

Incorporating species' correlations with Joint Species Distribution Models

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Outline

- ▶ JSMD
- ▶ GLLVMs background
- ▶ gllvm R-package

Questions so far?



Distribution Modelling

If you have presence-absence data of a species, you fit a Species Distribution Model of the form:

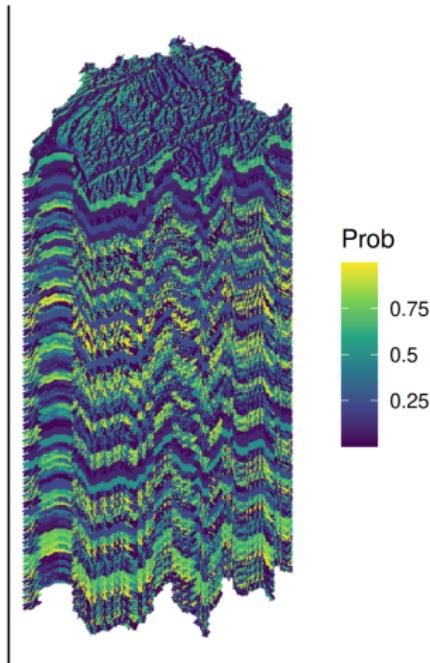
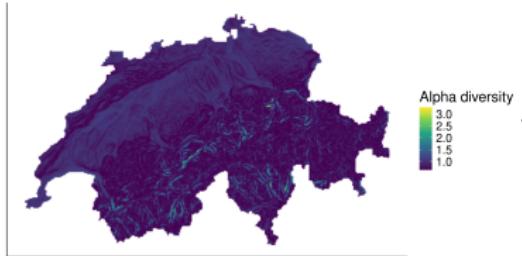
$$y_{ij} = \alpha + \mathbf{x}_i^\top \boldsymbol{\beta} \quad (1)$$

- ▶ \mathbf{x}_i is usually a bioclimatic variable
- ▶ Then you want to predict where a species may occur
- ▶ Potentially based on future climate scenarios
- ▶ Similar to the model from yesterday; it requires

Co-occurrence of Swiss birds

Can the distribution of one species inform us of another's?

Bird alpha diversity (due to mean abundance, aspect and slope)



Leveraging shared information

In our mixed-effects model yesterday, we had some components already shared for all species:

The random effect $\beta_j \sim \mathcal{N}(\mu, \Sigma)$:

- ▶ had mean μ the same for all species
- ▶ had covariance Σ the same for all species

Sharing information across species helps; on some species we have more information than others, which we can use to inform ourselves on the occurrence of less frequent species.

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Sharing information across species helps; on some species we have more information than others, which we can use to inform ourselves on the occurrence of less frequent species.

This is also the idea of JSMD: use co-occurrence information to improve the model's knowledge of the community

Co-occurrence patterns

- ▶ if one species occurs somewhere, we know another does too, for various reasons

Species correlation

If we fit a GLM to data of multiple species, we assume **independence** (so we need much more information for accurate estimates)

But, observations of the same species form groups. Co-occurring species have more similar observations than for other species

In GLMM language: **observations of species exhibit correlation**

- 1) Part of this can be explained by shared environmental responses
- 2) The other part remains

We never know how much of the “remainder” is explainable by the environment.

Independence

Correlation means non-independence. Violation of the independence assumption cannot be ignored:

- ▶ Fixed effect parameter estimates are biased (estimated environmental preferences are wrong)
- ▶ Standard errors are too small (inflated type I error; too optimistic)
 - ▶ Consequently, p-values and CIs are too small
- ▶ Predictions may be poor
- ▶ Equivalently, means we have pseudoreplication
- ▶ Random effect estimates can be inaccurate

So, there is also a statistical need to adjust the model

Assessing the independence assumption

This is done via:

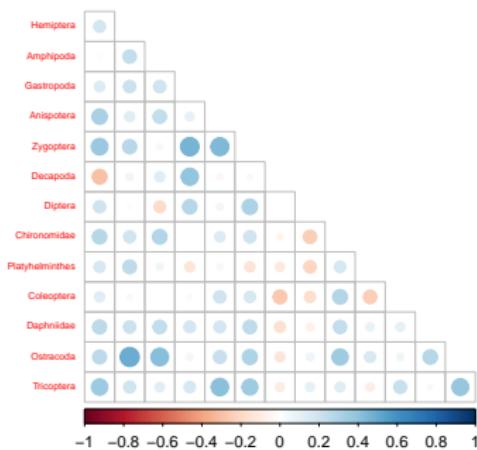
- ▶ Nature of the data (clustering)
- ▶ Visually via residual diagnostics (see yesterday)

The previous model

```
model4 <- gllvm::gllvm(y, X = X, formula = ~NO3, num.lv = 0,  
family = "negative.binomial")
```

We can see this in the correlations of the residuals from our model:

```
corrplot::corrplot(cor(residuals(model4)$resi), type = "lower", diag = FALSE, tl.pos = "l", tl.cex = 0.5)
```



Joint Species Distribution Modeling

A decade ago, Joint Species Distribution Models (JSMD) were introduced to model binary data of multiple species

- ▶ Pollock et al. (2015): co-occurrence of frogs and trees
- ▶ Clark et al. (2015): co-occurrence of trees

The goal: to incorporate covariation of species for better predictions

Species associations

What induces covariation between species?

- ▶ Shared environmental responses (abiotic conditions)
- ▶ Biotic interactions

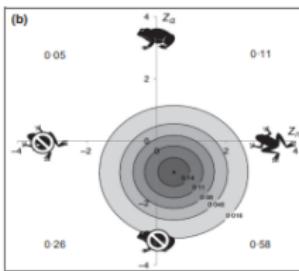
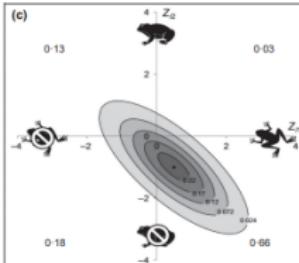
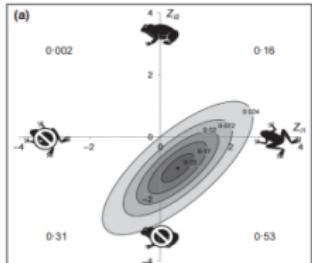


Figure 1: Pollock et al. (2015, fig. 1)



Interactions and co-occurrence

ECOLOGY LETTERS

Ecology Letters, (2020) 23: 1050–1063 doi: 10.1111/ele.13525

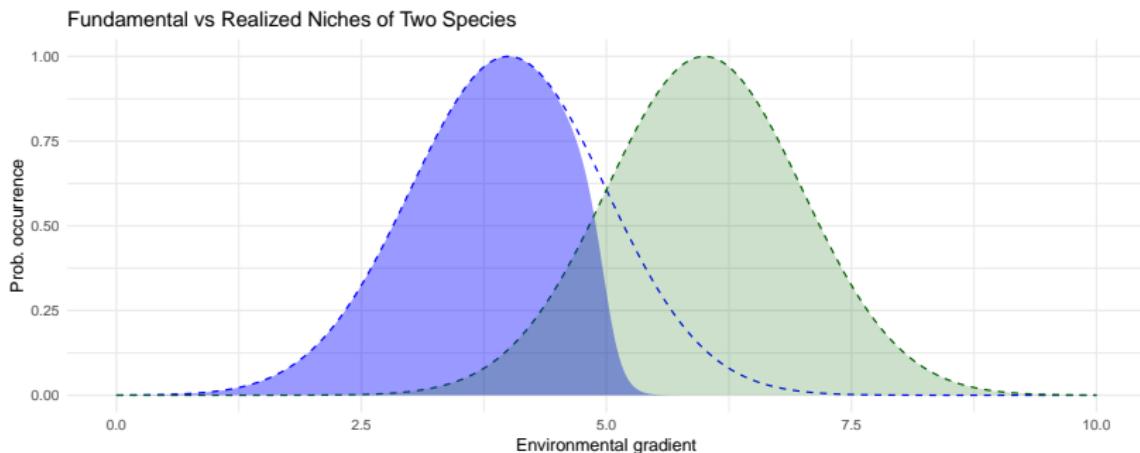
**IDEAS AND
PERSPECTIVES**

Co-occurrence is not evidence of ecological interactions

Interactions induce correlation, but we cannot infer interactions from (non-temporal) co-occurrence data.

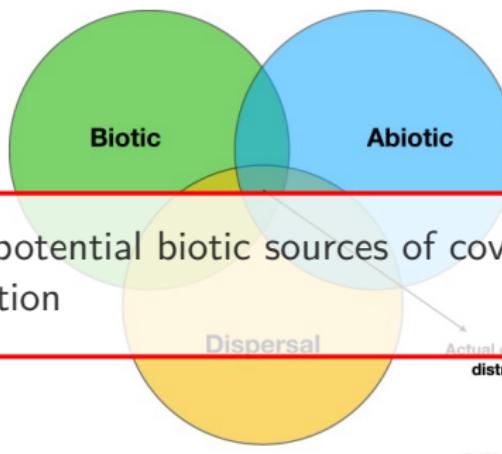
The niche concept

We can also take a different angle; correlation is introduced to improve our estimates for species' responses.



Fundamental niche: total occupiable space without other species' intervention
Realized niche: the space occupied due to other species

When reality kicks in



Incorporating potential biotic sources of covariation is a step in the right direction

Figure 2: Poggialto et al. (2021)

Niches are shaped more than by environment and interactions; historical limitations, dispersal, and other processes prevent us from estimating the fundamental niche.

JSDM vs. classical multivariate analysis

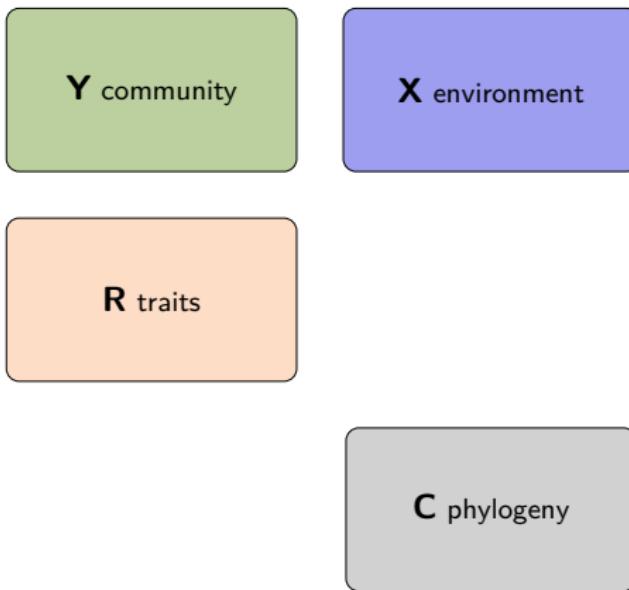
	Classic	JSDM
Focus	Low-dimensional space	Distributions
Goal	Inference	Prediction
Data type	Usually quantitative	Binary
Scale	Local	Regional
Covariates	Environmental	Bioclimatic
Presentation	Ordination diagram	Correlation plot/map
Audience	Community ecologists	Macro ecologists

JSDM vs. classical multivariate analysis

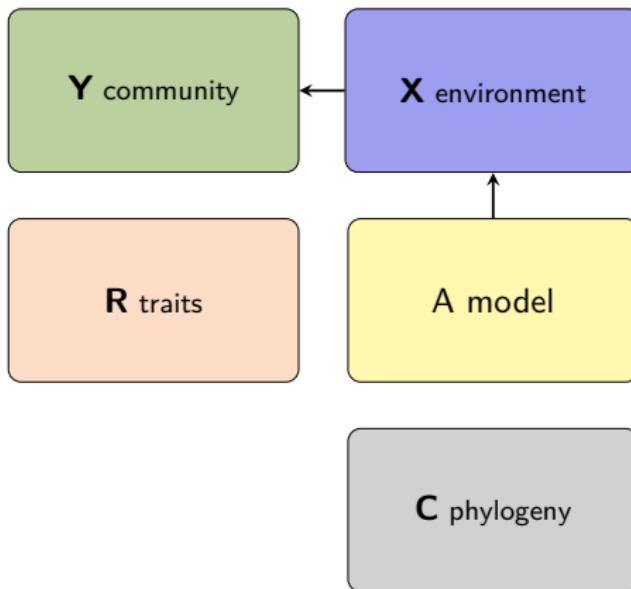
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That is not to say JSDMs cannot be used for non-binary data, for inference, or for local scales

Typical questions in the framework

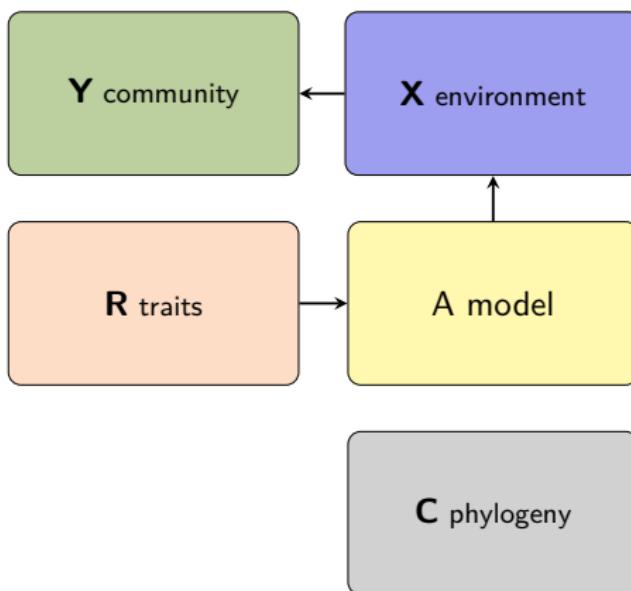


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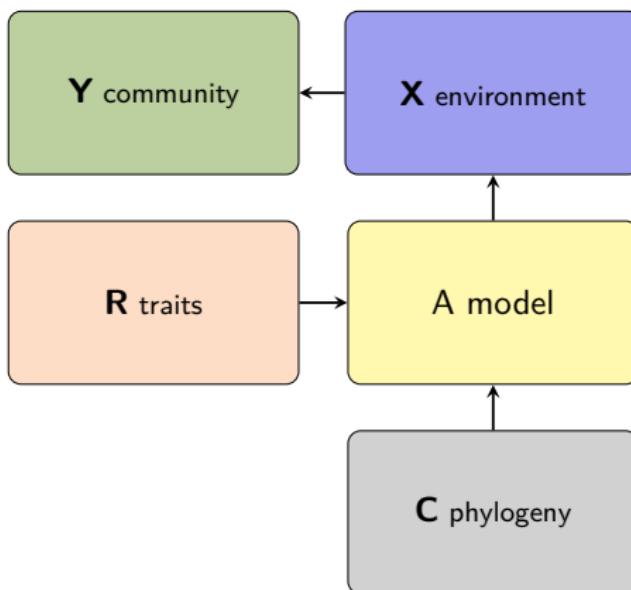
Q: How does the environment structure the community?
environmental filtering

Typical questions in the framework



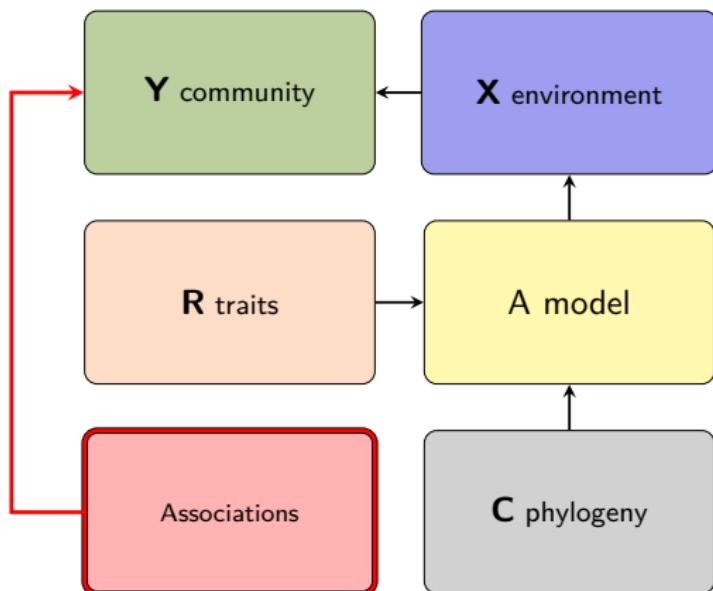
Q: How do traits affect species' responses to the environment?
environmental filtering (more later)

Typical questions in the framework



Q: Do species with shared evolutionary history co-occur?
(phylogenetic structuring) **environmental filtering**

Typical questions in the framework



Q: Do species co-occur **after** the environment has been considered? **biotic filtering**

Joint Species Distribution Modeling

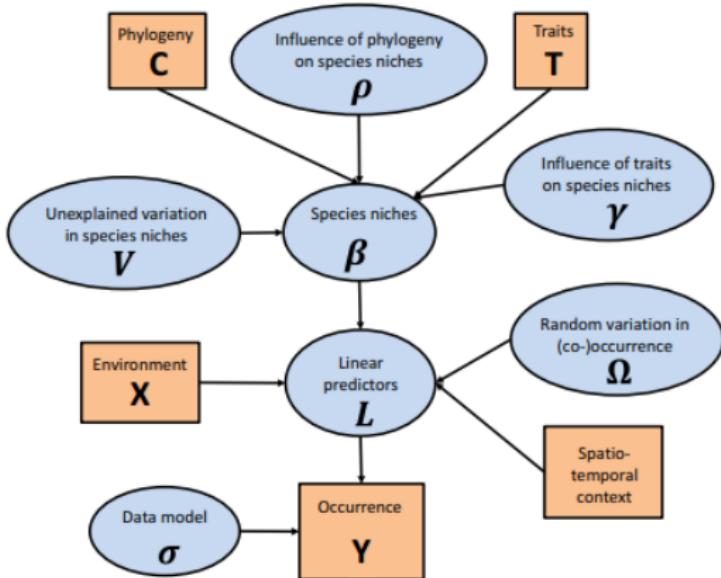


Figure 3: Figure from Ovaskainen et al. (2017)

Joint Species Distribution Modeling

The aim of JSDMs is to incorporate *species associations*

- ▶ Species may co-occur due to biotic interactions
- ▶ Due to similar environmental preferences
- ▶ Or because they have a similar history

Either how, it results in correlations between responses

Joint Species Distribution Model (JSDM)

- ▶ For community data, we want to incorporate correlation of species
- ▶ We have **Multivariate** data (in contrast to multivariable)

$$g\{\mathbb{E}(\mathbf{y}_i | \boldsymbol{\epsilon}_i)\} = \boldsymbol{\beta}_0 + \mathbf{x}_i^\top \boldsymbol{\beta} + \boldsymbol{\epsilon}_i \quad (2)$$

- ▶ we add $\boldsymbol{\epsilon}_i$ relative to the VGML(M)
- ▶ This random effect takes care of the left-over (co)variation of species
- ▶ so we assume $\boldsymbol{\epsilon}_i \sim \mathcal{N}(\mathbf{0}, \boldsymbol{\Sigma})$
- ▶ $\boldsymbol{\Sigma}$ is the matrix of **species associations**

JSDM: the model

$$\eta_{ij} = \beta_{0j} + \dots + \epsilon_{ij} \quad (3)$$

- ▶ The stuff from yesterday
- ▶ $\epsilon_i \sim \mathcal{N}(0, \Sigma)$
- ▶ Σ is the matrix of *species associations*
- ▶ So we expect a positive values of species co-occur, and negative if they do not

Species associations

- ▶ Difficult to estimate: there are usually too many parameters
- ▶ The number of pairwise associations grows quadratically
 - ▶ 2 with 2 species, 6 for 4 species, 45 for 10 species, 4950 for 100

$$\Sigma = \begin{bmatrix} 1 & sp_{12} & \cdots & sp_{1j} \\ sp_{21} & 1 & \cdots & sp_{2j} \\ \vdots & & \ddots & \vdots \\ sp_{j1} & sp_{j2} & \cdots & 1 \end{bmatrix} \quad (4)$$

This very quickly becomes an issue for fitting models

JSMD: it is just a mixed-effects model

The JSMD is “just” a mixed-effects model. So we can fit it with available software:

In lme4:

```
glmer(abundance ~ species + x:species + (0+species|sites), data = data)
```

- ▶ There are $p(p + 1)/2$ correlations between species
- ▶ This model becomes (very) large very quickly do not try this at home
- ▶ Will usually not fit
- ▶ So we need to do something smart!

JSDM software implementations

There are many!

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- ▶ Boral (Bayesian, slow and somewhat outdated)
- ▶ sJSDM (Bayesian, relatively slow, but faster than Boral)
- ▶ Hmsc (Bayesian, generally slow, loads of functionality)
- ▶ ecoCopla (Frequentist, very fast but limited functionality)
- ▶ CBFM (Frequentist, geared towards spatio-temporal analysis)
- ▶ sjSDM (Frequentist, very fast but limited functionality, requires python)
- ▶ glmmTMB (Frequentist, fast and very versatile, not purpose-coded)
- ▶ gllvm (Frequentist, fast and very versatile, purpose-coded)

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- ▶ gllvm (Frequentist, fast and very versatile, purpose-coded)

Which software is most suitable on your aim, data type, and model.

Example: alpine plants in France

- ▶ Data by Choler 2005
- ▶ Occurrence of 92 species at 75 5 by 5 plots
- ▶ 6 environmental variables: aspect, slope, microscale landform, disturbance level (physical and trampling/burrowing), and mean Julian snowmelt date
- ▶ In the jSDM package



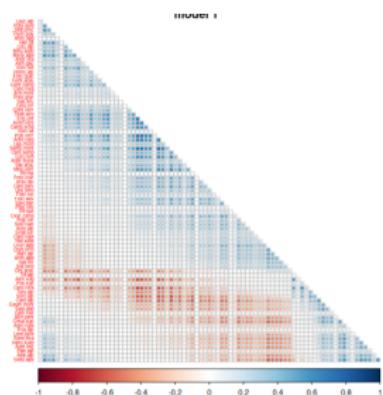
Example: fitting a JSDM

```
model1 <- gllvm(Y, family = "binomial")
```

Pretty straightforward!

Example: visualizing associations

```
cors <- getResidualCor(model1)
corrplot(cors, type = "lower", diag = FALSE, tl.pos = "l", order = "AOE",
```

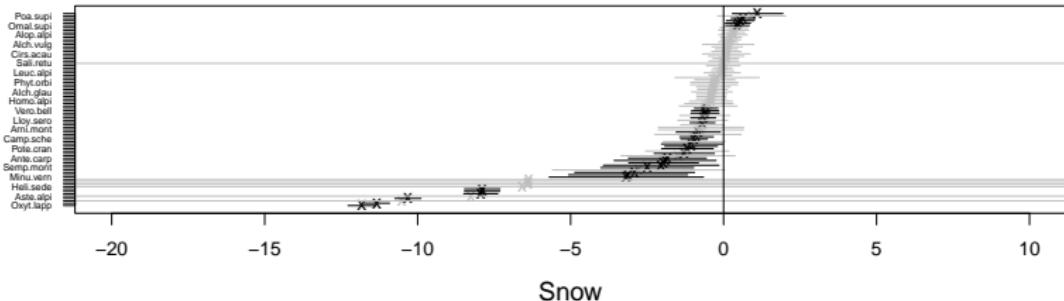


Blue: species that are predicted to co-occur
Red: species that are predicted to avoid each other

Example: adding a environmental variable

Now that we have incorporated associations, we can add in environmental variables as yesterday (fixed or random):

```
model2 <- gllvm(Y, X = X, formula = ~Snow, family = "binomial")
```



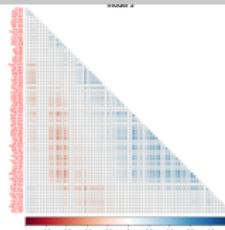
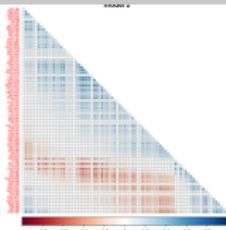
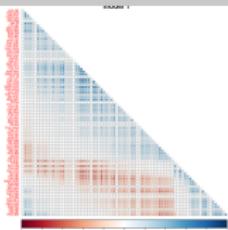
Adding environmental covariates tends to improve the model, but reduce the signal in the associations.

Example: comparing the models

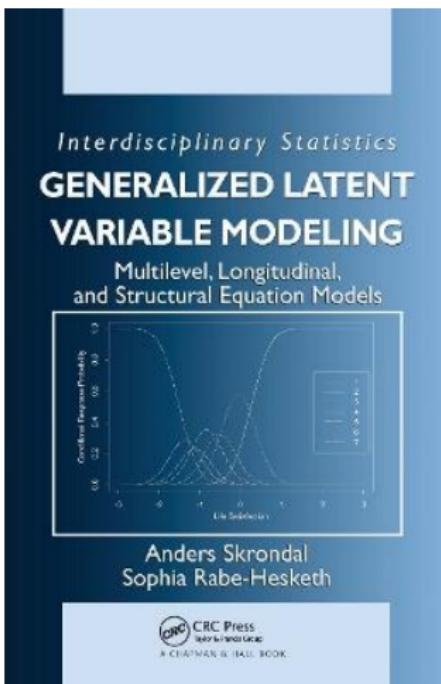
```
model3 <- gllvm(Y, X = X, formula = ~Snow+Form+Slope+Aspect, family = "binomial")
```

```
AIC(model1, model2, model3)
```

```
##          df      AIC
## model1 245 4148.531
## model2 327 4140.254
## model3 573 4171.055
```

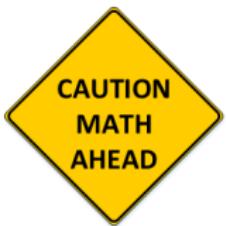


Generalized Linear Latent Variable Models (GLLVMs)



Generalized Linear Latent Variable Models (GLLVMs)

- ▶ A framework for model-based multivariate analysis
- ▶ That does dimension reduction
- ▶ Similarly as in VGLMM, you need to specify:
 1. A distribution
 2. A link function
 3. The model its structure
- ▶ But now also the number of dimensions for the associations



Factor analysis to the rescue

- ▶ GLLVMs were introduced to ecology as a technical solution to this problem
- ▶ We represent the covariance matrix with fewer **dimensions**:
 $\Sigma \approx \Gamma\Gamma^\top$

“The factor analytic solution” because factor analysis (Spearman, 1904) is the precursor of GLLVMs

GLVM: the model

$$\eta_{ij} = \beta_{0j} + \dots + \epsilon_{ij} \quad (5)$$

- ▶ The stuff from yesterday
- ▶ $\epsilon_i \sim \mathcal{N}(0, \Sigma)$
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- ▶ $\boldsymbol{\Sigma}$ is the matrix of *species associations*
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Prediction

So, we represent:

$$\Sigma \approx \Gamma\Gamma^\top \quad (6)$$

The number of columns in Γ is equal to the number of latent variables.

- ▶ The more latent variables we use, the better we represent the associations
- ▶ But, more latent variables slows down the model!
- ▶ So; it is a trade-off that we need to measure (somehow)
 - ▶ Can use information criteria or hypothesis tests
 - ▶ Variation explained
 - ▶ Cross-validation
 - ▶ Or some measure of predictive performance

Does it improve predictions?

Yes



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It depends how you evaluate it. Statistically, we need to incorporate non-independence.

Prediction of focal species

For a subset of species we are particularly interested in **A**, we can do **conditional** prediction: utilize information from other species **B** to improve its prediction. We define our residual covariance matrix:

$$\Sigma = \begin{bmatrix} \Sigma_A & \Sigma_{AB} \\ \Sigma_{BA} & \Sigma_B \end{bmatrix} \quad (7)$$

we set $\epsilon_{iA} = \Sigma_{AB} \Sigma_B^{-1} \epsilon_{iB}$

Now, even if species **A** is absent somewhere, we are also using its known relation with species **B**. But, this does not work if we don't have response data at a site.

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Note, this requires Σ to be full rank.

The residual variance

Σ is of full rank, as long as we also have residual variance.

We write our model with a residual:

$$\eta_{ij} = \beta_{0j} + \epsilon_{ij} + e_{ij} \quad (8)$$

- ▶ where ϵ_{ij} is our term for covariation as before
- ▶ $e_{ij} \sim f(0, \phi_j)$ is an independent residual

e_{ij} takes different forms depending on the response distribution. In some cases (Poisson) it is hard to define.

Link functions: probit

In probit regression, we use a latent variable η_{ij}^* for thresholding.

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and we model this auxiliary variable:

$$\eta_{ij}^* = \eta_{ij} + E_{ij} \sim \mathcal{N}(0, 1)$$

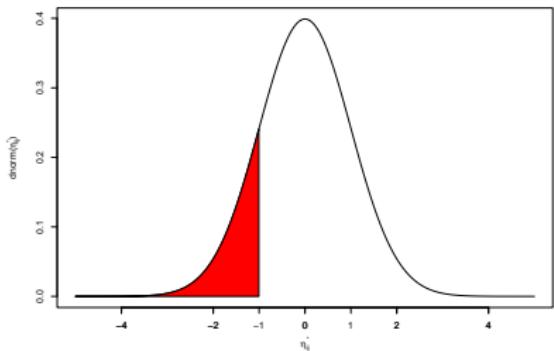
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$$p_i = \Phi(\eta_{ij})$$

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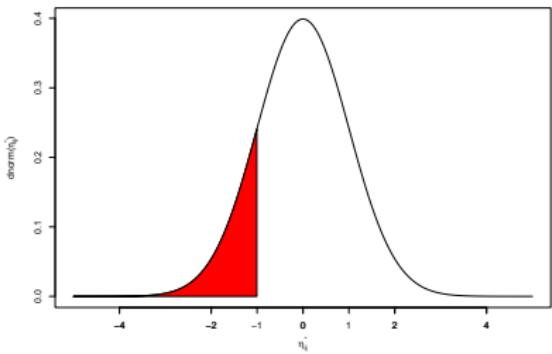
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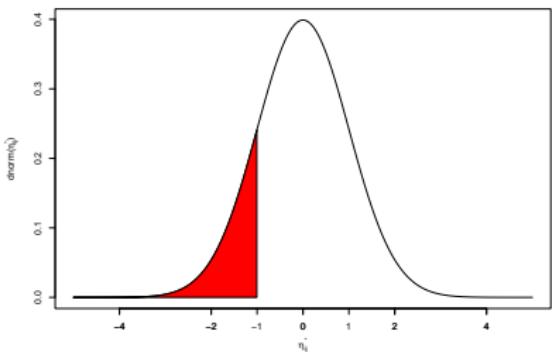
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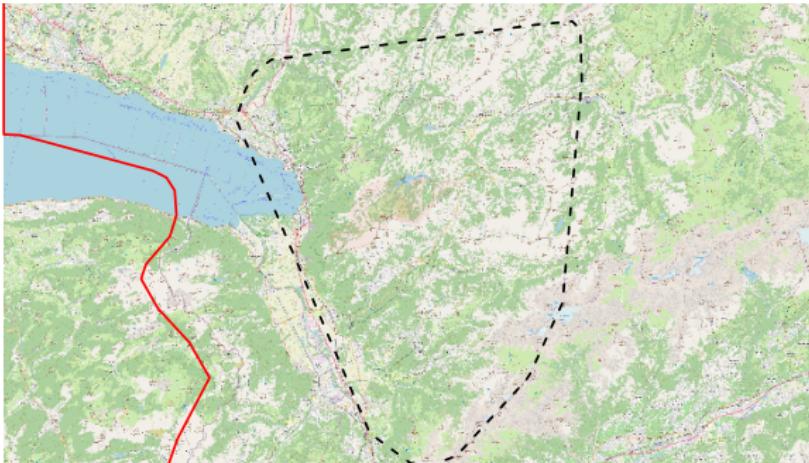


**if η_{ij}^* is positive, we have 1
and 0 if it is negative**

So, really, $\Sigma = \Gamma\Gamma^\top + I$

Example: alpine plants in Switzerland

- ▶ Data by D'amen et al. (2017)
- ▶ Occurrence of 175 species at 840 $4m^2$ plots
- ▶ Environmental variables: Degree days above zero, slope, moisture, solar radiation, topography (and coordinates)



Example: fit JSDMs

```
model5 <- gllvm(Y, num.lv = 2, family = "binomial", sd.errors = FALSE, diag.iter = 0, optim.method = "L-BFGS-B"
model6 <- gllvm(Y, num.lv = 3, family = "binomial", sd.errors = FALSE, diag.iter = 0, optim.method = "L-BFGS-B"
model7 <- gllvm(Y, num.lv = 4, family = "binomial", sd.errors = FALSE, diag.iter = 0, optim.method = "L-BFGS-B"
```

Calculate predictive performance

```
goodnessOfFit(Y, object = model5, measure = "RMSE")$RMSE
```

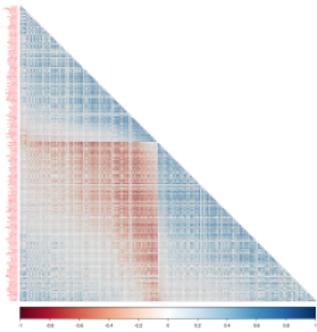
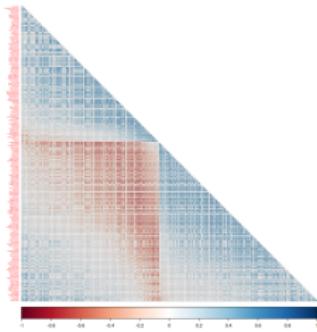
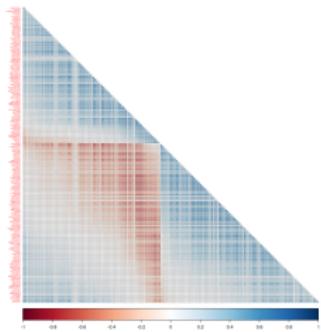
```
## [1] 0.2625214
```

```
goodnessOfFit(Y, object = model6, measure = "RMSE")$RMSE
```

```
## [1] 0.2454212
```

```
goodnessOfFit(Y, object = model7, measure = "RMSE")$RMSE
```

Example: resulting associations

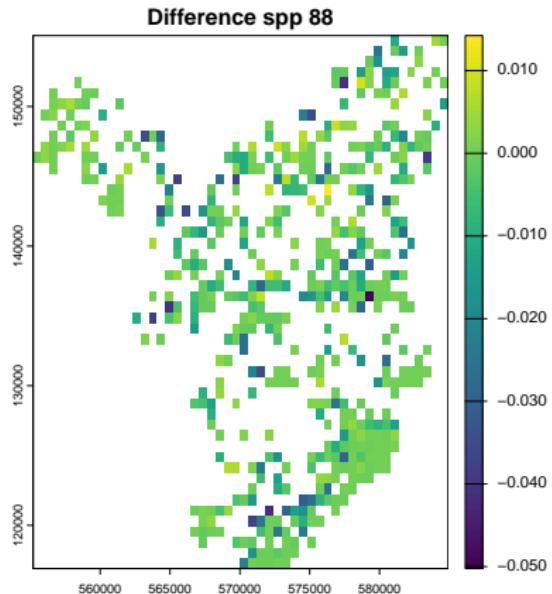
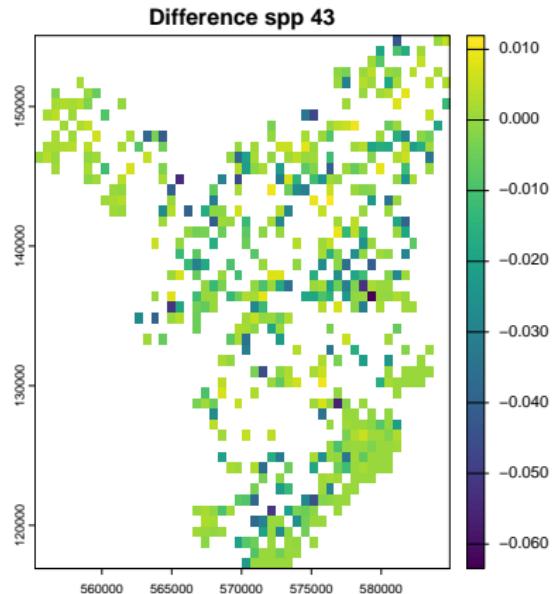


Example: conditional prediction

Let's take one of the models, and do a conditional prediction.

```
condPred <- pnorm(conditionalPredict(c(43,88),model7))
pred <- pnorm(predict(model7)[,c(43,88)])
colnames(pred) = NULL
pts = cbind(pts, condPred = condPred)
pts = cbind(pts, pred = pred)
pts2 <- terra::vect(pts)
```

Example: result of conditional prediction



Defining predictions



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Defining and evaluating predictions of joint species distribution models

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Wilkinson et al. defined multiple types of predictions:

- ▶ marginal (from predict)
- ▶ conditional marginal (aforementioned)
- ▶ joint: occurrence of multiple species simultaneously
- ▶ conditional joint: occurrence of two or more species together, given the information from another

Summary

- ▶ JSDMs were introduced: models to incorporate species' correlation
- ▶ JSDM mostly focuses on predicting (e.g., on a map)
- ▶ Usually, JSDMs are implemented using latent variables
 - ▶ The number used affects predictive performance
- ▶ Conditional predictions can facilitate a focus on focal species
- ▶ There are different types of predictions possible, to target particular ecological questions