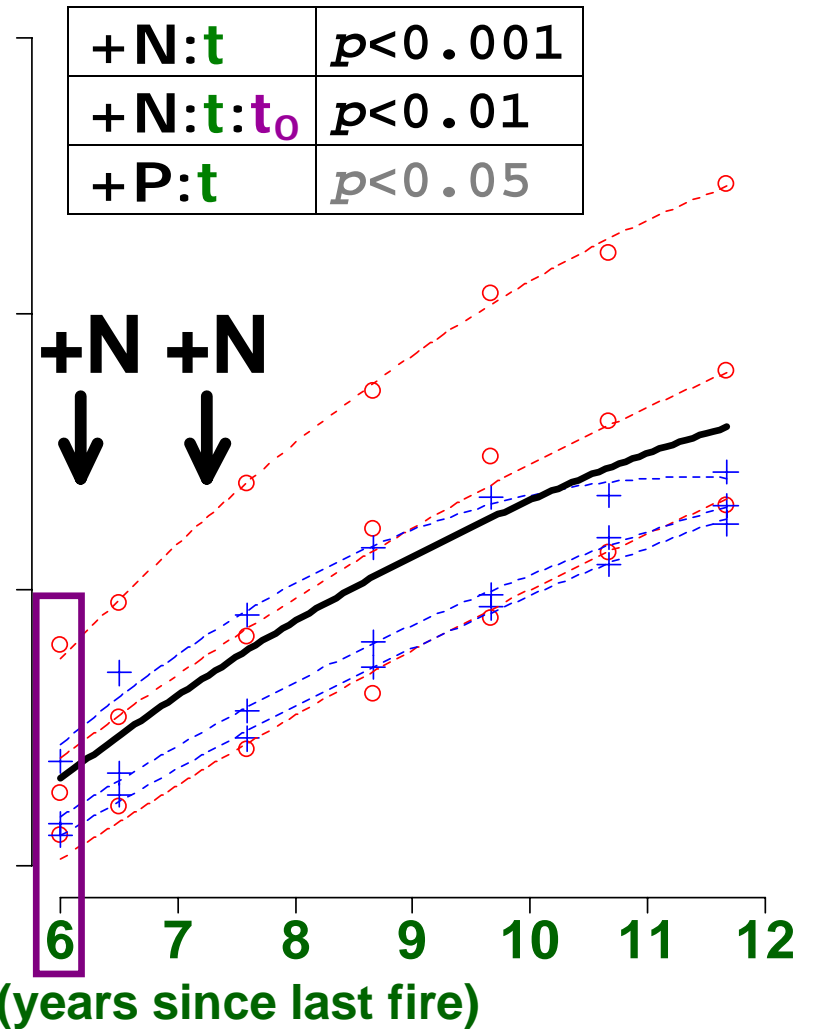
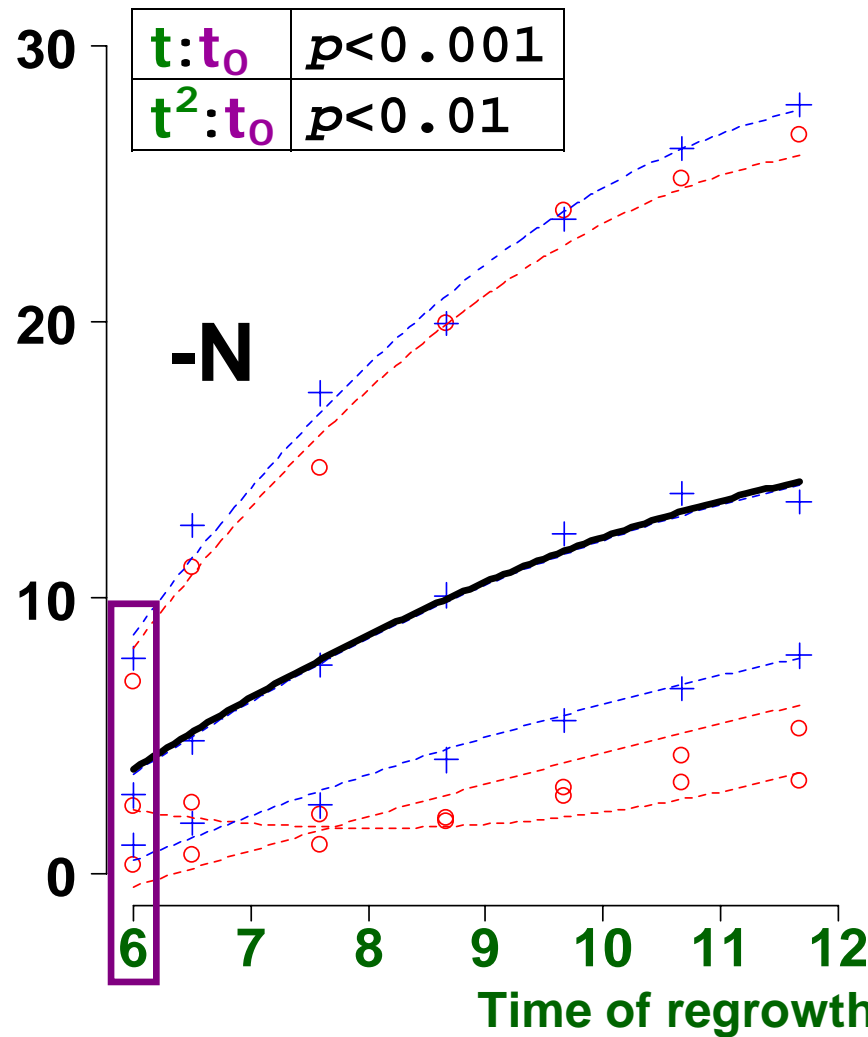
Measured Plots (3 Blocks each):	o -P	--- Individual Plot BLUPs
	+ +P	— Fixed Effects BLUPs (-P/+P pooled)

Nutrient effects on individual species

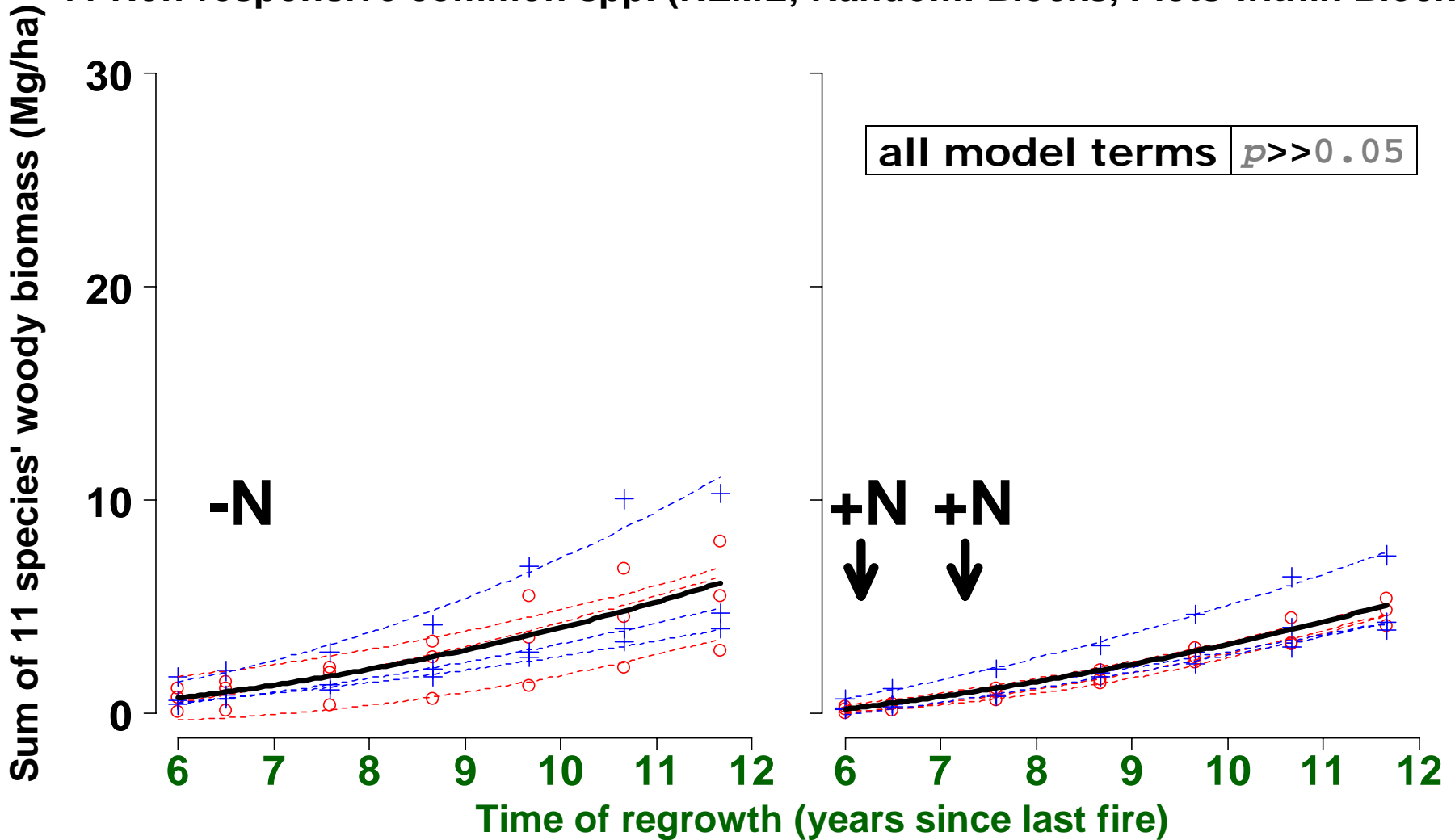
1. Select **common tree** species:
 - ✓ ≥ 9 individuals
 - ✓ persisting for ≥ 4 censuses
 - ✓ spread across ≥ 3 treatments
2. Fit **mixed model for individual species**
3. **Pool species** with significant responses to **same model terms**
4. Pool all other common species:
 - (a) **no significant treatment effects** with
 - (b) **no successful fit** (viol.assumptions)
5. **Re-fit mixed model** for these “functional groups” of species

2 N-responsive common spp. (REML; Random: Blocks, Plots within Blocks)

Rollinia+Banara woody biomass (Mg/ha)

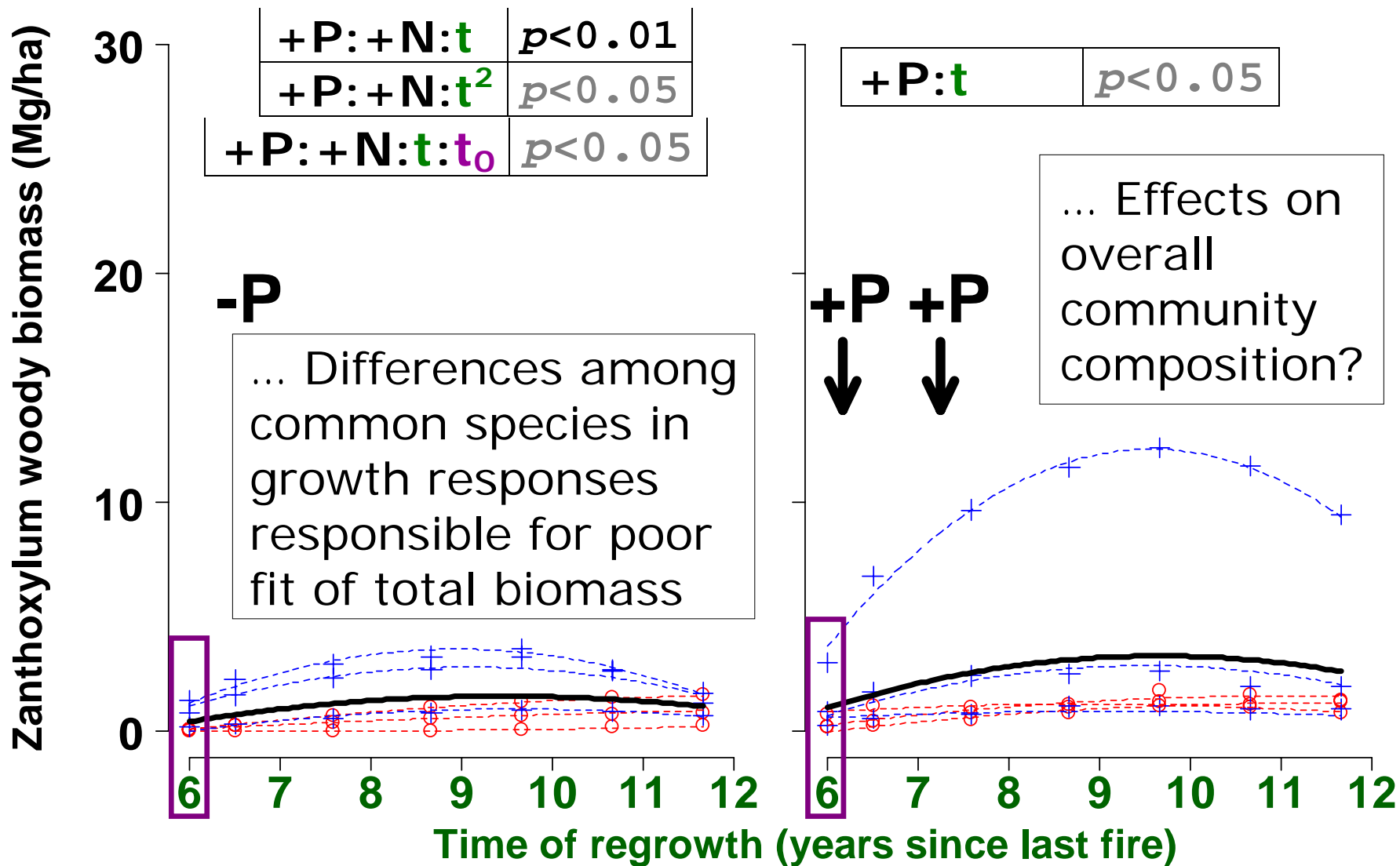


11 Non-responsive common spp. (REML; Random: Blocks, Plots within Blocks)



Measured Plots	○ -P	--- Individual Plot BLUPs
(3 Blocks each):	+ +P	— Fixed Effects BLUPs (-P/+P pooled)

1 P-responsive common sp (REML; Random: Blocks, Plots within Blocks)



Measured Plots (3 Blocks each):	o -N	--- Individual Plot BLUPs
	+ +N	— Fixed Effects BLUPs (-N/+N pooled)

Ecologically meaningful community dissimilarity

1. Zero-inflated data, mostly rare spp

X Metric ordination of raw data

Orlóci 1978 *Multivar. anal. in vegtn. research.* Junk

Faith et al. 1987 *Vegetatio* 69:57

2. Autocorrelated repeated measures

X Rank-based ordinations

✓ **Hellinger-standardization**

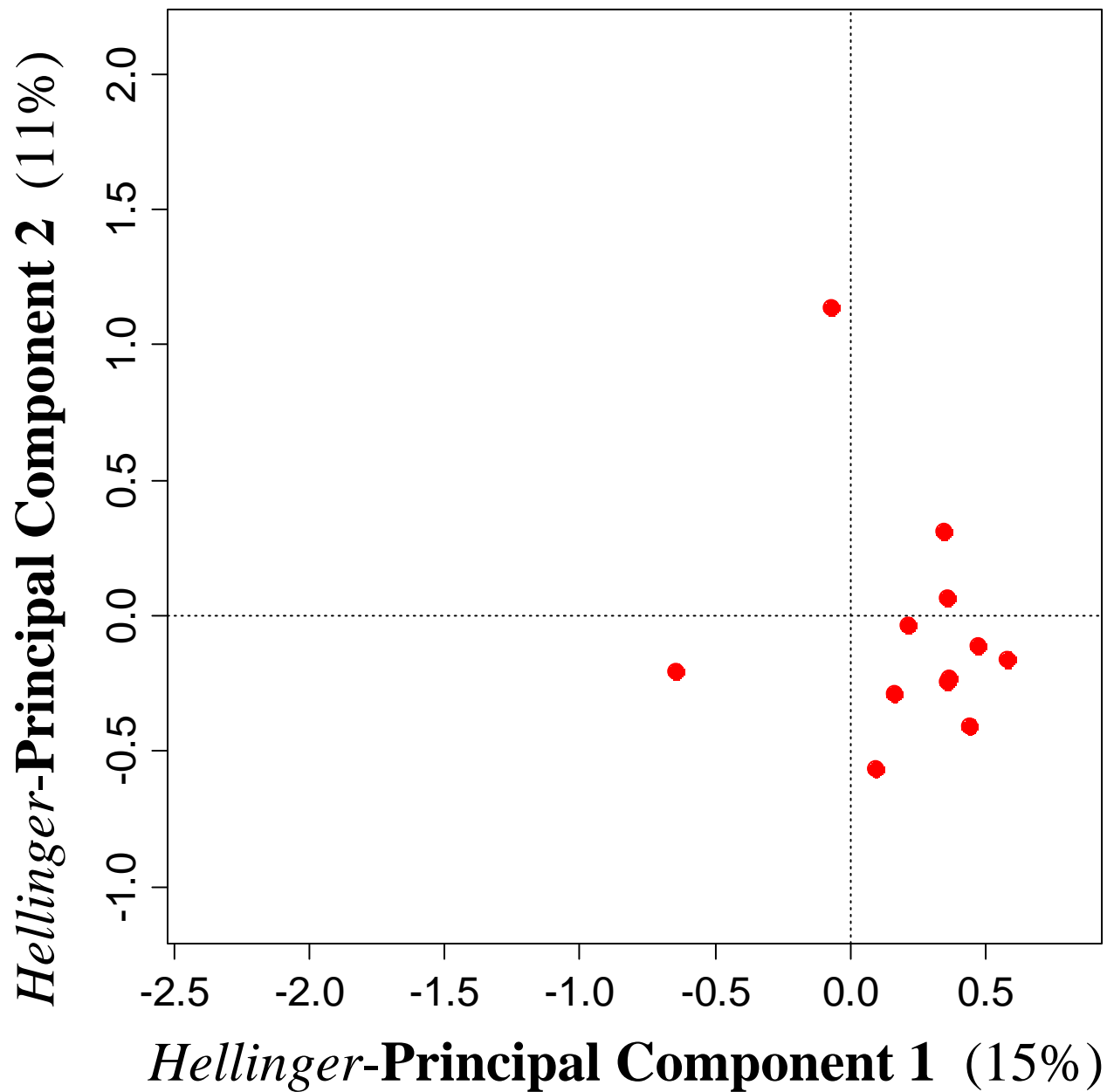
⇒ display changes in species woody biomass composition in fully Euclidian space (e.g. PCA, RDA):

$$y'_{ij} = \sqrt{\frac{y_{ij}}{y_{i+}}} \quad \begin{array}{l} y_{ij} = \text{sp } j \\ y_{i+} = \text{sum for all spp} \end{array}$$

Legendre & Gallagher 2001 *Oecologia* 129:271

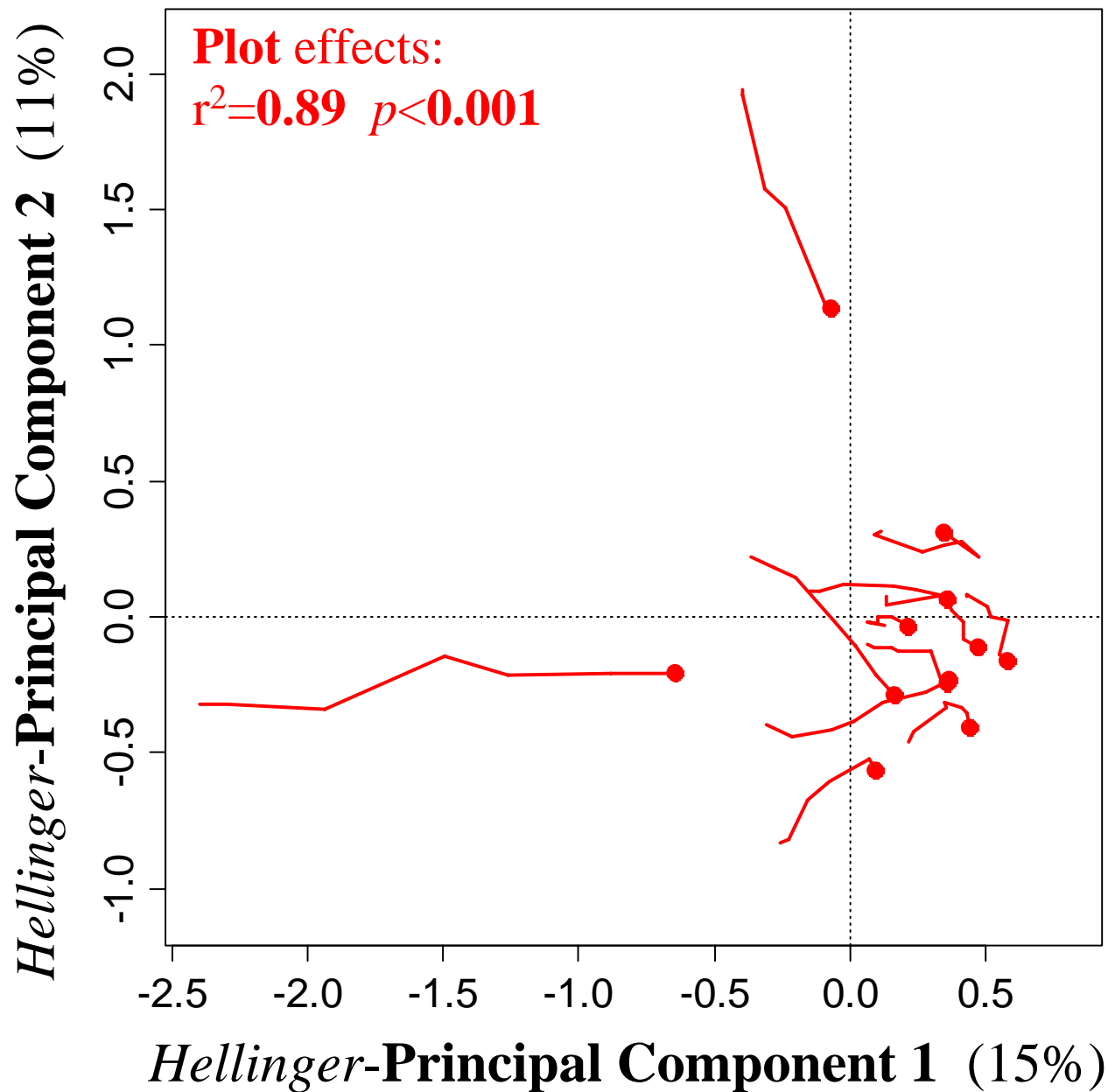
		Species' biomass					
Time of regrowth	Plot 1	0	0	0	0	0	0
		0	0	0	0	0	0
		0	0.04	0	0	0	0
		0	0.07	0	0	0	0
		0	0.08	0.04	0	0	0
		0	0.12	0.07	0	0	0
	Plot 2	0	0.13	0.09	0	0	0
		0	0	0	0	0.07	0
		0	0.03	0	0	0.08	0
		0	0.16	0	0.04	0.13	0
		0	0.28	0	0.06	0.19	0
		0	0.51	0	0.08	0.27	0
Plot 3	0	0.52	0.05	0.11	0.35	0	
	0	0.60	0.06	0.12	0.40	0	
	0	0	0	0	0.03	0	
	0	0	0	0	0	0	
	0	0.04	0	0	0	0	
	0	0.08	0	0	0	0	
		0	0	0	0		
		0.13	0	0	0		
		0	0	0	0		
		0	0.15	0.05	0	0.17	
		0	0.19	0.06	0	0.22	

Unconstrained Ordination:



• Plots at 1st census

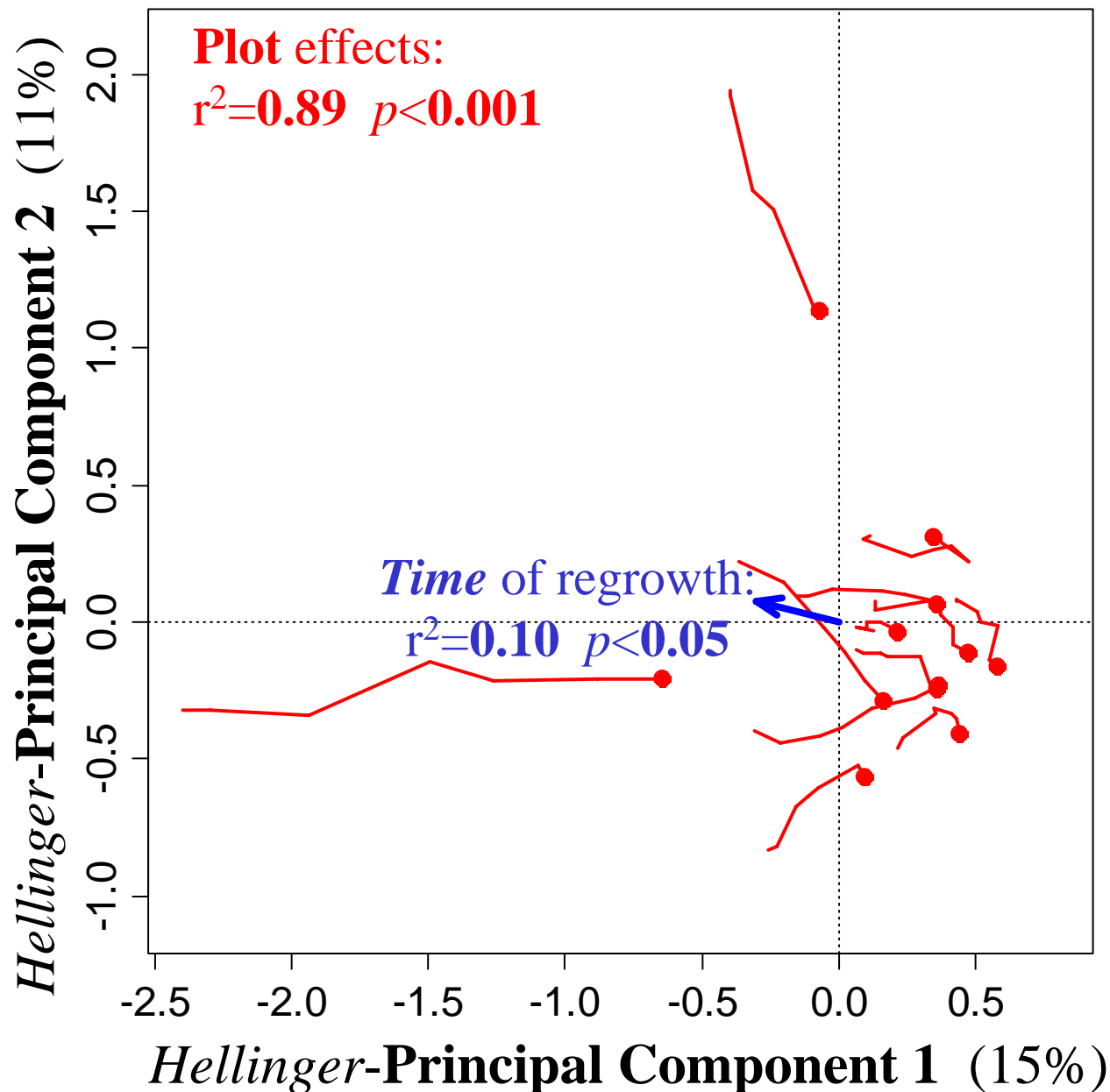
Unconstrained Ordination:



- Plots at 1st census
- Trajectory over subsequent 6 years

[All p-values based on permutations]

Unconstrained Ordination: Primarily Plot Effects

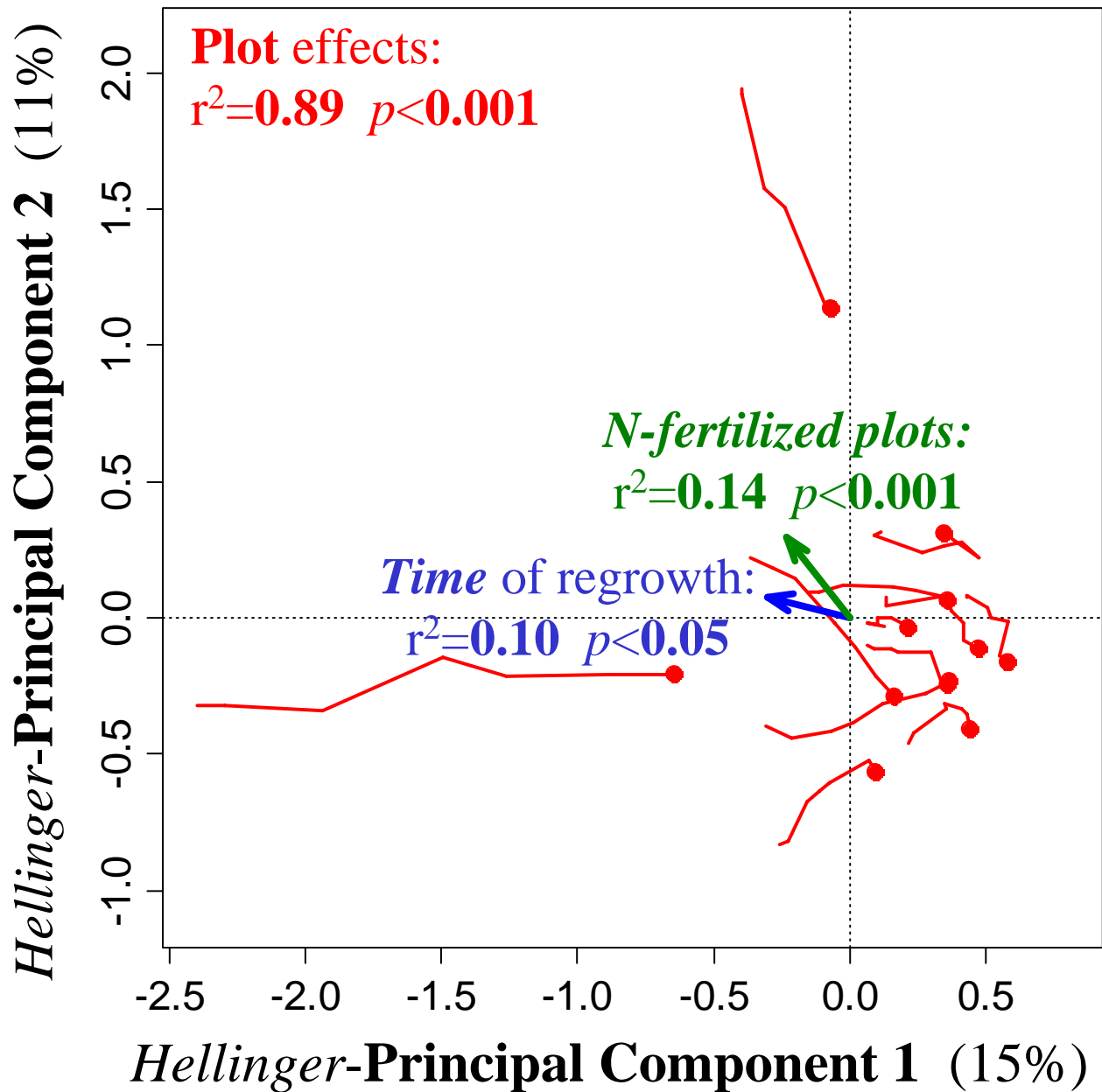


- Plots at 1st census
- Trajectory over subsequent 6 years

Superimposed experimental vectors (without constraining ordination):
→ *Time*

[All p-values based on permutations]

Unconstrained Ordination: Primarily Plot Effects



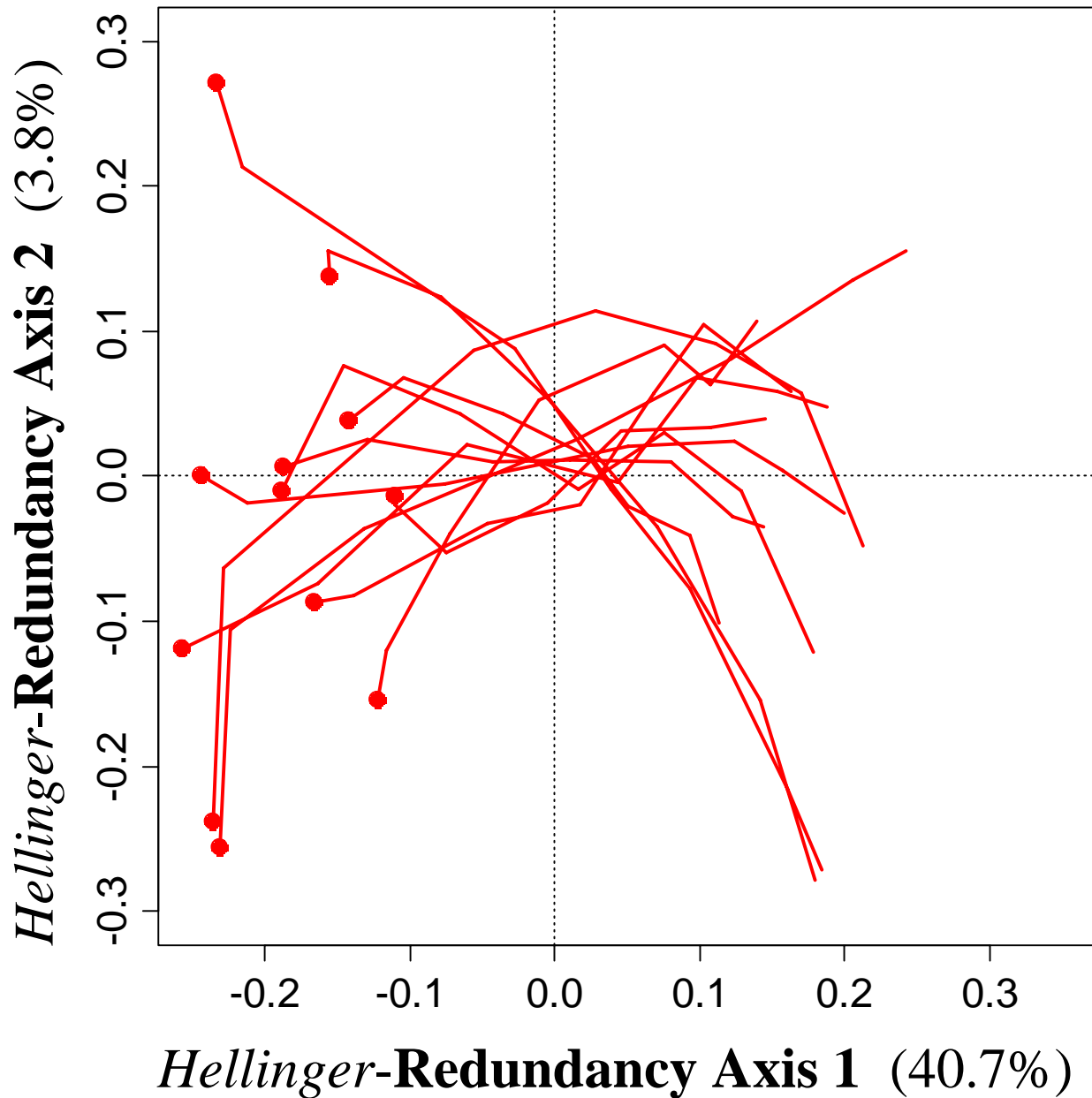
- Plots at 1st census
- Trajectory over subsequent 6 years

Superimposed experimental vectors (without constraining ordination):

- *Time*
- *N-fertilized plots (excl. 1st census)*

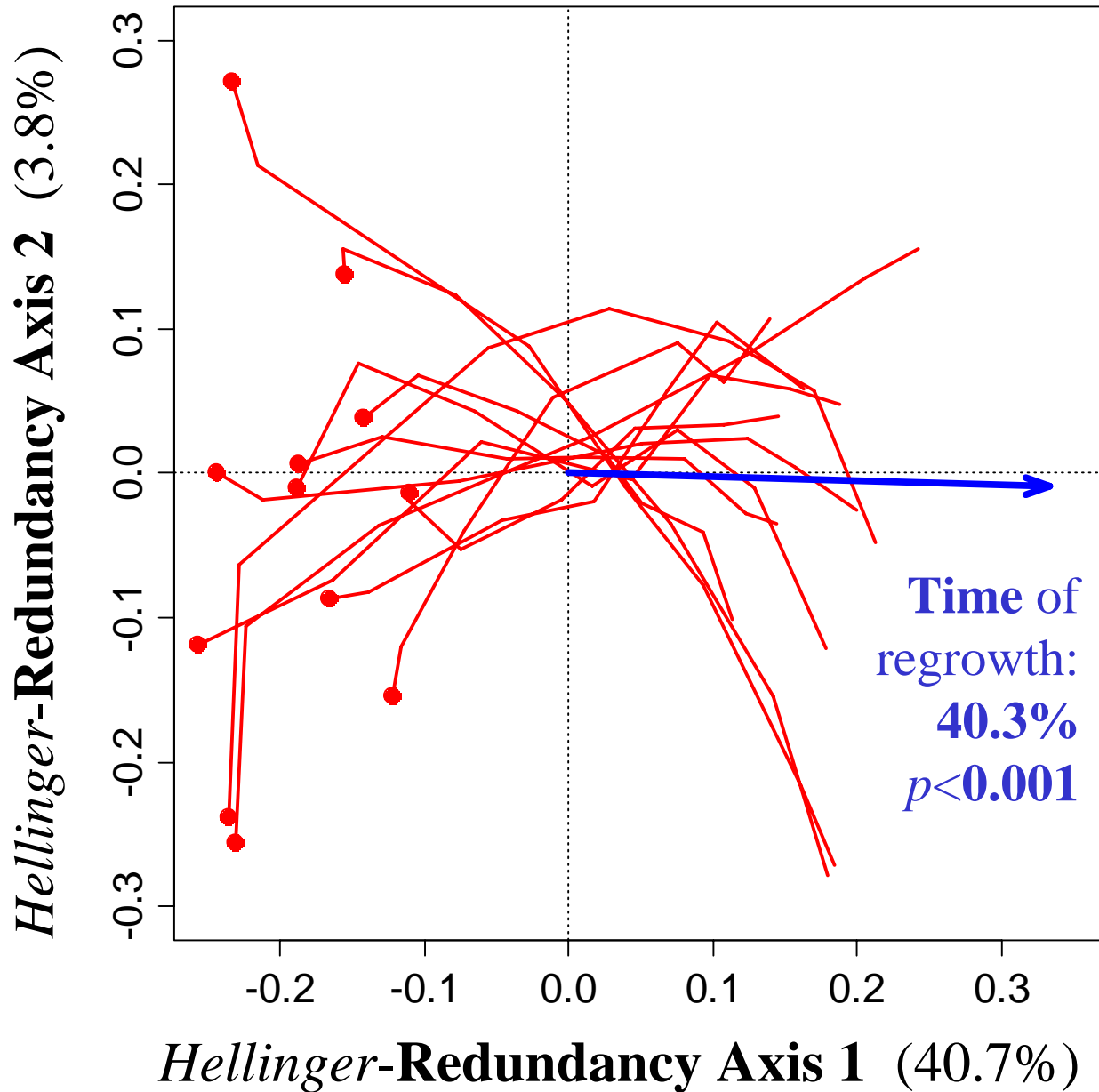
[All p-values based on permutations]

Partial Constrained Ordination: Interaction terms



- 0. Remove variance associated with plot differences (77% of Total Variance)
- 1. Extract linear axes most related to model constraints (time & fertilization)
- Plots at 1st census
- Trajectory over subsequent 6 years

Partial Constrained Ordination: Interaction terms



0. Remove variance associated with plot differences (77% of Total Variance)

1. Extract linear axes most related to model constraints (time & fertilization)

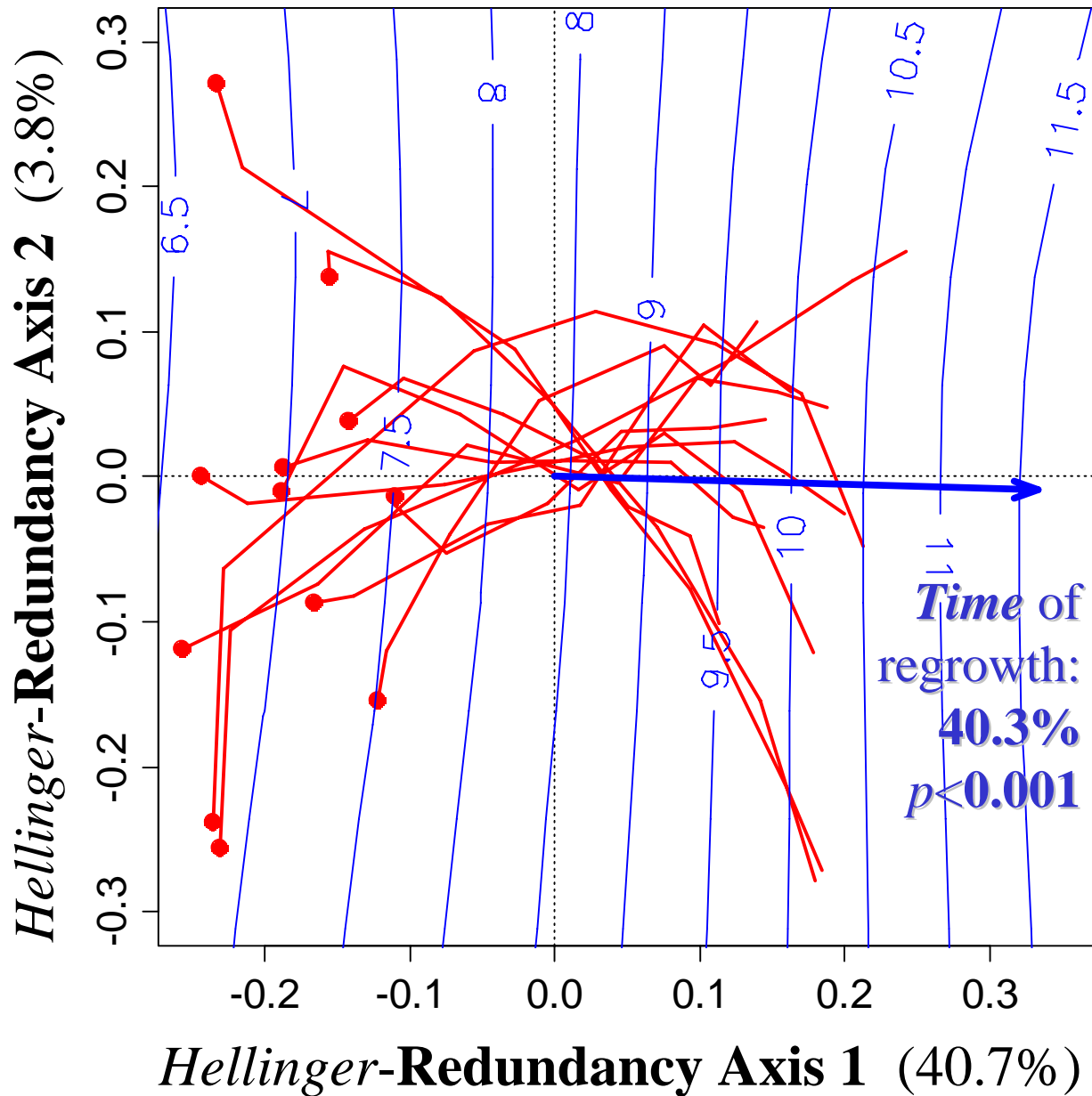
• Plots at 1st census

– Trajectory over subsequent 6 years

→ Main effect of time

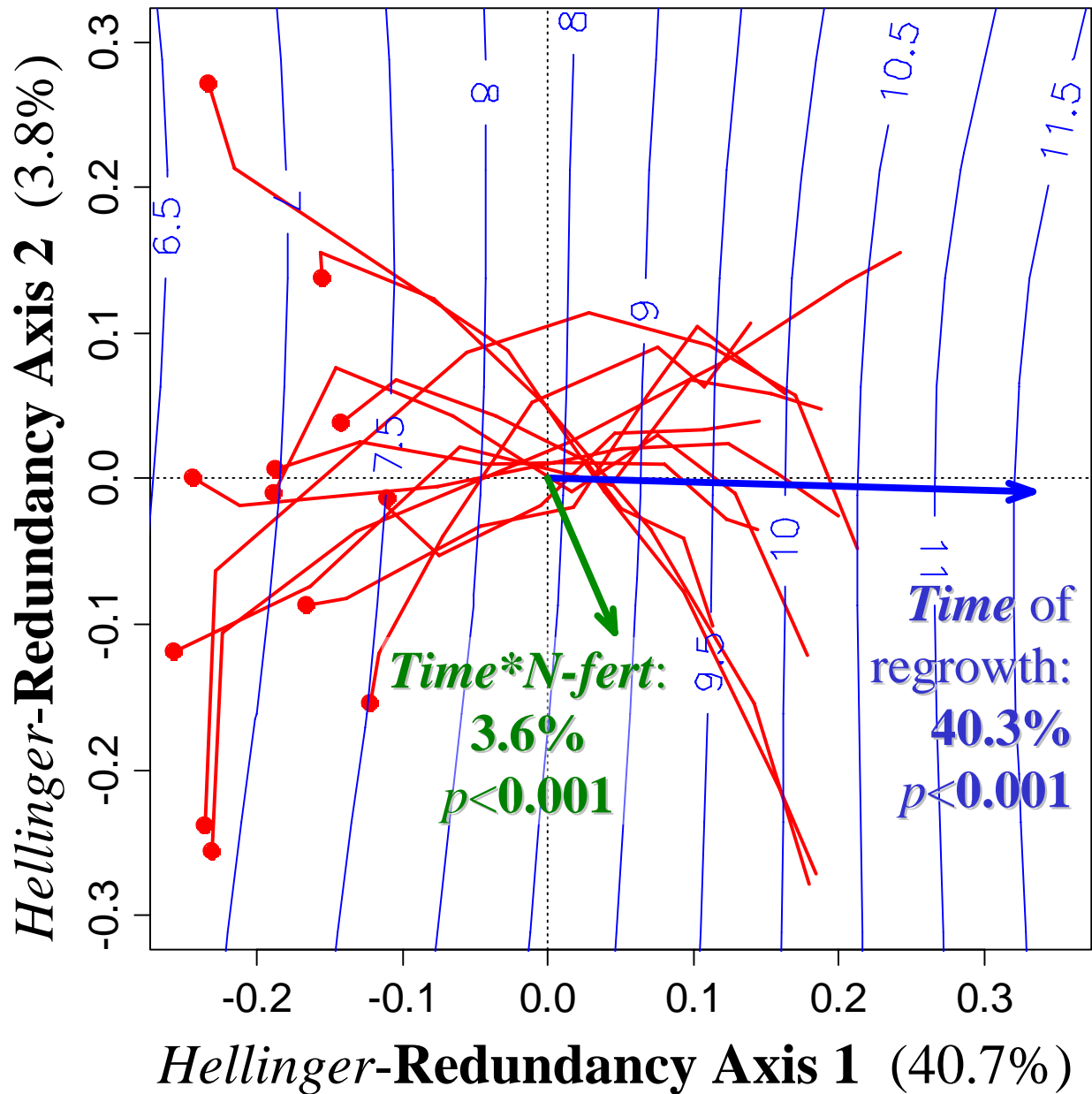
[All p-values based on permutations]

Partial Constrained Ordination: Interaction terms



- 0. Remove variance associated with plot differences (77% of Total Variance)
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- Trajectory over subsequent 6 years
- ➔ Main effect of *Time*; Thinplate splines (years)

Partial Constrained Ordination: Interaction terms



- 0. Remove variance associated with plot differences (77% of Total Variance)
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- Plots at 1st census
- Trajectory over subsequent 6 years
- ➔ Main effect of *Time*; Thinplate splines (years)
- ➔ *Time*N* interaction

Detect effects despite background variability?

- Mixed models of total plot measures:**
powerfully account for background variation, but best fit may hide distinct composite trajectories
- Mixed models of individual species:**
can reveal hidden patterns; but 0-inflation problem
- Hellinger community ordination:**
Constraint important (for BACI) to separate inherent plot differences from treatment* time interactions
- 4th-Corner Analysis (w.abundances & autocorr.):** Important gap in R...!?

Species abundances						Explanatory Variables					
	Species						Exper.Constants				
	sp1	sp2	...	sp58	time		+N	+P	Plot	Block	
Samples (=Plot-by-Time Combinations)	C0	1.6	0	2.39	1.5	C0	0	-	-	1	X
	C1	2.26	0	0	0	C1	1	-	-	1	X
	C2	0	2.39	5.66	0	C2	2	-	-	1	X
	...	1.63	0	3.57	1.44	-	-	1	X
	C6	0	5.66	0	0	C6	6	-	-	1	X
	...	0	0	5.56	0	-	-	...2...	...Y...
	...	2.27	0	6.41	1.18	-	-	...3...	...Z...
	N0	0	5.56	0	0	N0	0	-	-	4	X
	N1	0	0	5.39	0	N1	1	+	-	4	X
	N2	2.87	0	7.81	1.06	N2	2	+	-	4	X
	...	0	0	0	0	+	-	4	X
	N6	0	7.81	5.49	0	N6	6	+	-	4	X
	...	2.87	0	7.33	0.75	+	-	...5...	...Y...
	...	0	0	0	0	+	-	...6...	...Z...
	NP0	0	0	4.77	0	NP0	0	-	-	7	X
	NP1	3.04	1.18	7.12	0.75	NP1	1	+	+	7	X
	NP2	1.44	0	0	0	NP2	2	+	+	7	X
	...	0	0	0	0	+	+	7	X
	NP6	3.03	0	6.56	0.66	NP6	6	+	+	7	X
	...	1.16	0	0	0	+	+	...8...	...Y...
...	0	0	8.68	0	

Species traits						"Ecosystem traits"					
	Species						Exper.Constants				
	sp1	sp2	...	sp58	time		+N	+P	Plot	Block	
Spp Traits	Family	Mimo	Rut	...	Nac	Family	?	?	?	?	?
	N2-fixing	-	-	...	-	N2-fixing	?	?	?	?	?
	Leaf-N	1.39	2.23	...	0.12	Leaf-N	?	?	?	?	?
	Leaf-P	0.13	0.21	...	0.09	Leaf-P	?	?	?	?	?
	Succ.Grp.	1	2	...	3	Succ.Grp.	?	?	?	?	?
	Timb.dens.	1.3	1.1	...	1.9	Timb.dens.	?	?	?	?	?
	?	?	?	?	?



Acknowledgements

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base, car, ellipse, graphics,
gam, labdsv, lattice, MASS,
mgcv, nlme, rgl, stats, vegan

Contact: ILYAS
i.siddique@uq.edu.au

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