Spatially-explicit occupancy modeling with the spOccupancy R package

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Course Website

- https://doserjef.github.io/TWS23-spOccupancy/
- Single-species non-spatial/spatial occupancy models
- Multi-species non-spatial/spatial occupancy models
- Multi-season non-spatial/spatial occupancy models

Occupancy Models

Ecological Motivation

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  - Spatial autocorrelation

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Site	Survey
1	1
2	0
3	1
4	1
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1. The species does not exist at the site

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Assuming no false positives, if we detect the species, we know it exists at the site

A 0 (or nondetection) could mean:

1. The species does not exist at the site
2. The species exists at the site, but we failed to detect it.

Occupancy modeling

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- **Fundamental concept**: obtain "repeated surveys" at a given site during some period of closure
  - Key assumption: the species does not move in or out of the site during this time period
- "Repeated surveys" usually come in the form of multiple visits to a site during some time period, but can also take different forms (e.g., multiple observers, spatial replicates)

Data for occupancy modeling

Detection-nondetection matrix (y)

k

j

Site	Survey 1	Survey 2	Survey 3	Survey 4
1	1	0	0	1
2	0	0	0	0
3	1	1	0	NA
4	1	NA	0	NA
5	0	1	1	1
6	0	0	0	1

$y_{j,\,k}$

- *J* sites with K_j replicate surveys at each site *j*
- Assume no false positives
- Any variation in the observed data values across surveys is assumed to arise from imperfect detection.

Occupancy model structure

- Two distinct sub-models
    1. Model occupancy probability as a function of site-level covariates

Occupancy model structure

- Two distinct sub-models
  1. Model occupancy probability as a function of site-level covariates
  2. Model detection probability as a function of site and/or survey-level covariates
     - Can only detect a species if it truly occupies a site
     - Detection probability is modeled "conditional" on true occupancy

Single-species occupancy model

$j = 1, \ldots, J$ (site)
$k = 1, \ldots, K_j$ (replicate)

Occupancy (ecological) sub-model

$$z_j \sim \text{Bernoulli}(\psi_j)$$
$$\text{logit}(\psi_j) = \beta_1 + \beta_2 \cdot X_{2,j} + \cdots + \beta_r \cdot X_{r,j}$$

z_j True occurrence of the species at site *j*

ψ_j Occurrence probability at site *j*

$X_{r,j}$ The *r*th covariate at site *j* (e.g., habitat variable)

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$$\text{logit}(p_{j,k}) = \alpha_1 + \alpha_2 \cdot V_{2,j,k} + \cdots + \alpha_r \cdot V_{r,j,k}$$

$y_{j,k}$ Detection-nondetection data at site *j* during replicate *k*

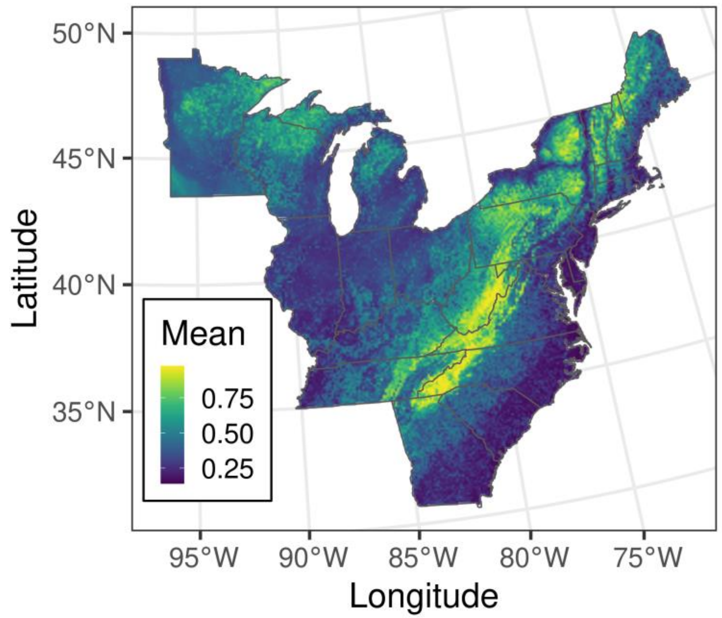
$p_{j,k}$ Detection probability at site *j* during replicate *k*

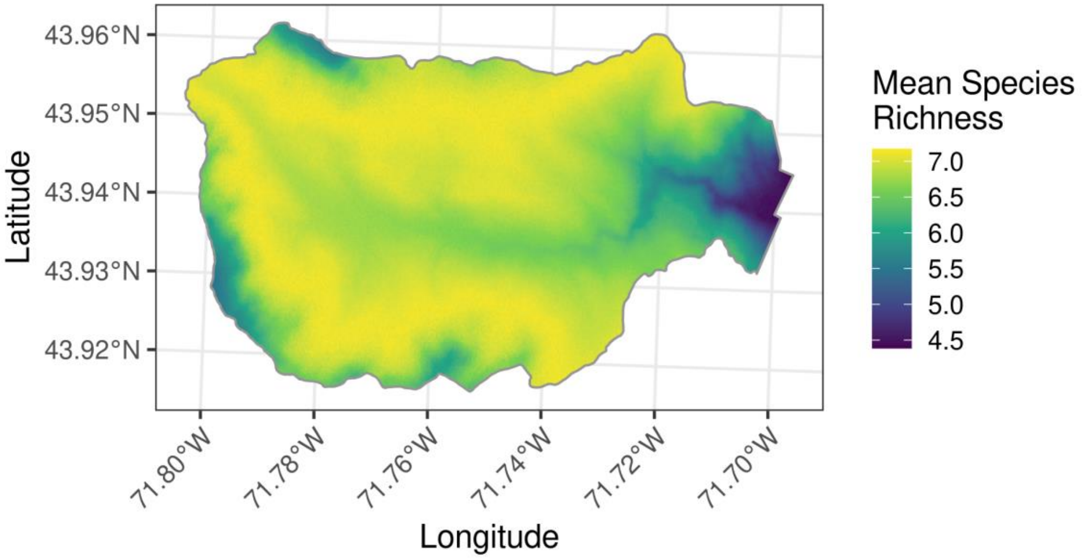
$V_{r,j,k}$ Covariate affecting detection at site j during replicate k

Spatial Occupancy Models

Spatial autocorrelation

- First Law of Geography: "Everything is related to everything else, but near things are more related than distant things." - Waldo Tobler





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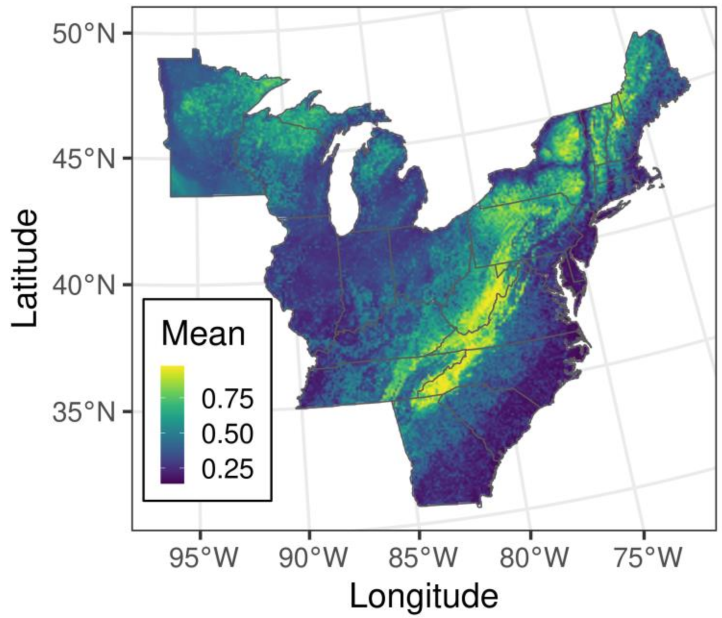
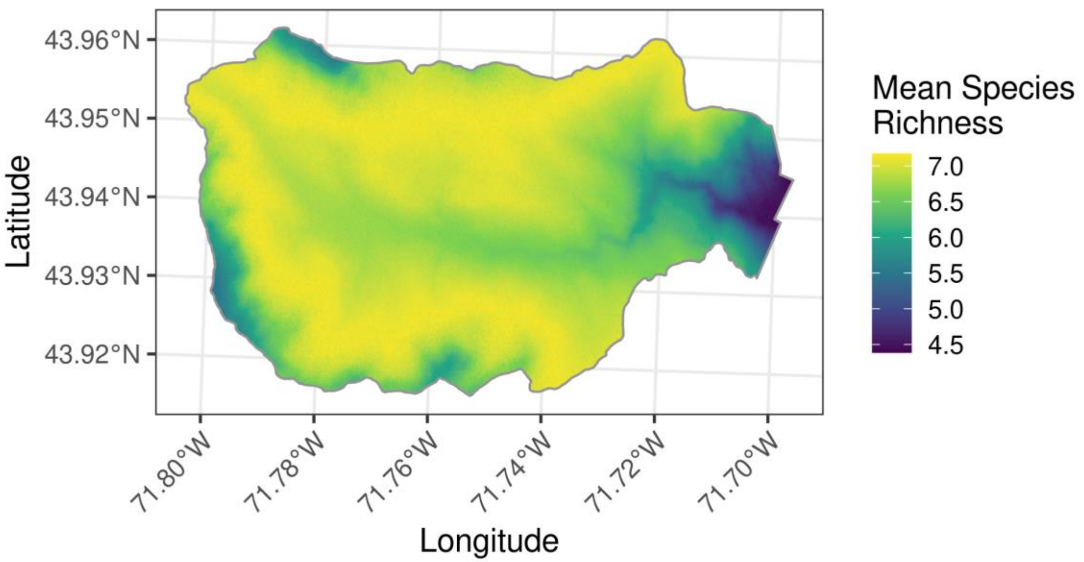
  - Environmental drivers, habitat requirements
  - Biotic factors (dispersal, conspecific attraction)





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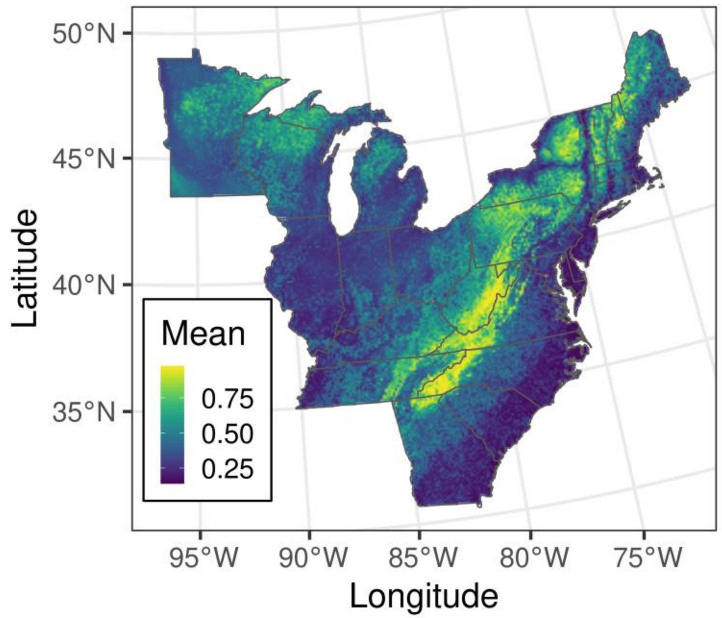
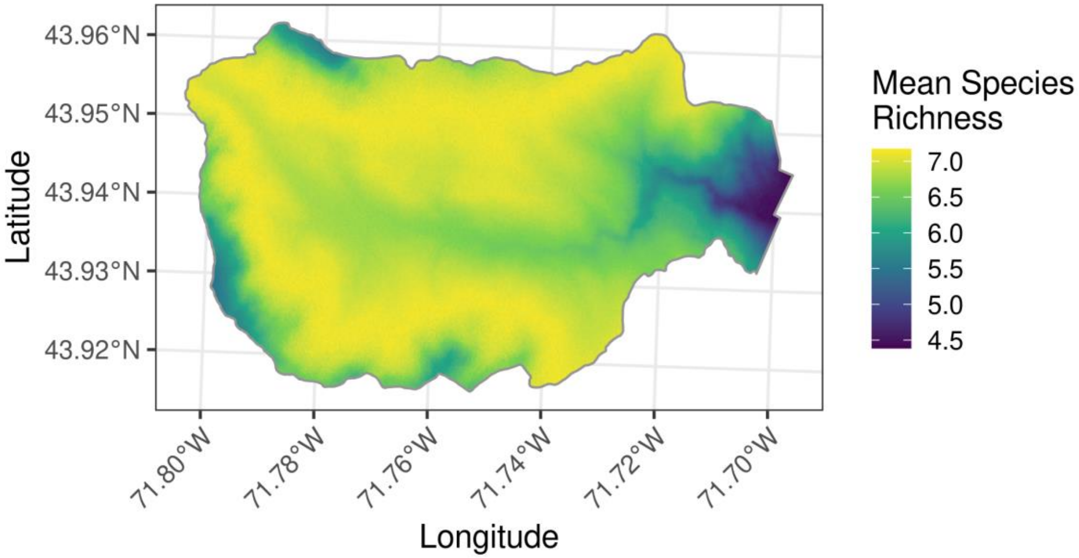
- Initial approach: attempt to explain spatial variation in species distributions with covariates (e.g., forest cover, temperature, elevation)





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- Spatial correlation in occupancy probability *after* including spatial covariates
- Often arises from missing/unavailable covariates
- Can lead to bias if unaddressed
- Account for using spatial random effects
  - Each site has a local adjustment in occupancy probability
  - The local adjustments are given a spatial structure
  - Estimated parameters: spatial variance and spatial decay

Single-species spatial occupancy model

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$$\text{logit}(\psi_j) = \beta_1 + \beta_2 \cdot X_{2,j} + \cdots + \beta_r \cdot X_{r,j} + \text{w}_j$$
$$\text{w}_j \sim \text{Normal}(0, \boldsymbol{\Sigma})$$

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- Covariance between two sites is determined by:
  - Distance between the sites
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- spOccupancy supports four covariance functions: **exponential**, Gaussian, spherical, Matérn
- Covariance between site A and site B using exponential covariance function:

$$\boldsymbol{\Sigma}(d_{A,B}, \sigma^2, \phi) = \sigma^2 \text{exp}(-\phi d_{A,B})$$

Intuition on spatial covariance

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$\frac{3}{\phi}$ "Effective spatial range" when using an exponential covariance function. This is the distance at which the spatial correlation between two sites is essentially negligible (0.05)

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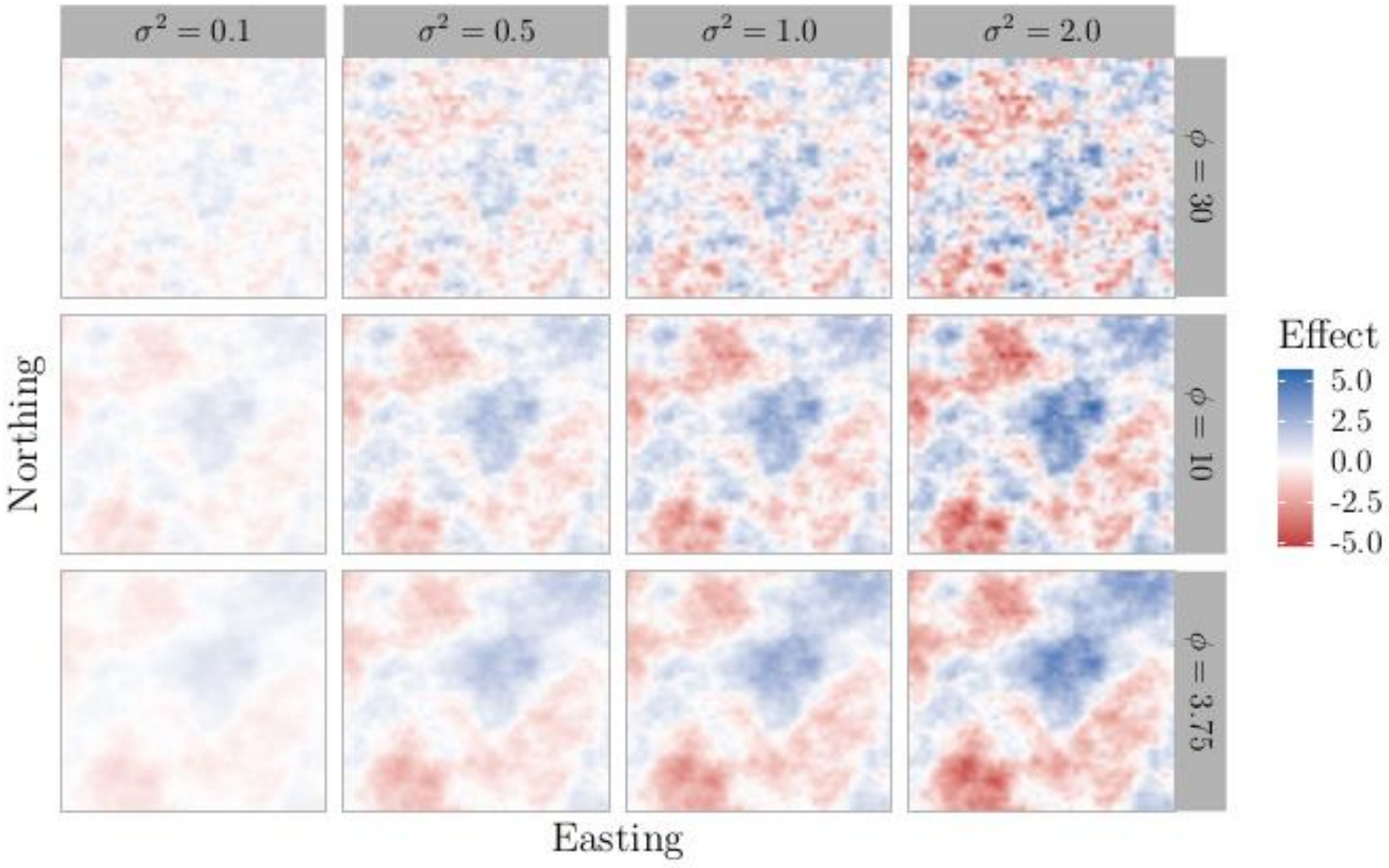

Gaussian process

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- Flexible approach to account for spatial autocorrelation
- But... becomes extremely slow as the number of sites increases
- Not practical for data sets with hundreds of data points, let alone thousands.
- Computational bottleneck: dealing with a large, dense J x J matrix
- Need a more efficient approach...

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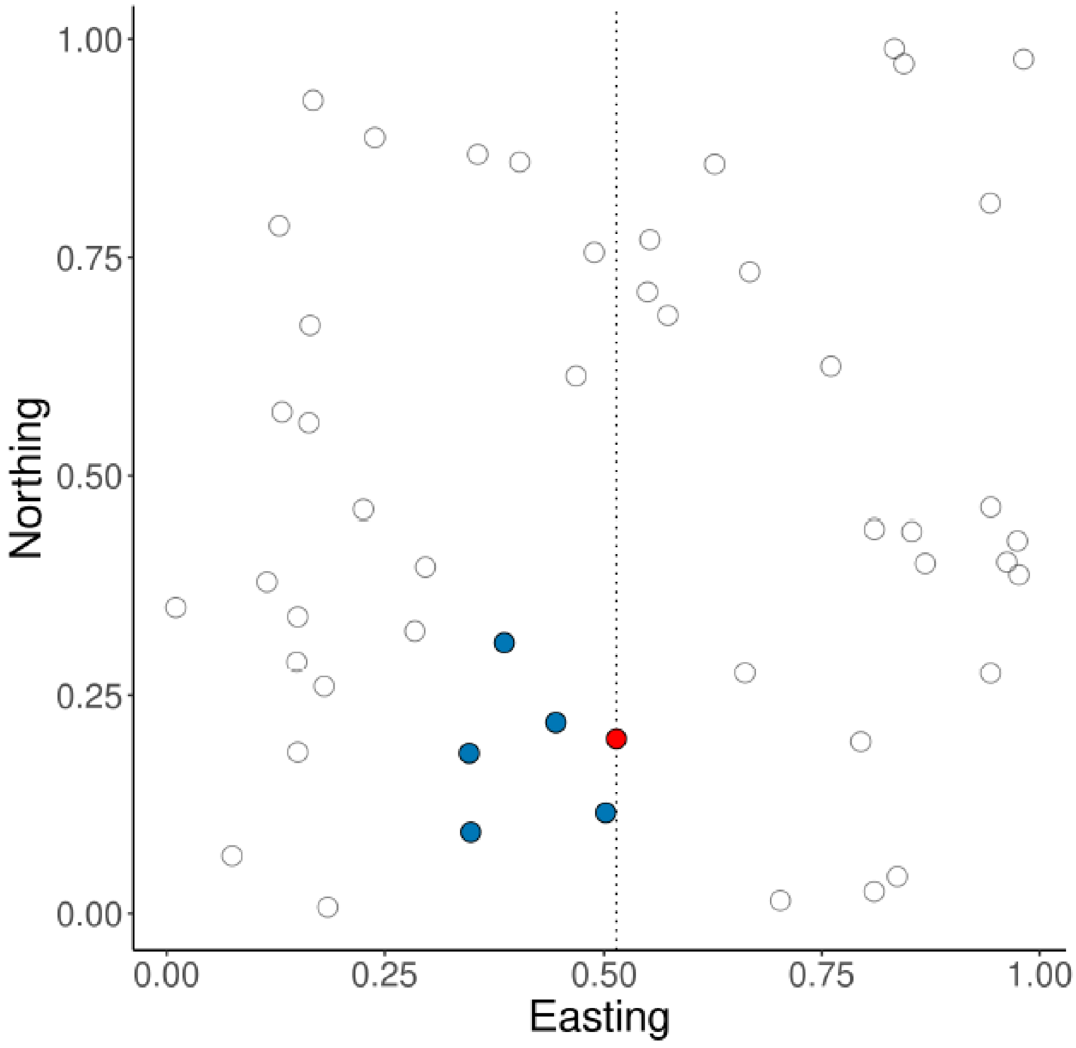
  3. The spatial random effect at each site only depends on values of its *m* nearest neighbors and is conditionally independent of all other values

Choosing the neighbors

- spOccupancy orders sites along the horizontal axis (i.e., Easting)
- Example: NNGP with 5 neighbors
- Red point denotes the current site
- Blue points denote sites in the "neighbor set"



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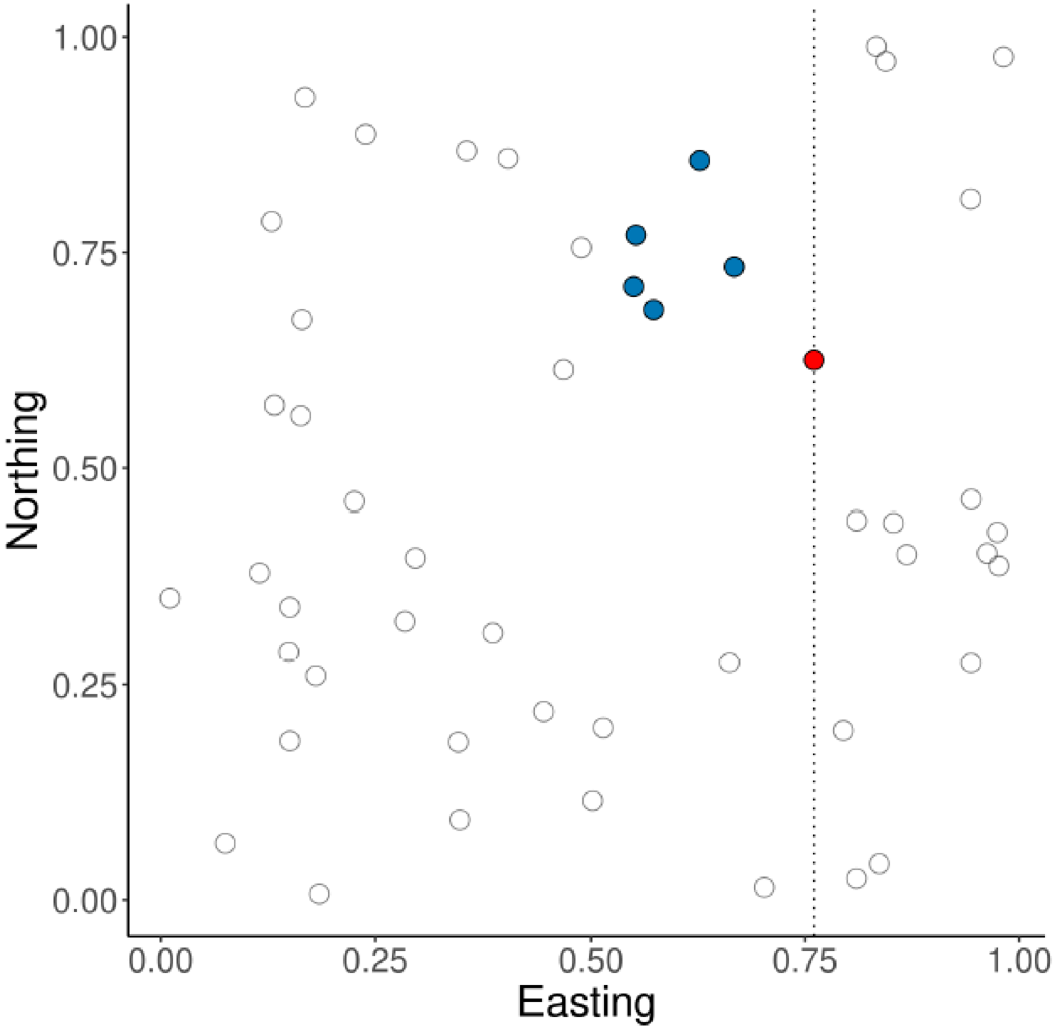

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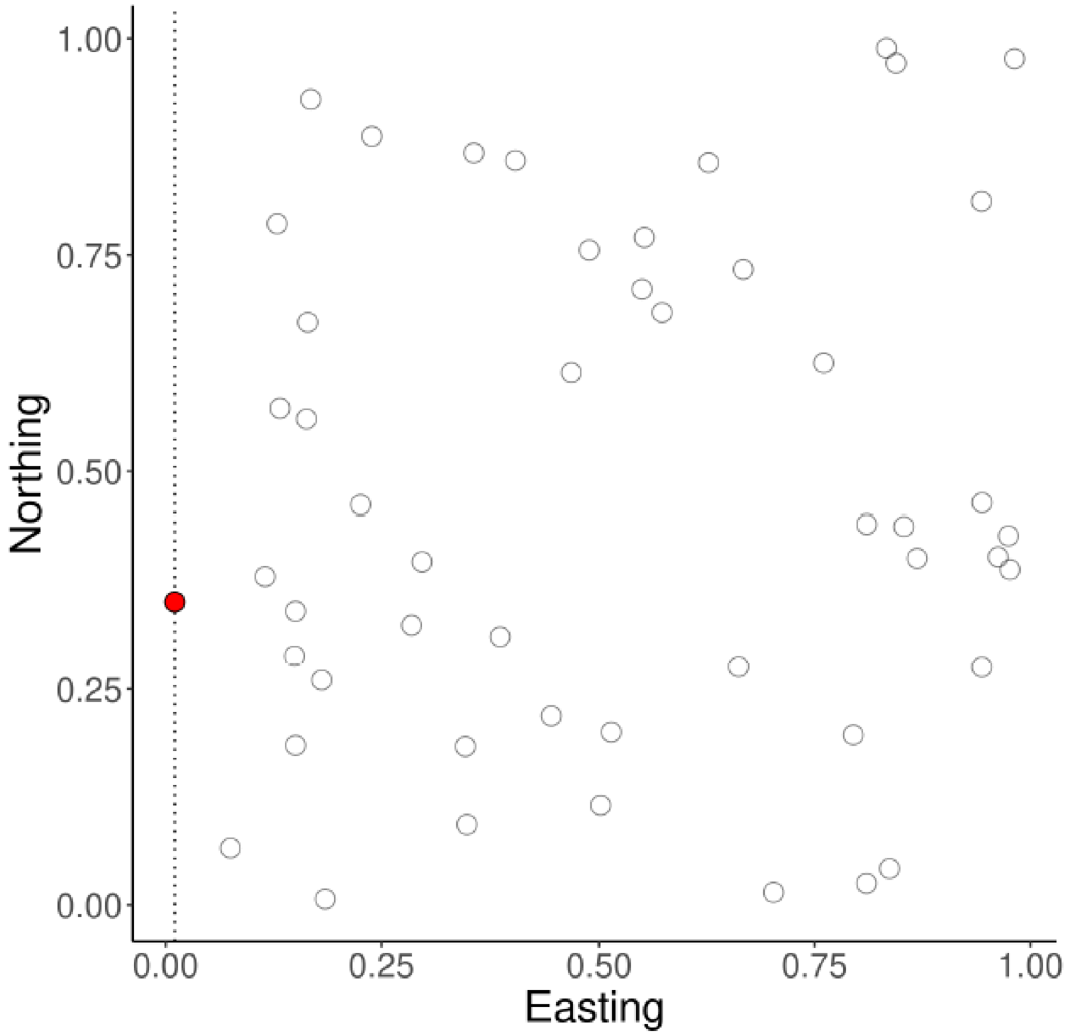

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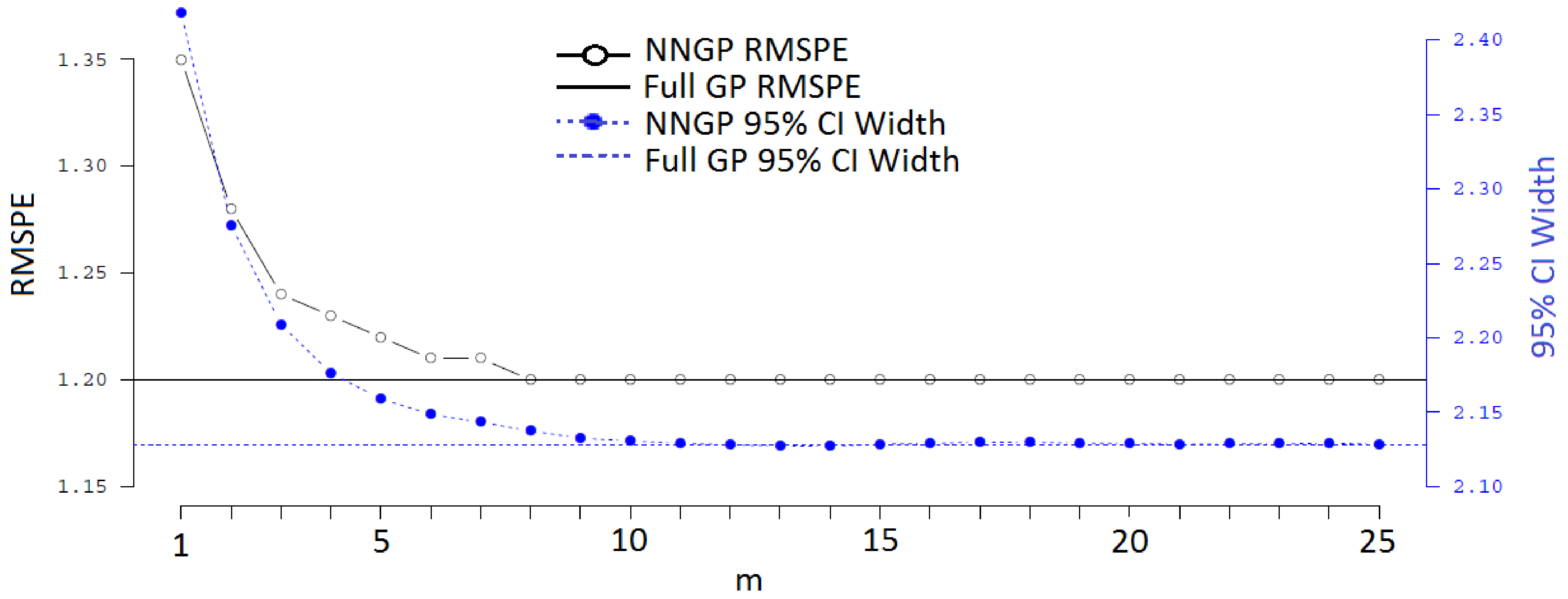

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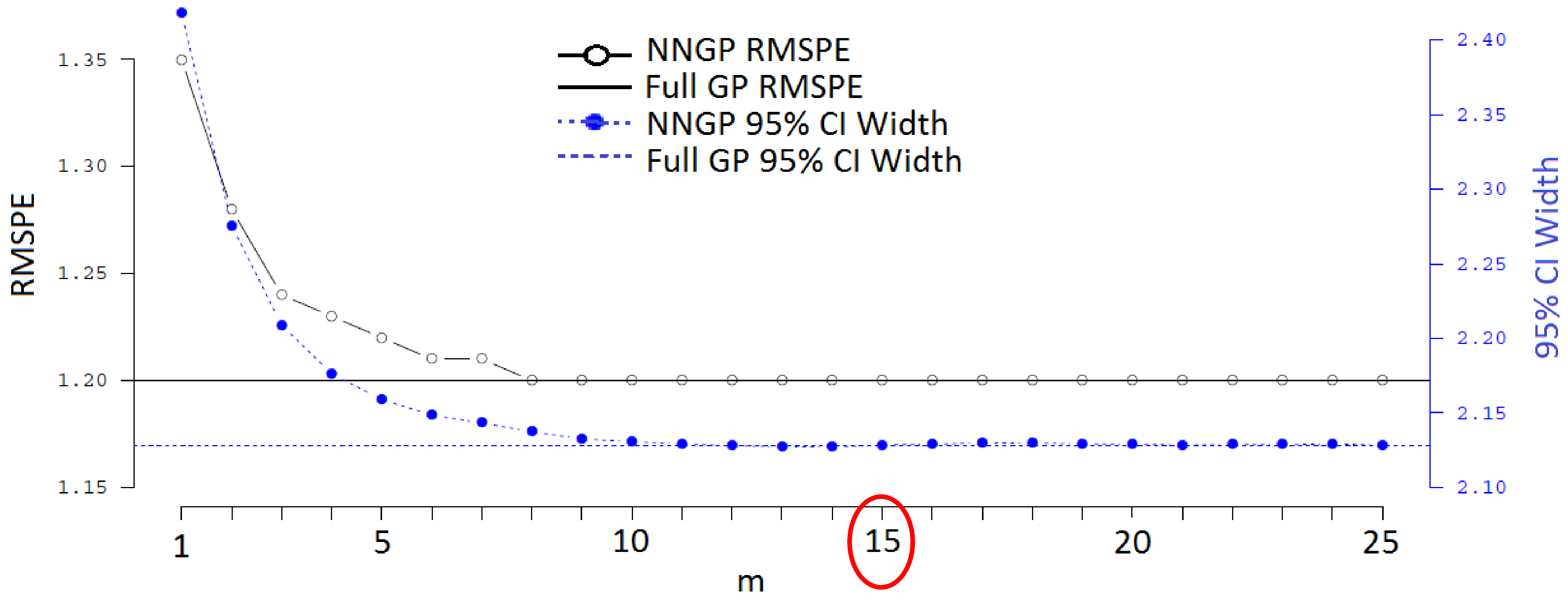

- m= 15 neighbors is often adequate (spOccupancy default)
- Can compare smaller m using WAIC

Datta et al. (2016) JASA

Pros/cons of spatial models

Pros

- More accurate species distribution maps (improved predictions)
- More accurate uncertainty estimates
- Provide insights on underlying drivers
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Cons

- Slower (but NNGPs help a lot!)
- Spatial confounding (Hanks et al. 2015, Mäkinen et al. 2022)
- More data hungry

Bayesian Basics

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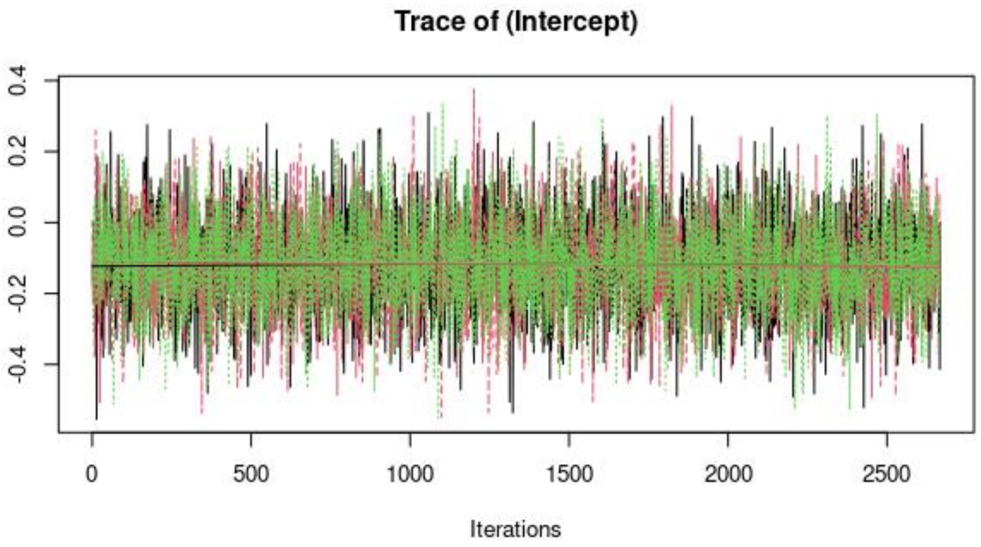
2. More flexible to accommodate spatial autocorrelation
3. Easy to extend to multispecies frameworks/integrate multiple data sources
4. Fully propagate uncertainty in all estimates (and derived quantities)

Bayesian basics: what to know to get started in spOccupancy

- Markov chain Monte Carlo (MCMC)
- MCMC chains eventually converge to a posterior distribution
  - Assess convergence by running multiple chains with different starting values



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Monte

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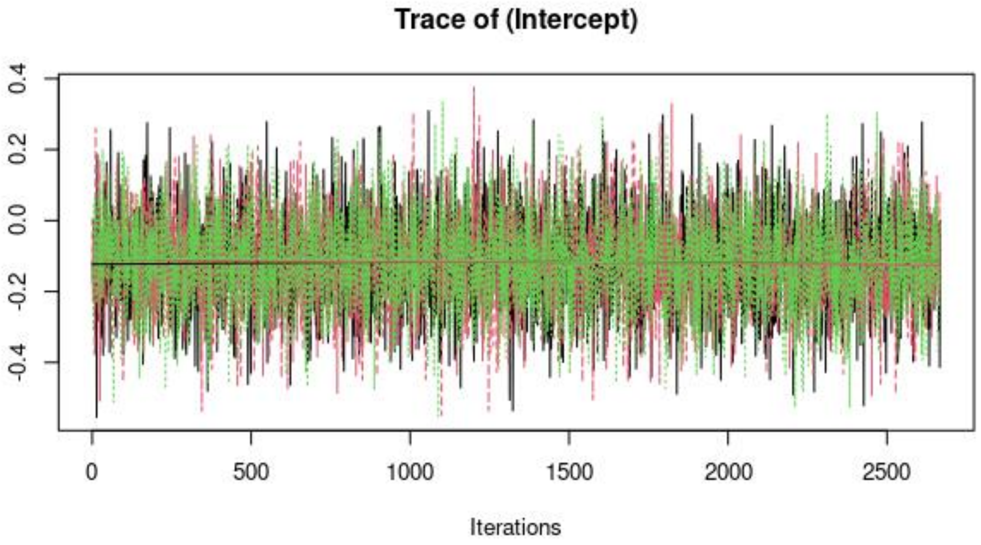


MCMC Step 1: Specify prior distributions

$$\begin{aligned}
\beta &\sim \mathrm{Normal}(\mu_\beta, \sigma^2_\beta) \\
\alpha &\sim \mathrm{Normal}(\mu_\alpha, \sigma^2_\alpha) \\
\sigma^2 &\sim \text{Inverse-Gamma}(a_{\sigma^2}, b_{\sigma^2}) \\
\phi &\sim \mathrm{Uniform}(a_\phi, b_\phi)
\end{aligned}$$

MCMC Step 2: Set initial values

- Set different values for each chain
- spOccupancy will set initial values by default
- Can be important for more complicated models (e.g., spatially-varying coefficient models)

MCMC Step 3: Propose new value

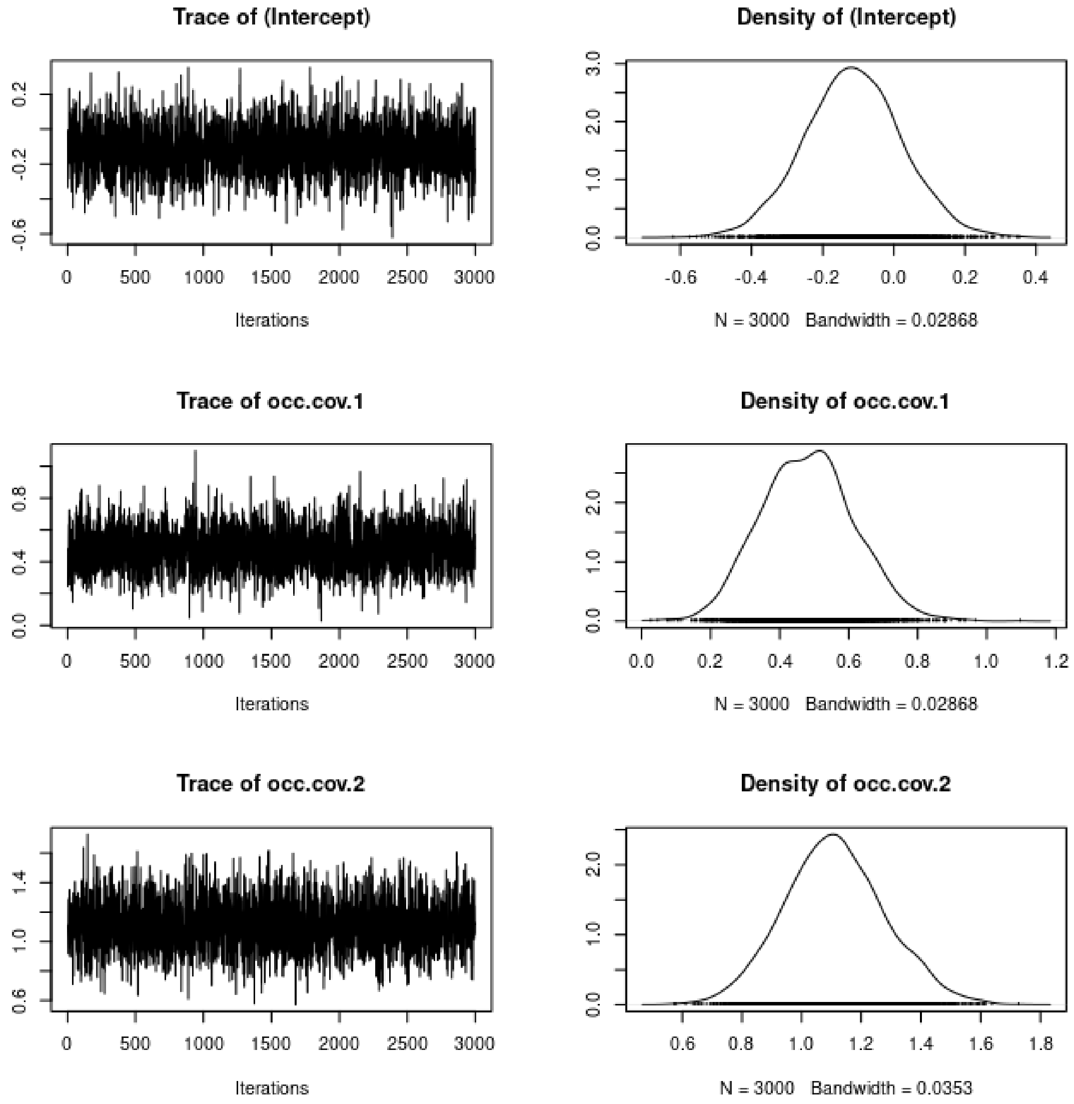
- Propose a new value for each parameter one at a time based on a statistical algorithm.
- For some parameters, we always accept the proposed value because our algorithm is efficient.
- For parameters with less efficient algorithms, we will accept the new value with some probability p.

MCMC Step 4: Repeat

- Repeat step 3 "many" times to generate a set of samples from the posterior distribution for each parameter.

MCMC Step 5: Summarize

- Point estimate: mean, median, mode
- Uncertainty: 95% credible (e.g., 2.5 and 97.5% quantiles of the samples)



What do you need to specify?

- Prior distribution (optional)
- Initial values (optional)
- Number of samples/iterations
- Burn-in: initial part of the MCMC chain that we throw away
- Thinning rate: how often do you want to save a sample?

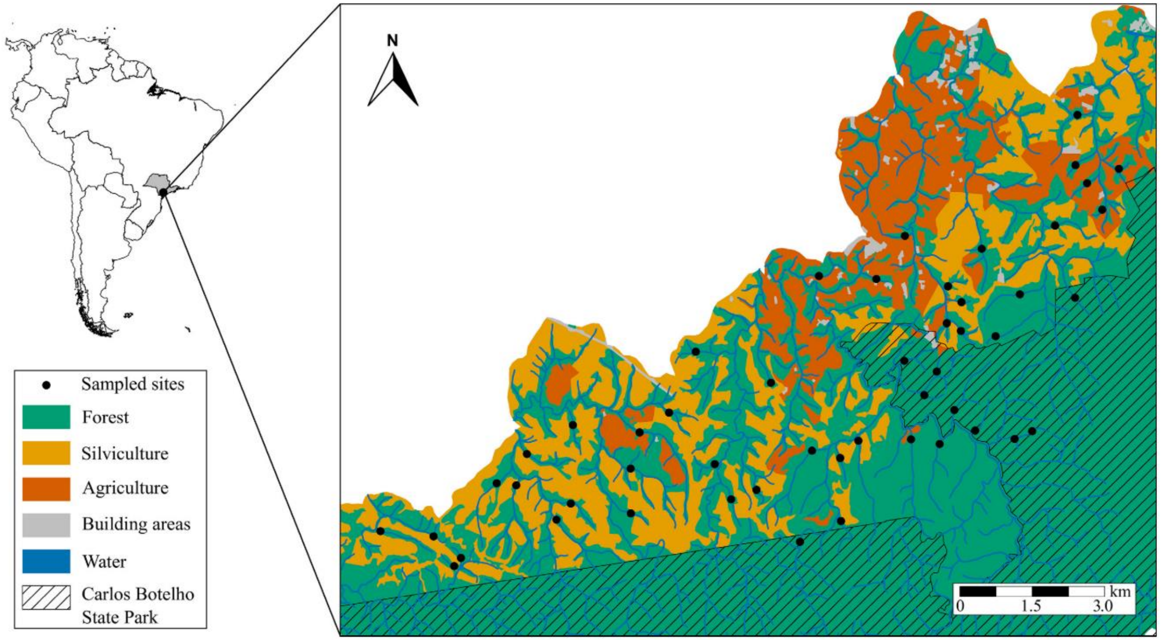
spOccupancy

spOccupancy

- Designed to fit Bayesian single-species and multi-species occupancy models
- Efficient options (NNGPs) to account for spatial autocorrelation
- Workflow completely in R (no Bayesian programming languages necessary)
- PGOcc -> single-species occupancy model
- spPGOcc -> spatial single-species occupancy model
- The "PG" stands for Pólya-Gamma (Polson et al. 2013)

Exercise 1: Amphibian occupancy in Brazil

- Data from [Ribeiro Jr. Et al (2018) *Eco Apps*]
- 50 sites along a gradient of landscape characteristics
- 3 ARU recordings at each site (repeat surveys/visits)
- 36 amphibian species analyzed
- Focus on *Crossodactylus caramaschii*



Ribeiro Jr. et al. (2018) *Eco Apps*

spOccupancy workflow

1. Data simulation/prep
2. Model fitting
3. Model validation
4. Model comparison
5. Posterior summaries
6. Prediction

Multi-species occupancy models

Multi-species detection-nondetection data

- Many types of multi-species inventories:
  - Point count surveys
  - Acoustic recording units
  - Camera traps
  - Citizen science checklists

Species	Site 1	Site 2	Site 3	Site 4
A	1	0	0	1
B	0	0	1	0
C	1	1	0	0
D	1	0	0	0
E	0	1	1	1
F	0	0	0	1

Multi-species detection-nondetection data

Visit 1

Species	Site 1	Site 2		
A	1	0		
B	0	0		
C	1	1		
D	1	0	0	0
E	0	1	1	1
F	0	0	0	1

Visit 2

Species	Site 1	Site 2		
A	0	NA		
B	0	NA		
C	1	NA		
D	0	NA		
E	0	NA	1	1
F	0	NA	0	0

Visit 3

Species	Site 1	Site 2	Site 3	Site 4
A	1	0	0	NA
B	0	1	1	NA
C	0	0	0	NA
D	0	0	0	NA
E	0	0	1	NA
F	0	0	0	NA

Ecological Motivation

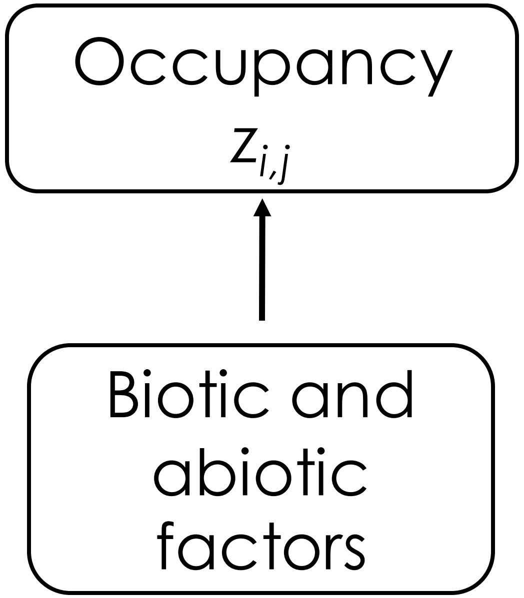
- Management has historically focused on individual species.
- Increased interest in multi-species management
- Biodiversity conservation
- Species are not independent of each other

Statistical Motivation

- Species of interest (e.g., SGCNs) are often the rarest species.
- Occupancy models are hard to fit when the number of detections is low
- Multi-species models can:
  - Improve ability to model rare species
  - Provide inference at both species and community-levels
  - Use information from other species to improve species-specific estimates

Multi-species occupancy model

i = 1, …, N (species)
j = 1, …, J (sites)
k = 1, …, K (replicates)



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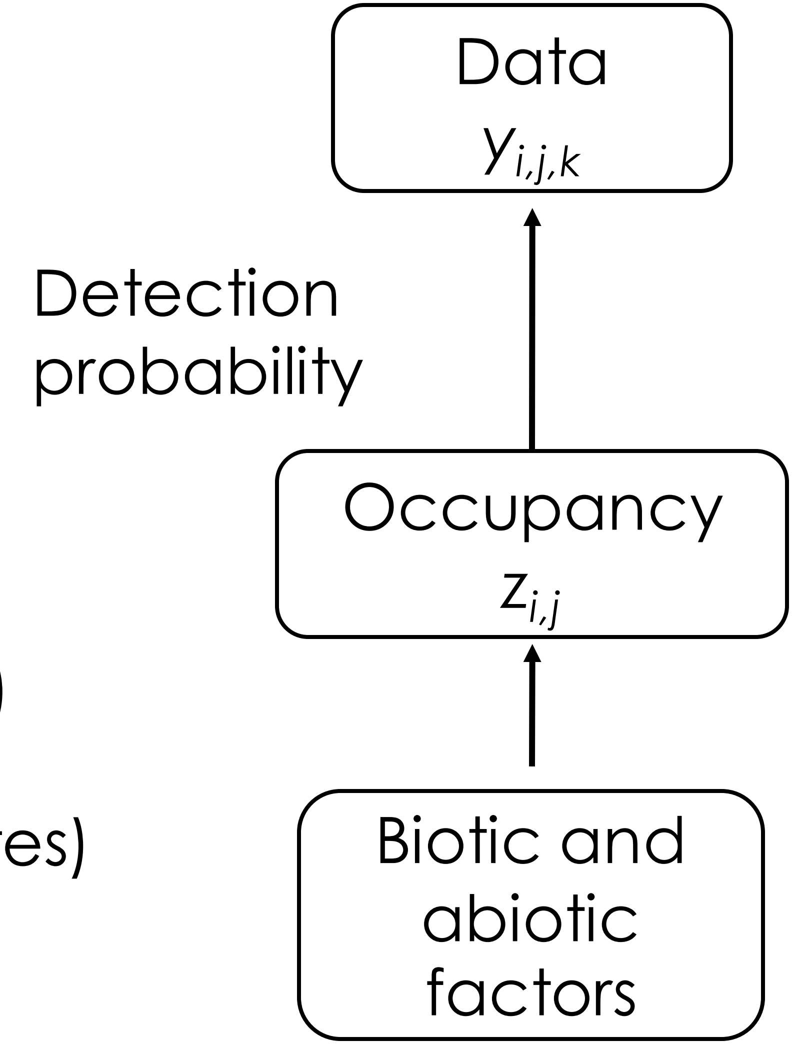

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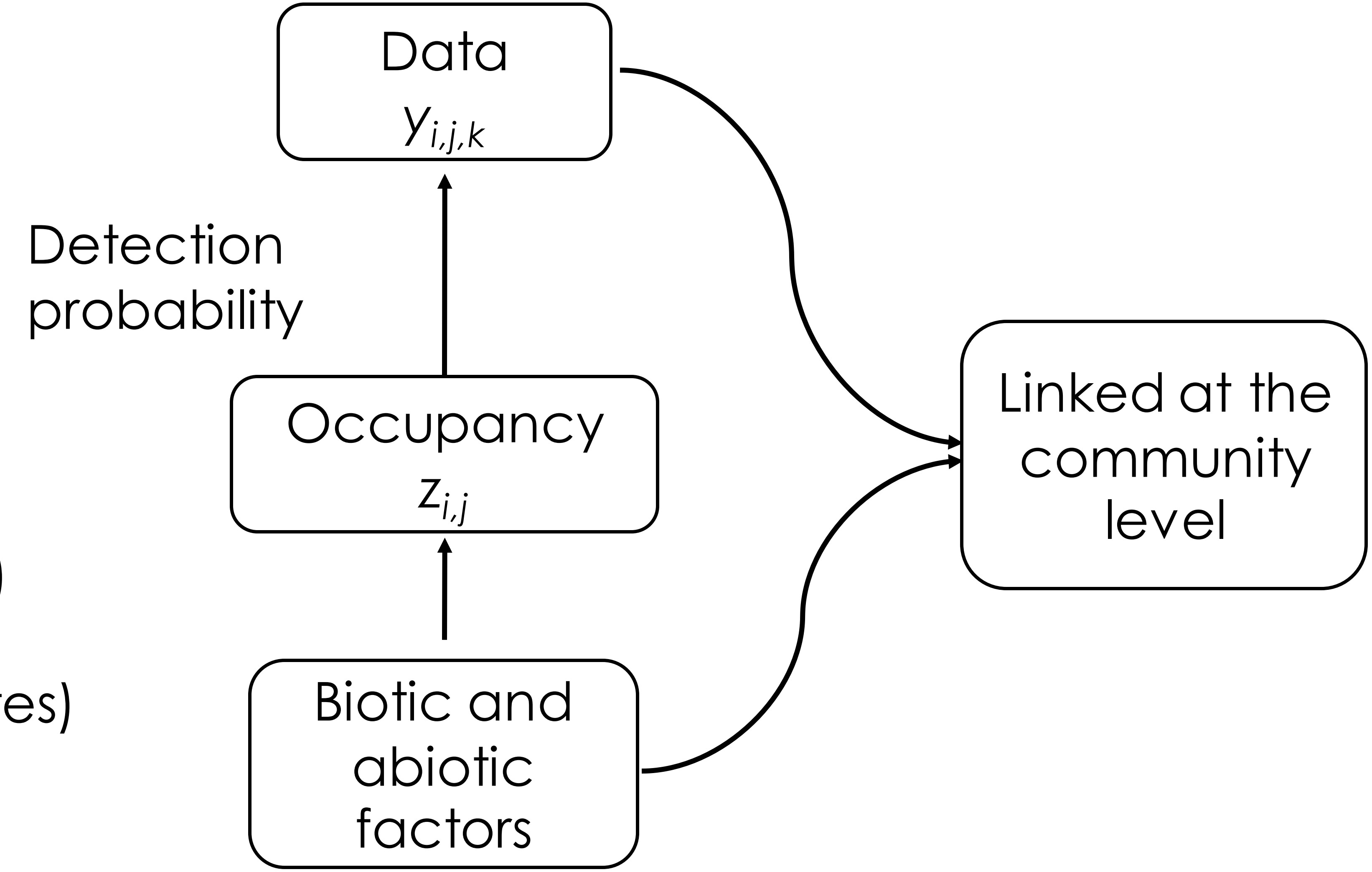

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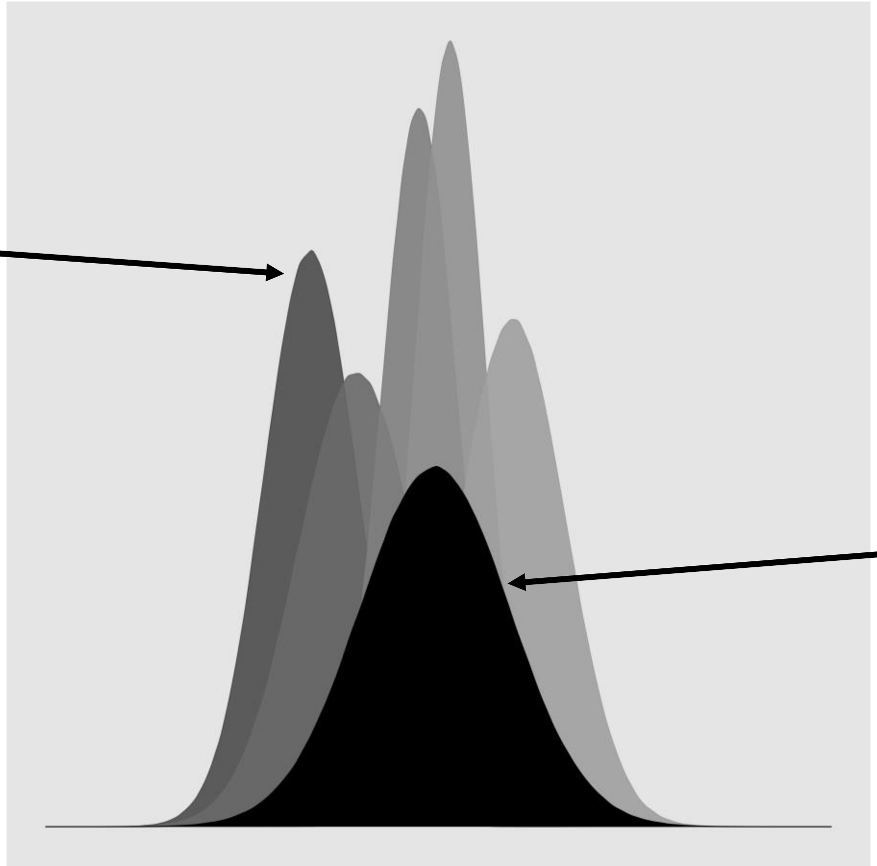
Species-specific and community effects

Species-specific effects



Community-level effect

Species-specific effects are drawn from a common, community-level distribution

Multi-species occupancy model

i = 1, …, N (species)
j = 1, …, J (sites)
k = 1, …, K (replicates)

Occupancy (ecological) sub-model

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z_{i,j} &\sim \text{Bernoulli}(\psi_{i,j}) \\
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Multi-species occupancy model

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μ_{β_r} Mean effect of covariate across all species

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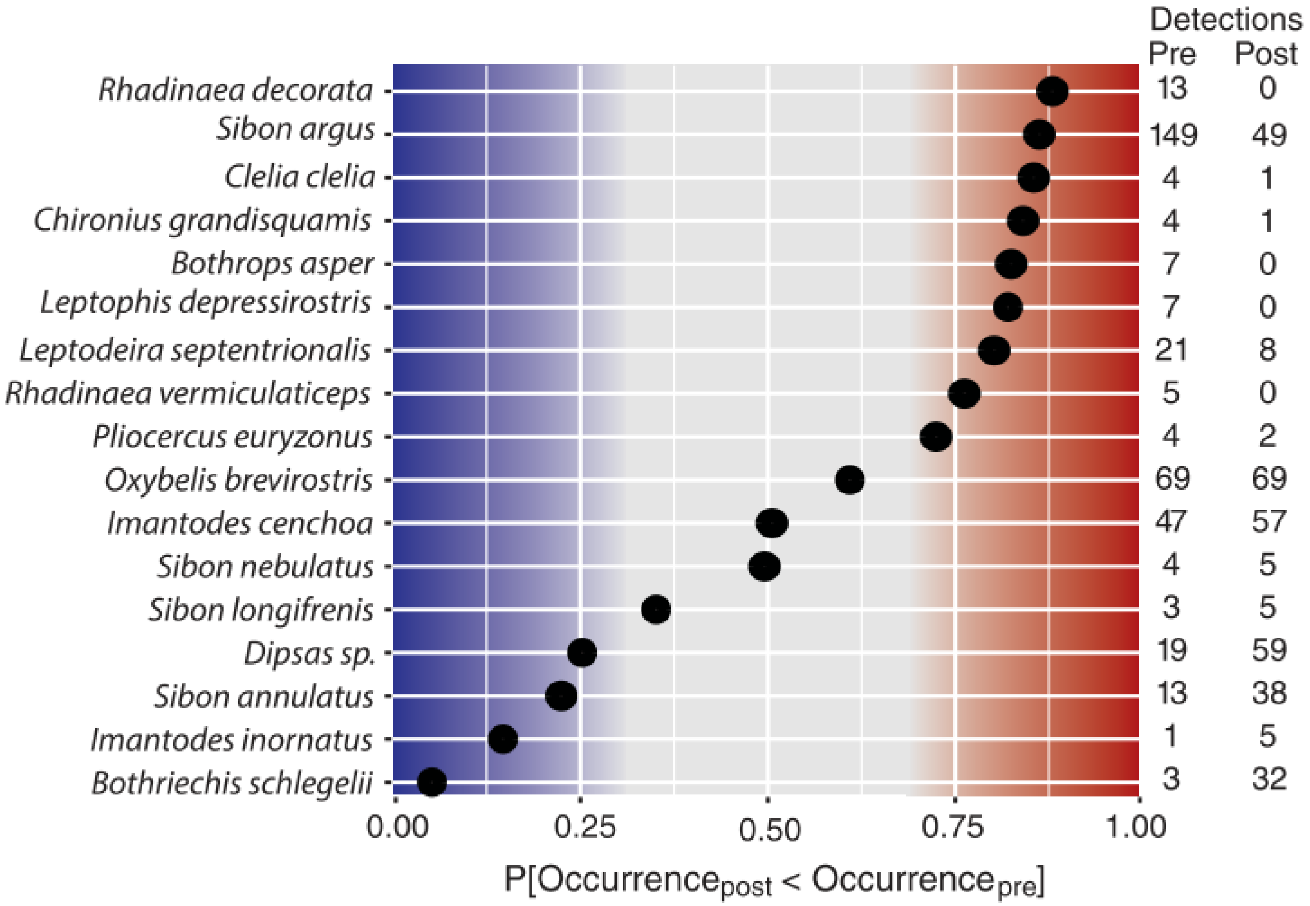
Random slopes!!

Why multi-species occupancy modeling?

Improved ability to model rare species



Potential downsides

- Longer model run times
- Coding often involves working with multi-dimensional arrays (but spOccupancy simplifies this!)
- Defining a "community" is not always straightforward:
  - Pacifici et al. 2014 Ecology and Evolution
- May not be ideal for the rarest of the rare species:
  - Erickson and Smith, 2023 Ecography

Spatial multi-species occupancy models

Spatial autocorrelation in multi-species models

- Spatial autocorrelation may be more relevant in multi-species models since different species are driven by different variables.

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- Each w is estimated using an NNGP as before
- Model run times become huge with even a moderate number of species (e.g., 10)

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- View the factors as "missing covariates" with a spatial structure
- Each species has a unique effect of each "missing covariate"
  - Called a "factor loading"
- This is a form of "factor analysis" (similar to PCA)

Spatial factor models

- Example: one covariate and two factors ("missing covariates")

$$\text{logit}(\psi_{i,j}) = \beta_{1,i} + \beta_{2,i} \cdot X_{2,j} + \lambda_{i,1} \cdot \mathrm{w}_{1,j} + \lambda_{i,2} \cdot \mathrm{w}_{2,j}$$

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"Missing covariates" that account for residual spatial autocorrelation

Spatial factor models

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Effects of the missing covariates

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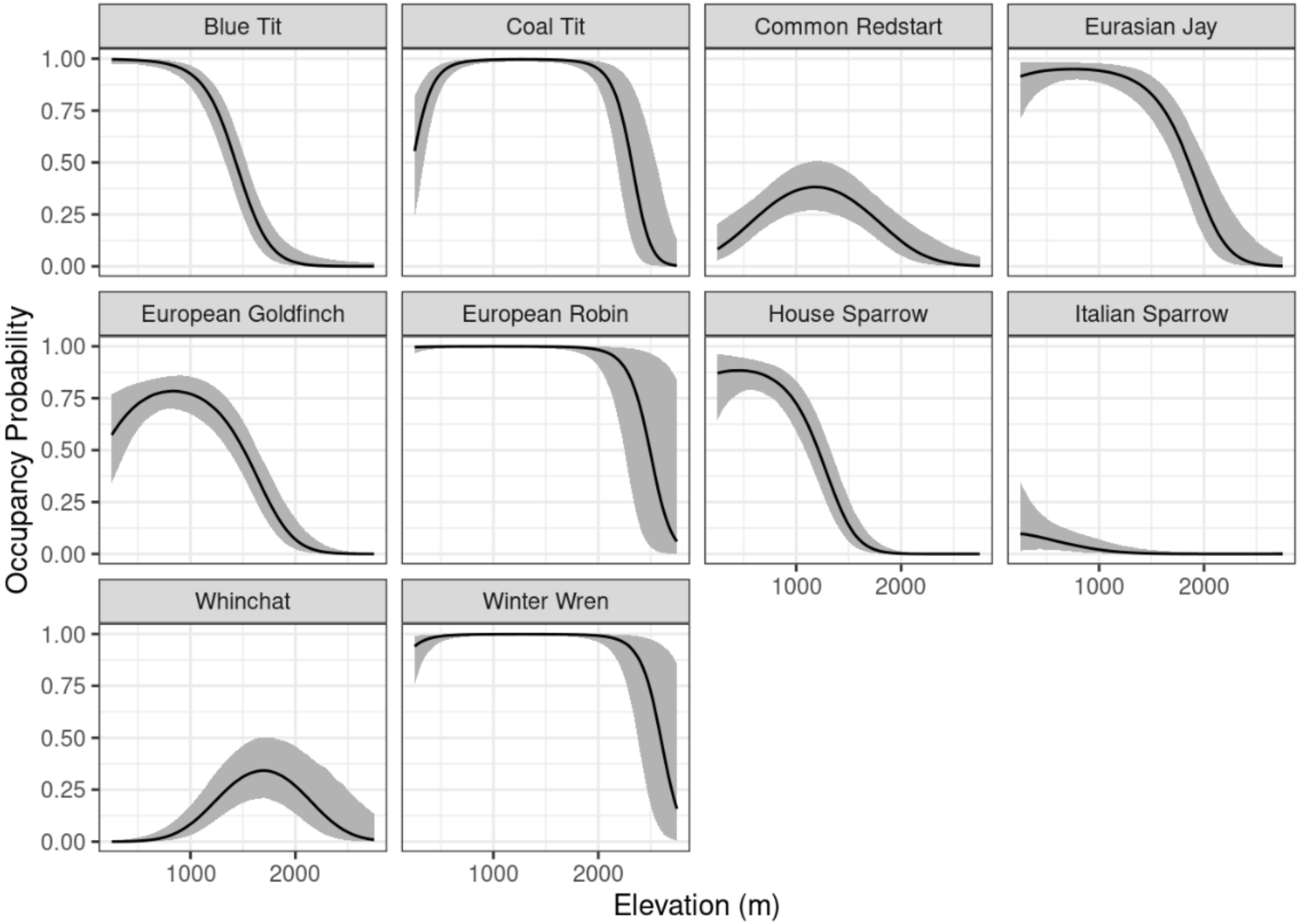
- Model run time increases with the number of factors
- See Doser et al. (2023) Ecology for details
- Downsides
  - Convergence can be tricky (see linked vignette above)
  - Requires more data than non-spatial multi-species models

Exercise 2: Swiss songbirds

- Data from the Swiss Breeding Bird Survey
- 3 visits at 267 1km squares across Switzerland
- We will focus on 10 passerine species



Multi-season occupancy models

Ecological Motivation

- How are species distributions shifting across space and time?

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- Assessment of occupancy trends over time:
  - Detection-nondetection data are easier to collect than count data
  - Occupancy-abundance relationship
  - Exact interpretation of occupancy trends depends on how data are collected (Steenweg et al. 2018 *Ecology*)

Multi-season detection-nondetection data

- Data follow the "robust design"
- A set of J sites are sampled across a set of T seasons/years
- Within each season t, each site *j* is sampled $K_{j,t}$ times.

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- Seasons are sometimes referred to as "primary replicates" and repeat visits within season as "secondary replicates"

Multi-species detection-nondetection data

- Example: 6 sites, 2 seasons, 3 surveys within a season

Season 1

Site	Survey 1	Survey 2	Survey 3
1	1	0	0
2	0	0	0
3	1	1	0
4	1	NA	0
5	0	1	1
6	0	0	0

Season 2

Site	Survey 1	Survey 2	Survey 3
1	0	1	NA
2	1	0	0
3	1	1	0
4	1	1	0
5	NA	NA	NA
6	0	0	1

Dynamic vs. multi-season occupancy models

Dynamic models

Multi-season models

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Dynamic models

- Estimate colonization and survival/extinction

Multi-season models

- Estimate occupancy probability per season

Dynamic vs. multi-season occupancy models

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Dynamic vs. multi-season occupancy models

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- MacKenzie et al. 2003 *Ecology*

Multi-season models

- Estimate occupancy probability per season
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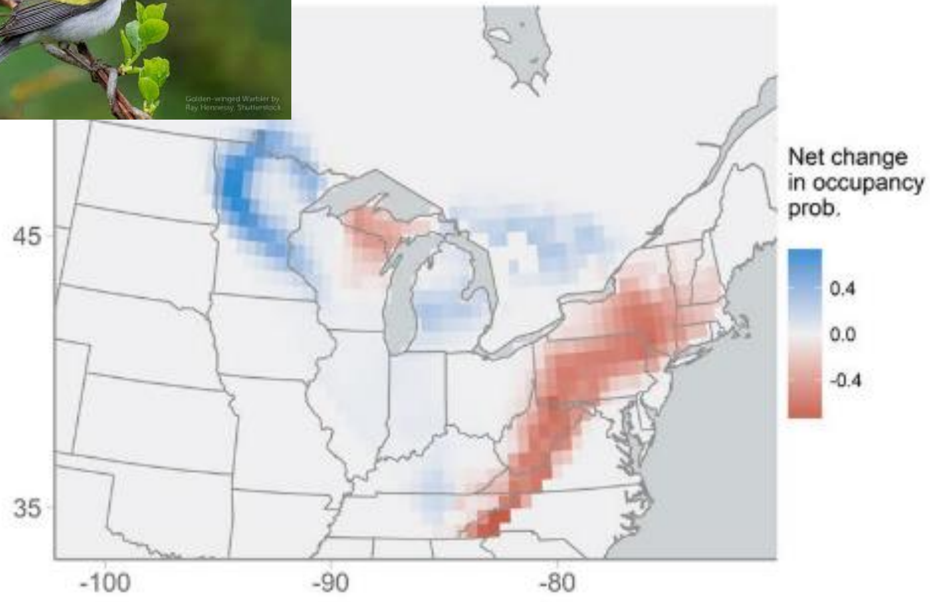
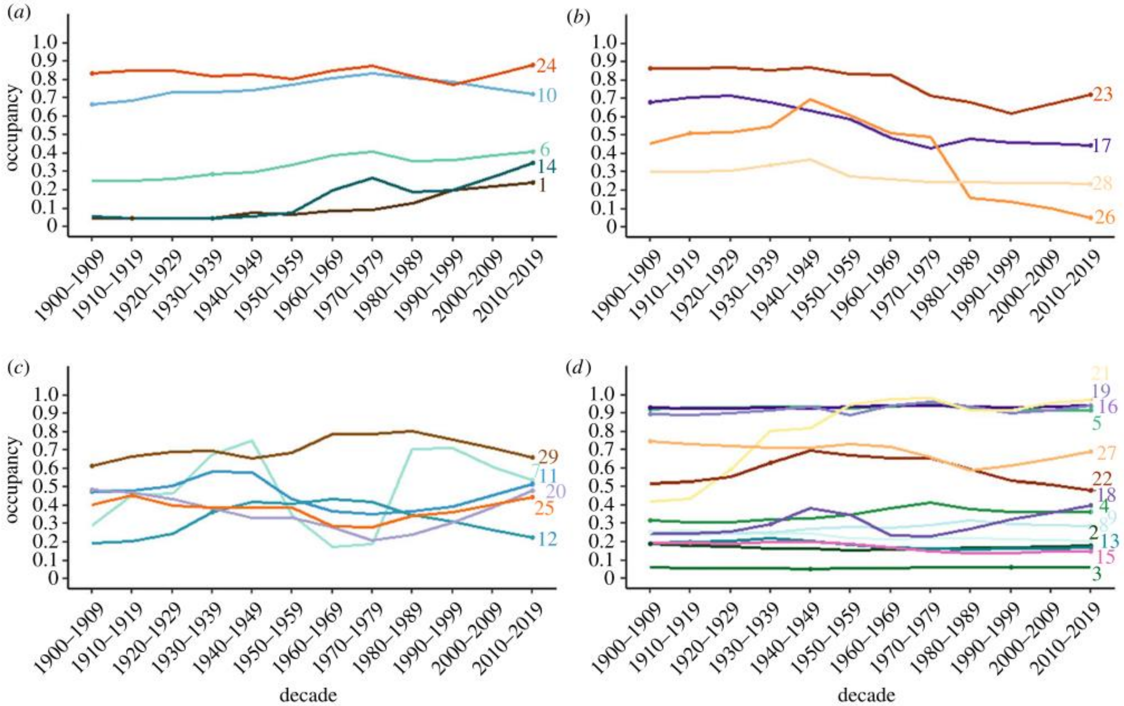
- Easier to fit and less data hungry
- In spOccupancy
- Package vignette
- Sometimes called "stacked" occupancy models

Examples of multi-season occupancy models





[Rushing et al. (2019) Sci Rep]

[Rushing et al. (2020) PNAS]

[Sheard et al. (2021) Curr Bio]

Multi-season occupancy model

$j = 1, \dots, J$ (site)
$t = 1, \dots, T$ (season)
$k = 1, \dots, K_{j,t}$ (replicate)

Occupancy (ecological) sub-model

$$z_{j,t} \sim \text{Bernoulli}(\psi_{j,t})$$
$$\text{logit}(\psi_{j,t}) = \boldsymbol{x}_{j,t}\boldsymbol{\beta} + \text{w}_j + \eta_t$$

$z_{j,t}$ True occurrence of the species at site *j* in season *t*

$\psi_{j,t}$ Occurrence probability at site *j* in season *t*

$\boldsymbol{x}_{j,t}$ Site and/or season-varying covariates

w_j Site-level random effect

η_t Season-level (temporal) random effect

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  2. Spatial NNGP -> same as before. This is the "spatial multi-season occupancy model"

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$$\eta_t \sim \mathrm{Normal}(0, \sigma_T^2)$$

    2. AR(1) -> random temporal effects follow an autoregressive structure. Covariance between two time points is:

$$\sigma_T^2 \rho^{|t-t'|}$$

Multi-season occupancy model

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Detection (observation) sub-model

$$y_{j,t,k} \sim \text{Bernoulli}(p_{j,t,k} \cdot z_{j,t})$$
$$\text{logit}(p_{j,t,k}) = \boldsymbol{v}_{j,t,k} \cdot \boldsymbol{\alpha}$$

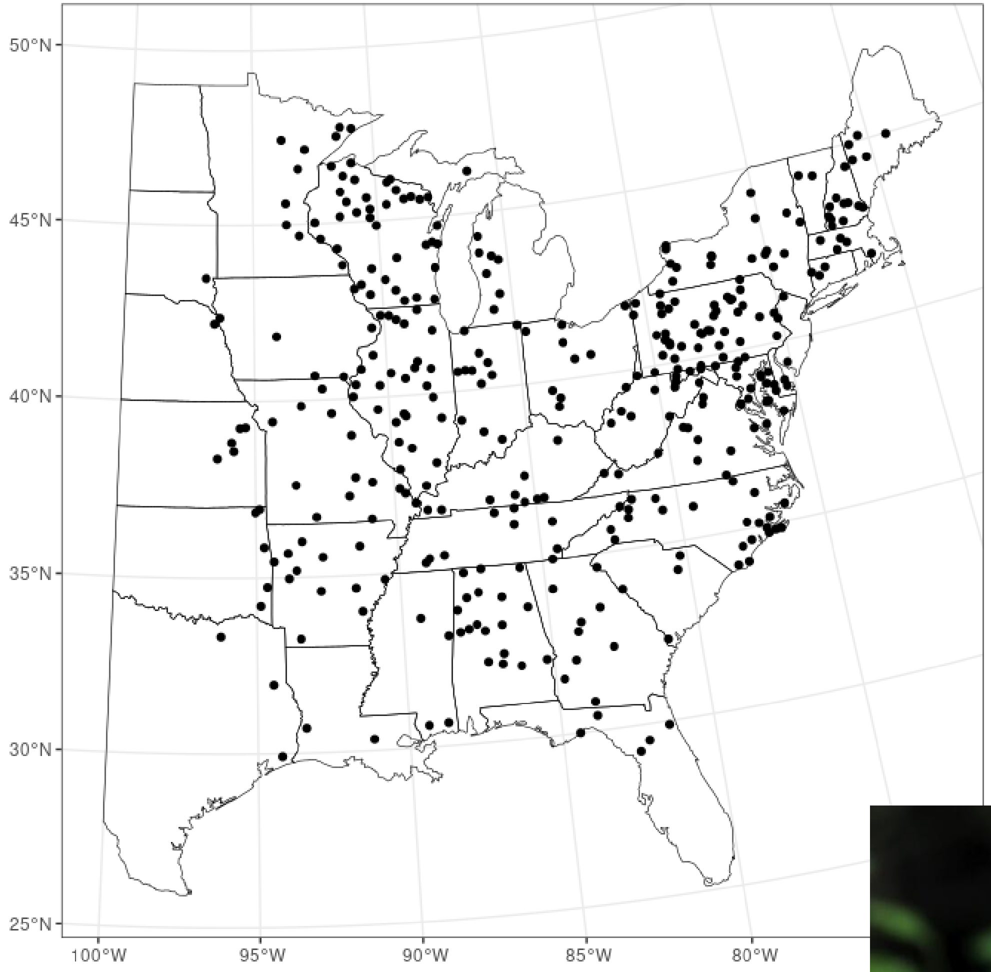
$y_{j,t,k}$ Detection-nondetection data at site *j* during replicate *k and season t*

$p_{j,t,k}$ Detection probability at site *j* during replicate *k and season t*

$\boldsymbol{v}_{j,t,k}$ Covariates affecting detection at site j during replicate k and season t

Exercise 3: Wood Thrush trend in eastern US

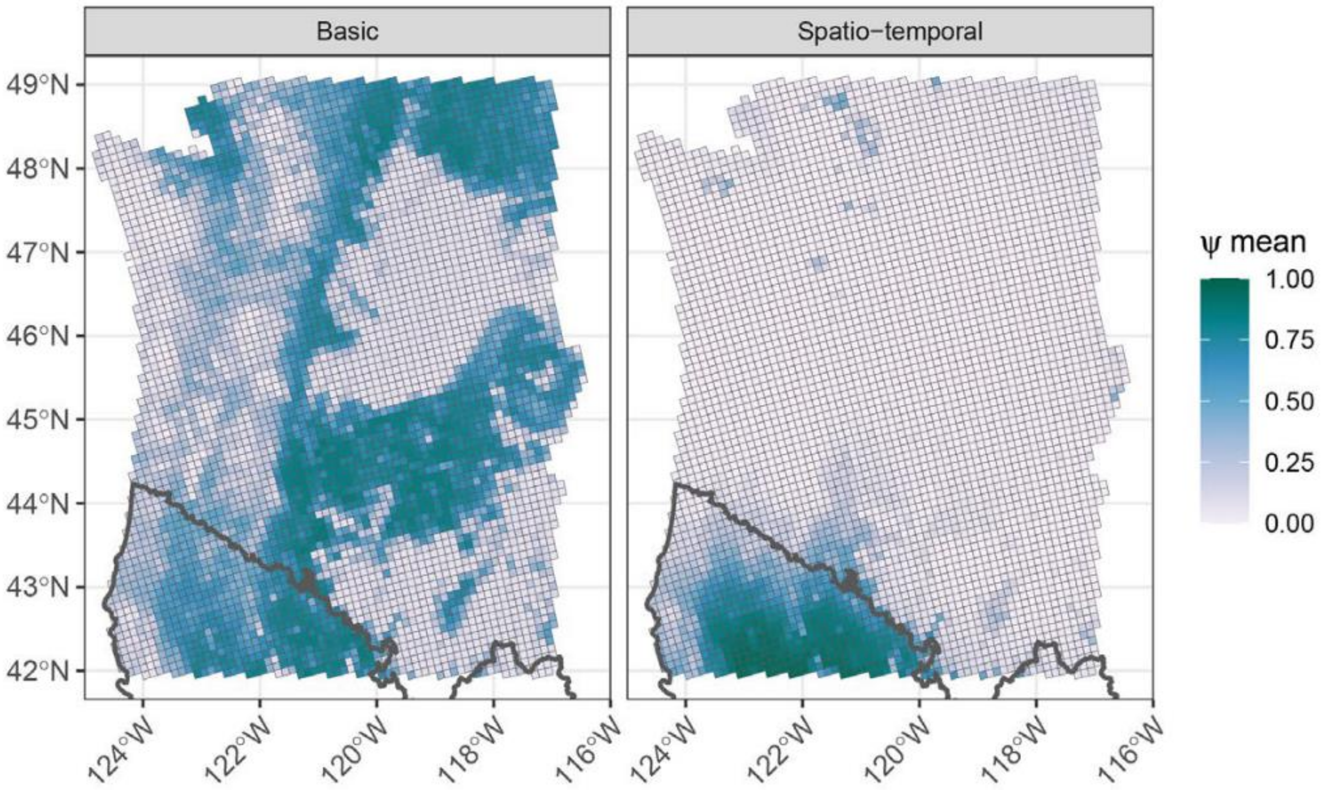
- Wood Thrush (*Hylocichla mustelina*) data from North American Breeding Bird Survey
- Replicates are spatial replicates (5 replicates per route)
- Each replicate is a group of 10 stops
- Data from 368 routes sampled in 2000-2009



Additional topics and resources

Multi-season multi-species occupancy models

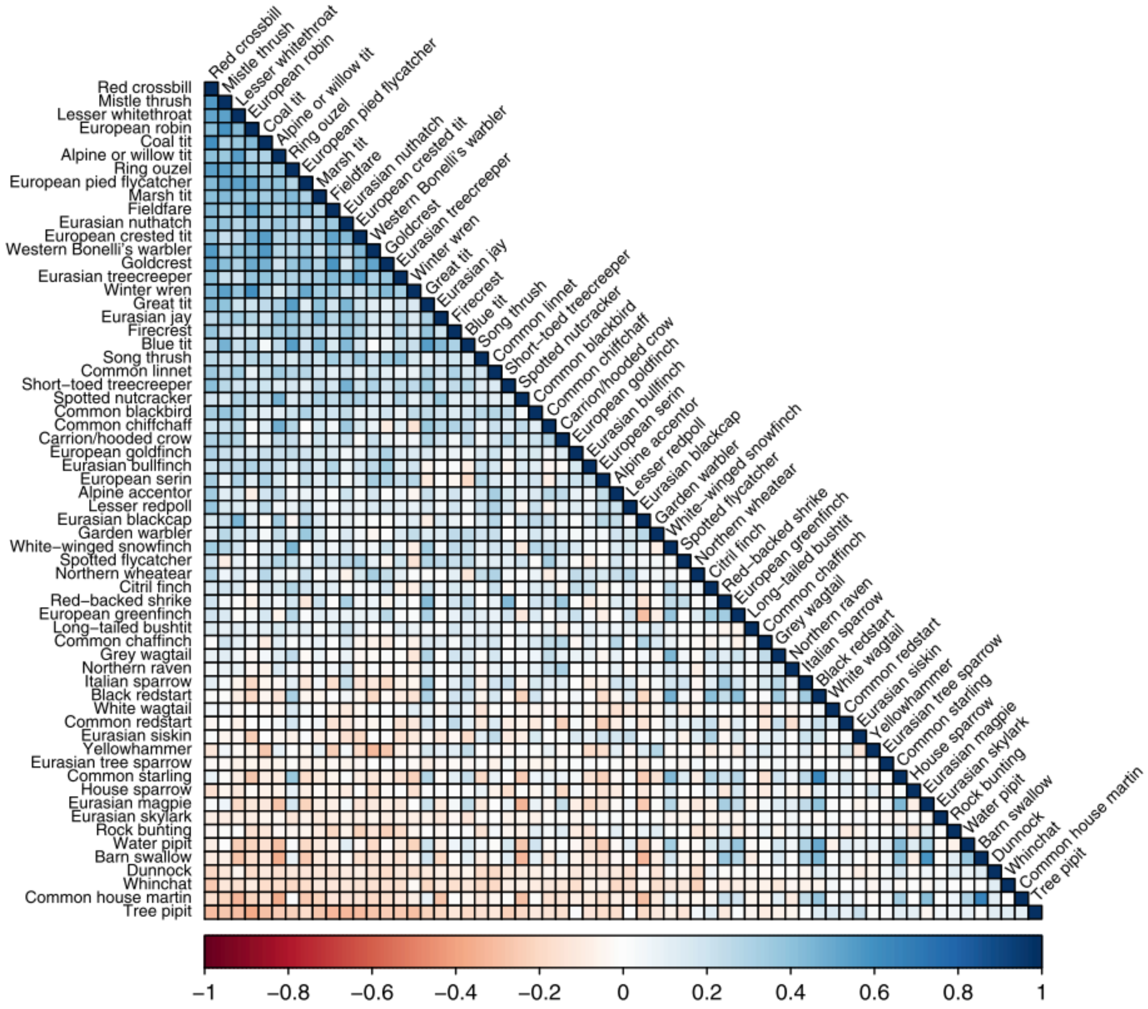
- Model spatio-temporal occupancy patterns for multiple species simultaneously
- Can help estimate trends for very rare species
- See functions tMsPGOcc() and stMsPGOcc()
- Data formatted in a four-dimensional array



[Wright et al. (2021) Eco and Evo]

Species correlations

- The factor modeling approach for multi-species models inherently accounts for residual species correlations (vignette)
- Can derive a species x species correlation matrix
- This is a spatially-explicit joint species distribution model (JSDM) with imperfect detection
- See lfMsPGOcc() function for a non-spatial JSDM



[Tobler et al. (2019) *Ecology*]

Spatially-varying coefficient occupancy models

- Allow the effects of covariates to vary spatially in addition to the intercept
- Applications: spatially-varying trends, quantify "nonstationarity" in covariate effects
- [Vignette]

Guidelines for the use of spatially-varying coefficients in species distribution models

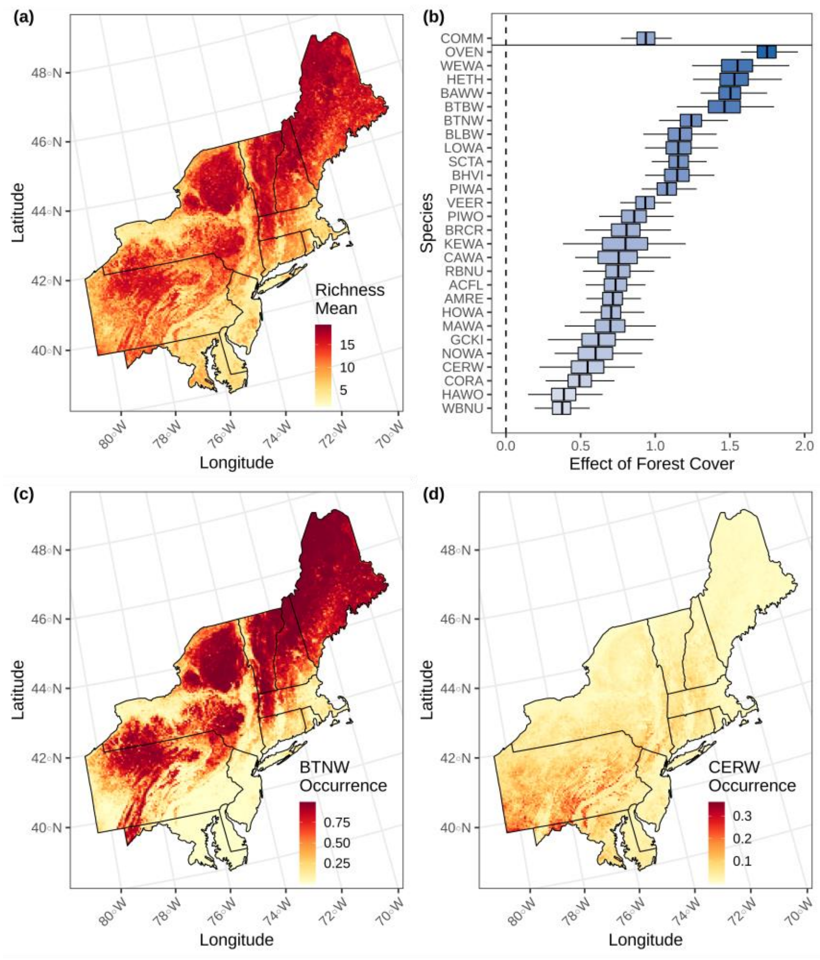
Jeffrey W. Doser[1, 2], Marc Kéry[3], Sarah P. Saunders[4], Andrew O. Finley[2,5,6], Brooke L. Bateman[4], Joanna Grand[4], Shannon Reault[4], Aaron S. Weed[7], Elise F. Zipkin[1, 2]

Modeling complex species-environment relationships through spatially-varying coefficient occupancy models

Jeffrey W. Doser[1, 2], Andrew O. Finley[2, 3, 4], Sarah P. Saunders[5], Marc Kéry[6], Aaron S. Weed[7], Elise F. Zipkin[1, 2]

Integrated occupancy models

- Fit occupancy models using multiple data sources
- Single-species: spatial and non-spatial models
- Multi-species: non-spatial models only (spatial coming soon)
- Examples:
  - Vignette for [single-species]() and [multi-species]()
  - [Code for single-species example with bottlenose dolphins]()
  - [Code for multi-species example with eBird and BBS data]()



[Zipkin et al. (2023) JAE]()

spAbundance

- Spatial and nonspatial N-mixture models, hierarchical distance sampling models, and GLMMs
- Single-species and multi-species models
- Syntax nearly identical to spOccupancy
- Website and preprint

Additional resources

Articles

Fit occupancy models

[Introduction to spOccupancy]
Learn how to get started with the core spOccupancy functionality

[Formatting data for use in spOccupancy]
Learn how to format raw data to fit occupancy models in spOccupancy

[Joint species distribution models with imperfect detection in spOccupancy]
Learn how to account for species correlations within multi-species occupancy models

[Multi-season occupancy models for assessing species trends and spatio-temporal occurrence patterns (PDF)]

[Multi-season occupancy models for assessing species trends and spatio-temporal occurrence patterns]
Learn how to fit multi-season occupancy models in spOccupancy

[Fitting occupancy models with random intercepts in spOccupancy]
Learn how to include random effects in spOccupancy

[Spatially varying coefficient models in spOccupancy]
Learn how to fit spatially varying coefficient models to quantify spatially varying trends and species-environment relationships

[Integrated multi-species occupancy models in spOccupancy]
Learn how to fit multi-species occupancy models with multiple data sources

[Convergence diagnostics and other considerations when fitting spatial occupancy models]
Ideas related to convergence, identifiability, priors, and other potential problem areas in spatial occupancy models

[Exploring model identifiability with a stress-testing framework]

- Website:
  - https://www.jeffdoser.com/files/spoccupancy-web/
- GitHub development page
  - https://github.com/doserjef/spOccupancy
- Package updates announced on Twitter/X (@jeffdoser18)
- Email: doserjef@msu.edu