

**Covariate-informed latent interaction models**  
**Addressing geographic & taxonomic bias in predicting bird-plant interactions**

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# Motivation

- Measured networks are often
  - ~> **incomplete**  
*we observed some interactions and recorded them*
  - ~> measured with error  
*incomplete + recorded interactions might not be truly present*
- Incomplete measured networks might occur because researchers
  - ~> target specific individuals
  - ~> have access to only a subset of nodes
- Interest:
  - ~> Infer the true interaction network from limited measured networks
  - ~> Understand the covariates that drive node interaction

- Not necessarily a problem:
  - ↪ If our inferential interest is the population we followed
- Could be a problem:
  - ↪ If the population we want to learn about is dissimilar than the one followed
  - ↪ measured interactions are not representative of interactions among target population

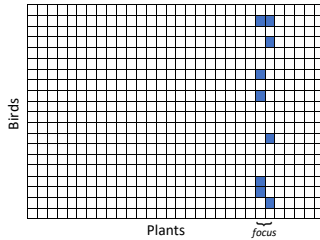
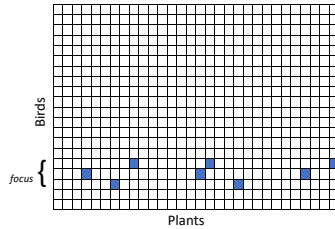
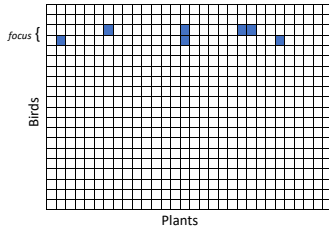
## Bipartite interaction networks in ecology

- Measured networks of species interactivity are incomplete

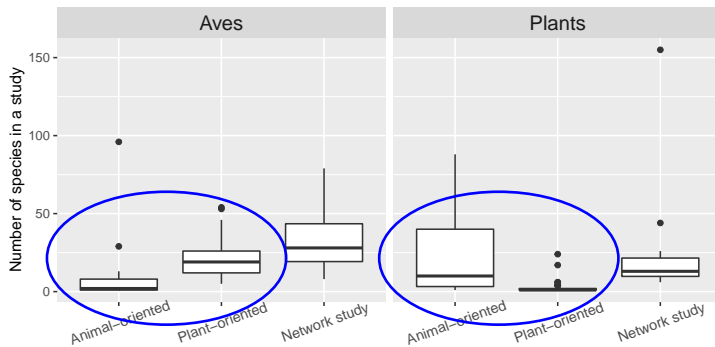
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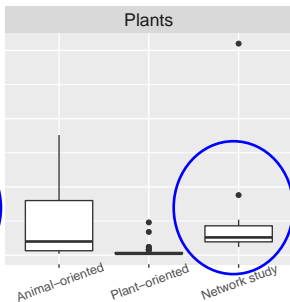
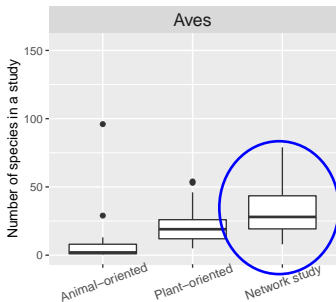
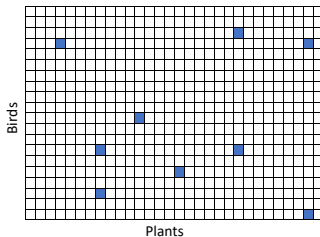
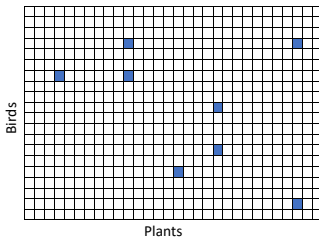
*Number of unique species by study type*

## Bipartite interaction networks in ecology

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- Network studies are most useful for studying species interactions



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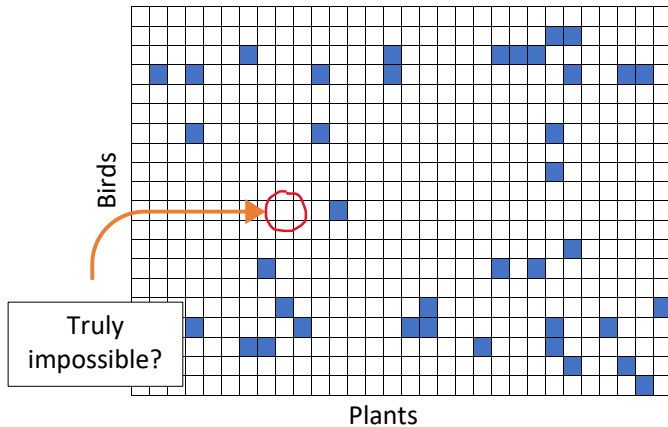




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- Individual studies on species' interactivity often focus on specific species
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- Under or over-representation of species
- Combined network is **taxonomically** and **geographically** biased

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### Goals:

- 1 Understand species interactivity while “adjusting” for these biases
- 2 Learn which covariates are most important in driving species interactions & detectability

## Motivation

- The Atlantic Forest currently includes only 12% of its original biome
- Plants rely on frugivore populations for seed dispersal
- Reductions in frugivore populations lead to disruptions in the regeneration of ecosystems
- Climate change, reductions in natural habitats, deforestation
- How will biological communities respond?

## Goals:

- Understand species interactivity
- Would a given bird consume the seed of a given plant, if given the opportunity?
- What are the drivers of species interactions?



## Our setup

- $S = 85$  individual studies  
     $\leadsto$  19 animal-oriented, 45 plant-oriented, and 19 network studies
- bird  $i = 1, 2, \dots, n_B$       ( $n_B = 232$ )
- plant  $j = 1, 2, \dots, n_P$       ( $n_P = 511$ )
- $A_{ijs} = 1$  or  $0$ : recorded or unrecorded interaction in study  $s$
- $\mathbf{X}_i, \mathbf{W}_j$ : covariate information

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## Goals (in statistical terms):

- Learn **bipartite network** of possible interactions  
     $\leadsto L_{ij} = 1$  if interaction is possible,  $0$  otherwise  
     $\leadsto$  unrecorded interactions are not necessarily impossible  
     $\leadsto$  recorded networks are prone to biases
- Study **covariate importance** in latent network models

## Our Approach

- Elucidate likelihood for  $(\mathbf{A}, \mathbf{X}, \mathbf{W})$

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- The measured covariates might not include all relevant information

Introduce **latent factors**:

$\mathbf{U}_i = (U_{i1}, \dots, U_{iH})^T$  for bird species

$\mathbf{V}_j = (V_{j1}, \dots, V_{jH})^T$  for plant species

- ↪ Representation of species covariate information
- ↪ Arbitrarily close to species' measured covariates

## Our Approach

- Elucidate likelihood for  $(A, X, W)$
- For a measured network to have recorded a given interaction, **all** of the following need to happen:
  - species co-occur
  - researchers are interested in the pair of species
  - species truly interact
  - an interaction was detected

## Our Approach

- Elucidate likelihood for  $(A, X, W)$
- Species occurrence:  $O_{ijs} = 1$  if  $i, j$  both occur at the study site
  - important for addressing geographical bias
  - fixed here

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- **True interactions:**  $L_{ijs} = 1$  if  $ij$ -pair is possible to interact
- **Species' detectability:**  $p_i, q_j$  for bird  $i$  and plant  $j$

## Our Approach – Dependencies

- Focus on

$$P(\mathbf{A} = \mathbf{a} \mid \mathbf{L}, \mathbf{F}, \mathbf{O}, \{p\}, \{q\}, \{U\}, \{V\}, \{\mathbf{X}\}, \{\mathbf{W}\})$$

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- ↪ geographic proximity ( $O_{ijs}$ )
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- and specify:

$$P(A_{ijs} = 1 \mid L_{ij} = l, F_{ijs} = f, O_{ijs} = o, p_i, q_j) = \begin{cases} 0, & \text{if } lfo = 0 \\ p_i q_j, & \text{if } lfo = 1 \end{cases}$$

# Our Approach – Dependencies

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## ■ We can write it as

$$\begin{aligned} & \prod_{i,j,s} P(A_{ijs} = a_{ijs} \mid L_{ij}, F_{ijs}, O_{ijs}, p_i, q_j) \\ &= \prod_{\substack{i,j,s \\ F_{ijs} O_{ijs} L_{ij}=1}} (p_i q_j)^{a_{ijs}} (1 - p_i q_j)^{1-a_{ijs}} \prod_{\substack{i,j,s \\ F_{ijs} O_{ijs} L_{ij}=0}} I(a_{ijs} = 0) \end{aligned}$$

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- Need to specify joint distribution on unobserved quantities:

$$\mathbf{L}, \{\mathbf{U}\}, \{\mathbf{V}\}, \{p\}, \{q\}$$

- Still need distribution on measured covariates  $\{\mathbf{X}\}, \{\mathbf{W}\}$ !

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↪ Recorded interactions depend on species' characteristics:

$$\text{logit}P(L_{ij} = 1 \mid \mathbf{X}_i, \mathbf{U}_i, \mathbf{W}_j, \mathbf{V}_j) = \lambda_0 + \sum_{h=1}^H \lambda_h U_{ih} V_{jh}$$



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↪ Species' detectability depends on species' characteristics:

$$E[\text{logit}(p_i) \mid \mathbf{U}_i, \mathbf{X}_i] = \delta_0 + \mathbf{U}_i^T \boldsymbol{\delta}$$

$$E[\text{logit}(q_j) \mid \mathbf{V}_j, \mathbf{W}_j] = \zeta_0 + \mathbf{V}_j^T \boldsymbol{\zeta}$$

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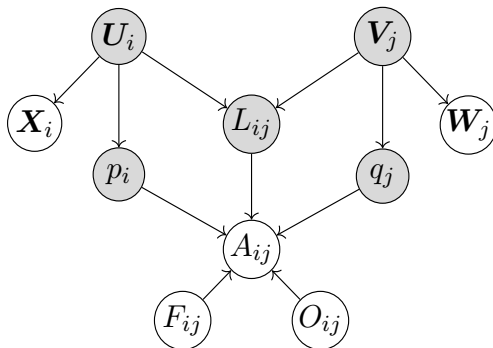
$$E[\text{logit}(q_j) \mid \mathbf{V}_j, \mathbf{W}_j] = \zeta_0 + \mathbf{V}_j^T \boldsymbol{\zeta}$$

↪ Latent factors are “close” enough to measured covariates

$$f_m^{-1}(E(X_{im} \mid \mathbf{U}_i)) = \beta_{m0} + \mathbf{U}_i' \boldsymbol{\beta}_m, \quad m = 1, 2, \dots, p_B, \quad \text{and}$$

$$g_l^{-1}(E(W_{jl} \mid \mathbf{V}_j)) = \gamma_{l0} + \mathbf{V}_j' \boldsymbol{\gamma}_l, \quad l = 1, 2, \dots, p_P$$

## Our approach (schematically)



## Our Approach (prior distributions)

- $U_{.h} \sim \mathcal{N}(\mathbf{0}, \Sigma_U)$ , and  $V_{.h} \sim \mathcal{N}(\mathbf{0}, \Sigma_V)$ 
  - $\leadsto$  independently across  $h$
  - $\leadsto \Sigma_U, \Sigma_V$  phylogenetically structured across species

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→ independently across  $h$

→  $\Sigma_U, \Sigma_V$  **phylogenetically structured** across species

---

- Model coefficients:  $\beta_{mh} | \tau_{mh}^\beta, \theta_h \sim N(0, \tau_{mh}^\beta \theta_h)$  *similarly for others*

$\theta_h$ : The increasing shrinkage prior of Legramanti et al. (2020)

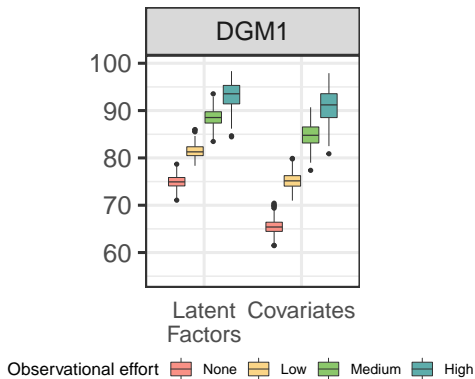
→ Increasingly penalizes coefficients with larger  $h$

$\tau_{mh}^\beta$ : Coefficient-specific additional variation

- We approximated the posterior distribution using MCMC
- Most updates were performed using Gibbs / MH
- Pólya-Gamma data augmentation scheme for parameters of logistic models

- We considered 24 scenarios:
  - Same or different covariates important for interactions and detectability
  - Important covariates are measured, mixed or unmeasured
  - Covariates are correlated or not
  - High and low information scenarios
- Alternative approaches using covariates, ignoring biases, fixed latent factor dimension ...

## AUROC – predicting missing interactions

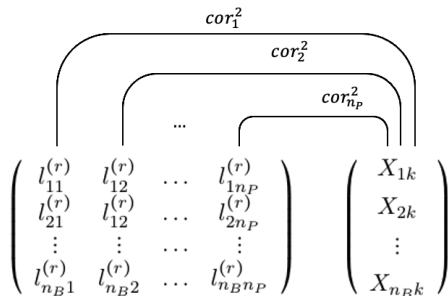




## Variable importance in latent network models

- Interaction model does not include covariates
- We cannot interpret coefficients
  - ~> lack of identifiability of latent factors
- Covariates are not included in the interaction model
  - ~> by design
  - ~> interpreting coefficients in models with structured latent factors has challenges (Van Ee et al., 2021)

# Variable importance in latent network models



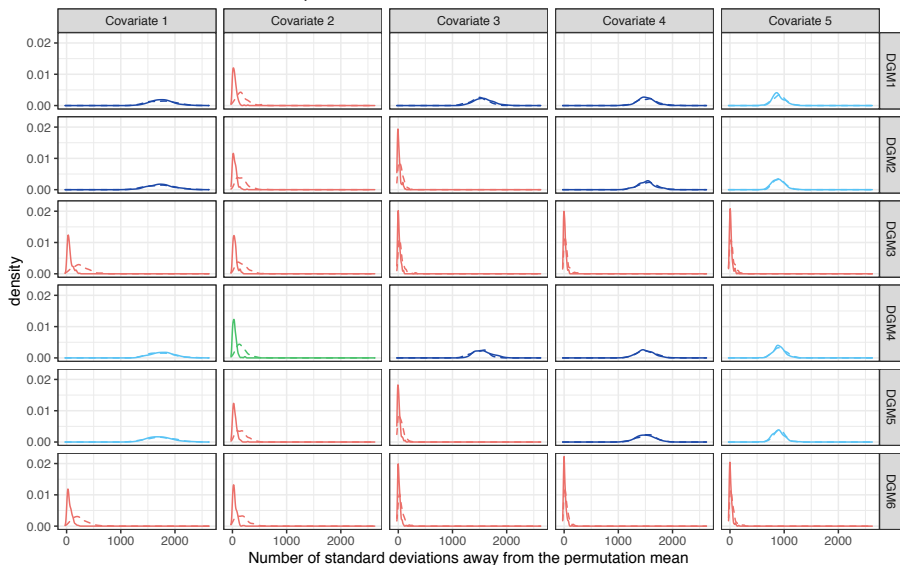
$l_{ij}^{(r)}$ :  $r^{th}$  posterior sample of (logit) probability of interaction between bird  $i$  and plant  $j$

- 1 Calculate  $T^{obs}$  by averaging across species and posterior samples
- 2 Permute the covariate vector  $B$  times  $\rightsquigarrow T^{(b)}, b = 1, 2, \dots, B$
- 3 Use

$$T^{obs} - \text{avg}\left(T^{(b)}\right) \quad / \quad \text{sd}\left(T^{(b)}\right)$$

as the variable importance metric

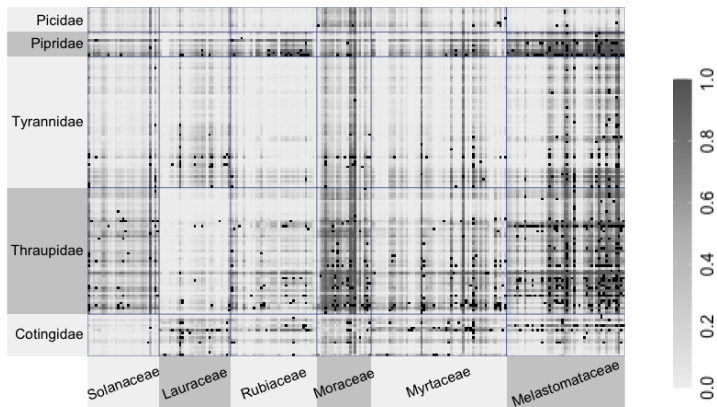
# Covariates for the first set of species



True importance — Not important — Forming & Detecting — Forming — Detecting

Correlation 0 0.3

## In our study...

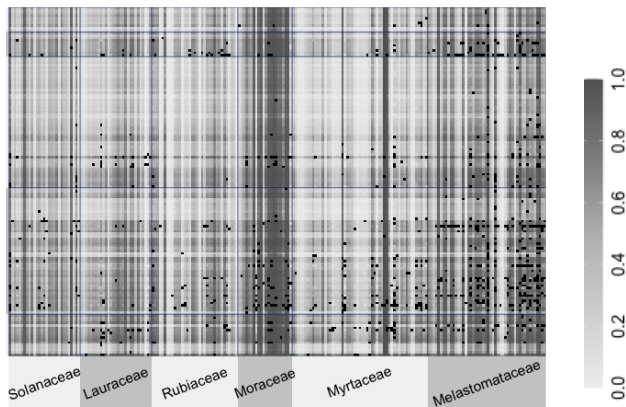


*Our approach*

## In our study...

- Species' interaction profiles appear to be taxonomically structured
- 5% of pairs are predicted to interact (post. prob.  $> 80\%$ )
- 41% of pairs are predicted to *not* interact (post. prob.  $< 10\%$ )

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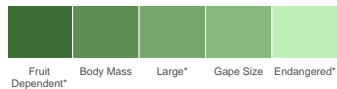


*Alternative approach using covariates directly*

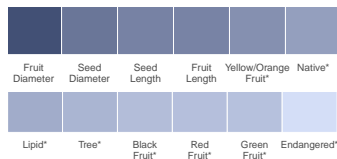
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- Cross validation:
  - ↪ compare post. prob. of interaction in held-out pairs compared to all pairs
  - ↪ covariates: (post.prob. interacting) 1.4 times higher (all)
  - ↪ latent factors: (post.prob. interacting) 3.2 times higher (all)
- Latent factor model differentiates truly possible interactions better

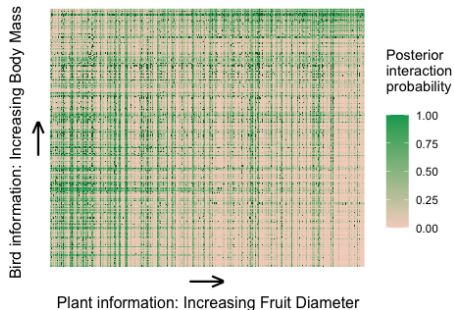
# Variable importance on species interactions



(a) Bird Traits Importance



(b) Plant Traits Importance



(c) Interaction matrix ordered by traits



# Final thoughts

- Latent network models for noisy bipartite networks
  - [covariates](#) inform the latent factors via separate models
  - quantifies our [uncertainty](#) around the estimated graph
  - posterior samples + permutation for [variable importance](#)
- Study species interactions based on meta-analysis data set
  - [complete the bipartite graph](#) of species interdependence
  - incorporates the [missingness mechanism](#) caused by the taxonomic and geographic bias of individual studies
- **EXTENSION:** simultaneous modeling of [co-occurrence](#) and [interactions](#)
  - incorporate geographic information and environmental variables
  - investigate the importance of species abundance and competition

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**Preprint:**     [arXiv:2103.05557](https://arxiv.org/abs/2103.05557)

**Rpackage:**   <https://github.com/gpapadog/BiasedNetwork>

**Analysis:**    [https://github.com/gpapadog/Bird\\_Plant\\_Interactions](https://github.com/gpapadog/Bird_Plant_Interactions)

*Thank you!*