Counting niches: Can spatial patterns reveal niche partitioning in tropical forests?

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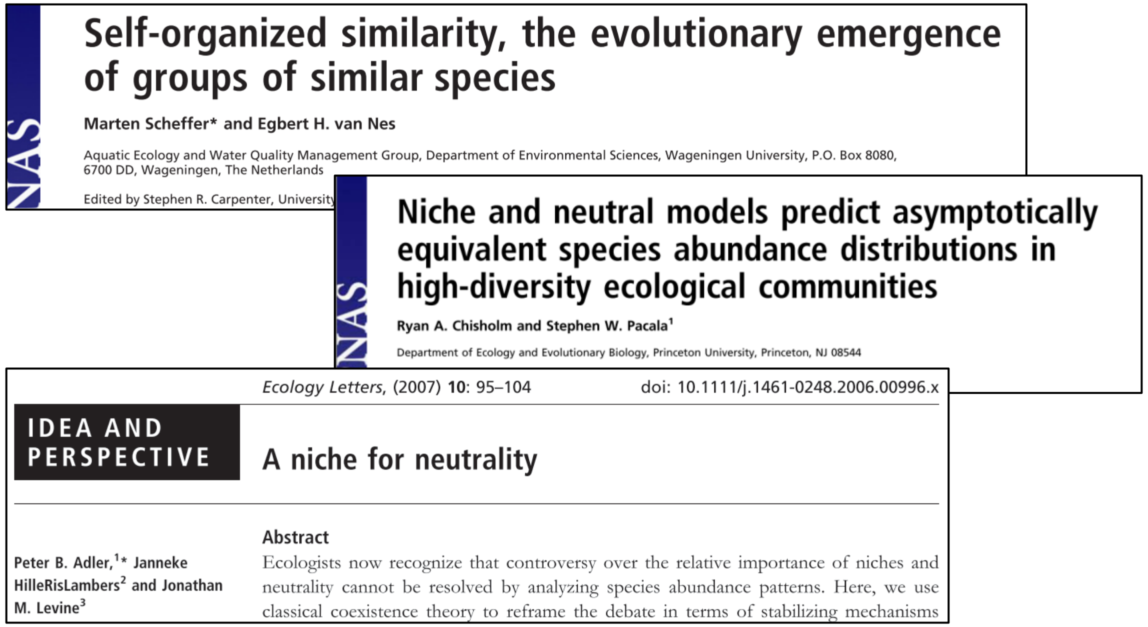
Big-picture questions

What forces assemble ecological communities? (Focus: niche partitioning/ sharing)

Is niche structure a primary component of biodiversity patterns in high-diversity communities such as tropical forests?

Niche sharing

The idea that multiple species may occupy the same niche on any given niche axis



PNAS

Self-organized similarity, the evolutionary emergence of groups of similar species

Marten Scheffer* and Egbert H. van Nes

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Edited by Stephen R. Carpenter, University

PNAS

Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities

Ryan A. Chisholm and Stephen W. Pacala[1]

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

Ecology Letters, (2007) **10**: 95–104 doi: 10.1111/j.1461-0248.2006.00996.x

IDEA AND PERSPECTIVE

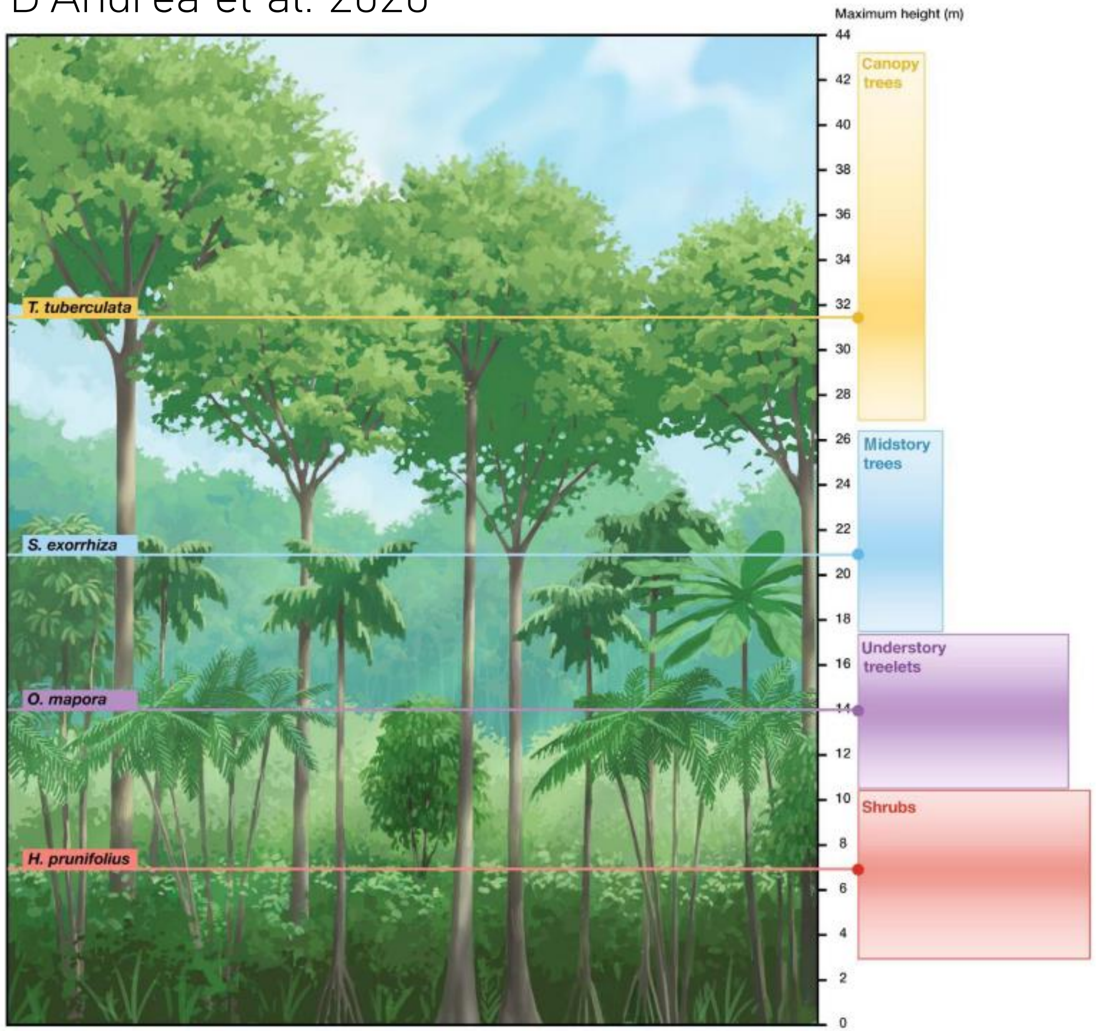
A niche for neutrality

Peter B. Adler,[1]* Janneke HilleRisLambers[2] and Jonathan M. Levine[3]

Abstract

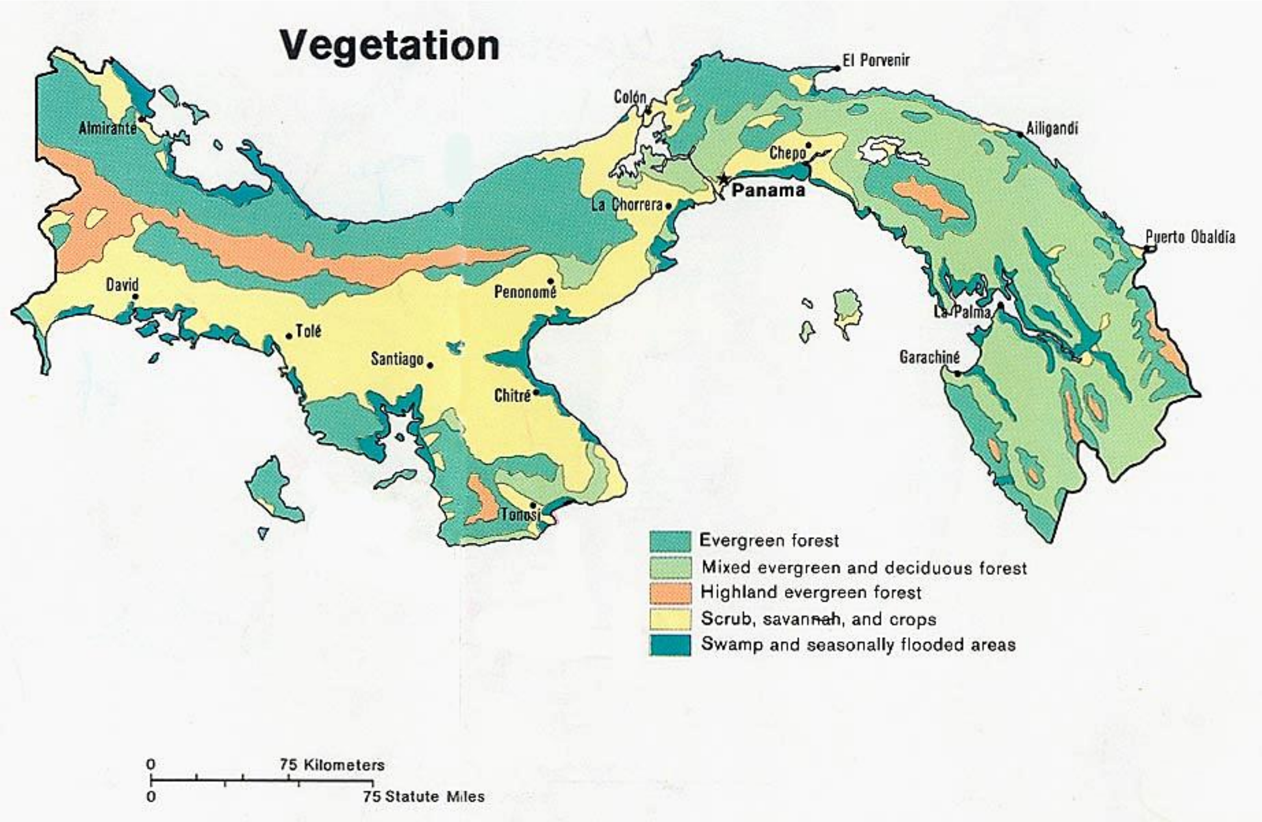
Ecologists now recognize that controversy over the relative importance of niches and neutrality cannot be resolved by analyzing species abundance patterns. Here, we use classical coexistence theory to reframe the debate in terms of stabilizing mechanisms

D'Andrea et al. 2020

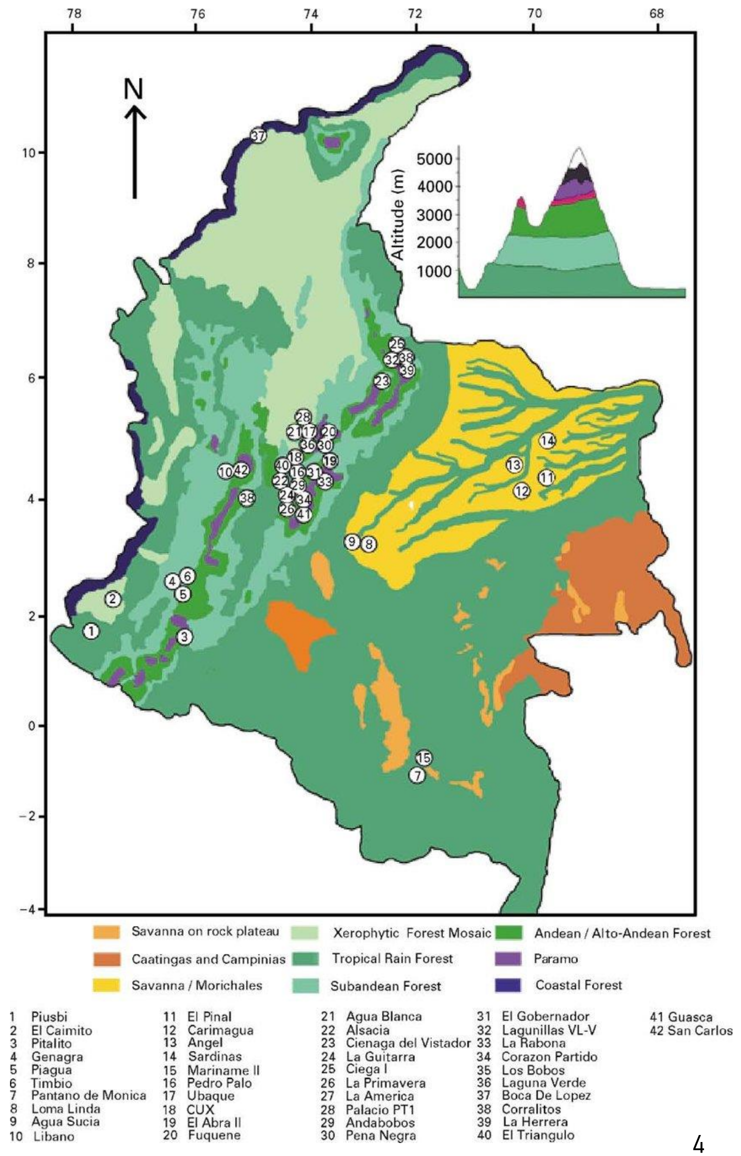


Regional variation

Panama



Colombia



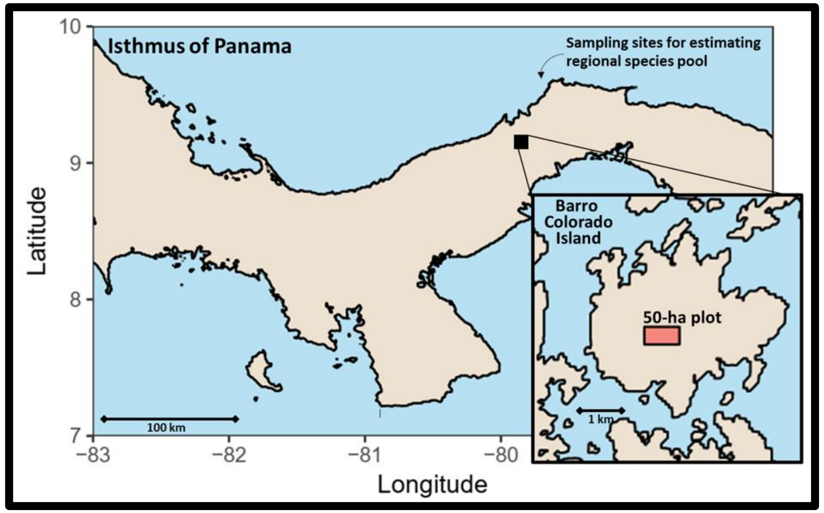
This talk

Do tropical species segregate spatially at local scales ($< 1km^2$)?

If so, does the pattern reflect adaptations to local abiotic environments?

If so, is this spatial niche structure reflected in species traits?

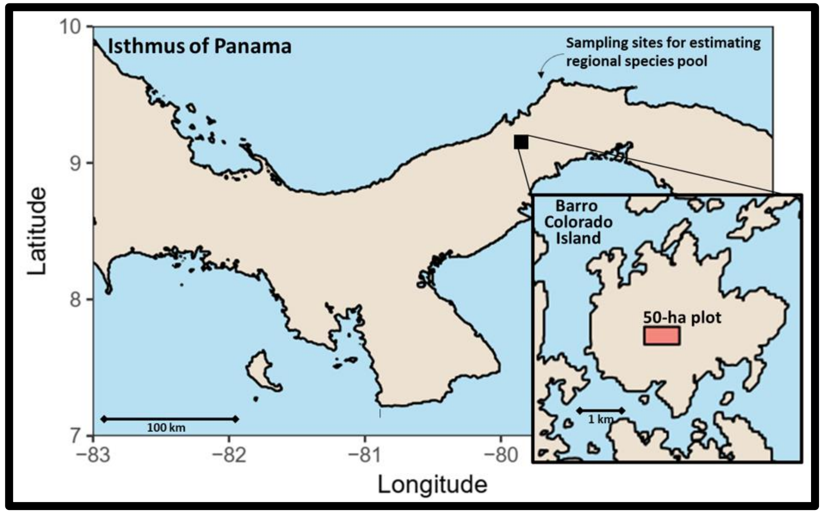
Barro Colorado Island

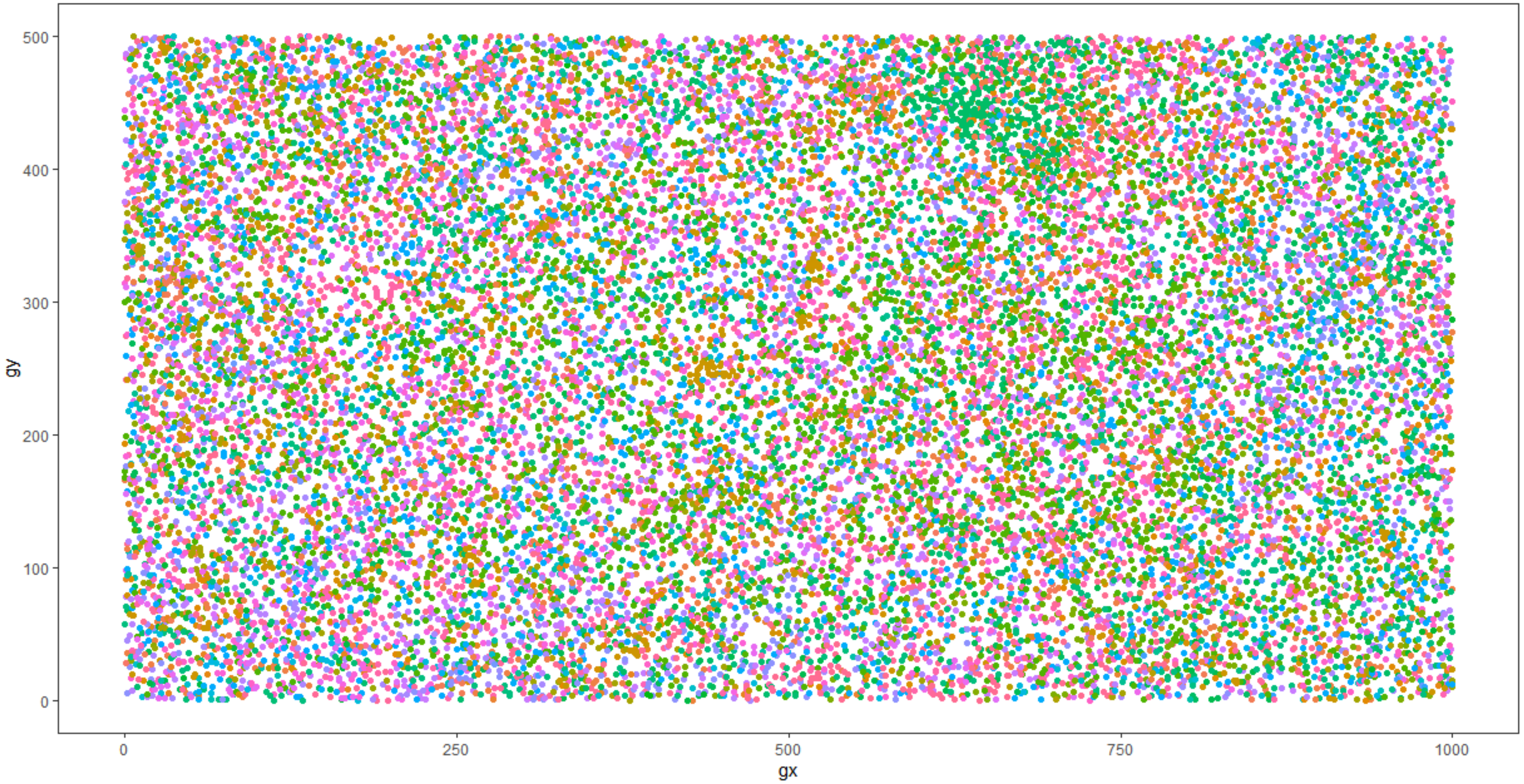


1,000 m x 500 m plot
207k trees
300 species

Data: STRI

Barro Colorado Island

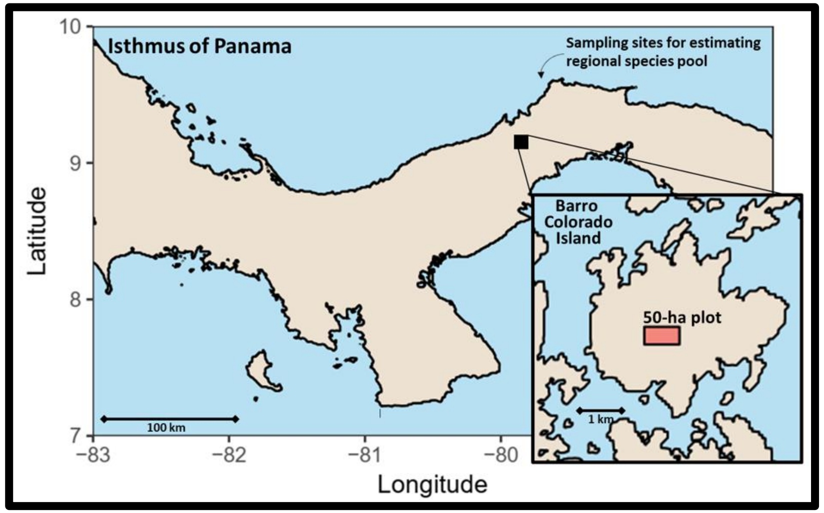


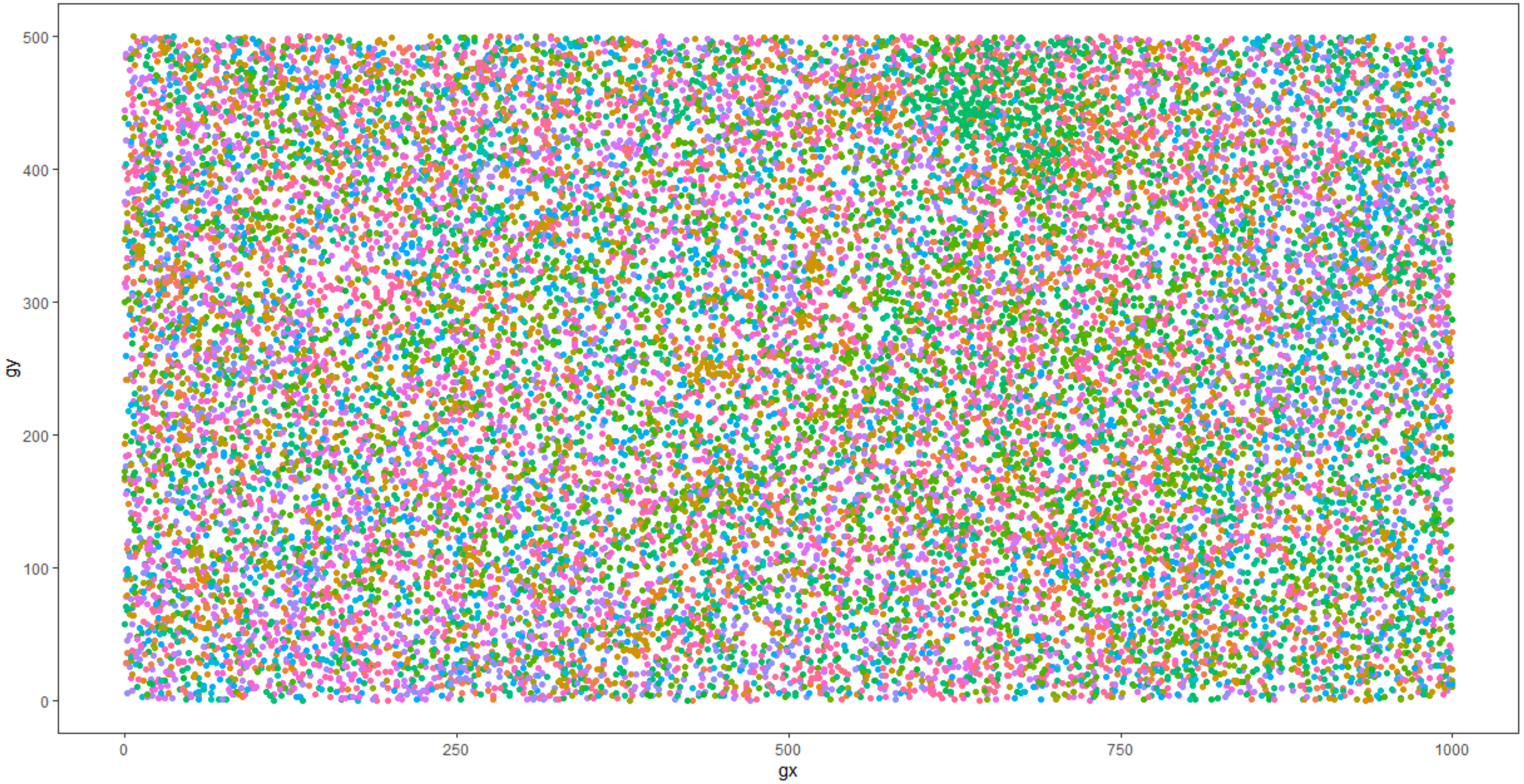


Data: STRI

Q: Signs of spatial niche structure (i.e. niche partitioning/sharing)?

Barro Colorado Island



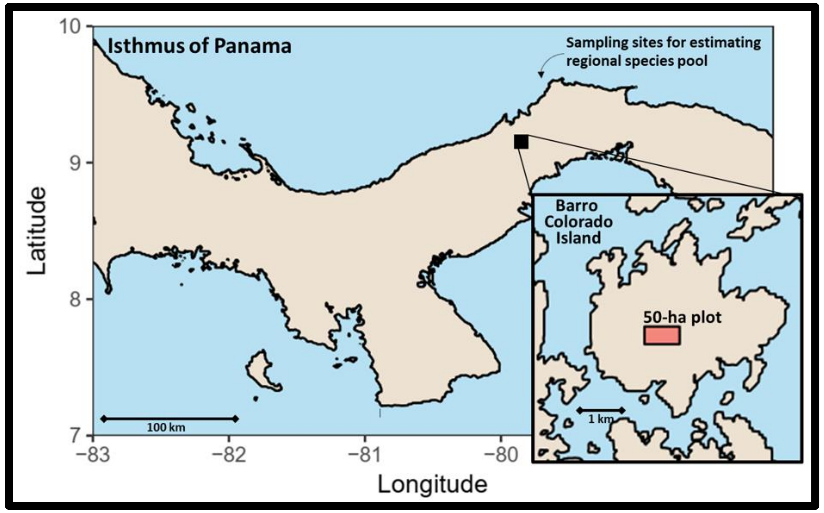


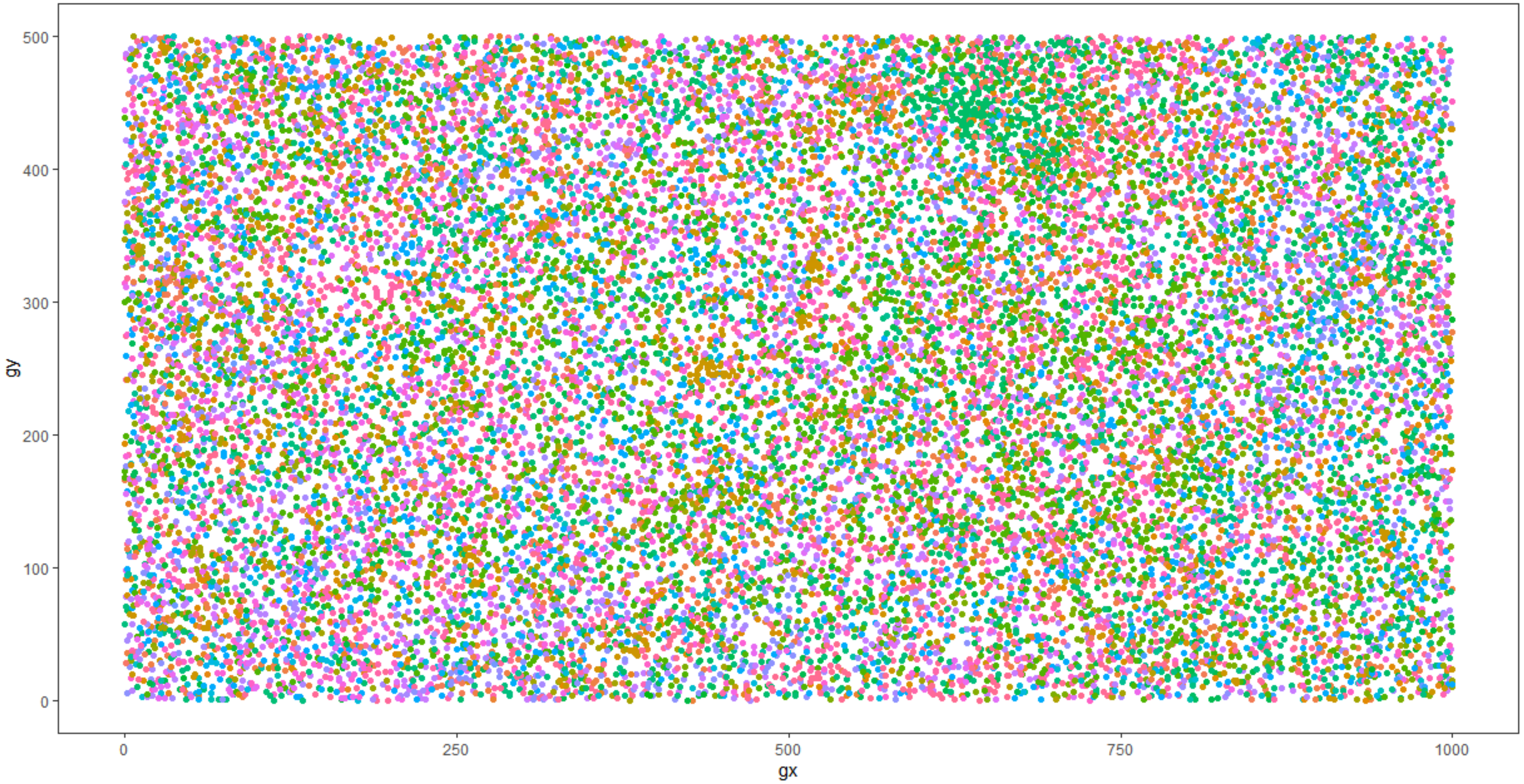
Data: STRI

John et al. 2007:

- The spatial distributions of 36–51% of tree species at these sites show strong associations to soil nutrient distributions
- Result cannot be explained by neutral dispersal

Barro Colorado Island

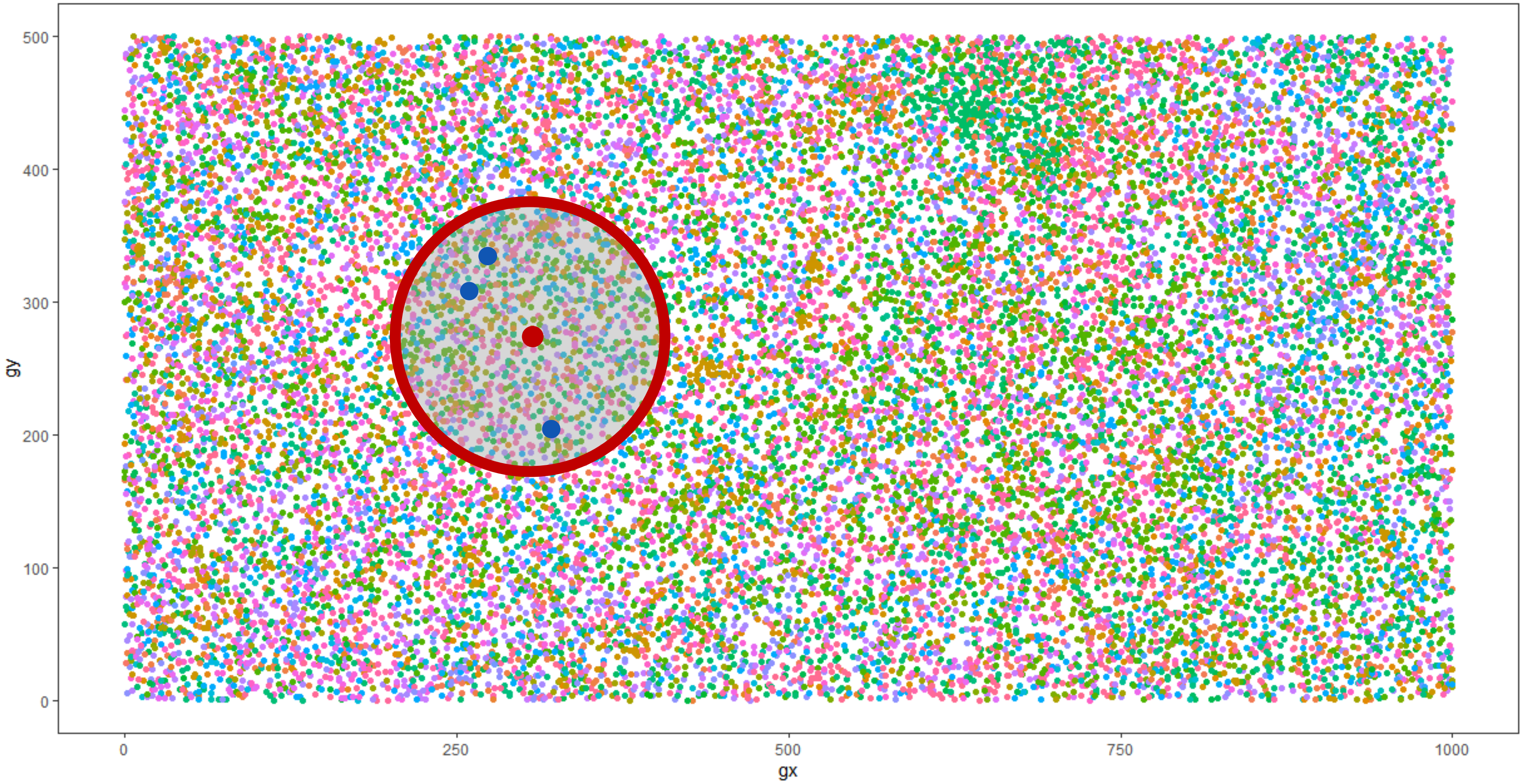




Data: STRI

Q: Yes but can we draw an anatomy of spatial niche structure?

Step 1: Look for spatial associations among species

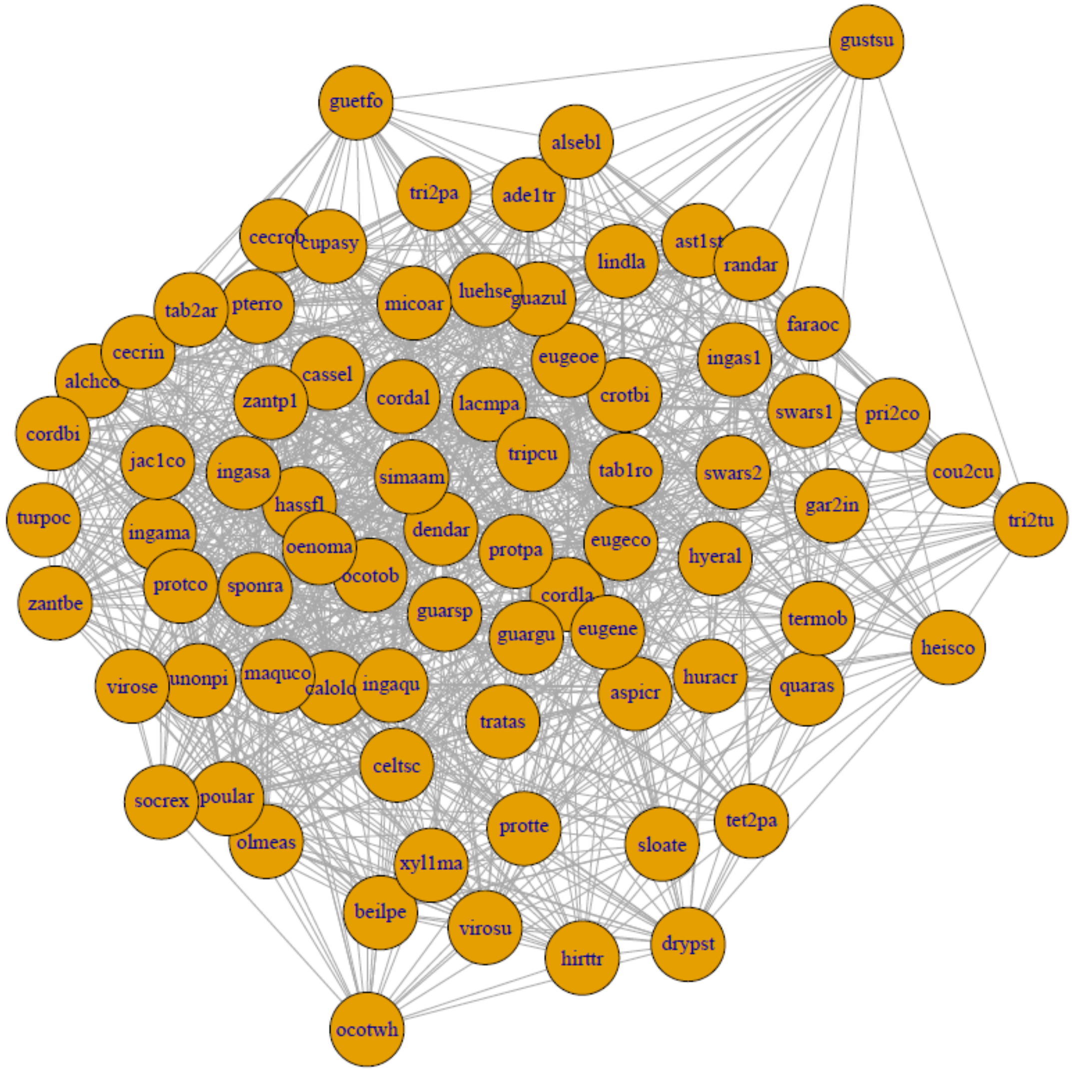


For each two species:

More near-neighbor tree pairs than expected by chance?

Yes → connected
No → not connected

Step 1: Look for spatial associations among species



For each two species:

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Step 1: Look for spatial associations among species

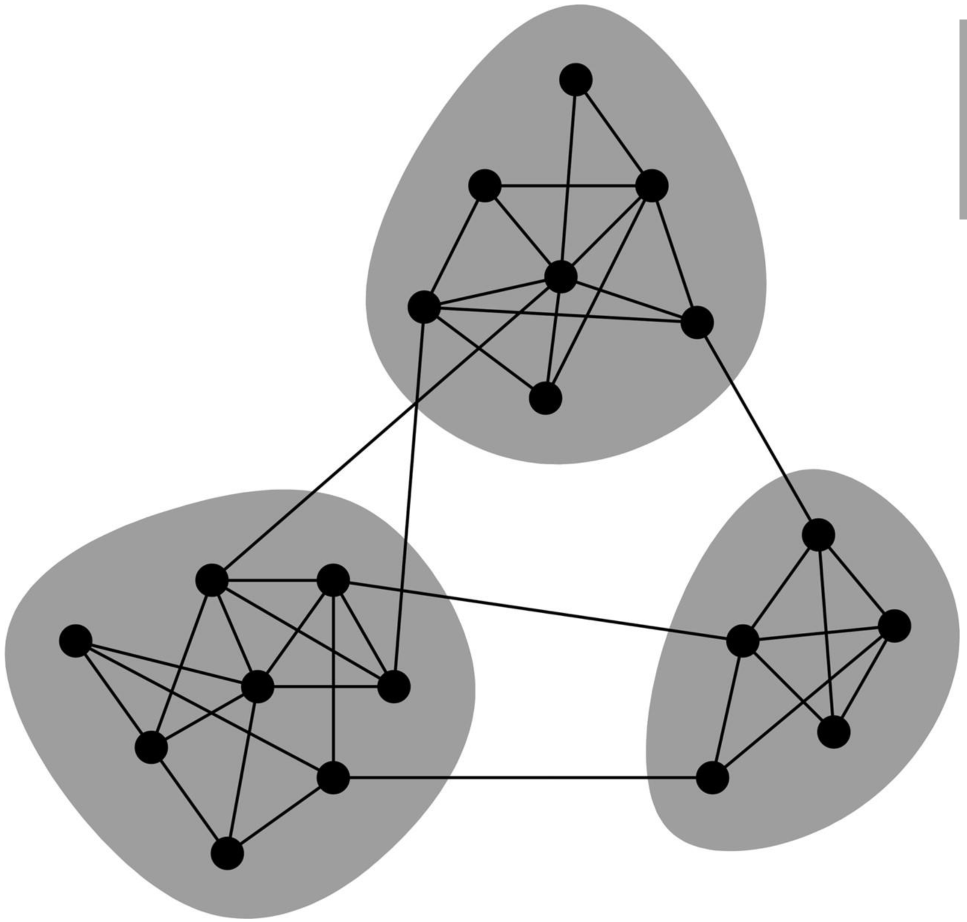
Adjacency matrix

For each two species:

More near-neighbor tree pairs than expected by chance?

Yes → connected
No → not connected

Step 2: Optimize modularity in the network

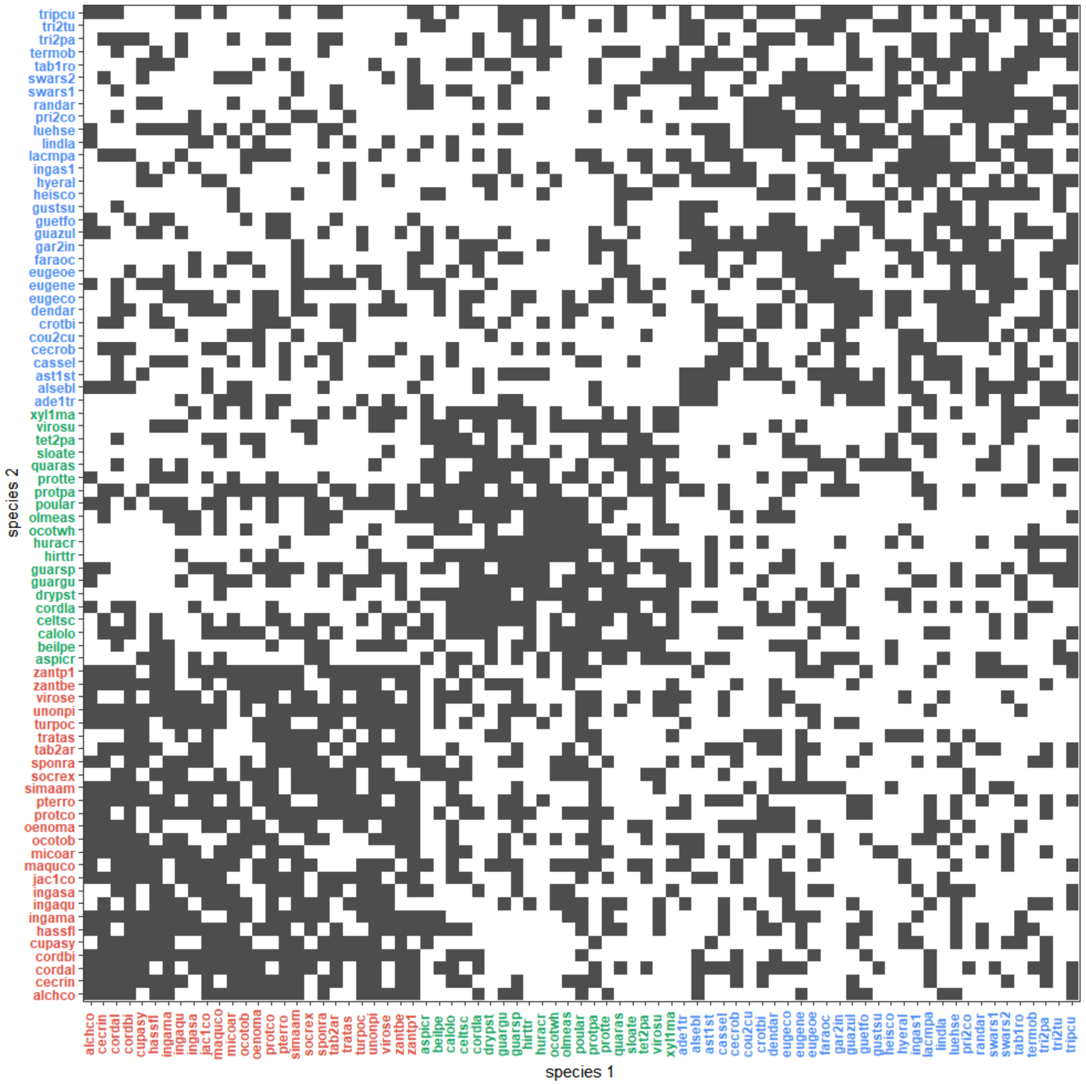


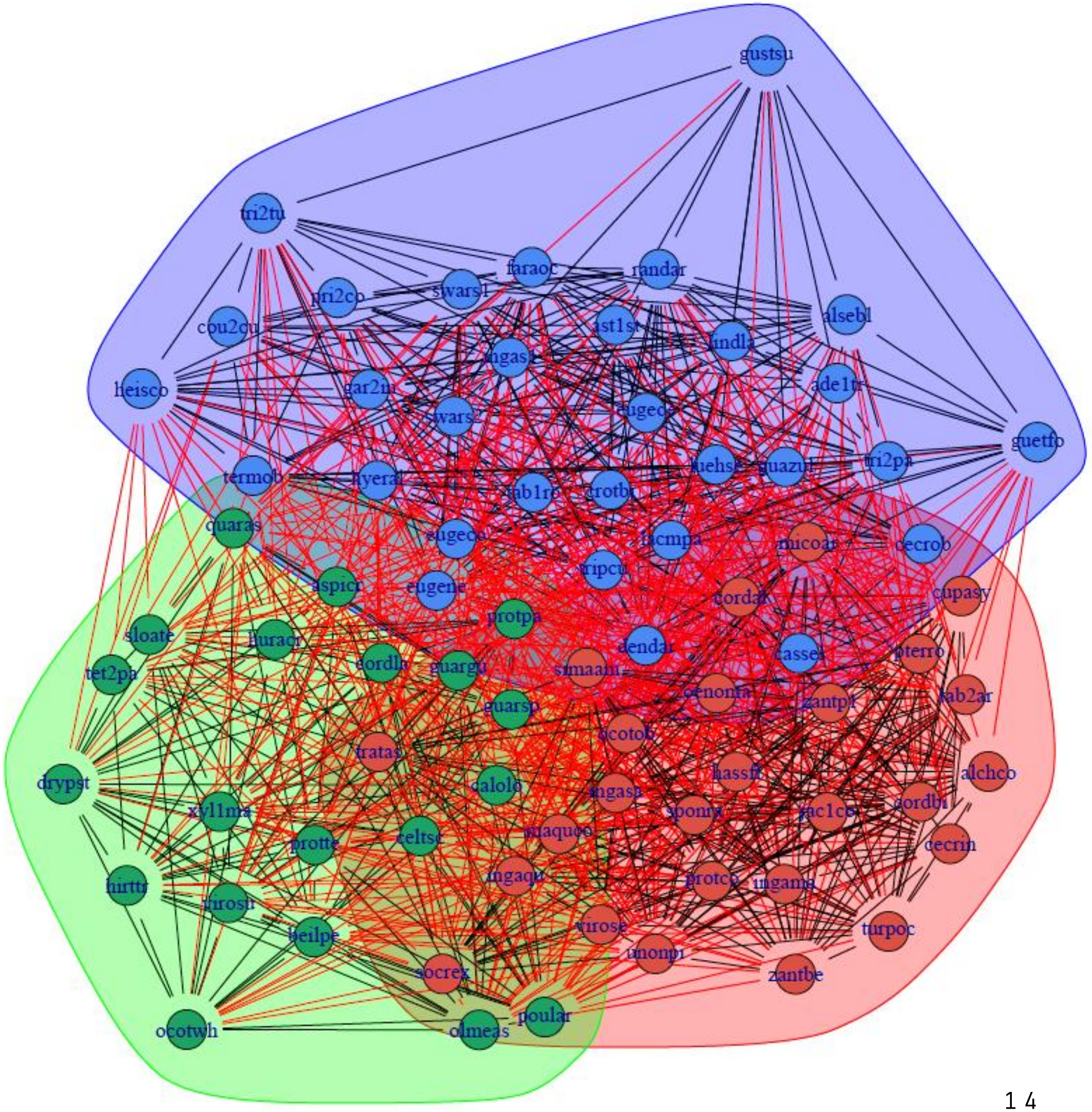
$$\text{Modularity} = \sum_{\text{modules}} \left[\begin{pmatrix} \text{fraction of edges} \\ \text{within module} \end{pmatrix} - \begin{pmatrix} \text{expected} \\ \text{fraction of edges} \\ \text{within module} \end{pmatrix} \right]$$

Several algorithms are available

- Walk trap (Pons and Latapy 2005)
- Spin glass (Reichardt and Bornholdt 2006)
- "Louvain" (Blondel et al. 2008)
- Etc

Step 2: Optimize modularity in the network





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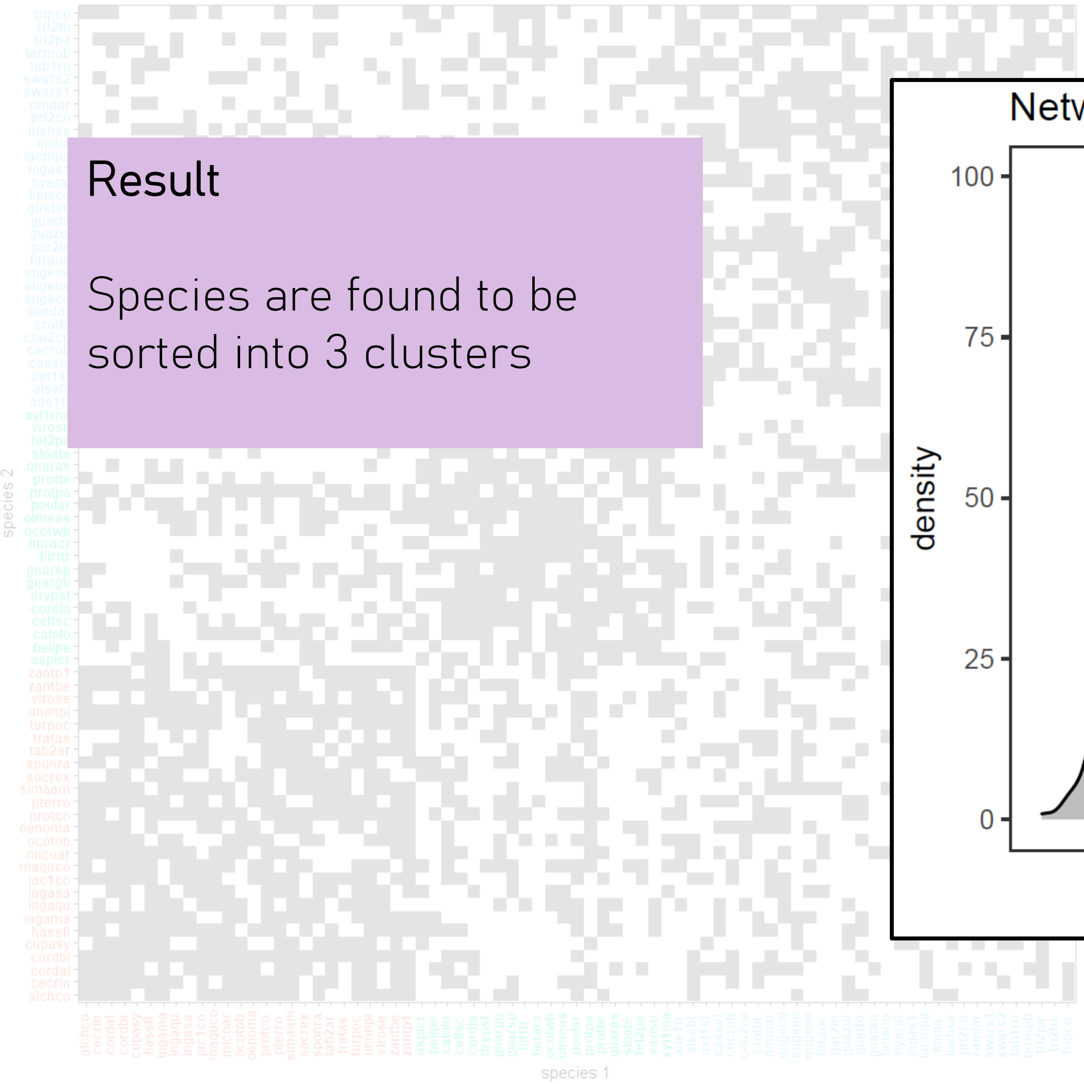
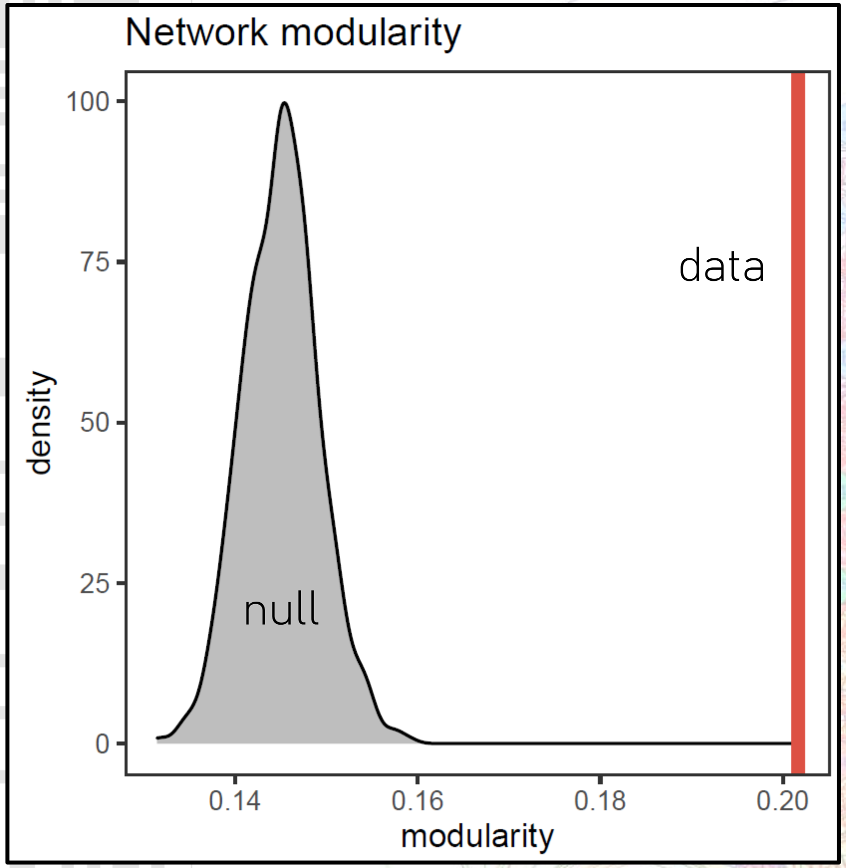
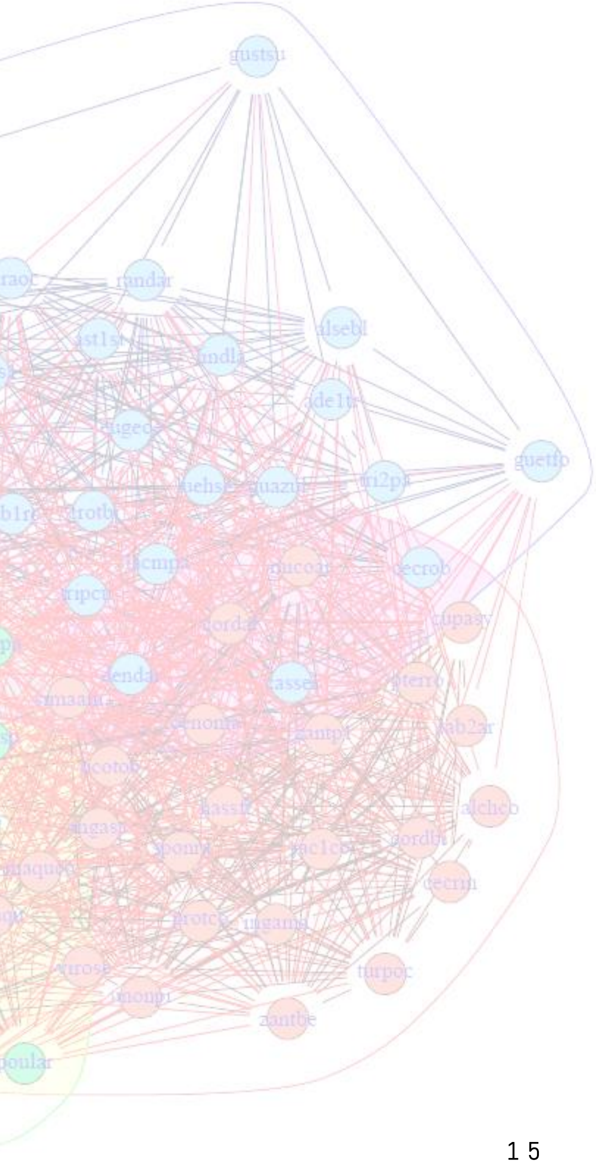


Result

Species are found to be sorted into 3 clusters





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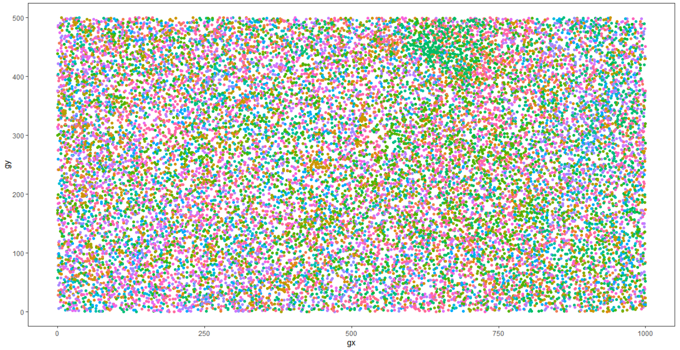
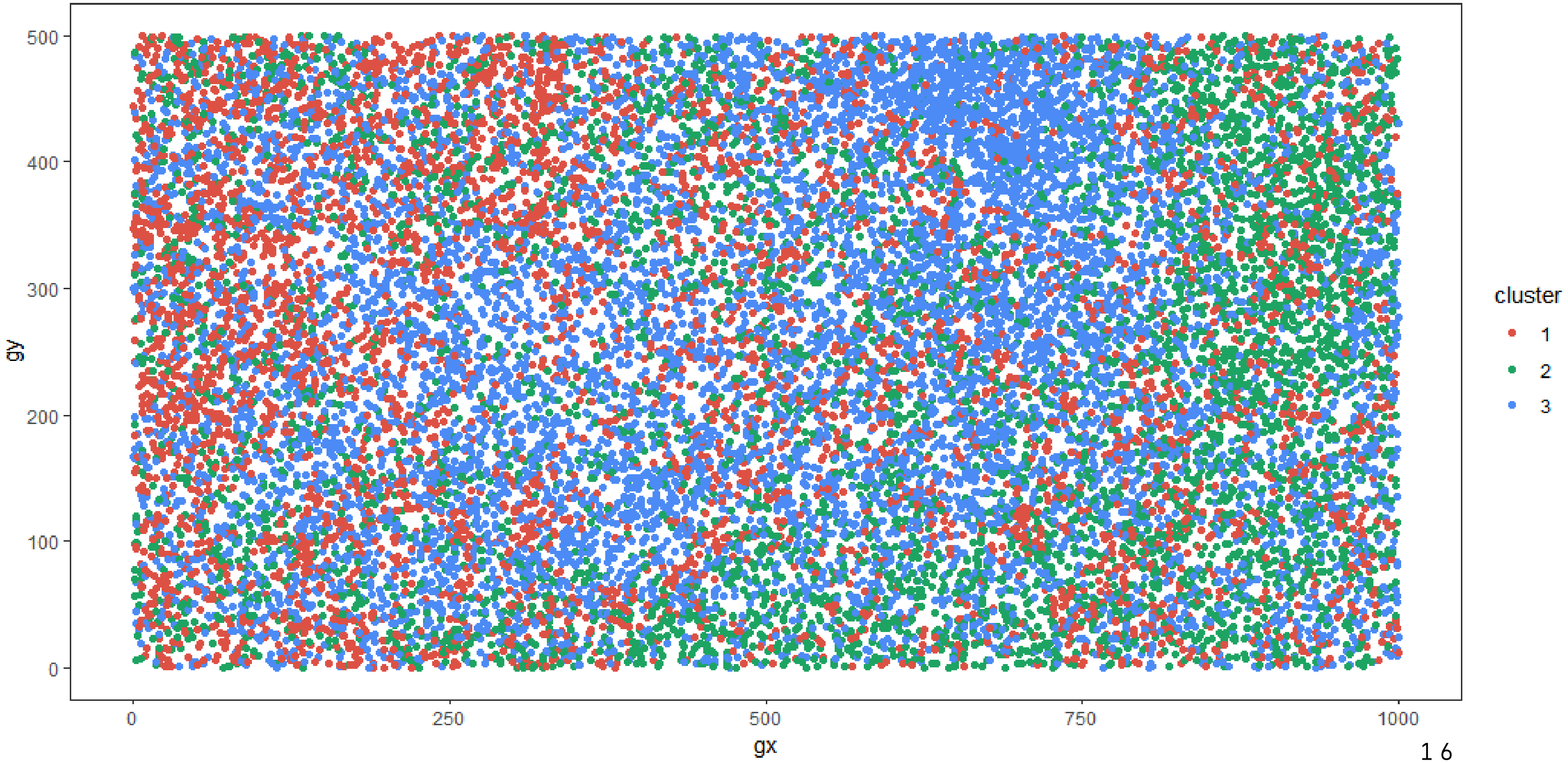




This talk

Do tropical species segregate spatially at local scales? ✔

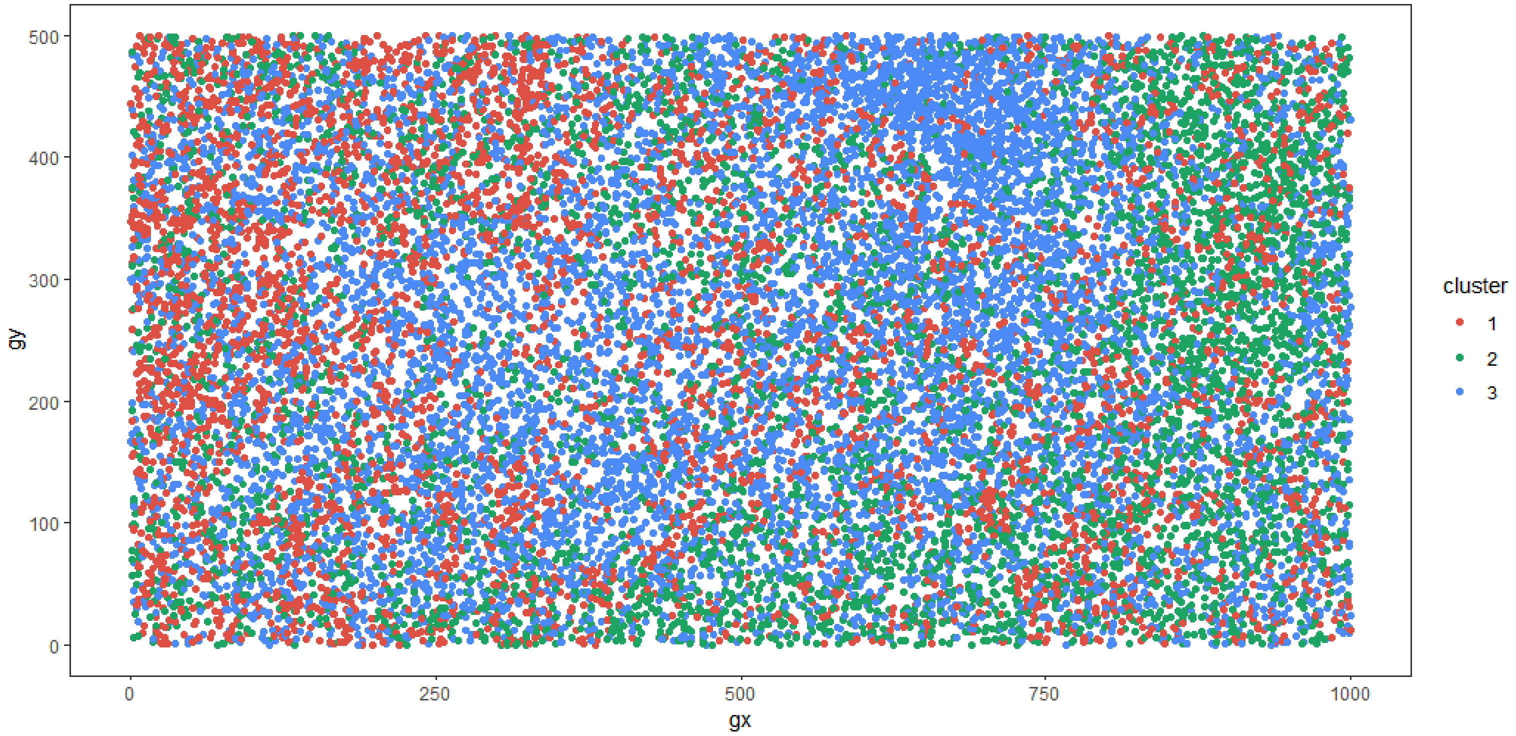
If so, does the pattern reflect adaptations to local abiotic environments?

If so, is this spatial niche structure reflected in species traits?

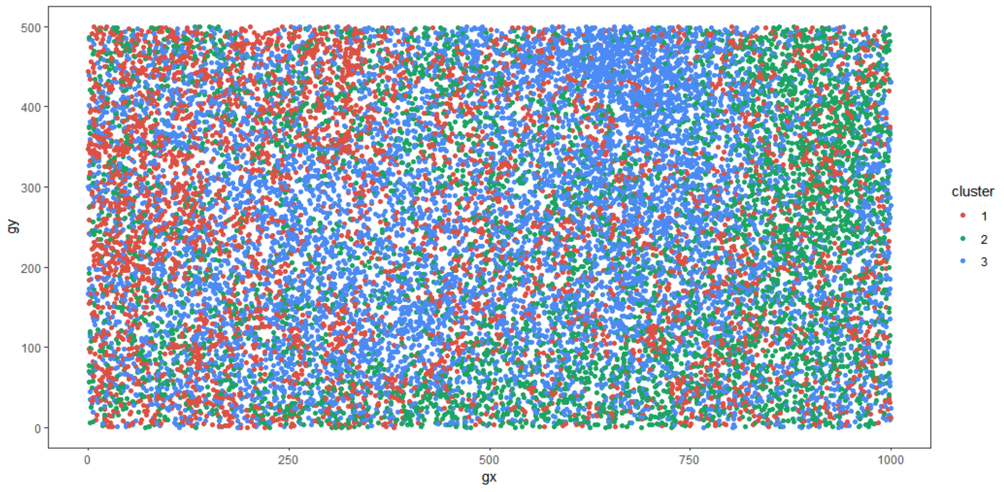
Step 3: Infer local abiotic conditions

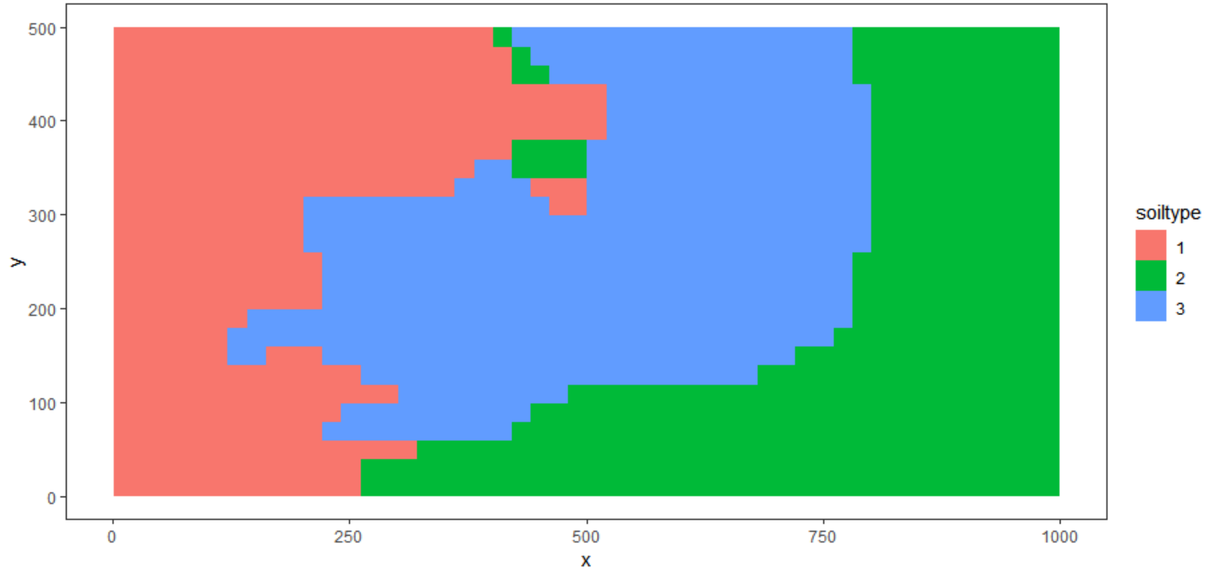
Assumptions:

- Each species group has its own preferred abiotic environment ("soil type")
- Soil type varies smoothly in space

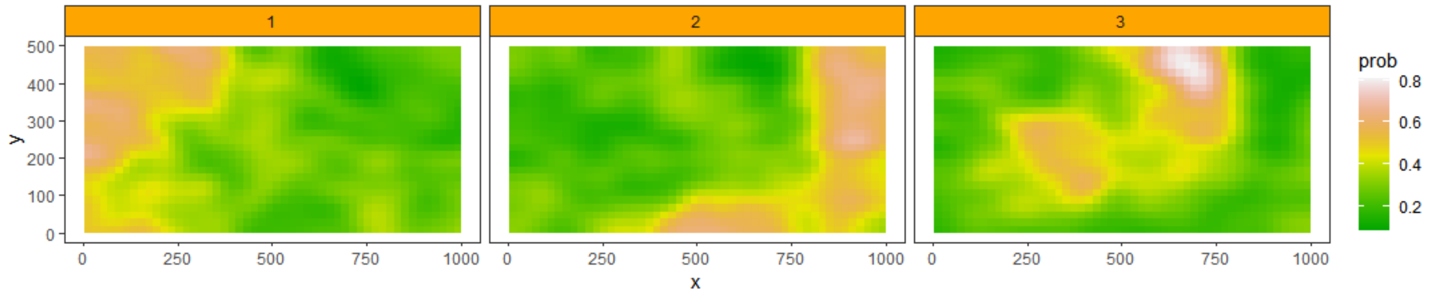


Step 3: Infer local abiotic conditions

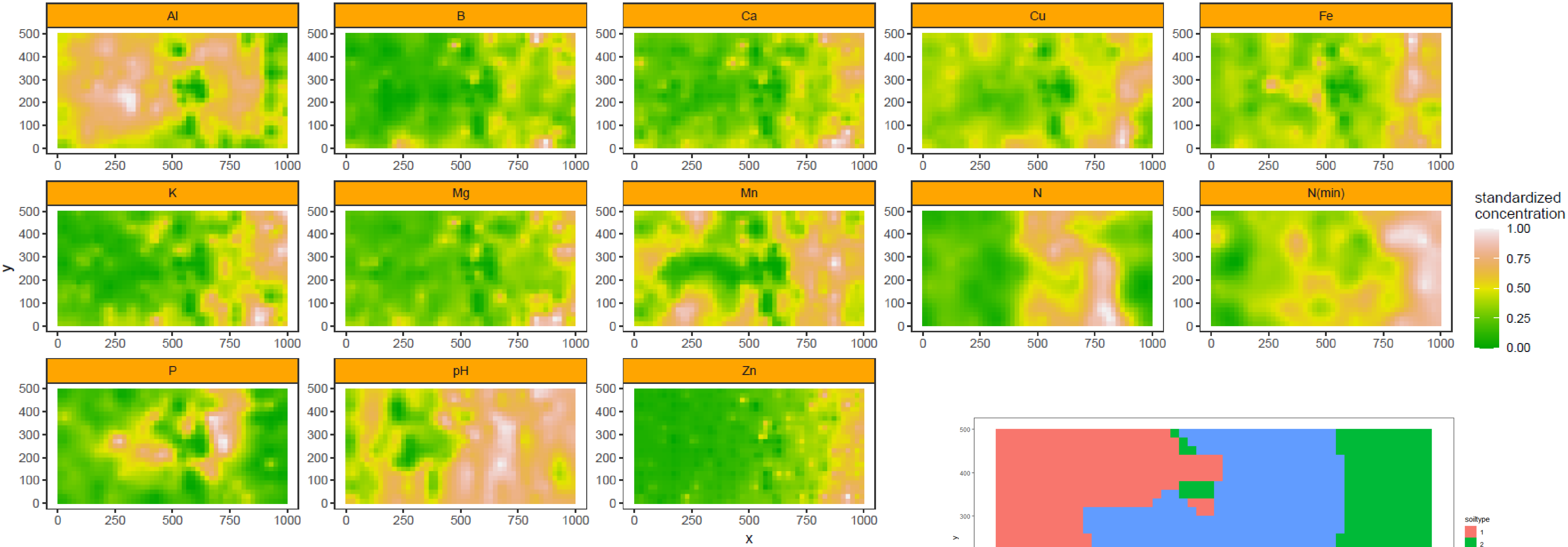




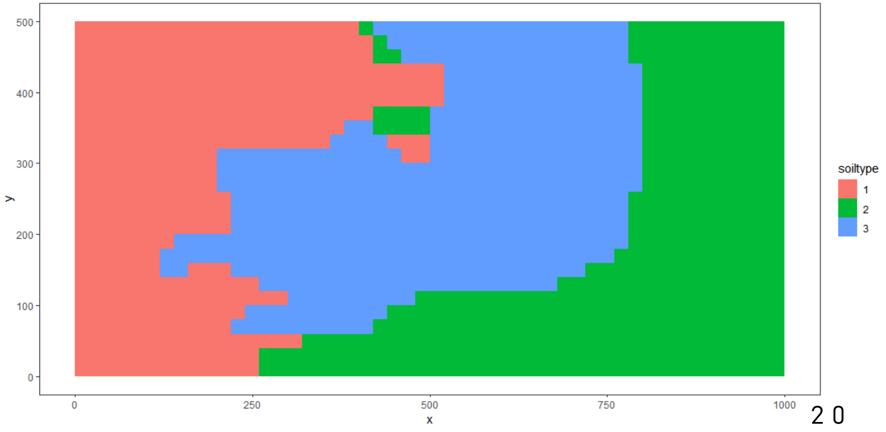
Kernel density estimation



Step 4: Compare with measured soil conditions



Krigged soil nutrient levels at 20 x 20 m quadrats.
Data courtesy of Jim Dalling

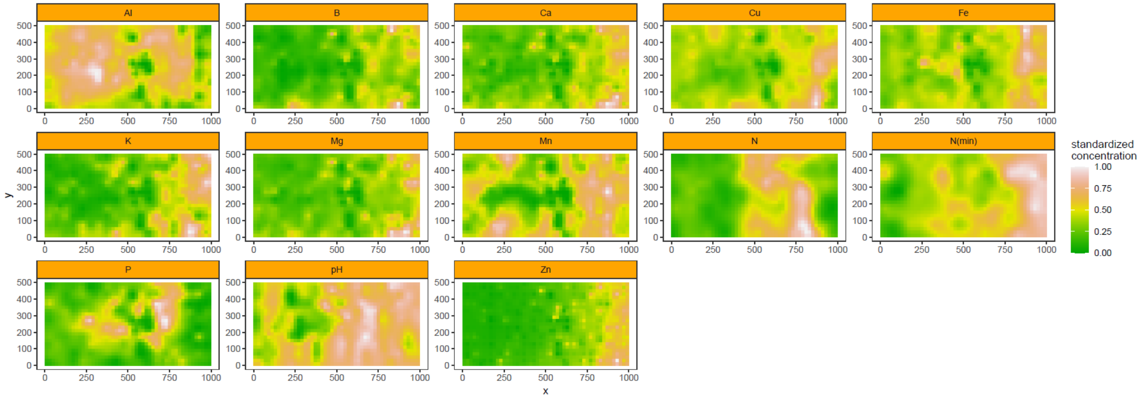


Step 4: Compare with measured soil conditions

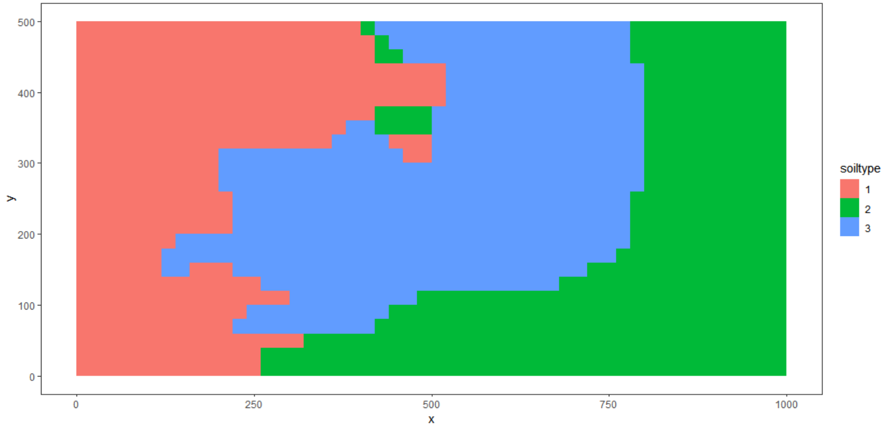
Game plan

- Train a statistical classifier to predict the inferred soil type based on local nutrient levels, and check for quality of predictions

- High-accuracy predictions would indicate that trees are sorting by local soil nutrients



predict

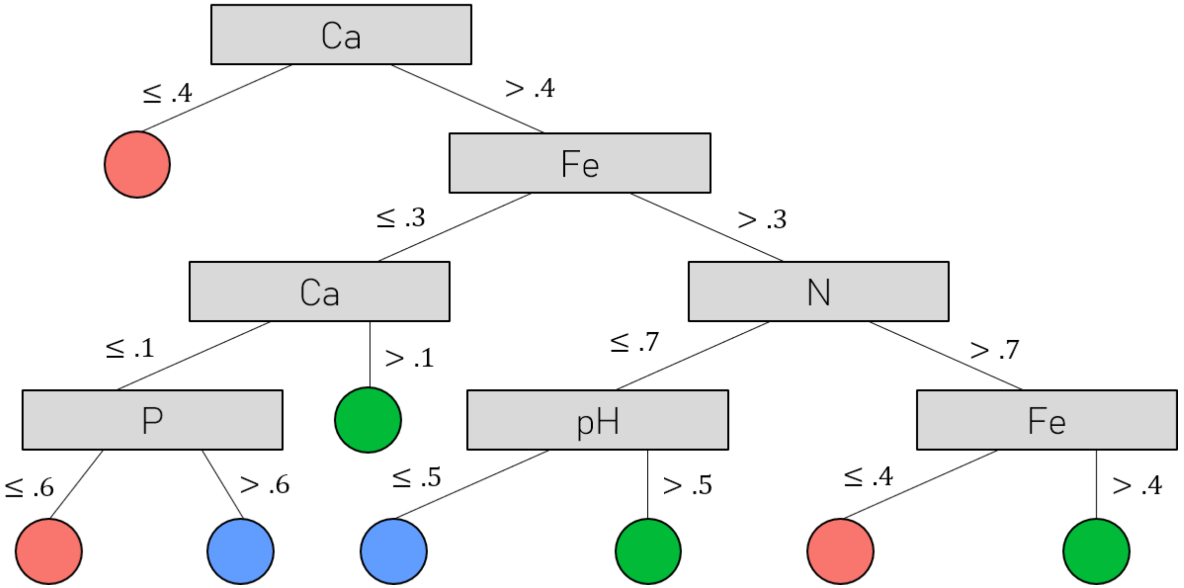


Step 4: Compare with measured soil conditions

Methods

- Statistical classifier:
  C5.0 decision tree algorithm
  - Builds decision trees by splitting data based on features
  - Finds rules that maximize information gain (i.e. increase within-group similarity) per split

Decision tree example



Step 4: Compare with measured soil conditions

Methods

- Assaying quality of prediction: Cohen's kappa
    - Compares observed accuracy to expected accuracy

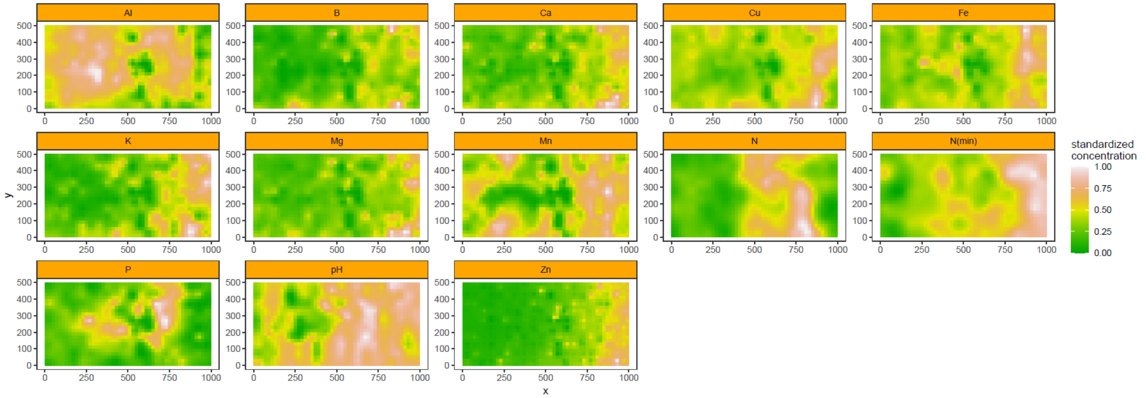
$$\kappa = \frac{\begin{pmatrix}\text{observed}\\ \text{agreement}\end{pmatrix} - \begin{pmatrix}\text{expected}\\ \text{agreement}\end{pmatrix}}{1 - \begin{pmatrix}\text{expected}\\ \text{agreement}\end{pmatrix}}$$

kappa	interpretation
< 0.2	poor agreement
0.2 to 0.4	fair agreement
0.4 to 0.6	moderate agreement
0.6 to 0.8	good agreement
> 0.8	very good agreement

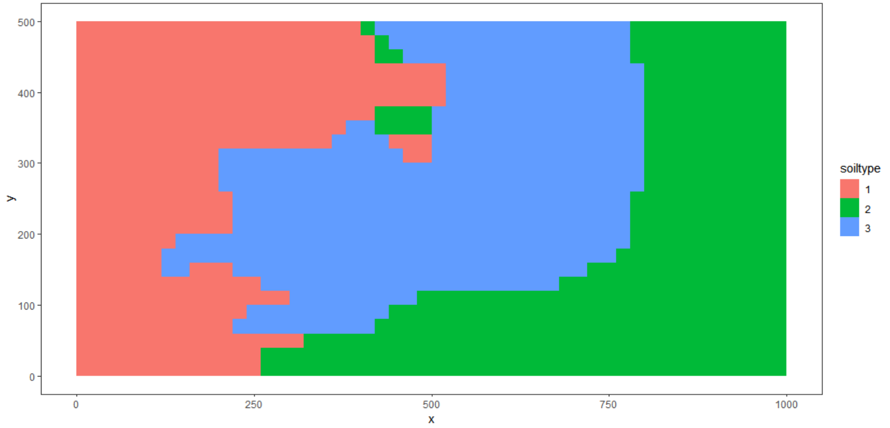
Step 4: Compare with measured soil conditions

Problem

- Both the data features and the predicted variable are spatially autocorrelated
- Some better-than-chance agreement is expected



predict



Step 4: Compare with measured soil conditions

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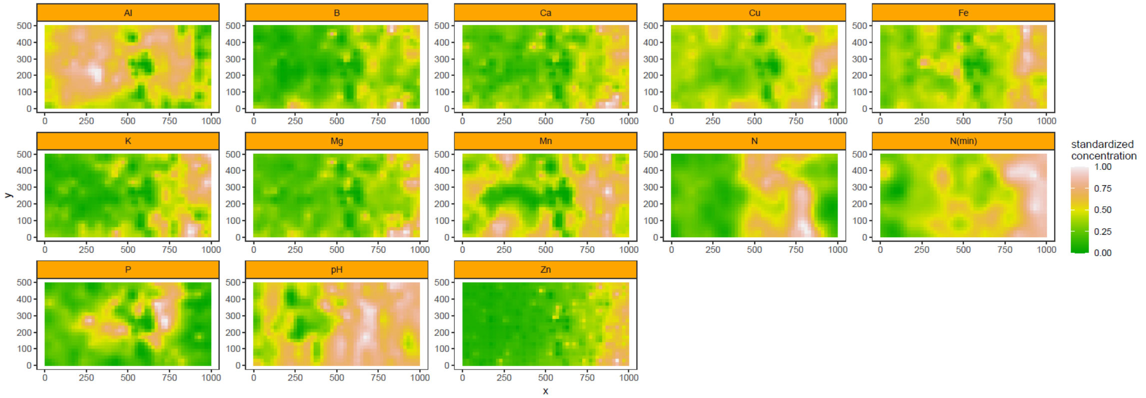


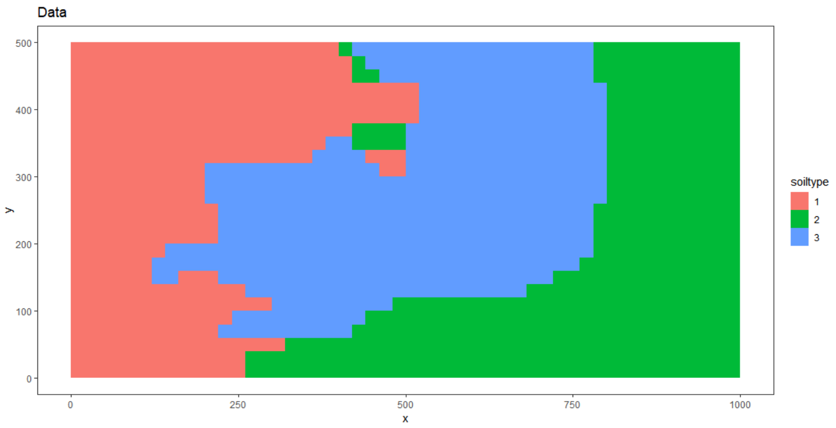
predict

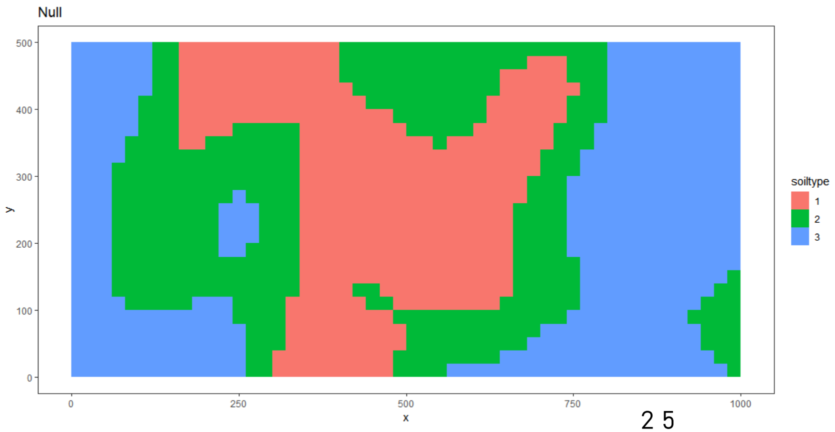
predict

compare

Solution

- Train the algorithm on mock autocorrelated data and compare results

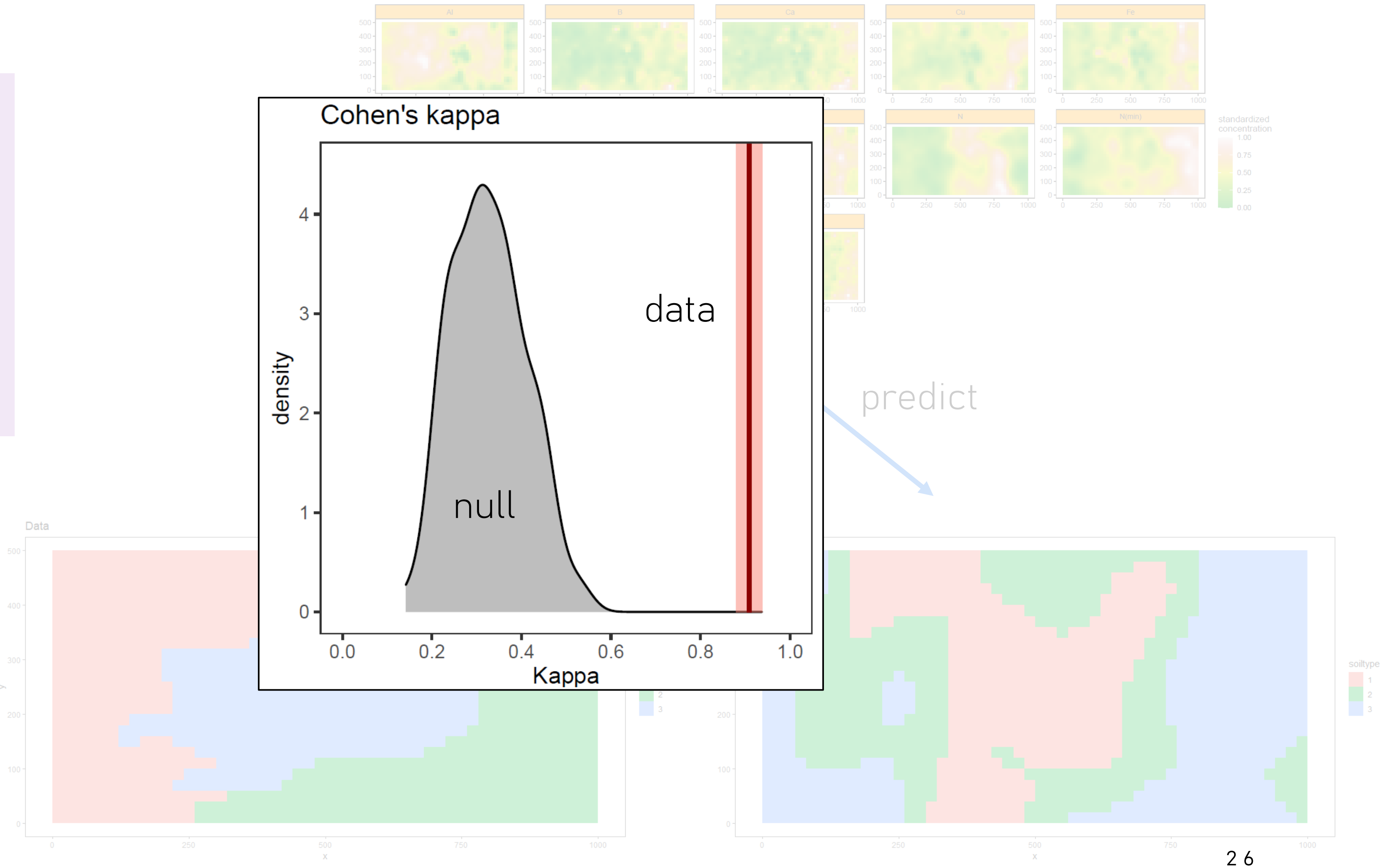




Step 4: Compare with measured soil conditions

Results

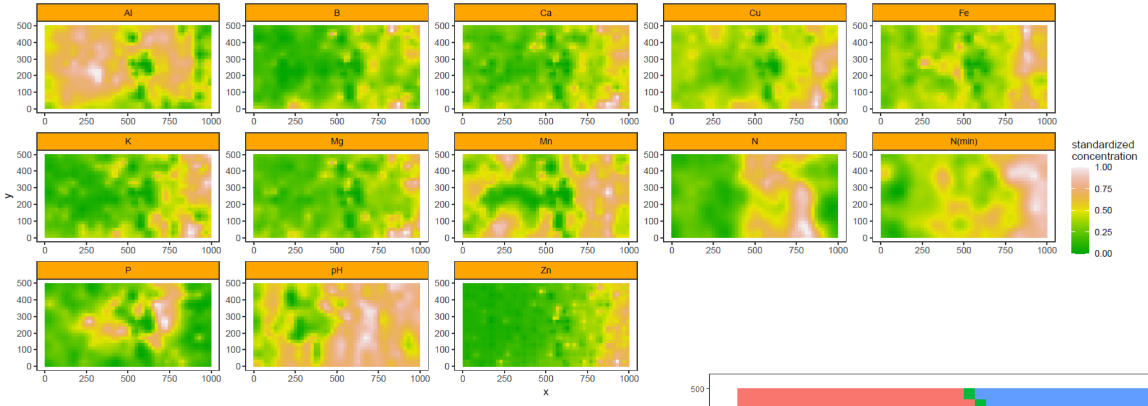
- Nutrients are highly predictive of inferred local conditions
- Association is much tighter than with null autocorrelated data

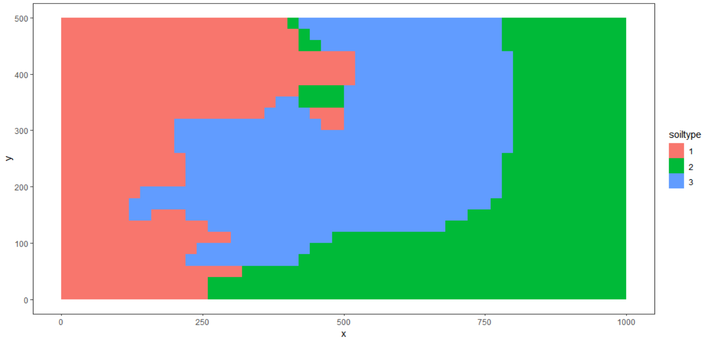


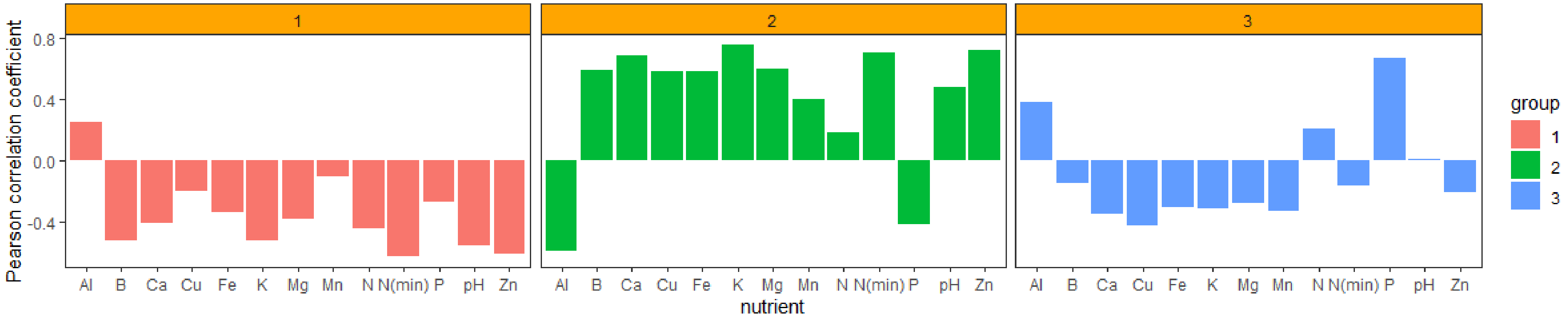
Step 4: Compare with measured soil conditions

Results

- Red group → low-nutrient sites
- Green group → high-nutrient sites
- Blue group → high P and organic N







This talk

Do tropical species segregate spatially at local scales? ✔

Does the pattern reflect adaptations to local abiotic environments? ✔

Is this spatial niche structure reflected in species traits?

Step 5: Compare with species traits

BCI trait data

- 77 species
- 32 traits
- 5 trait categories

Seed

Mass of seed (fresh, dry)
Mass of fruit (fresh, dry)
Mass of diaspore (fresh, dry)

Vital rates

Max DBH growth

Mortality at low DBH growth

Wood

Density after drying at 60C

Density after drying at 100C

Leaf

Lead area (sun leaf, shade leaf)
LMA disc (sun leaf, shade leaf)
LMA lamina (sun leaf, shade leaf)
Dry matter content
Thickness
Toughness
Etc

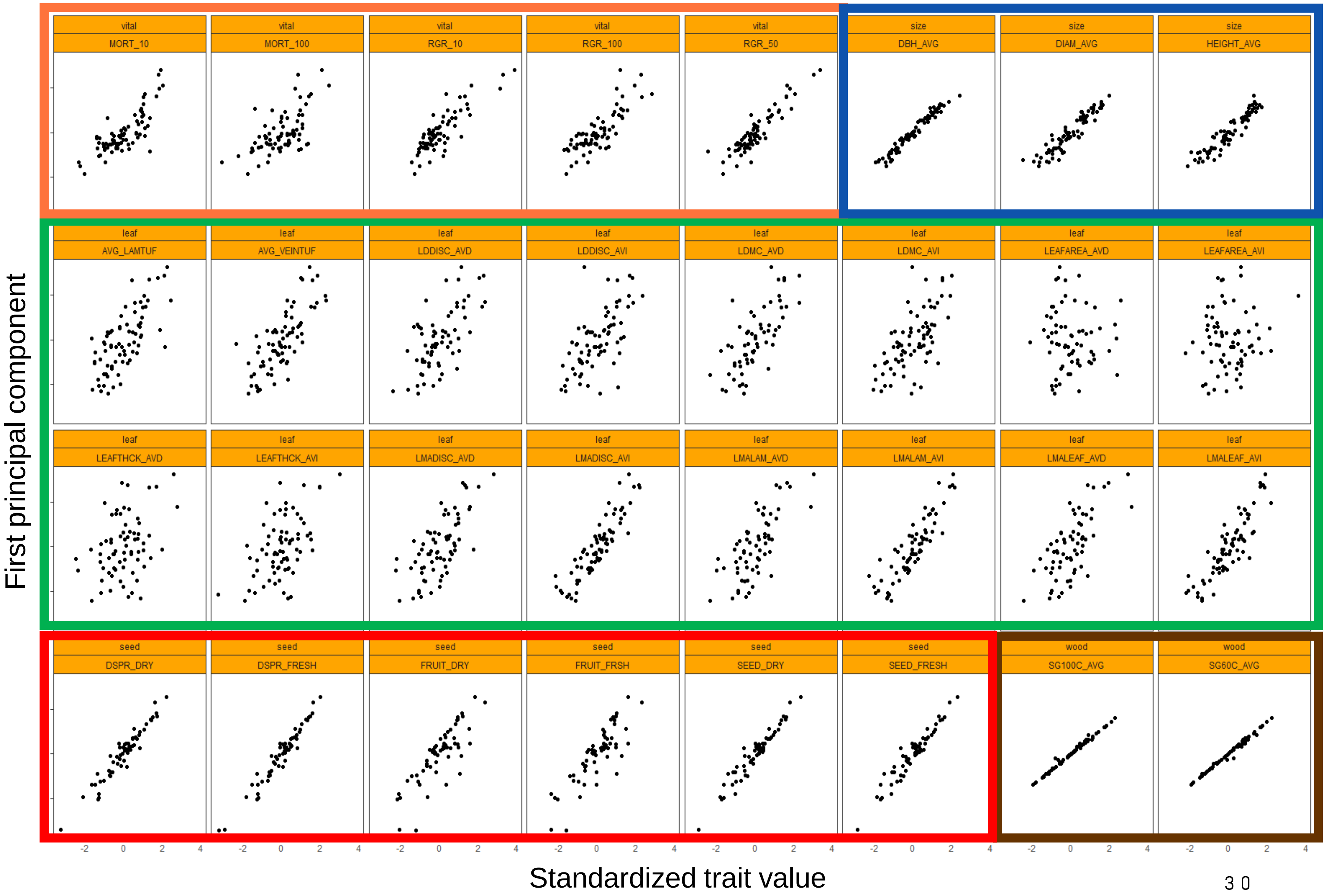
Size

Max DBH
Max height
Max canopy diameter

Trait data courtesy of Joe Wright

Step 5: Compare with species traits

- Traits of the same type are highly correlated/ redundant
- Ordination via PCA
- Keep 1st PC of each trait type

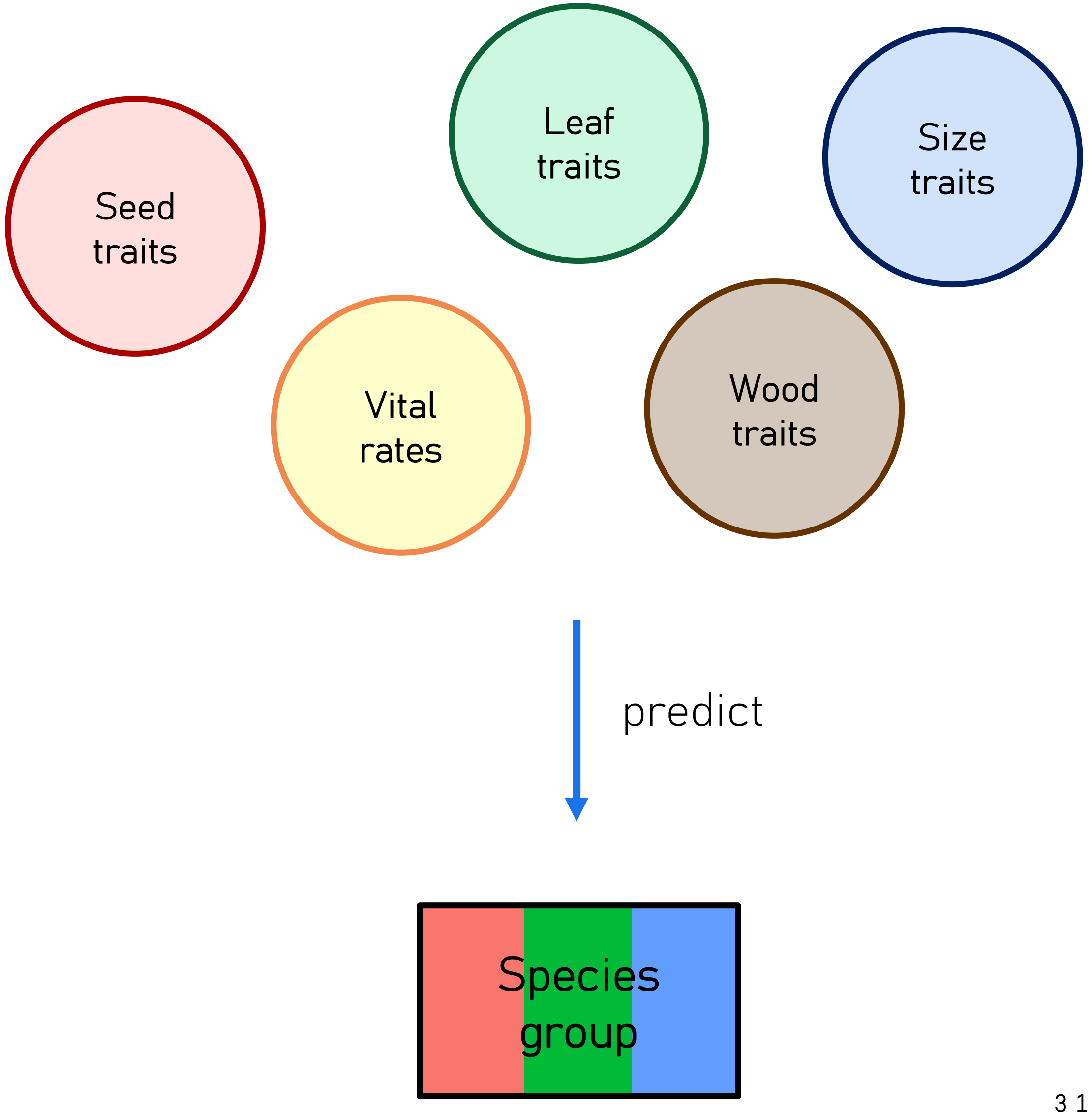


Trait data courtesy of Joe Wright

Step 5: Compare with species traits

Game plan

- Train C5.0 learner on species traits, predict species group
- No need to worry about autocorrelation
- Cohen's kappa will measure how informative species traits are in re to spatial groups

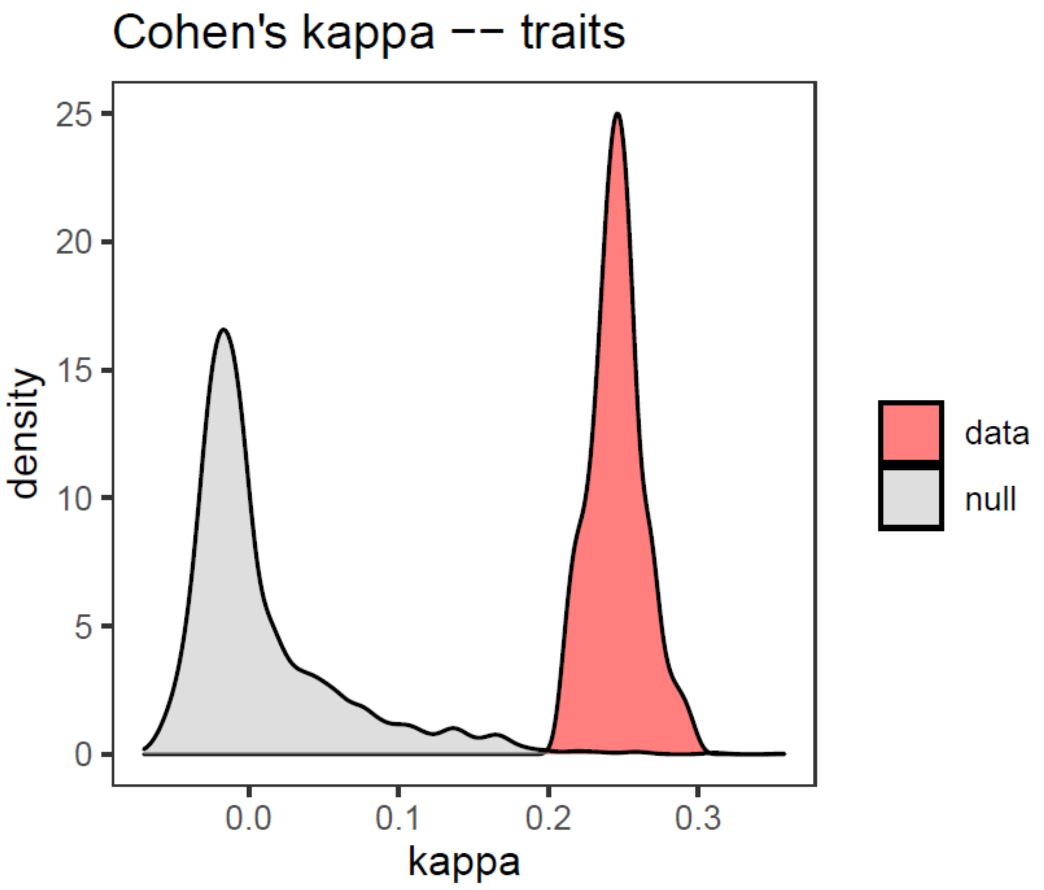


Step 5: Compare with species traits

Results

Q: Do traits predict species spatial cluster?

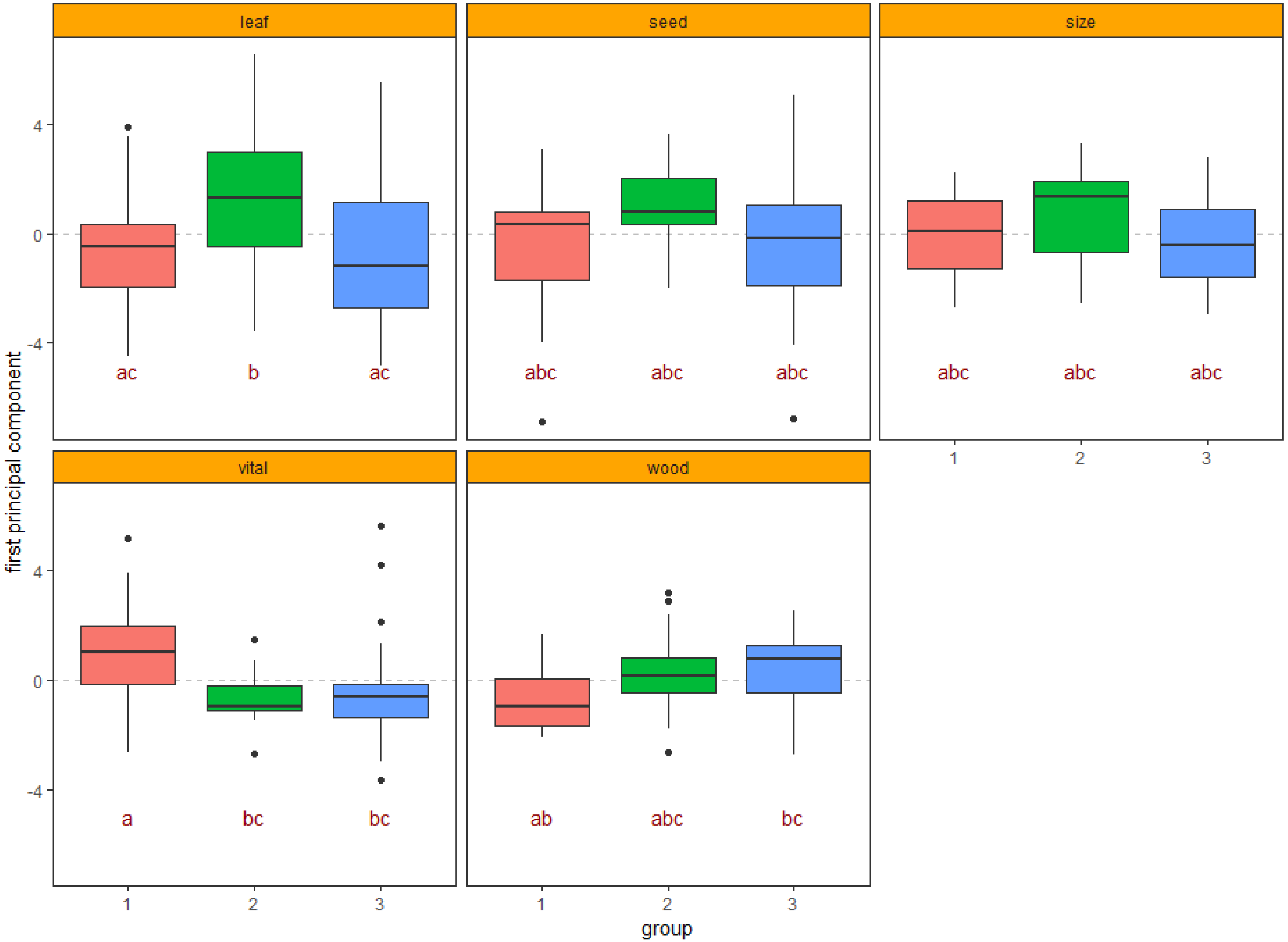
A: Yes, better than chance



Step 5: Compare with species traits

Results

- Red group has higher vital rates and lower wood density than Green and Blue groups
- Green group has higher leaf density, toughness, etc, than Red and Blue groups



Unshared letters (abc) denote significant differences ($\alpha = 0.05$, pairwise Wilcox test)

This talk

Do tropical species segregate spatially at local scales? ✔

Does the pattern reflect adaptations to local abiotic environments? ✔

Is this spatial niche structure reflected in species traits? ✔

Step 6: Tie it all together

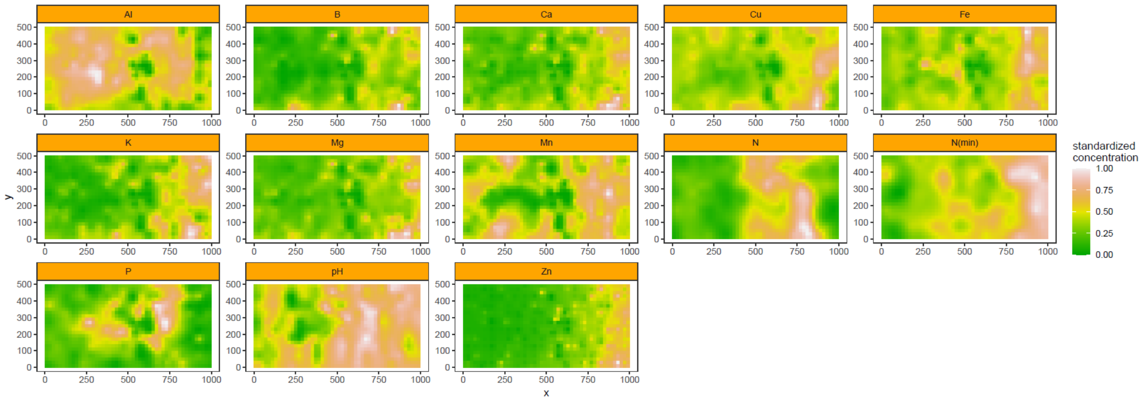
Q: Do the trait results match the nutrient results?

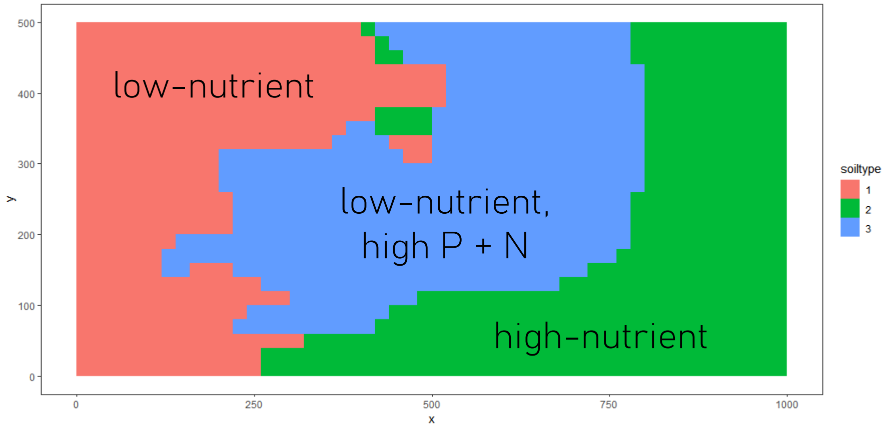
1. If local soil conditions filter among dispersing species, we would expect local species to be adapted to local soil conditions
   - E.g., live-fast-die-young species may disproportionately recruit in high-nutrient soils

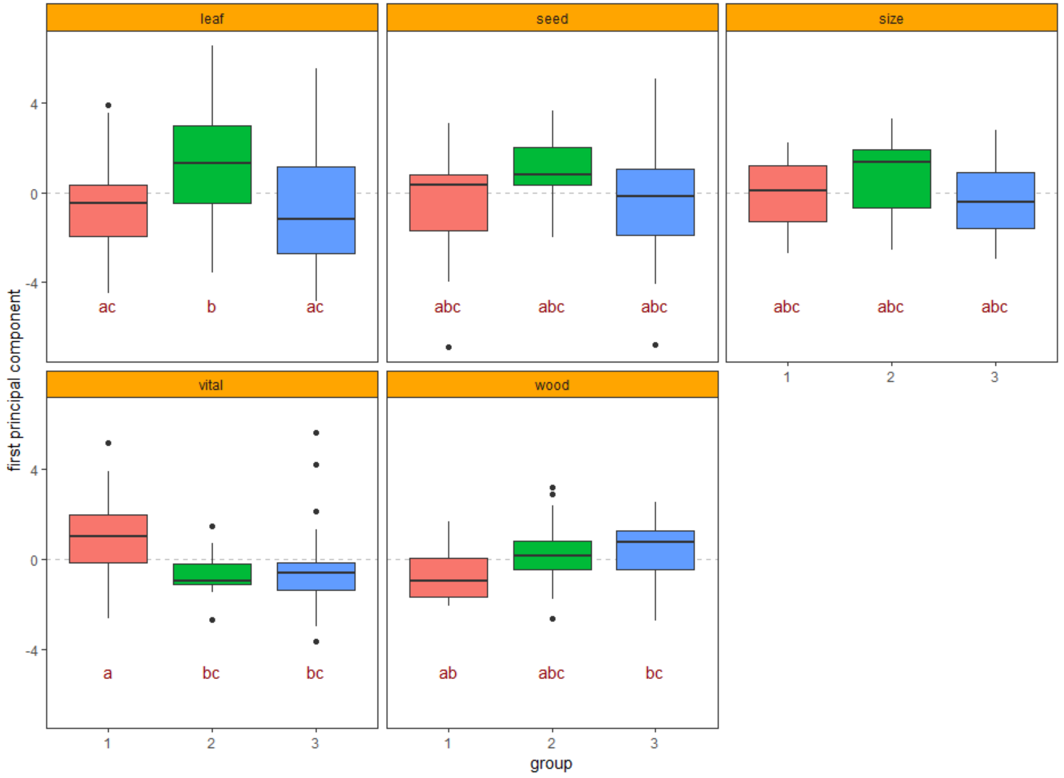
2. If species modulate the local environment, we would expect local soil conditions to reflect species composition
   - E.g., live-fast-die-young species may deplete local soil nutrients, and will then be found in low-nutrient areas

Hypothesis	Prediction
1. soil → species	vital rates $\overset{+}{\leftrightarrow}$ nutrients
2. species → soil	vital rates $\overset{-}{\leftrightarrow}$ nutrients

Step 6: Tie it all together







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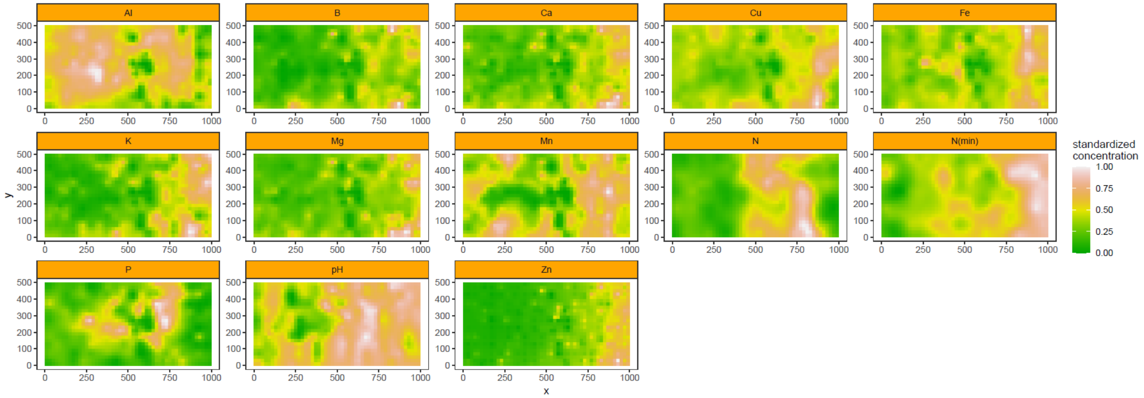
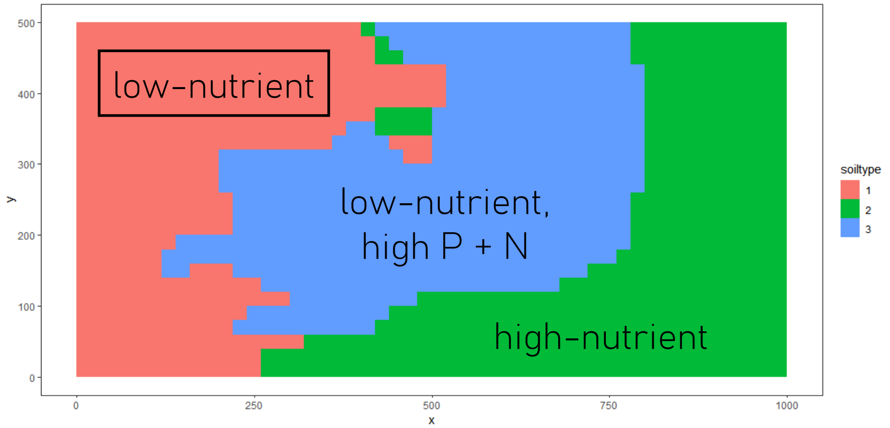
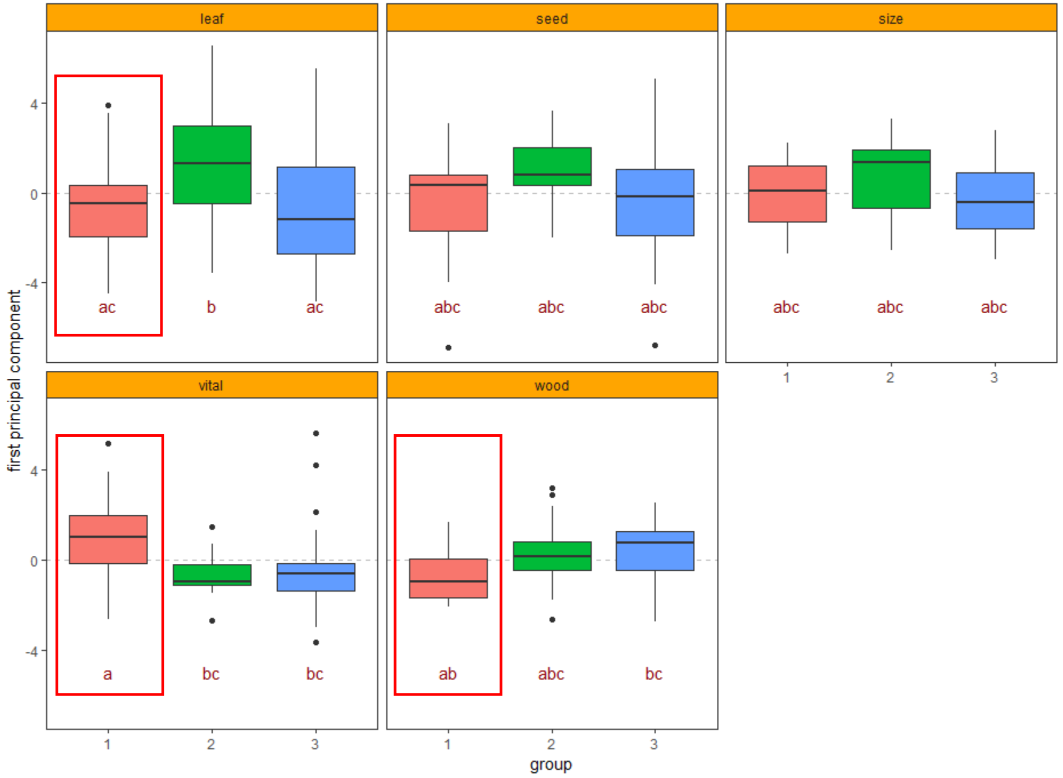


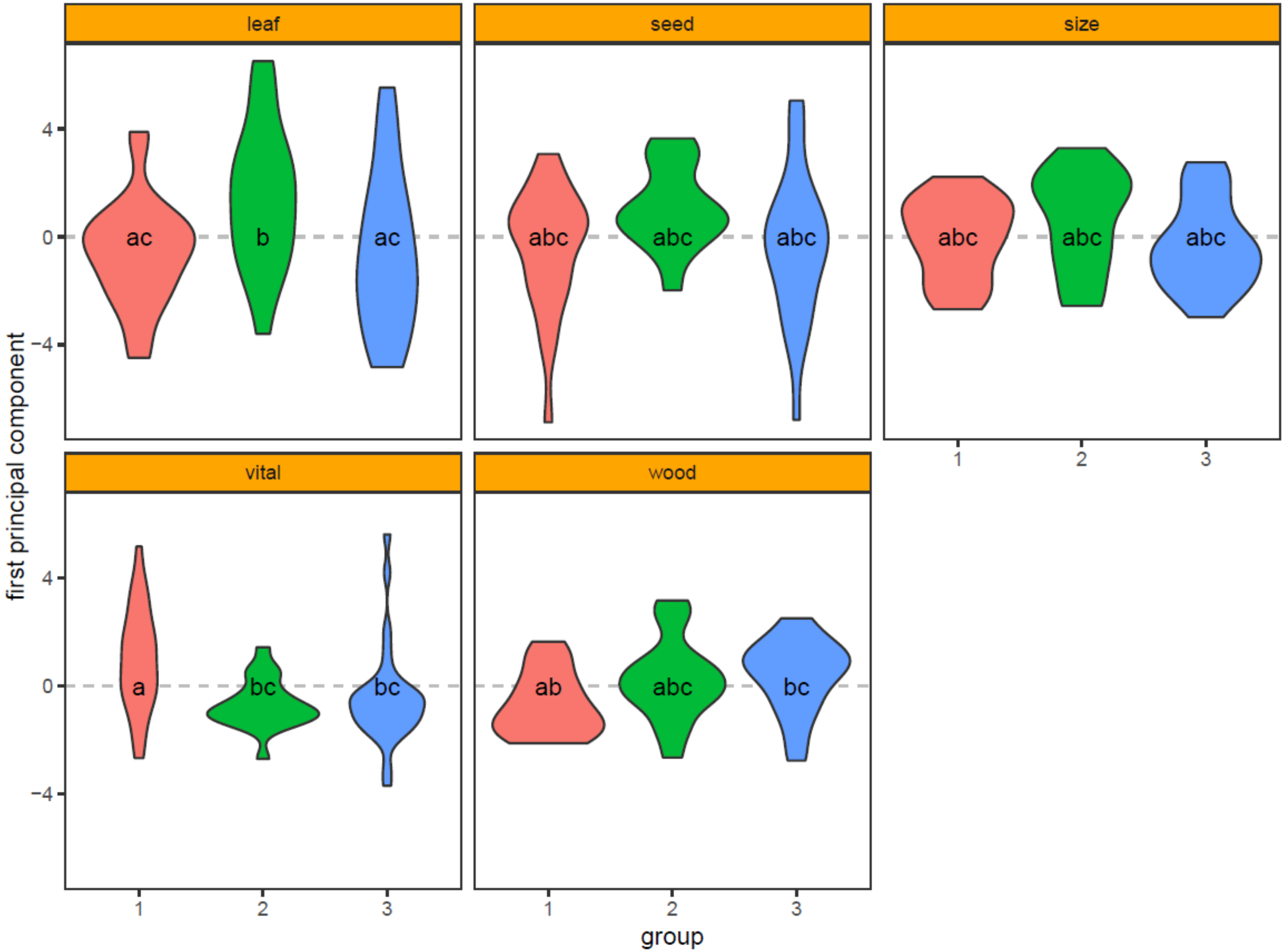




Step 6: Tie it all together

Note

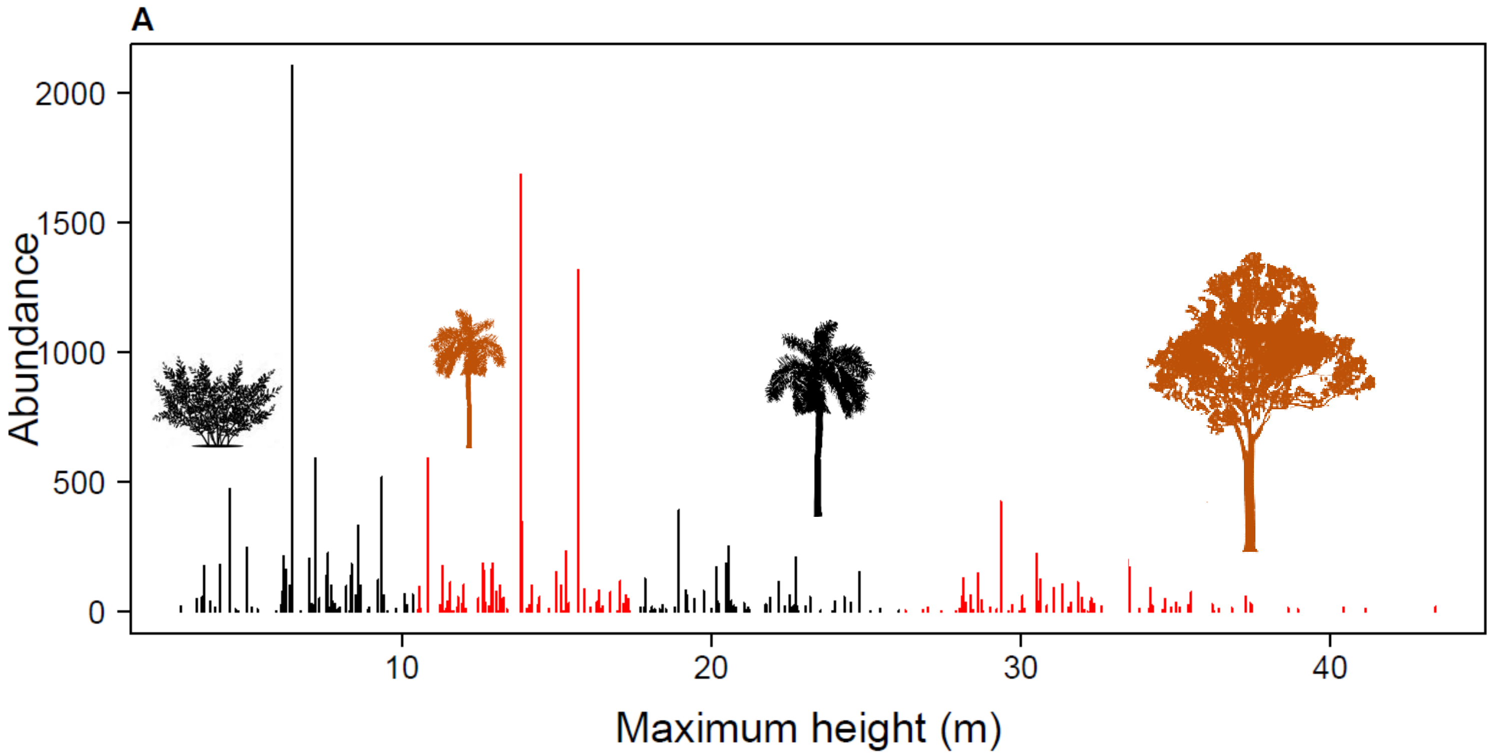
- Only a crude description of trait distribution
- Possible substructure – trait clusters within groups?



Unshared letters (abc) denote significant differences ($\alpha = 0.05$, pairwise Wilcox test)

Step 6: Tie it all together

- D'Andrea et al. 2020: BCI trees fall into height clusters revealing niche structure in competition for light
- When species are sorted by "soil niches", might their light-related clustered trait structure become even more apparent?



Conclusions

BCI trees are spatially sorted into groups of common neighbors

These groups are strongly associated with local soil conditions

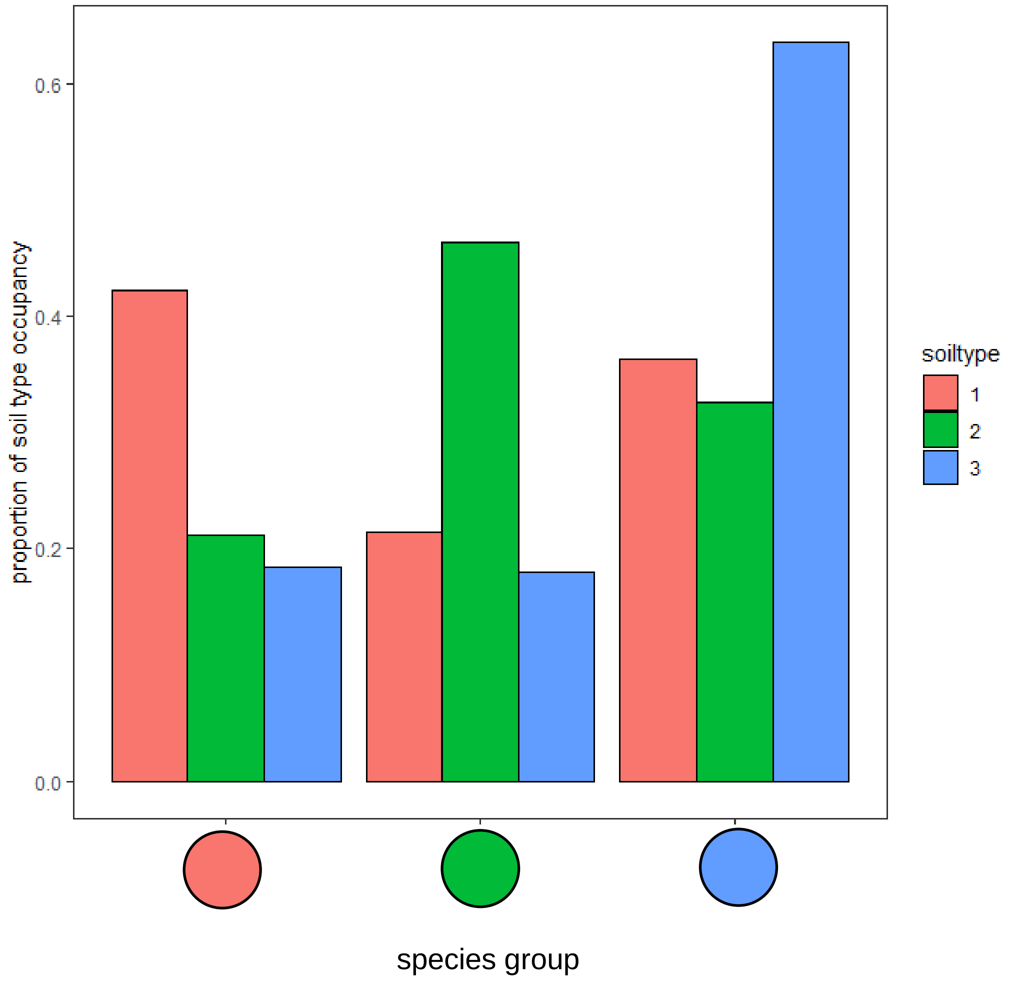
The groups also sort by life-history traits

Results suggest local flora modulates soil conditions rather than the reverse.

Deeper trait-based analysis may reveal further niche structure

Coda: Quantifying niche differentiation

- Estimating degree of niche differentiation:
  - Compare proportion of time trees of each group are found in their best "soil type" to proportion of time they are found in other "soil types".
- BCI: 2.1 ± 0.3
- D'Andrea et al. 2020b: consistent with emergent neutral behavior
- Compare to other spatial methods of estimating species interactions (e.g. Volkov et al. 2009)

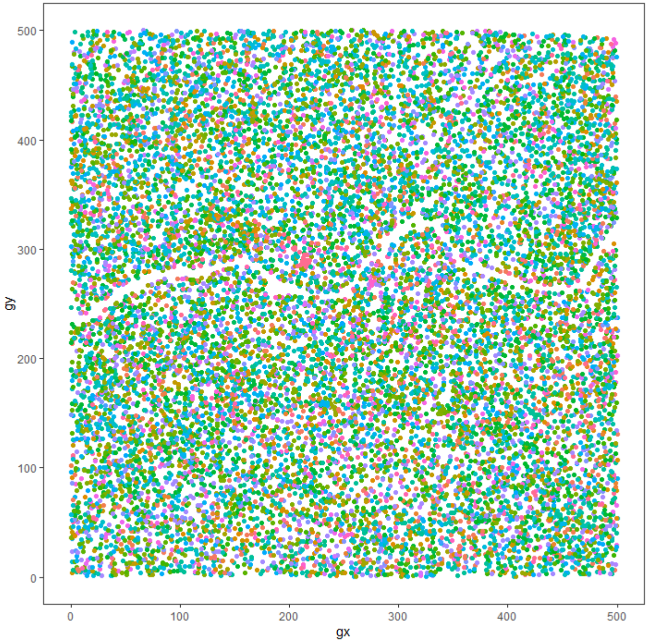


What about other forests?

La Planada

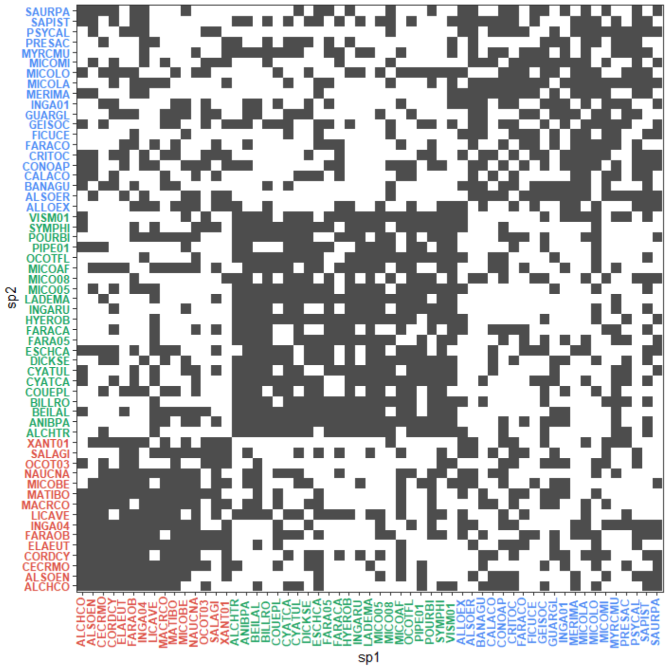

Photo credit: ForestGEO


Photo credit: ForestGEO

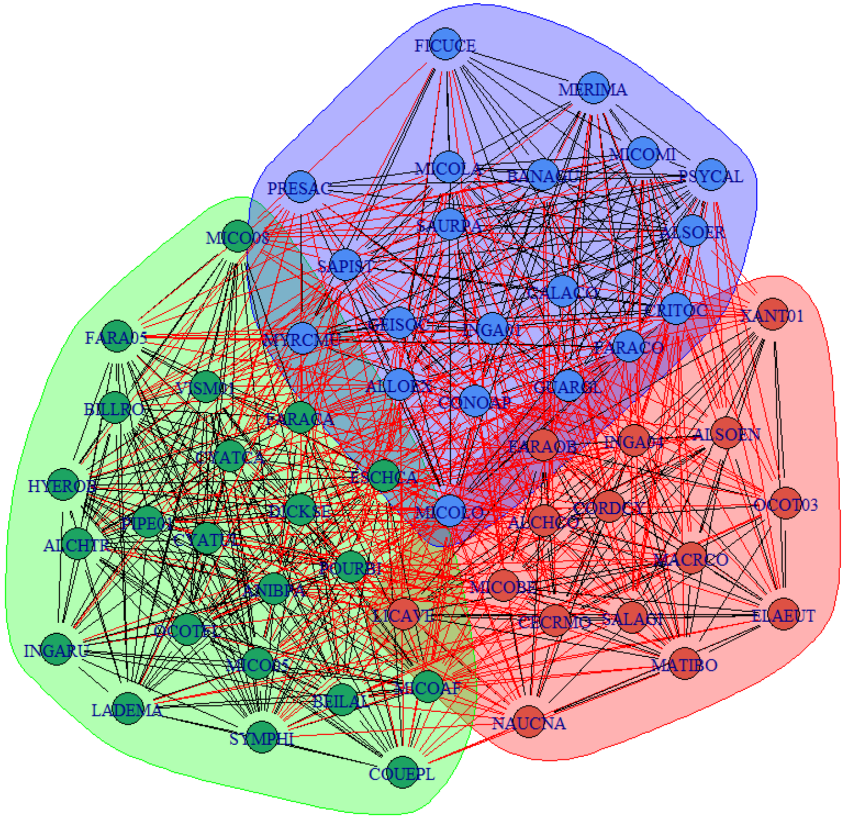


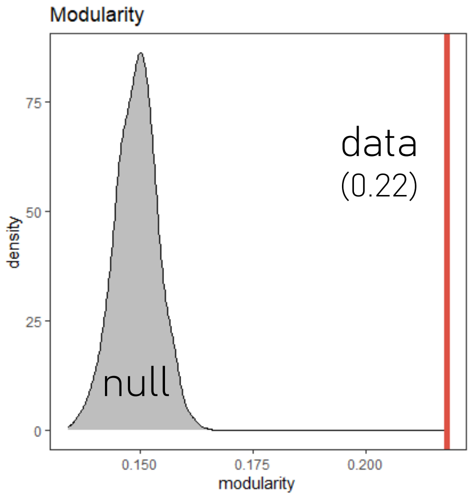
Data courtesy of Dr Natalia Norden

La Planada

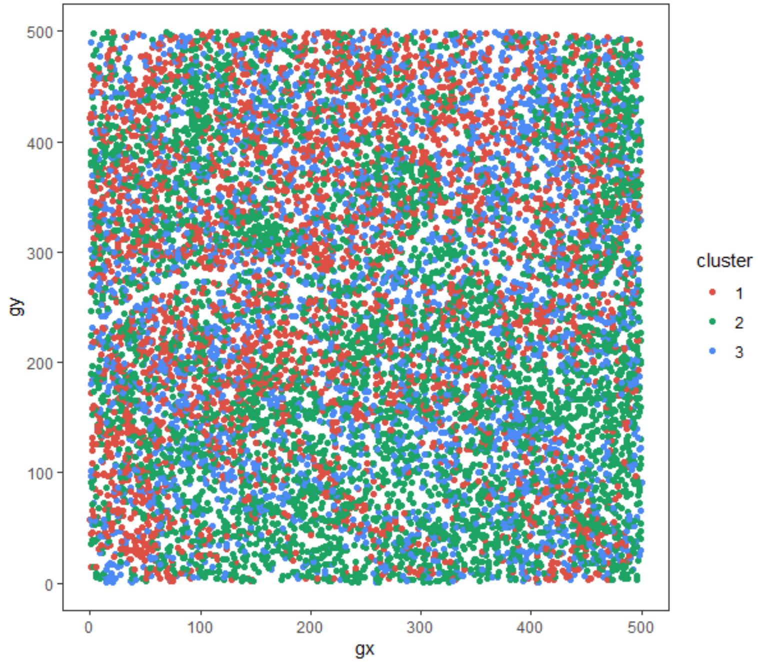


sp2
sp1



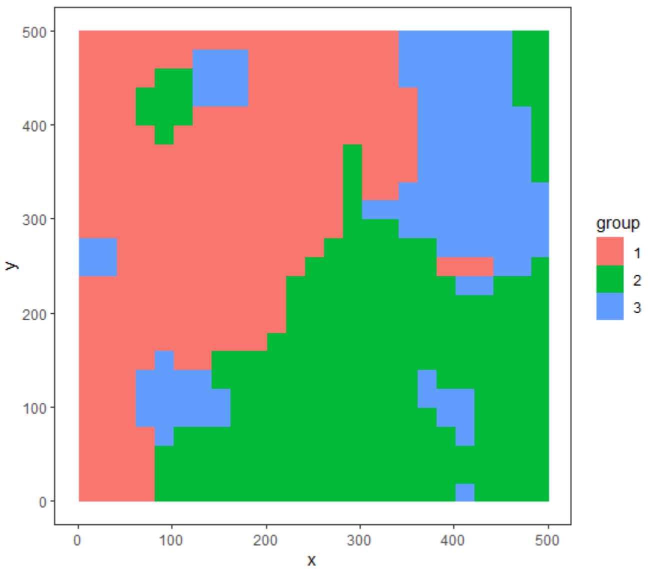


Modularity
density
75
50
25
0
0.150
0.175
0.200
modularity
data
(0.22)
null

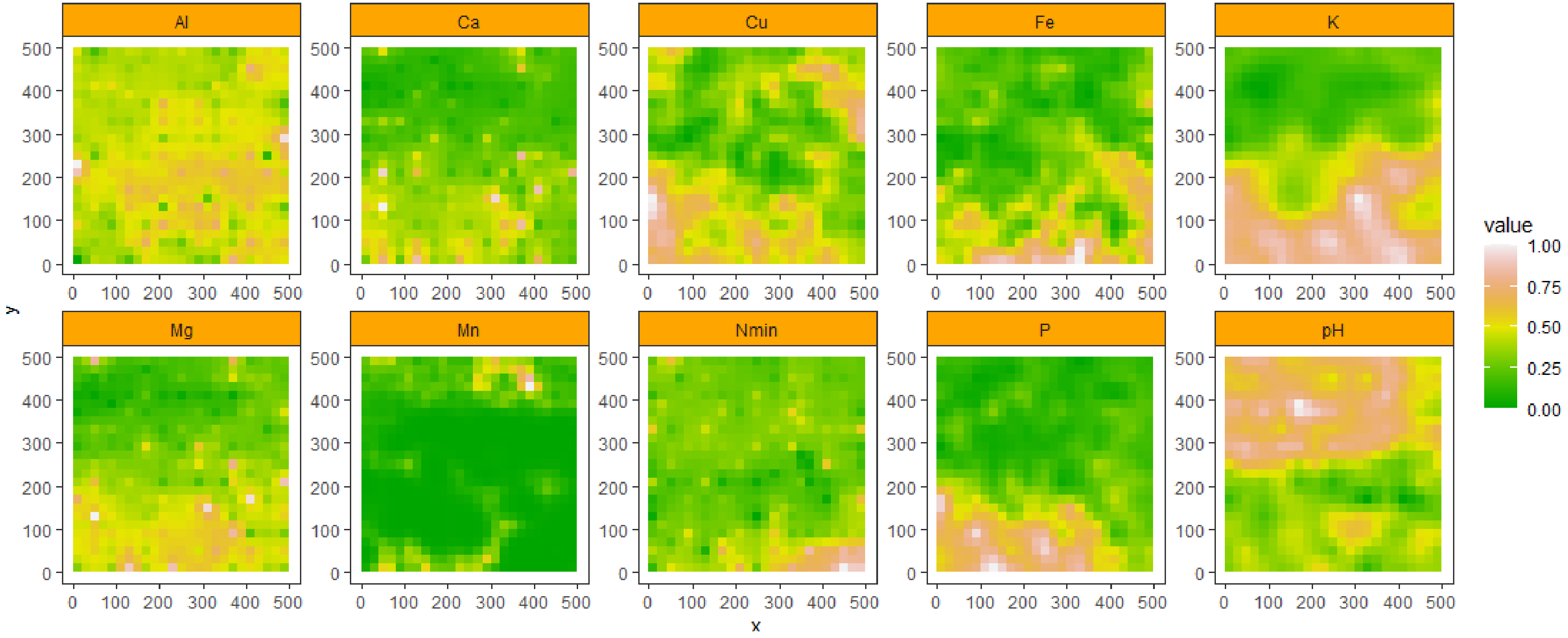


gy
500
400
300
200
100
0
0
100
200
300
400
500
gx
cluster
1
2
3

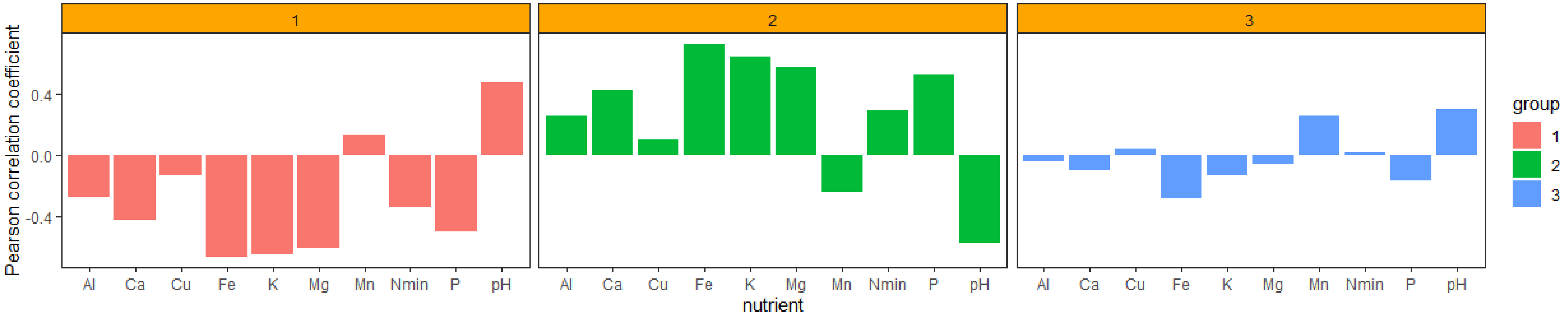
La Planada



group
1
2
3
x
y



Al
Ca
Cu
Fe
K
Mg
Mn
Nmin
P
pH
value
1.00
0.75
0.50
0.25
0.00
x
y



1
2
3
Pearson correlation coefficient
0.4
0.0
-0.4
Al Ca Cu Fe K Mg Mn Nmin P pH
nutrient
group
1
2
3

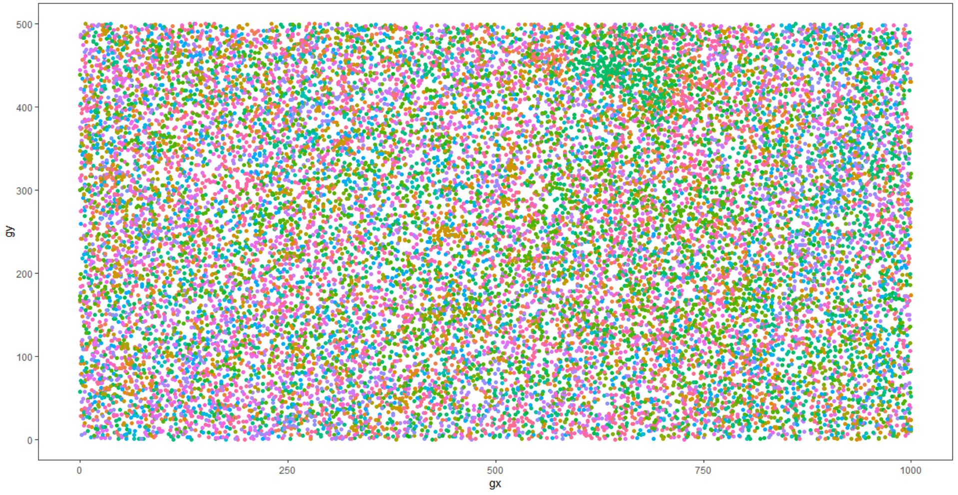
BCI vis-à-vis La Planada

BCI	La Planada
1,000 m x 500 m plot 207k (18k) trees 298 (77) species	500 m x 500 m plot 105k (12k) trees 241 (56) species

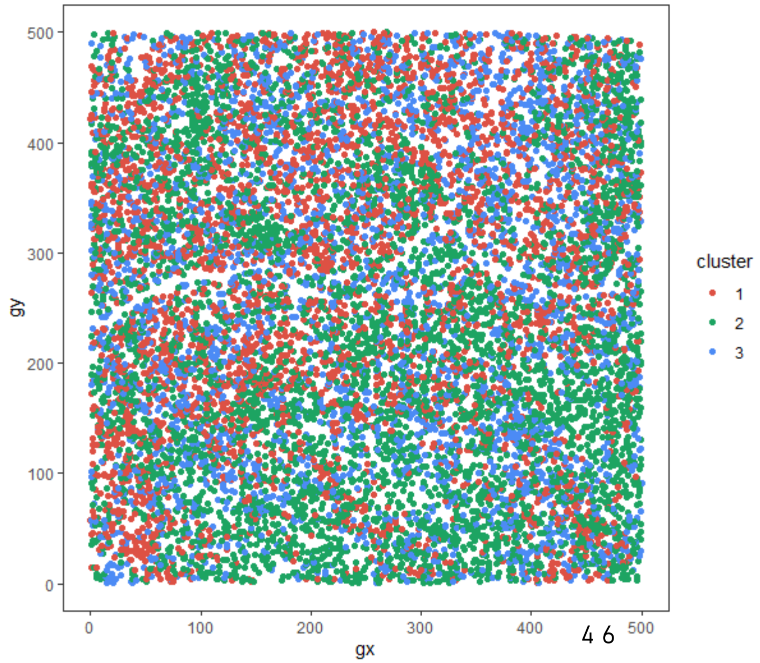
Idea:
Compare group membership of shared species

Problem:
Only one shared species in the analysis (12 total)

BCI

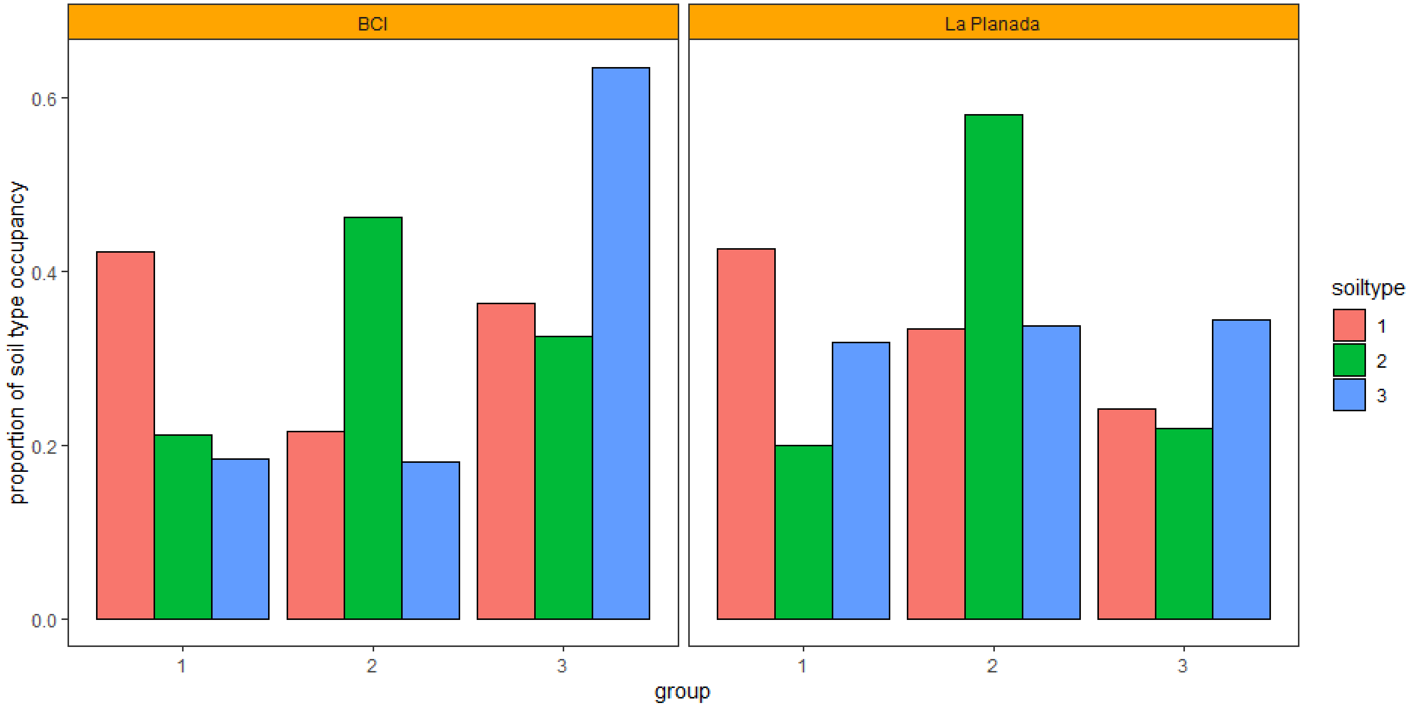


La Planada



BCI vis-à-vis La Planada

- Estimating degree of niche differentiation:
  - Compare proportion of time trees of each group are found in their best "soil type" to proportion of time they are found in other "soil types".
- **BCI**: 2.1 ± 0.3,
  La Planada: 1.6 ± 0.1



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What are your questions?

Trait type correlations

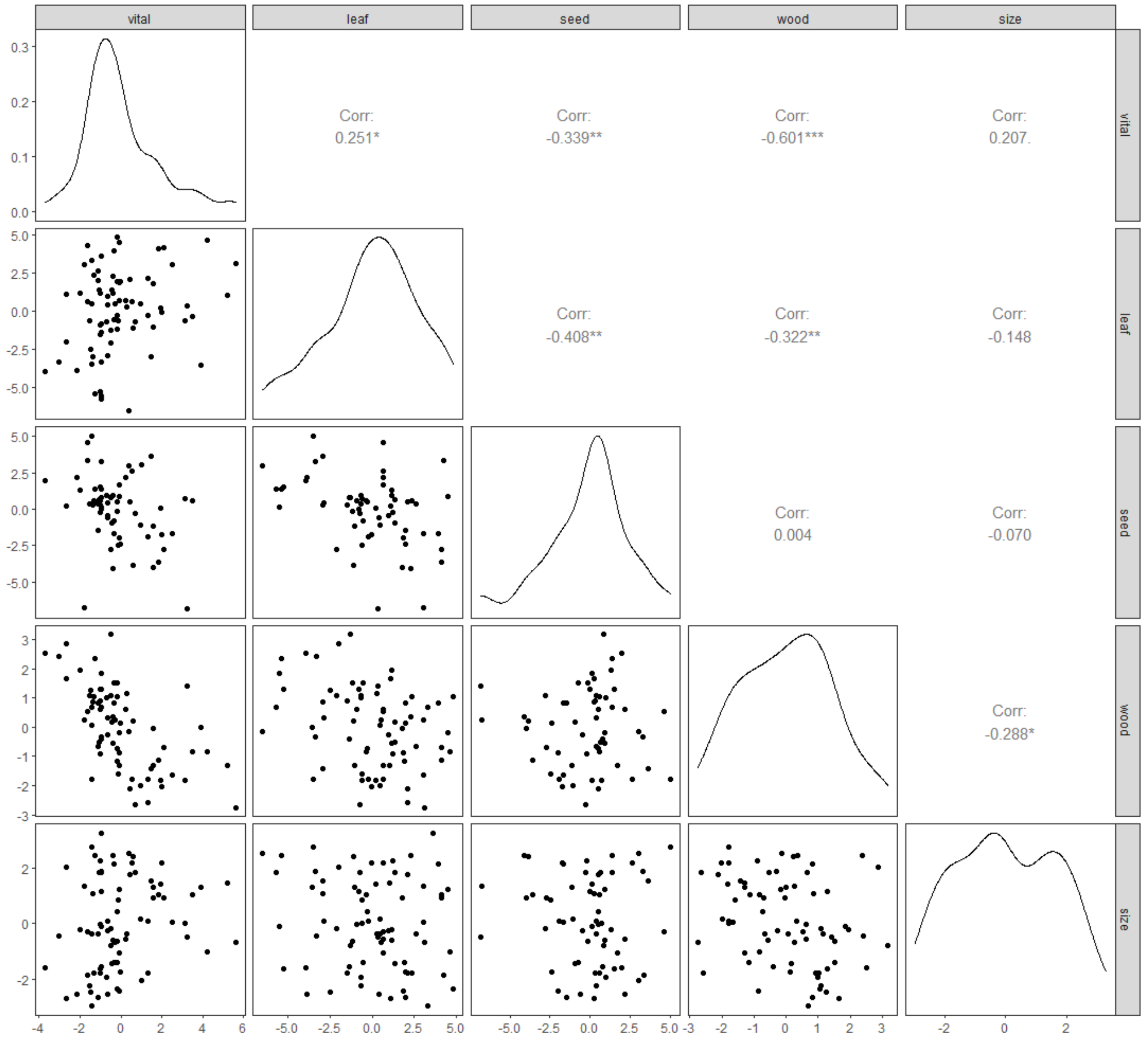
Correlations between trait types:

vital $\overset{-}{\leftrightarrow}$ wood

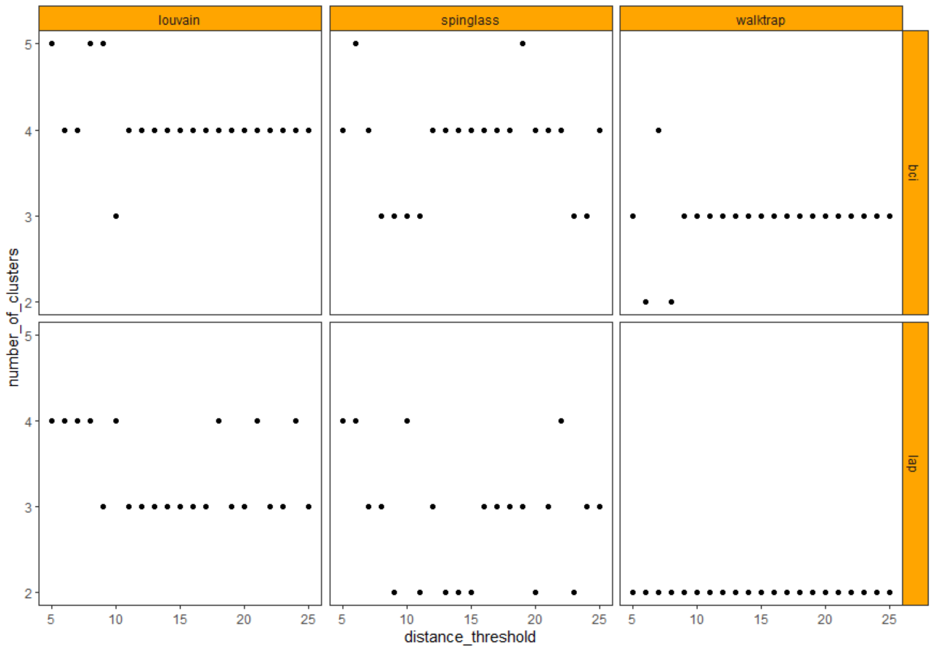
vital $\overset{-}{\leftrightarrow}$ seed

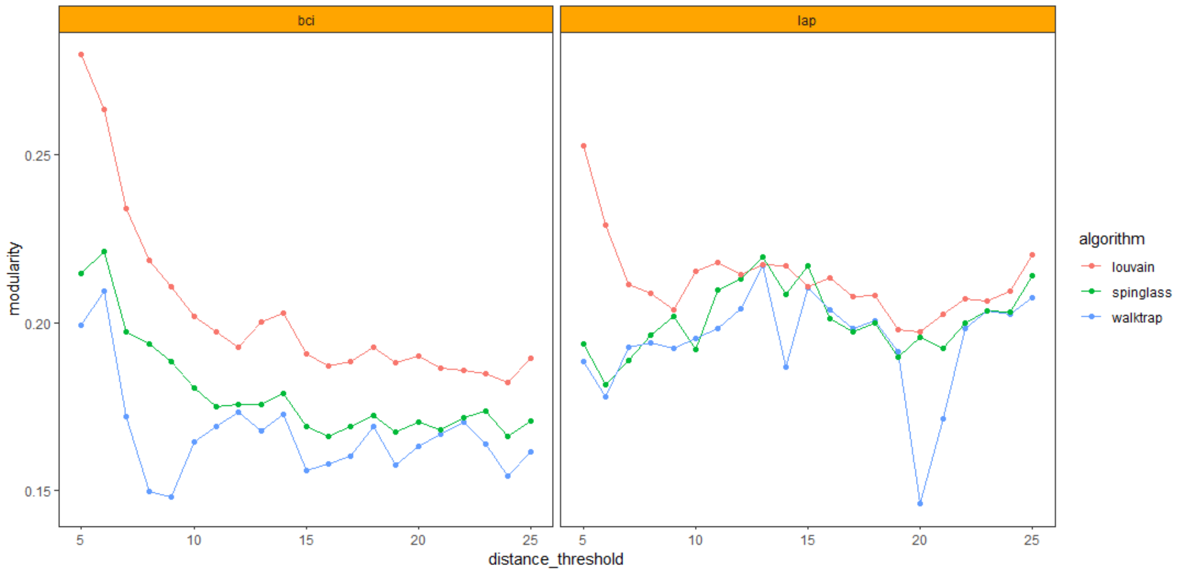
leaf $\overset{-}{\leftrightarrow}$ seed

leaf $\overset{-}{\leftrightarrow}$ wood



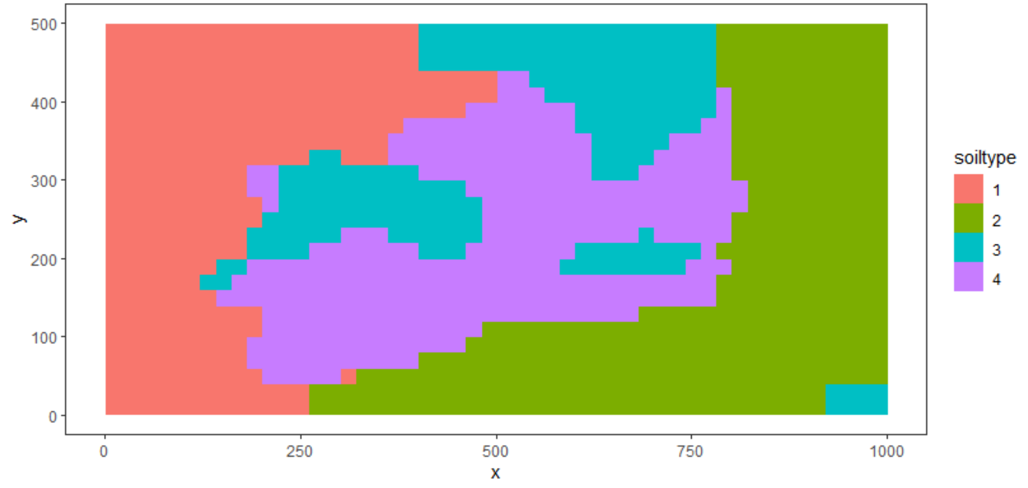
Robustness analysis

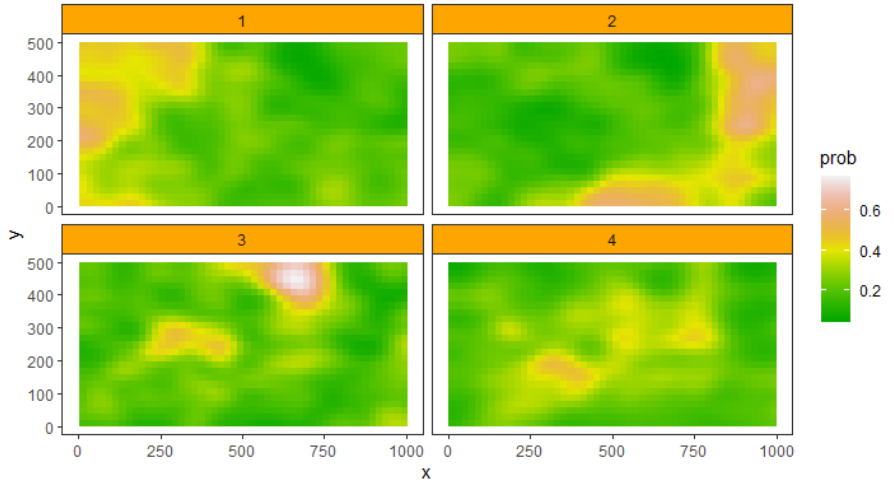


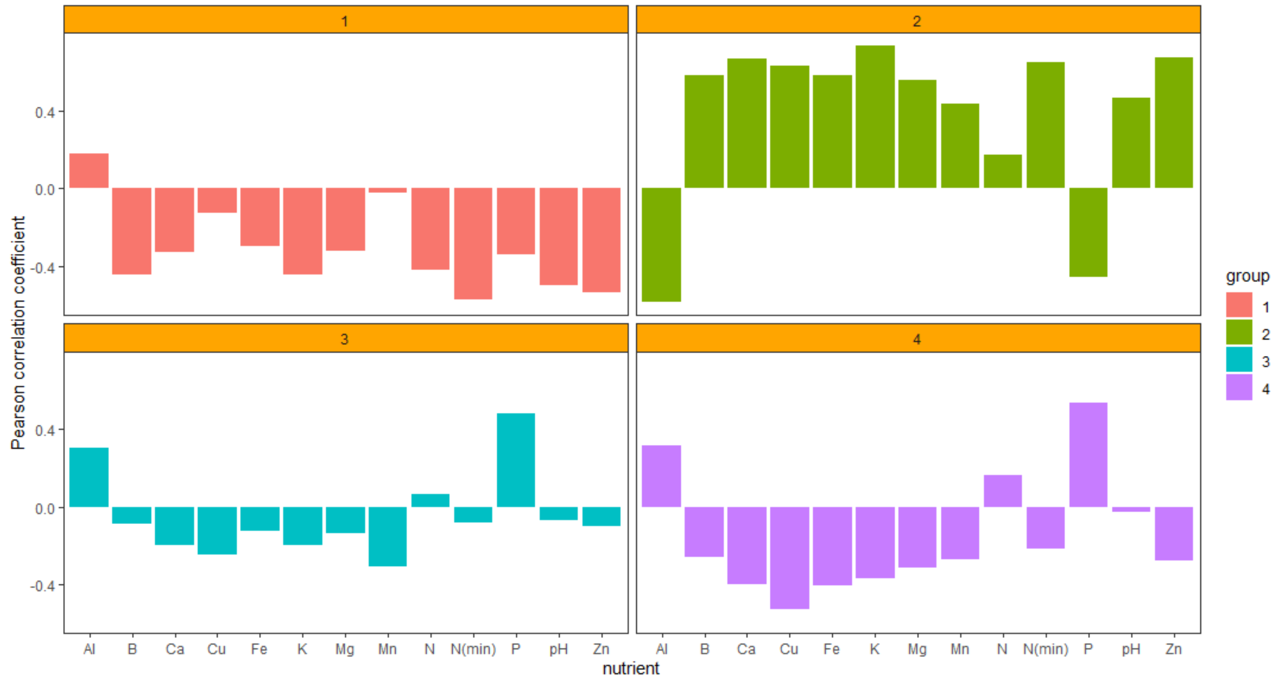


Robustness analysis

BCI: 4 clusters



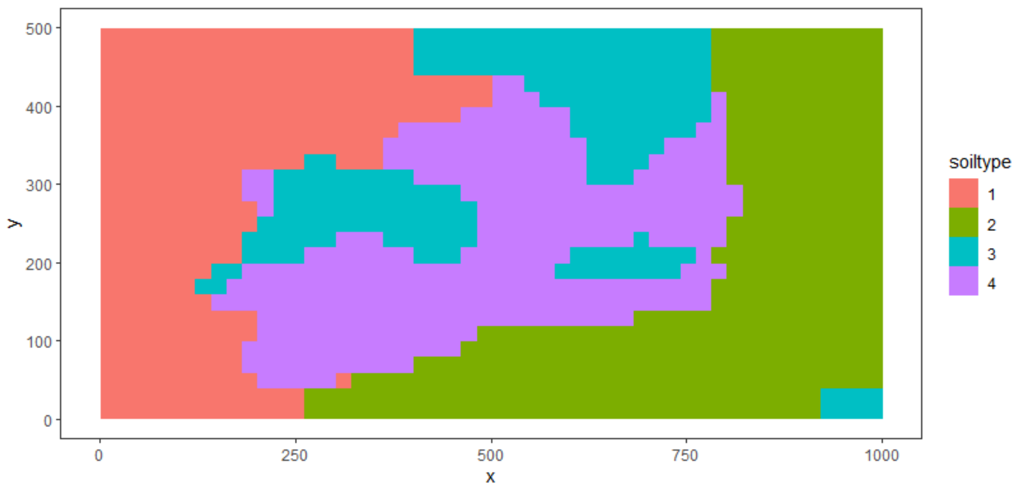


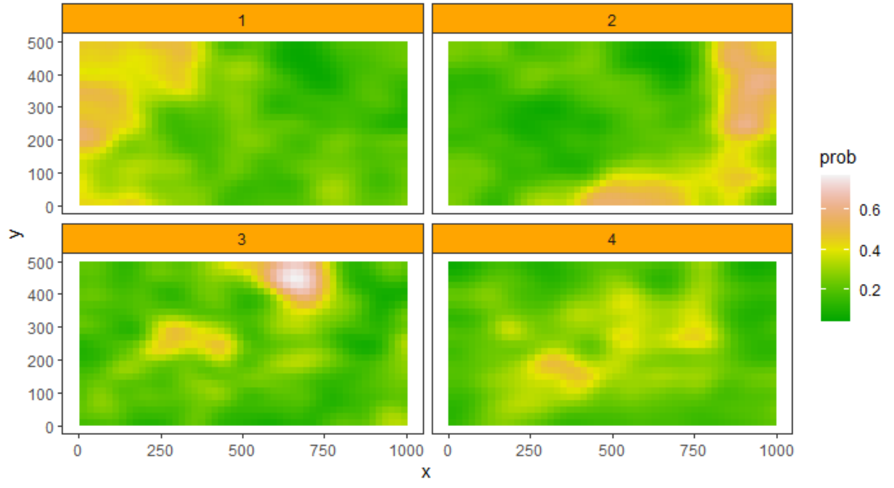


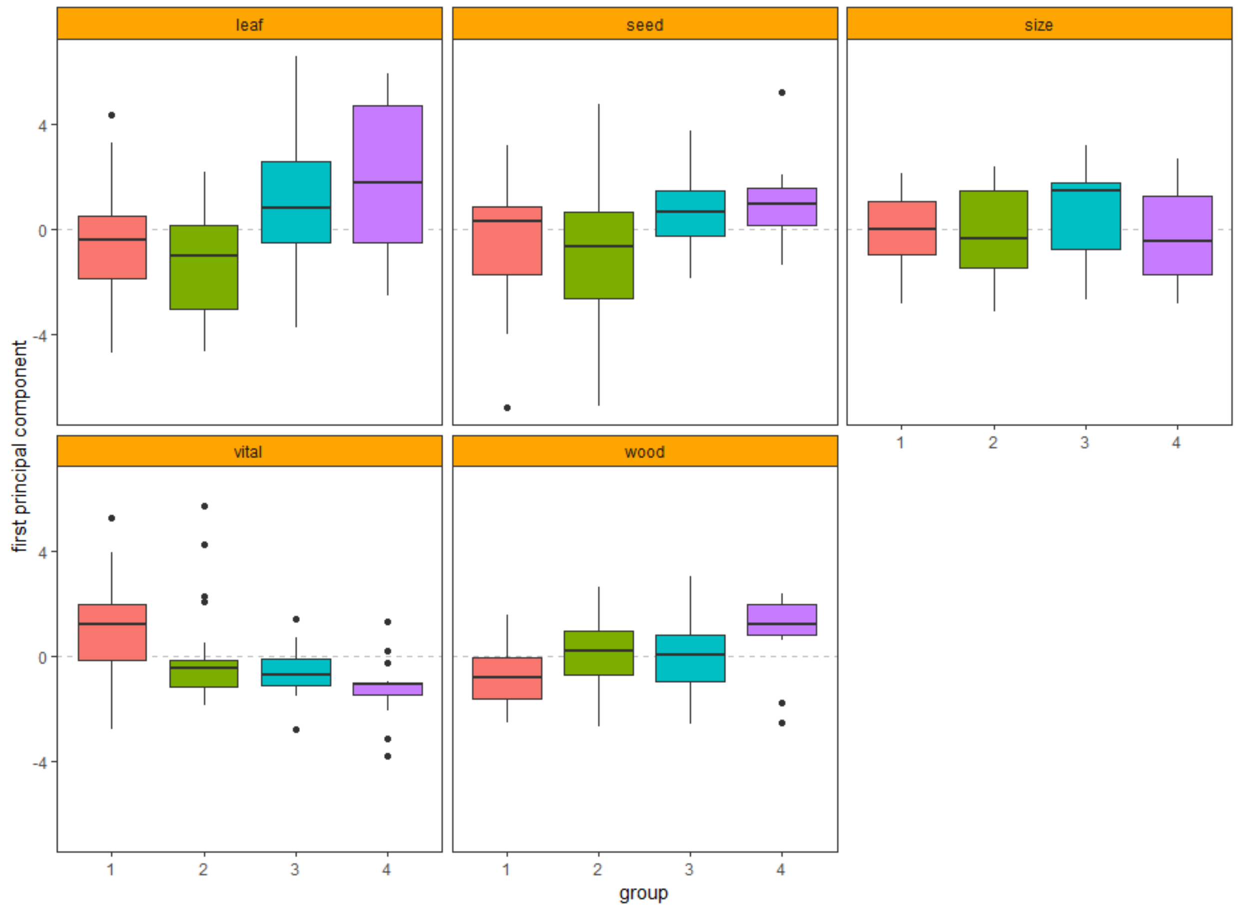
Cohen's κ = 0.88 $\pm$ 0.03
(compare to 0.91 $\pm$ 0.03)

Robustness analysis

BCI: 4 clusters



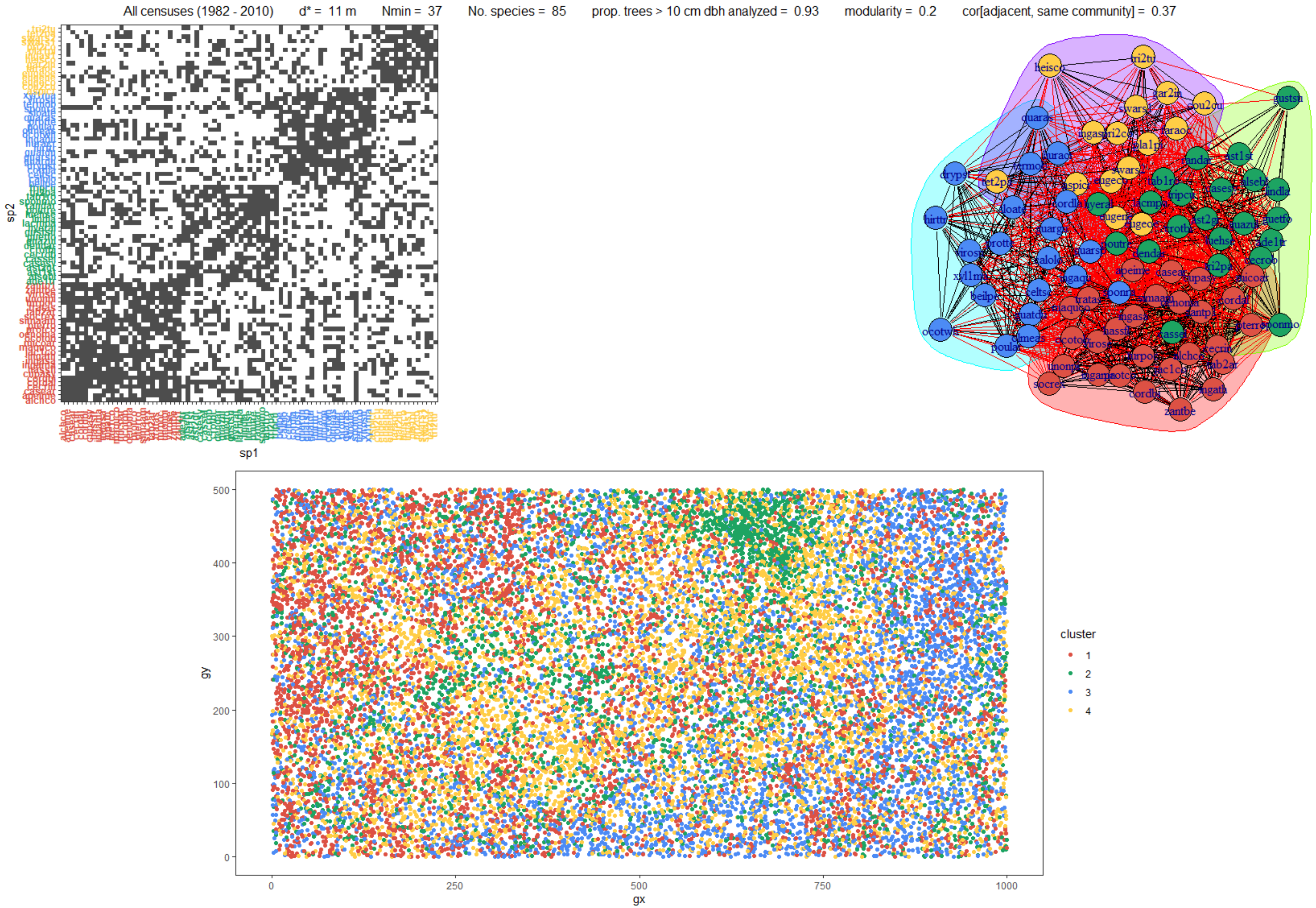




Cohen's κ = 0.2 ± 0.2
(compare to 0.24 ± 0. 3)

Robustness analysis

BCI: 4 clusters



Robustness analysis

BCI: 3 clusters