

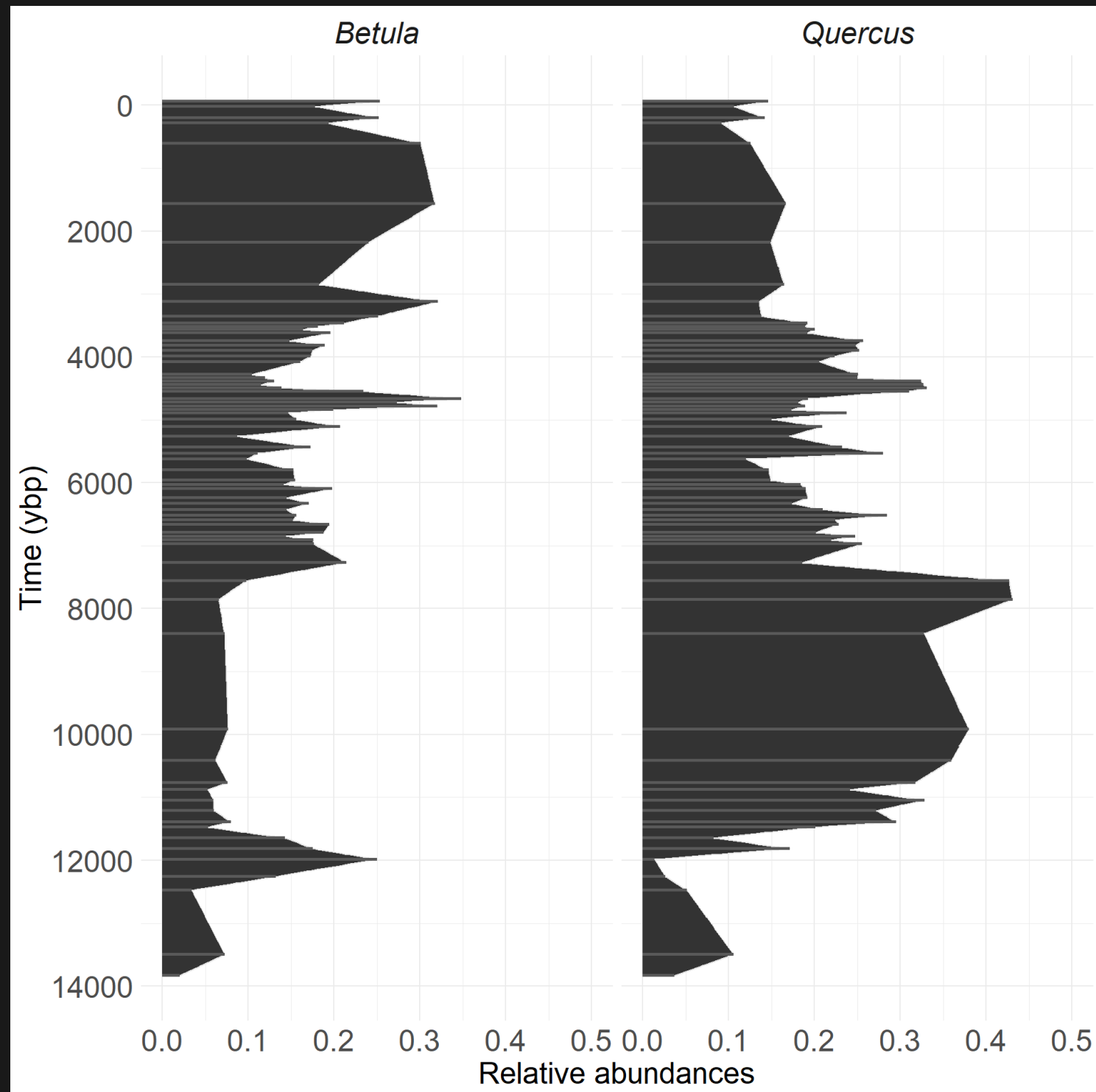
Modelling palaeoecological community data: a state-space approach

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Is the past recoverable from the data?



Palaeoecologists are concerned with questions such as:

- what are the drivers of community change?
- what role do species-environment interactions play?
- what role do density dependence and species interactions play?
- how can palaeoecological information inform present and future ecosystem states?

Palaeoecological proxy data

Proxy data typically:

- comprise multiple time-series (response):
- e.g., pollen, diatoms...
- include environmental covariates (predictors):
 - e.g., isotopic data, charcoal data, lake level...

Pose many statistical challenges:

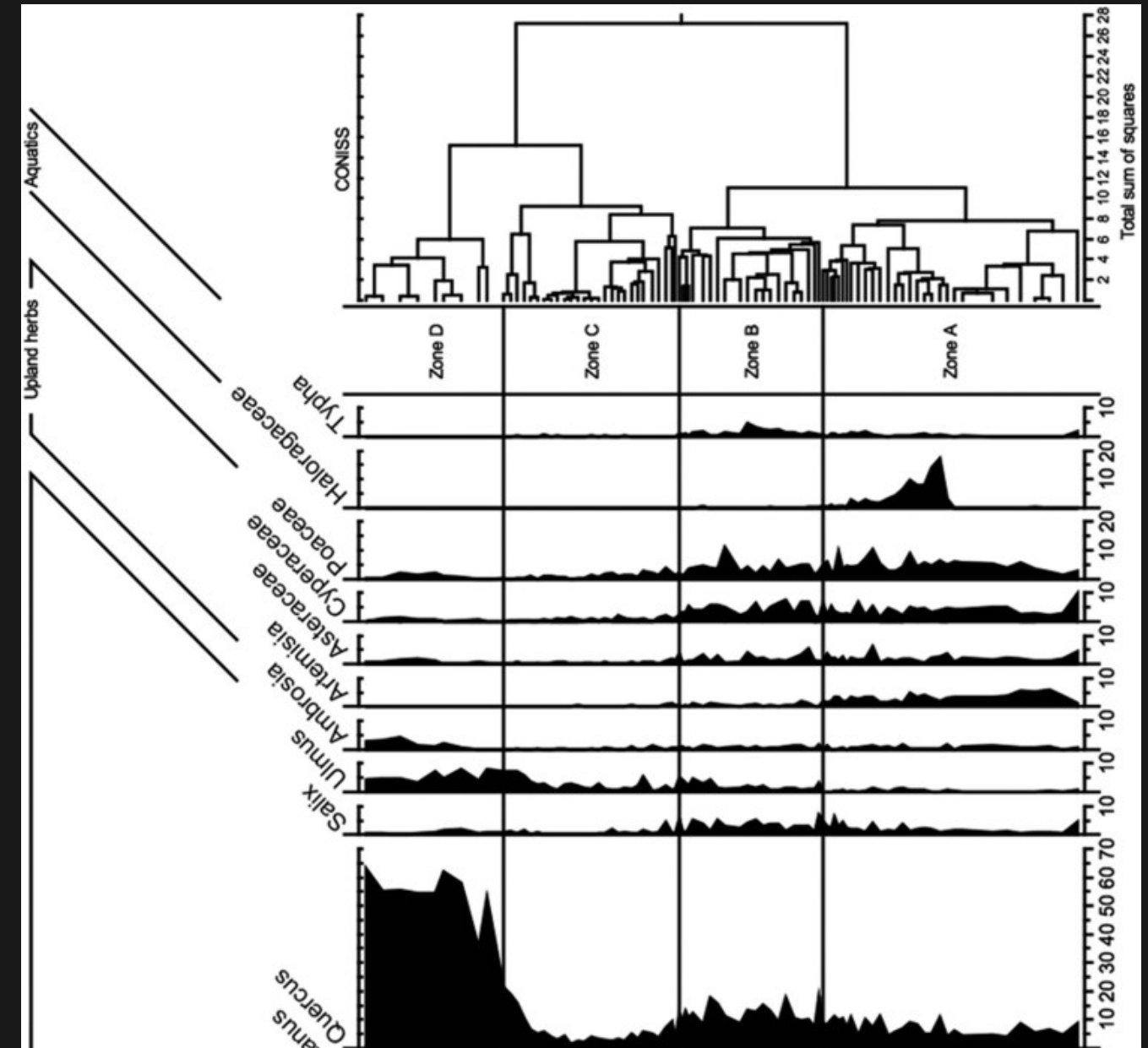
- Uneven sampling through time
- Time averaging
- Measurement uncertainty
- Relative abundances

Descriptive approaches

Many descriptive approaches exist for analysing multivariate time-series:

- Cluster analyses: CONISS
- Ordination: PCA, NMDS...
- Machine learning: MVRT, LDA (fancy cluster analyses)

Descriptive methods allow us to see patterns in the data but not determine potential causes of those patterns.



Jensen *et al.*, 2020

Beyond pattern recognition

The cutting edge in palaeoecology is to establish potential causes of observed patterns in species relative abundances. For example, are observed patterns driven by:

- species interactions?
- climate variability?
- fire regime?
- ...

This is what we want to know if we are to use palaeoecology to inform management of contemporary ecosystems or inform potential future ecosystem states. No easy task!

State-space modelling

State-space modelling goes beyond descriptive approaches and attempts to estimate:

- autoregressive / density dependent processes
- interspecific interactions (C matrix)
- species-environment interactions (B vector)
- combinations of the above

State-space modelling

State-space modelling attempts to predict the “true” unobservable state of a system from observable variables. It does so via two equations, one that models the *process of the system*:

Process equation:

$$Z_t = B0 + C(Z_{t-1} - B0 - BX_{t-1}) + BX_t$$

and one that models the *observations* from the system:

Observation equation:

$$Y_t = Multinomial(Z_t)$$

State-space modelling

State-space models are not new to ecology and have been used for:

- estimating animal populations
- animal movement
- plant cover data
- and much more

However, state-space models are not well explored in palaeoecology.

State-space modelling

This new variant of a state-space model:

- uses a multinomial distribution: accepts raw count data
- accepts multiple predictor data streams in the same model: e.g., isotopic data, charcoal accumulation rates, fungal spores...
- simultaneously fits multiple coefficients
- models autocorrelation structure

$$Z = B0 + C(Z_{t-1} - B0 - BX_{t-1}) + BX_t$$

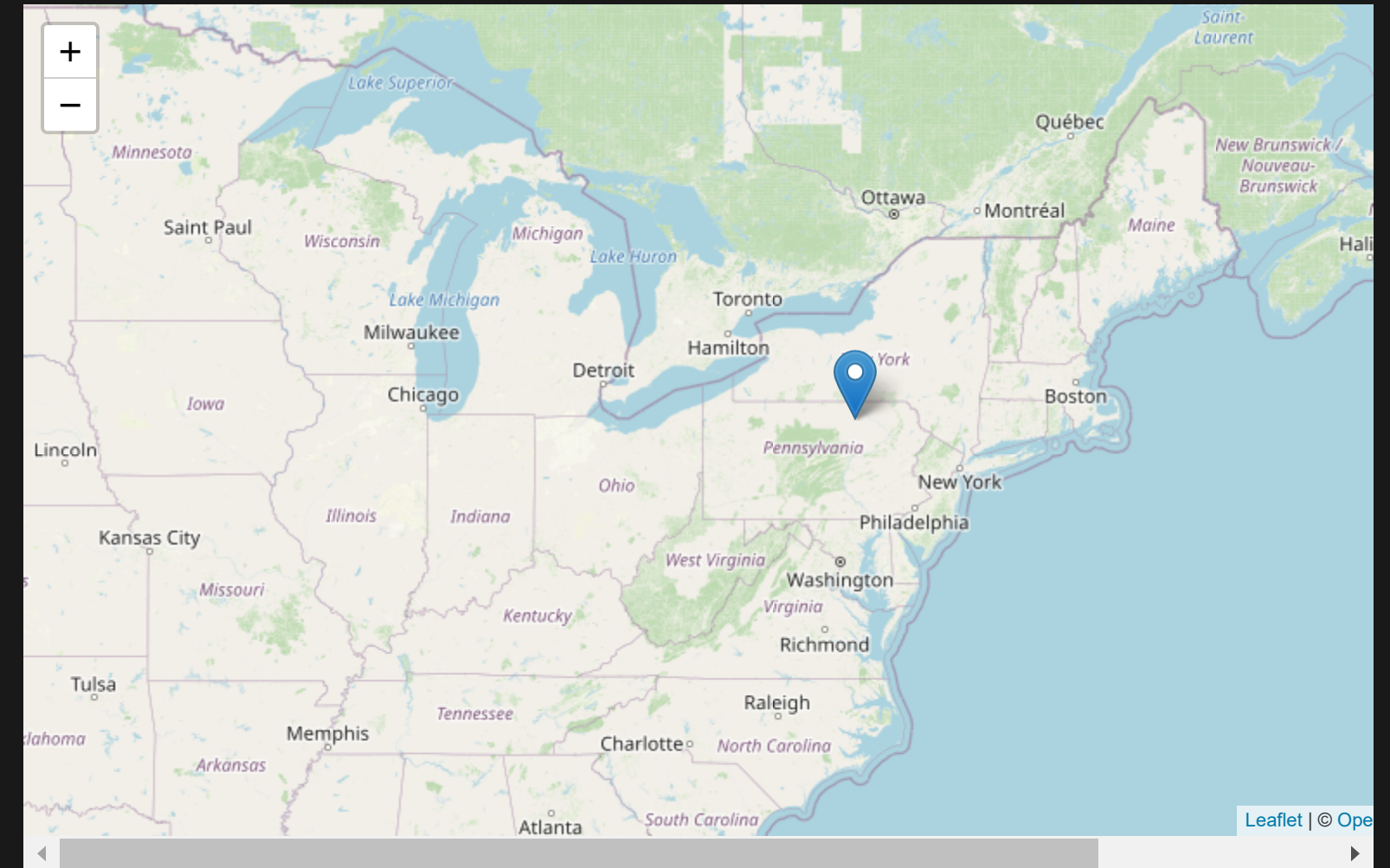
$$Y_t = \textit{Multinomial}(Z_t)$$

Can be used to assess a range of possible causes of observed patterns in palaeo-data.

Empirical example

Demonstrating a three-taxon model from Sunfish Pond:

- unpublished data: not presenting the dataset, focusing on the modelling approach (Johnson *et al.*, unpub)
- ACES project interested in abrupt transitions between dominant species



Jonathon Johnson (JJ)



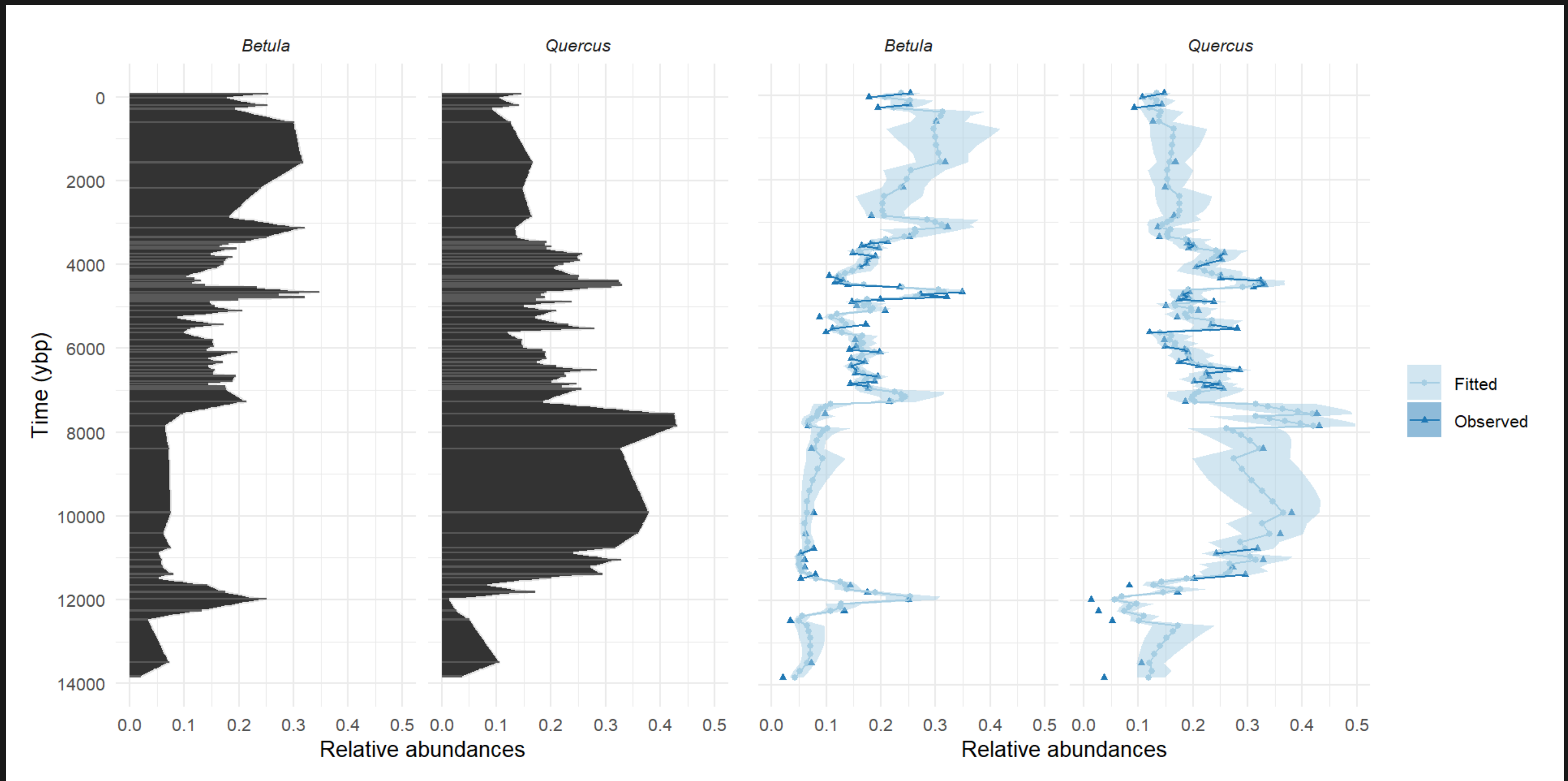
Empirical example

This example is a three-taxon model:

- two focal species (*Betula* and *Quercus*)
- third 'species' is an aggregate of all other species
- we fit species interactions
- estimate species change through time

Remember, this is a multinomial problem which accounts for unavoidable correlations in frequency data.

Time-forward model enables uneven intervals



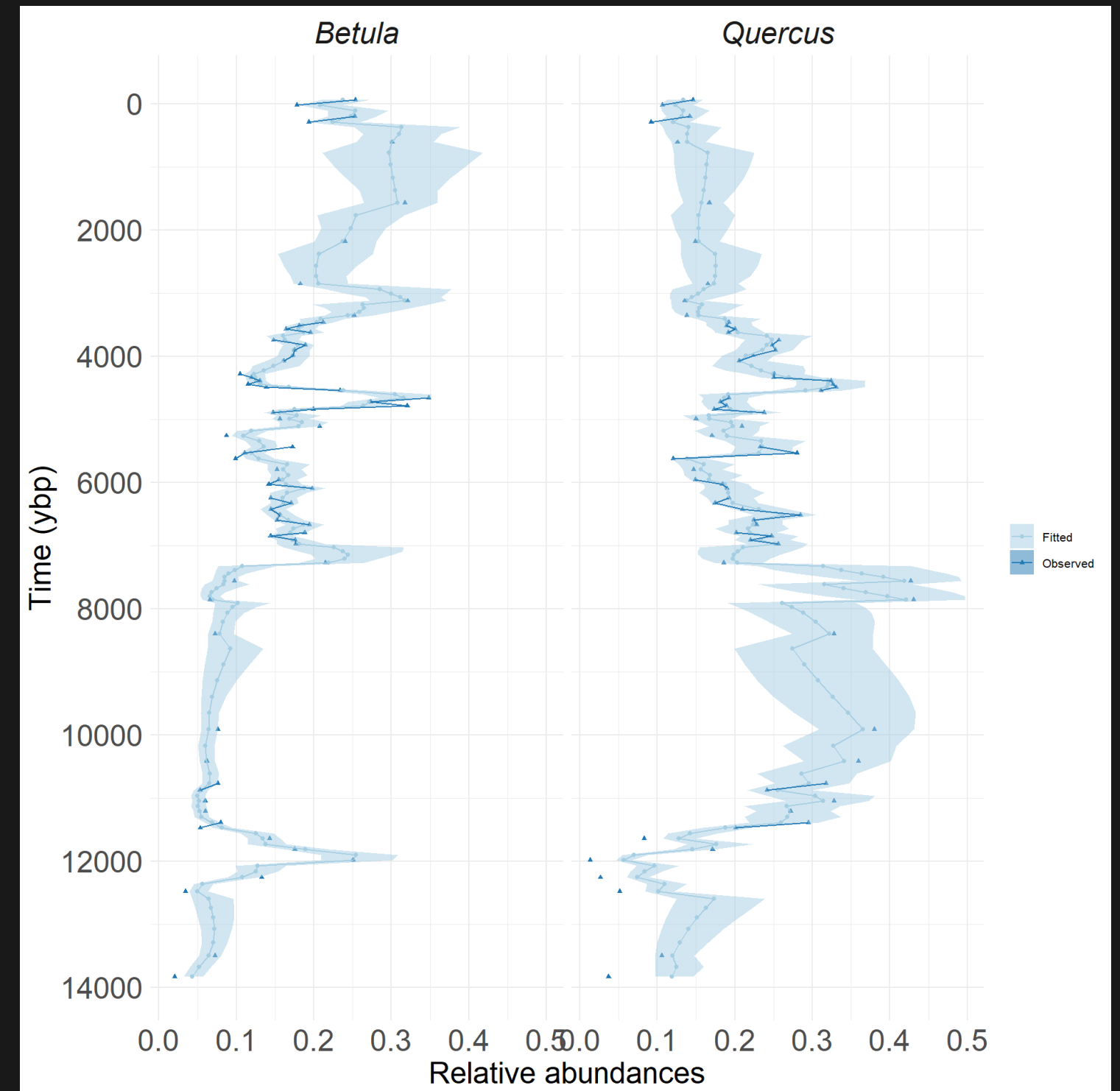
Johnson *et al.*, unpublished

Species interaction estimates

C matrix

	other	Quercus	Betula
other	-0.074	0.000	0.000
Quercus	0.000	-0.006	0.121
Betula	0.000	-0.702	-0.459

- columns = abundance; rows = change in abundance
- density dependence on the diagonal
- *Quercus-Betula* -0.7 means that abundance of *Quercus* affects the change in *Betula* abundance



Estimating the effect of covariates

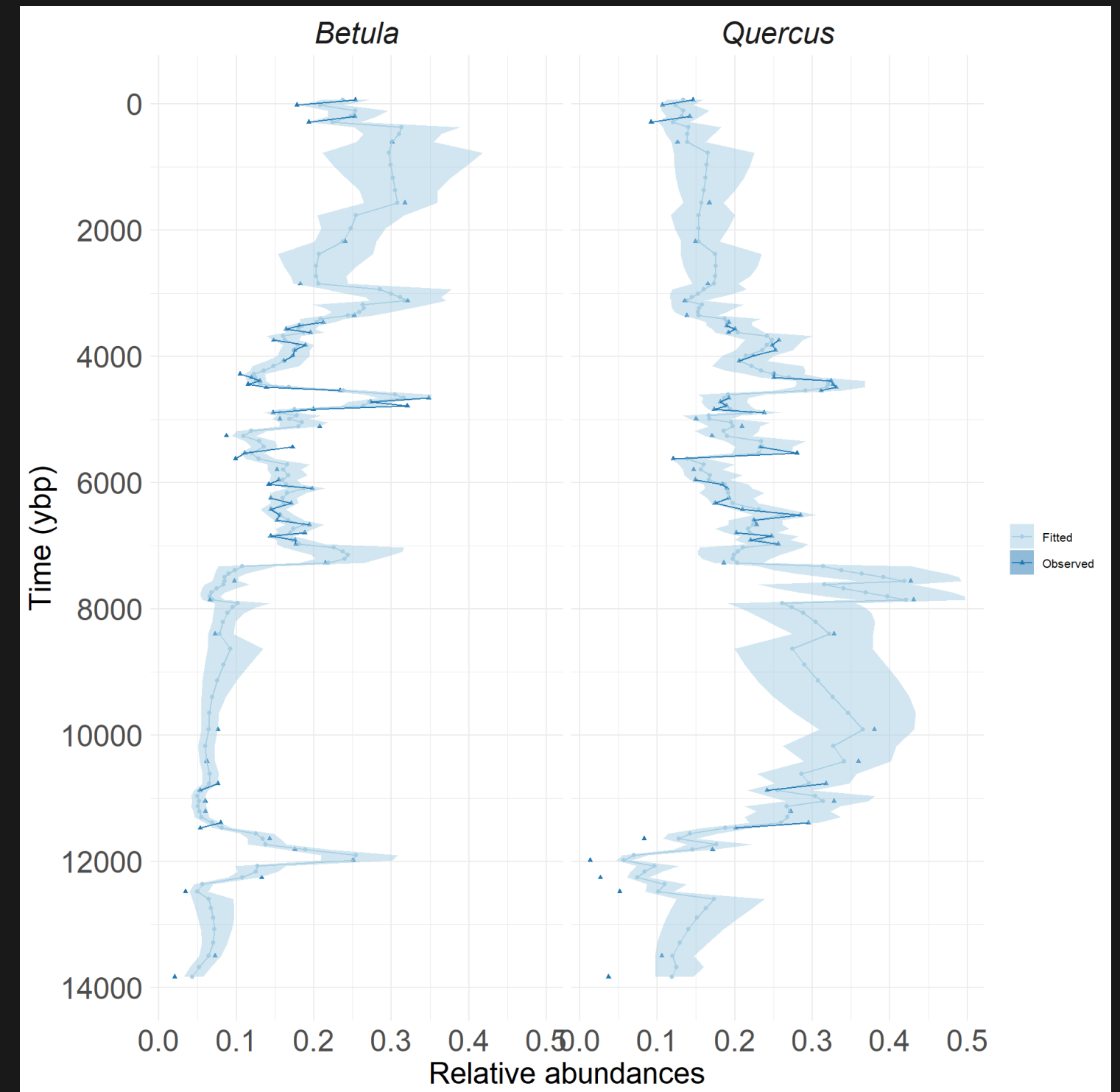
Estimate of change over time

B vector

```
other Quercus Betula  
0    0.048 -0.532
```

Overall:

- *Quercus* increases with time
- *Betula* decreases with time
- estimates are relative to “other” taxa

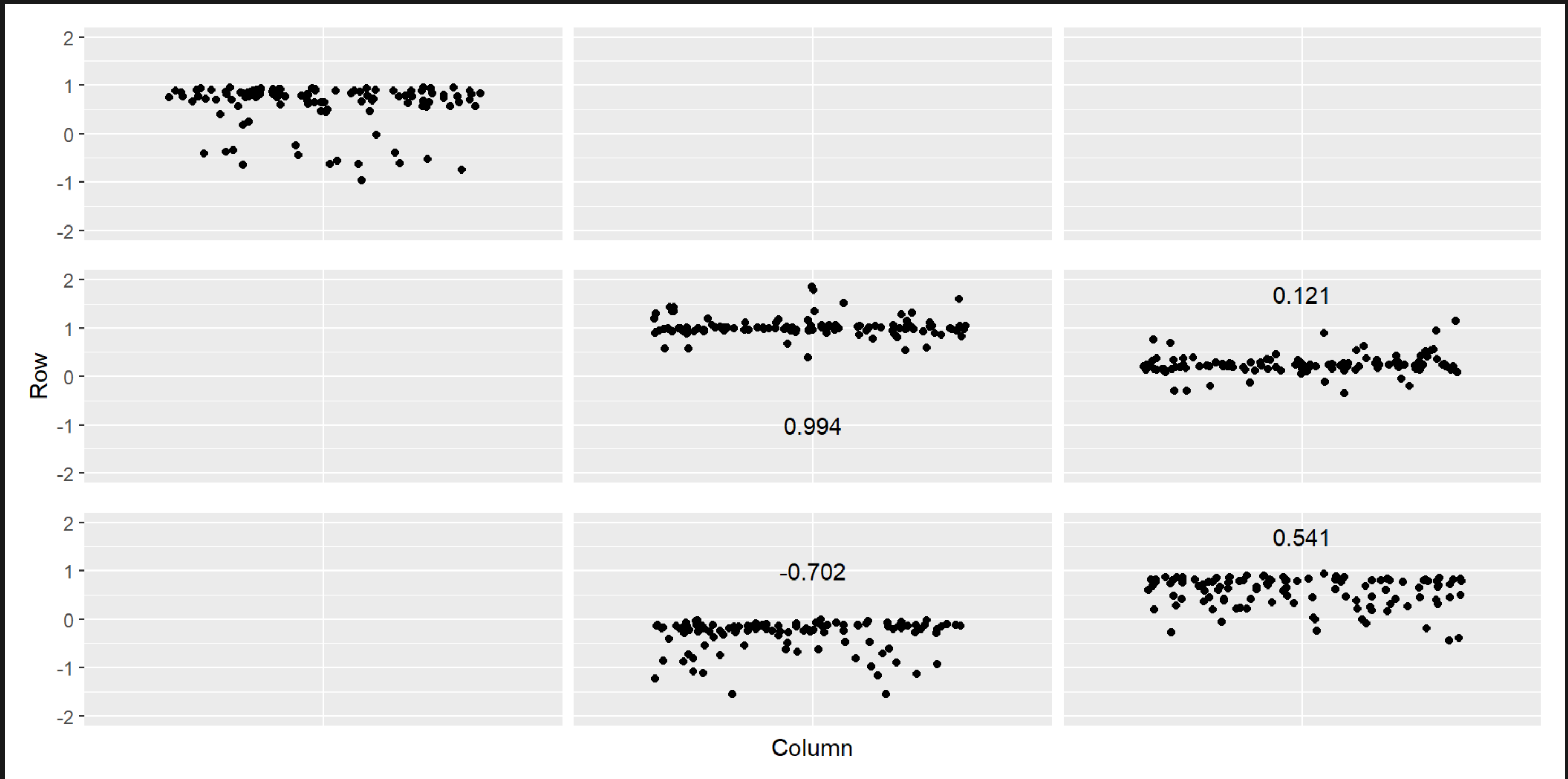


Evaluating the model with simulated data

- We cannot determine the accuracy of fitted coefficients empirically from palaeoecological data.
- Simulation experiments are used to assess the success of recovering parameters:
 1. data are simulated under known conditions with replication
 2. the model is fit to the simulated replicate datasets
 3. fitted models are assessed for how well input parameters are recovered

Evaluating the model with simulated data

C matrix estimates vs inputs



Hypothesis testing

We cannot determine with certainty, outside of simulation, causation from palaeo-data.

What we can do is:

- set up multiple working hypotheses (Chamberlin, 1897)
- couple descriptive methods with inferential ones
- assess which results lend support to the likelihood of each hypothesis being true

Given the data at hand the interaction matrix (C) indicates some competition between *Quercus* and *Betula*. Such an inference lends support to one hypothesis.

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