

*Euclid would approve with glee
How territoriality
Of bunting perched upon a stone
Is asymptote to hypercone*



– Bruce G. Marcot, “ODE TO THE NICHE
(AN ECOLOGIST’S NIGHTMARE)”

Hierarchical Modeling in Ecology

Andy Crosby

Cesar Estavo



Since that time, I have sometimes been accused of being a “modeler.” I wish to state that I am not now nor have I ever been a “modeler.” I was (and am) an ecologist who needed a model.

– David J. Mladenoff (Creator of the LANDIS forest simulation model)

Likely describes the majority of us!

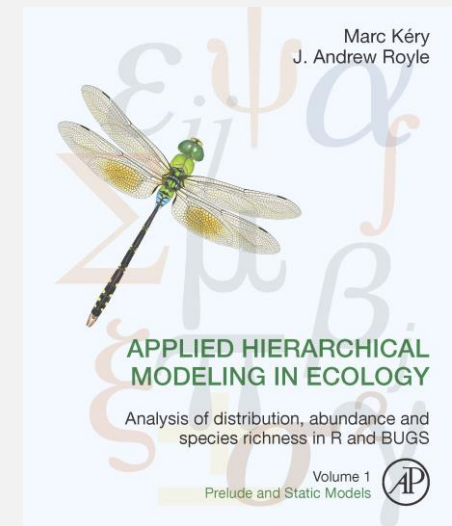
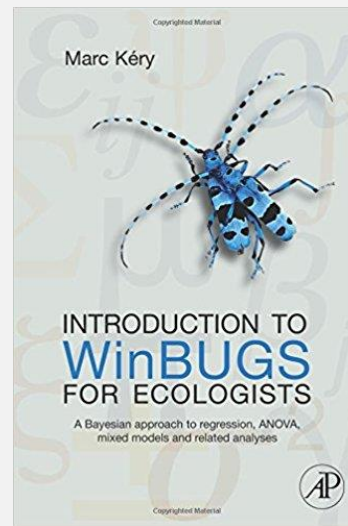
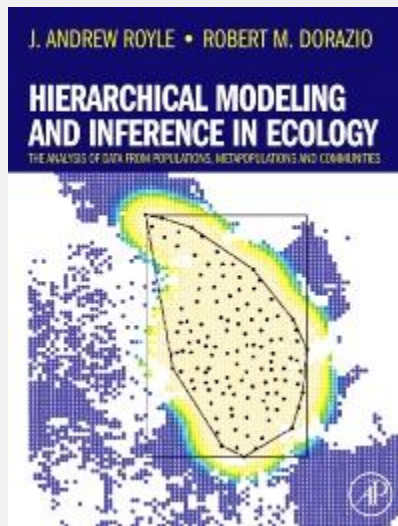


Objectives:

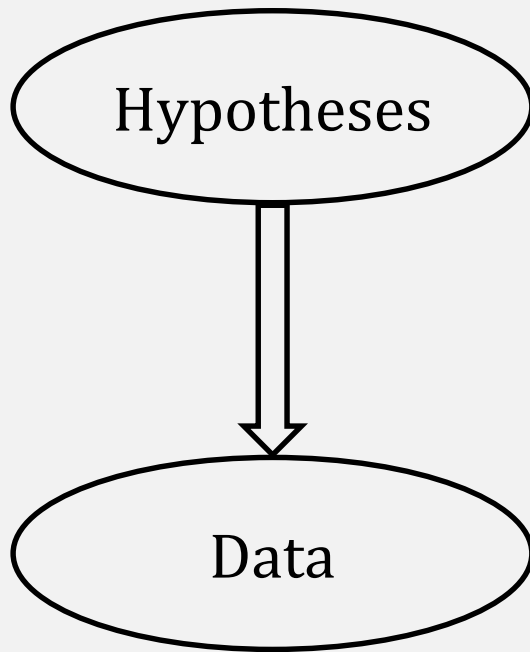
- Introduce hierarchical models as a way to think about ecological data
- De-mistify the modeling process
- Give some examples of HM applications



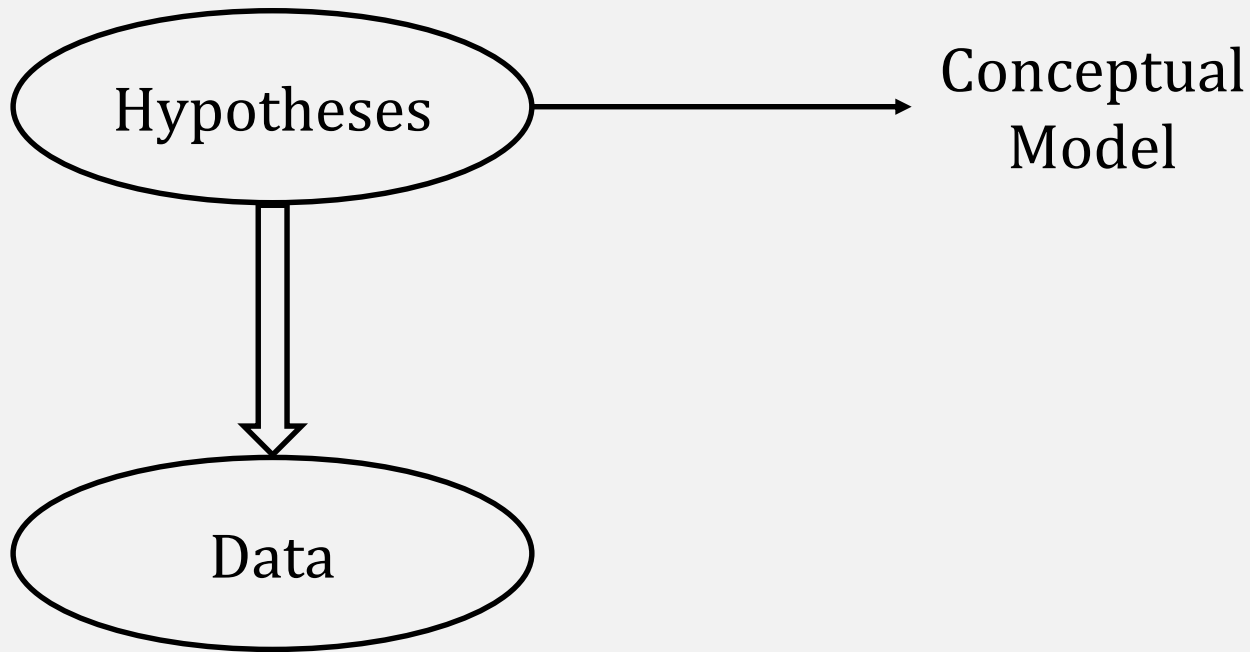
Resources:



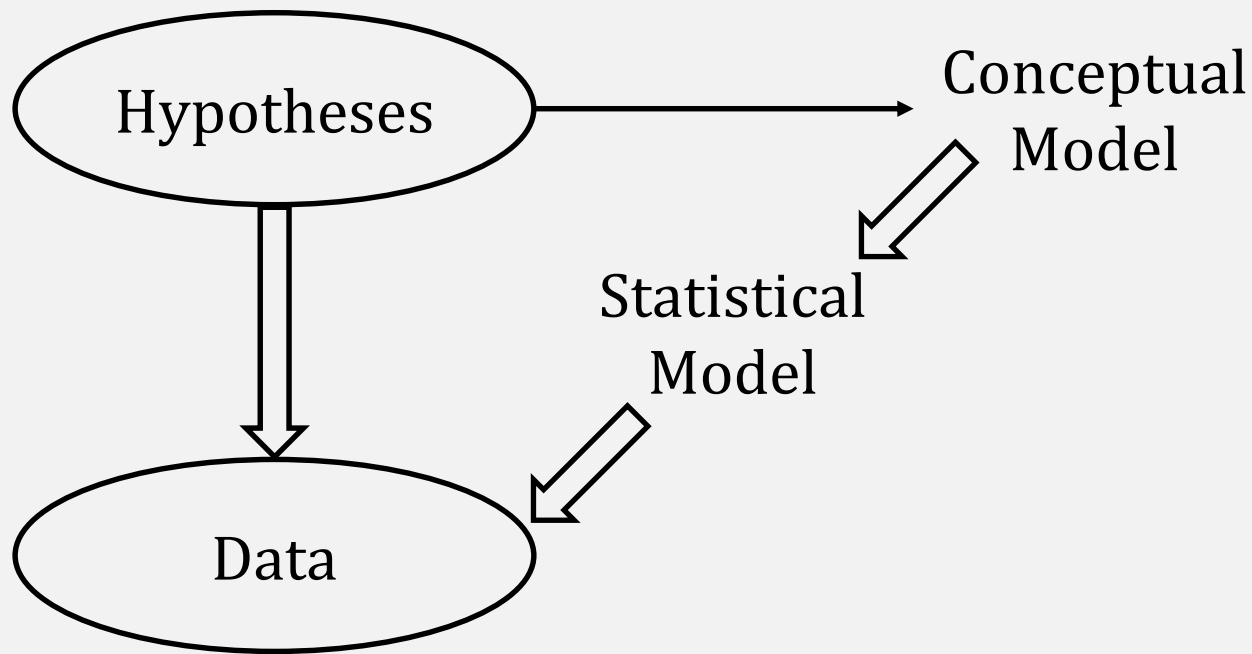
Why models?



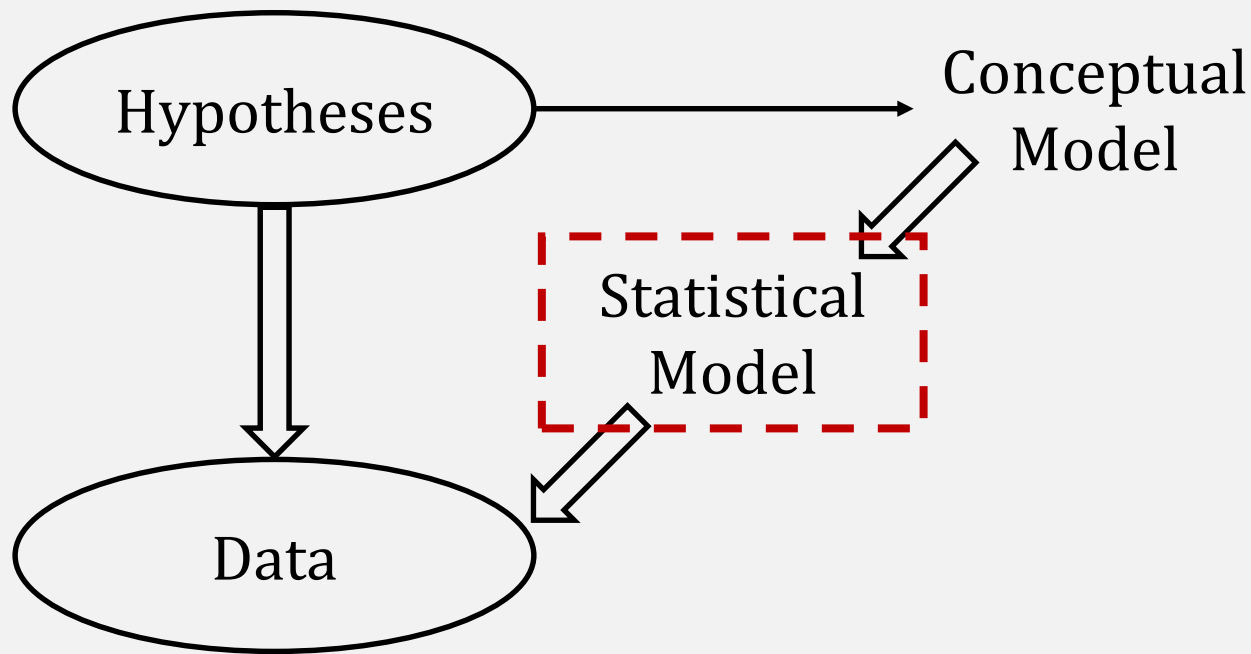
Why models?



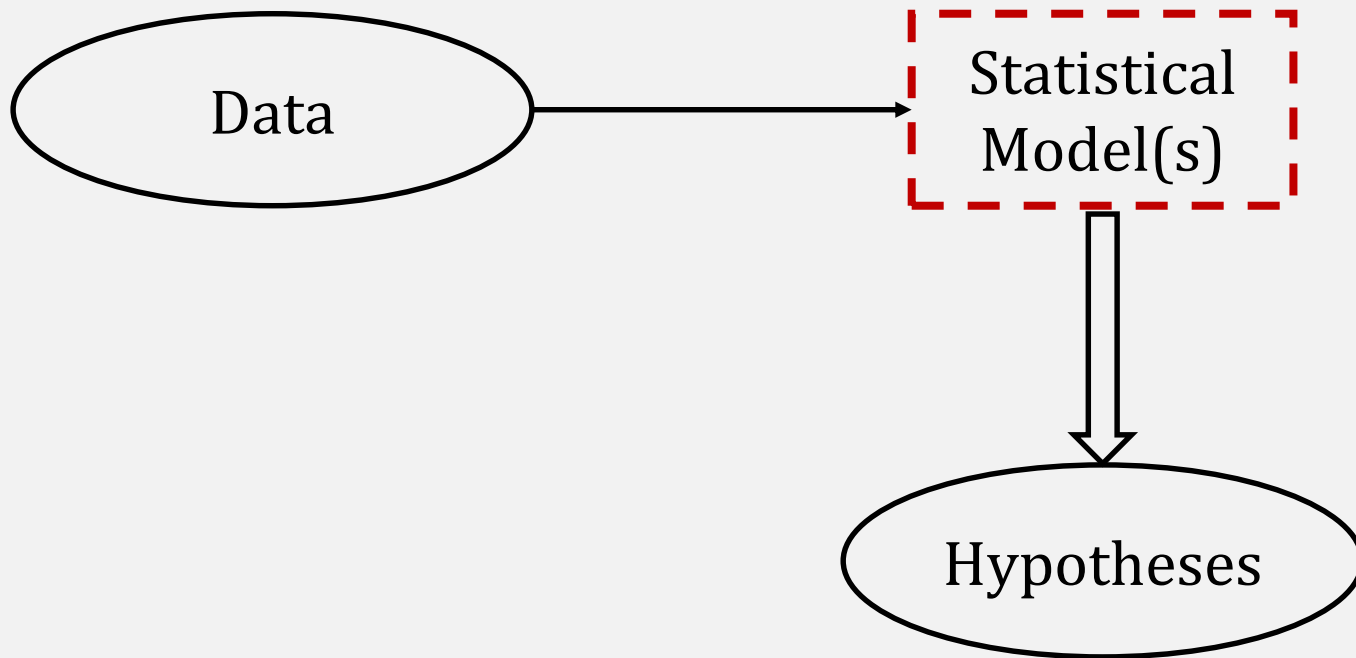
Why models?



H-D Method (Romesburg 1981)



Retroduction



Why hierarchical models?

1. Data reflects multiple distinct processes
 - A. Ecological process of interest
 - B. Observation process that produced the count



Why hierarchical models?

2. Hierarchically-structured systems



Why hierarchical models?

2. Hierarchically-structured systems

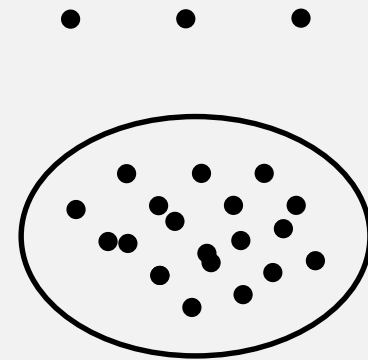
Individuals



Why hierarchical models?

2. Hierarchically-structured systems

Individuals
↓
Populations



Why hierarchical models?

2. Hierarchically-structured systems

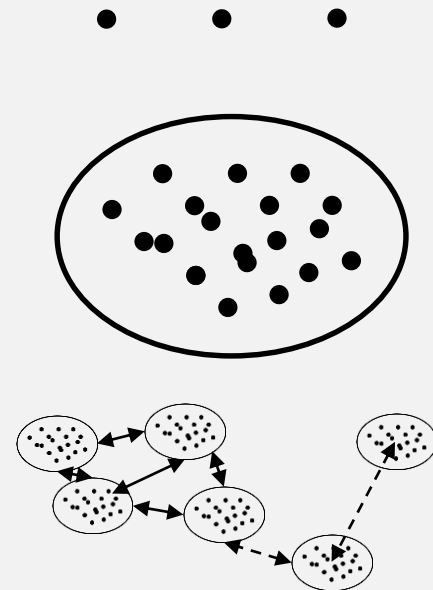
Individuals



Populations

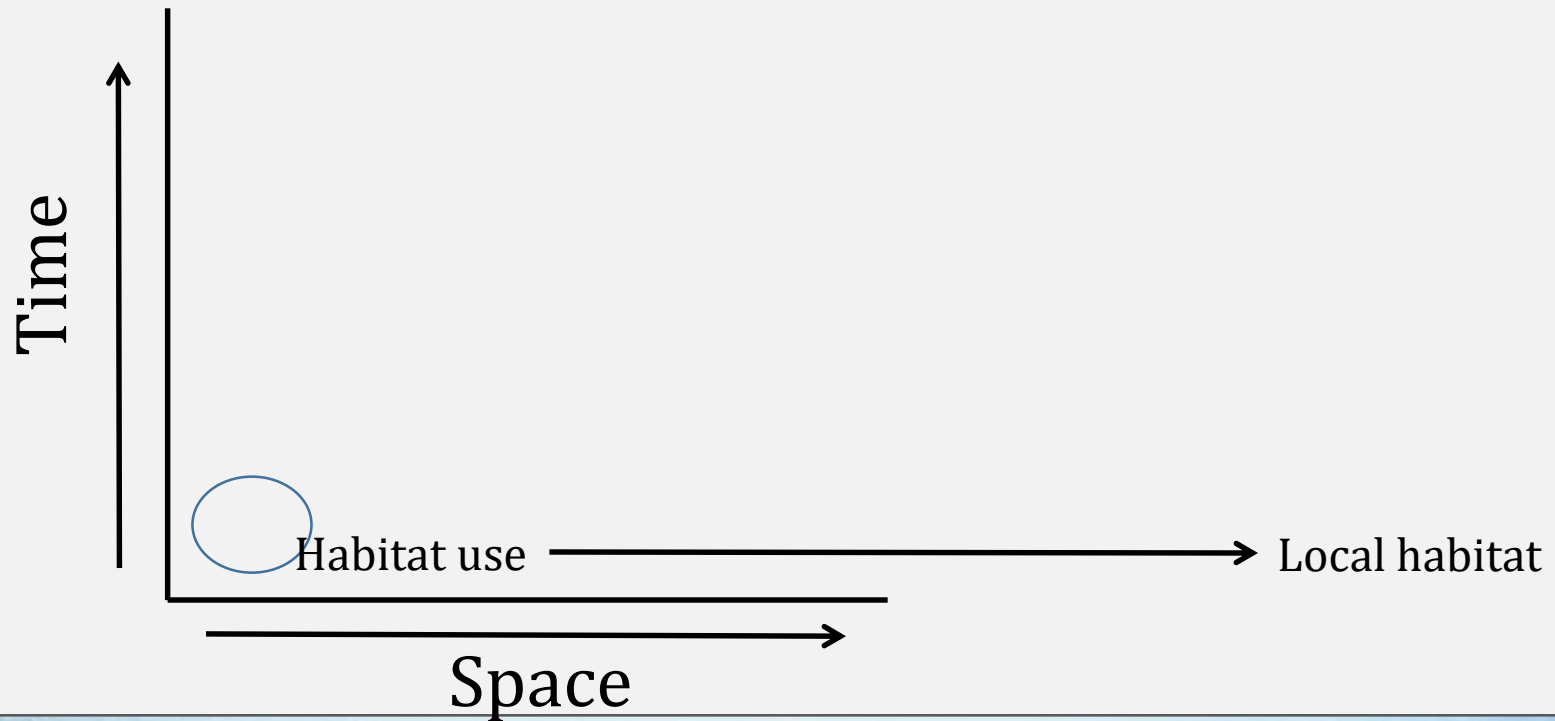


Metapopulations



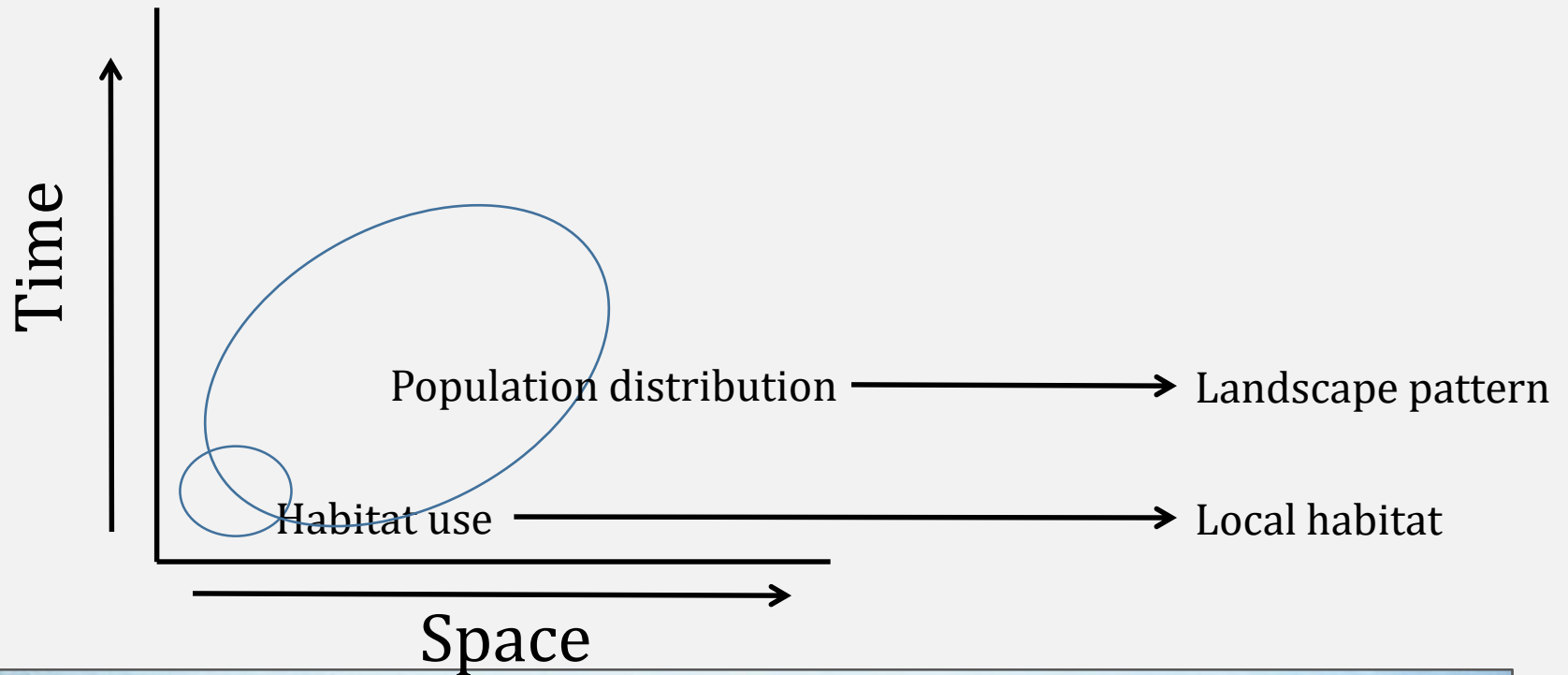
Why hierarchical models?

3. Scale-dependent processes



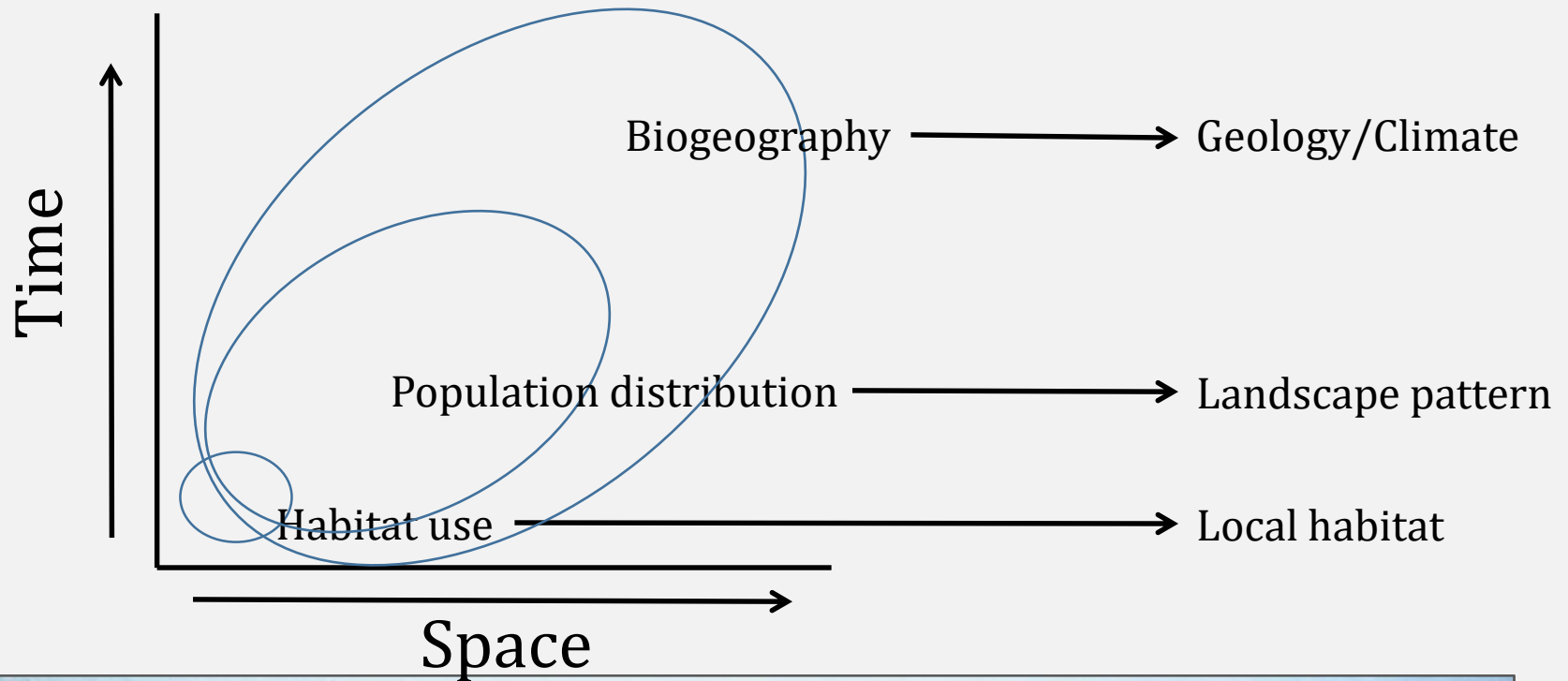
Why hierarchical models?

3. Scale-dependent processes



Why hierarchical models?

3. Scale-dependent processes



Conceptual correspondence

1. Levels of organization
2. Scales of different processes
- 3. Hierarchical models**



What do we mean by hierarchical?

- Coupled sets of models that are conditionally related (e.g. the simplest occupancy model)

- Model 1: the ecological process:

$$z_i \sim \textit{Bernoulli}(\psi) - \text{where } z \text{ is 0 or 1}$$

- Model 2: the observation process

$$y_{i,j} | z_i \sim \textit{Bernoulli}(z_i p) - \text{where } y \text{ is 0 or 1}$$

- **y is the data**



Translation: Ecological model

- ψ is the probability that a site is occupied
- z_i (occupied or not) is a random variable where success ($z_i=1$) has probability ψ

$$z_i \sim \text{Bernoulli}(\psi)$$

- ψ can be modeled as a function of covariates

$$\text{logit}(\psi_i) = \alpha + \beta \mathbf{X}_i$$



Translation: Observation model

- p is the probability of detection
- $y_{i,j}$ (detected or not) is a random variable where success ($y_{i,j}=1$), **conditional on \mathbf{z}** , has probability $z_i \times p$

$$y_{i,j} | z_i \sim \text{Bernoulli}(z_i p)$$

- p can be modeled as a function of covariates

$$\text{logit}(p_{i,j}) = \alpha + \boldsymbol{\beta} \mathbf{X}_{i,j}$$



English translation:

1. Site i has probability ψ of being occupied

$$z_i \sim \text{Bernoulli}(\psi)$$

2. Conditional on site i being occupied, we can detect the species with probability p

$$y_{i,j} | z_i \sim \text{Bernoulli}(z_i p)$$



What **don't** we mean by hierarchical

- Doesn't imply Bayesian or Frequentist
- Doesn't have to be about detection
- Doesn't have to be complicated



Example: zero-inflated abundance model

- Model 1: the occupancy process:

$$z_i \sim \text{Bernoulli}(\psi) - \text{where } z \text{ is 0 or 1}$$

- Model 2: the abundance process

$$N_i | z_i \sim \text{Poisson}(z_i \lambda) - \text{where } N \text{ is an integer}$$

- Model 3: the detection process

$$y_{i,j} | N_i \sim \text{Binomial}(N_i, p) - \text{where } y \text{ is the count}$$



English translation:

1. Site i has probability ψ of being occupied

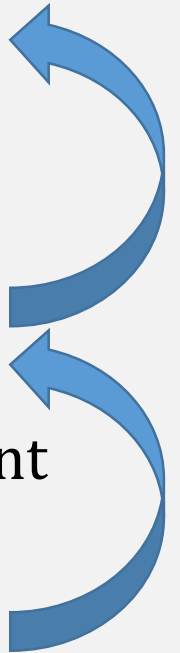
$$z_i \sim \text{Bernoulli}(\psi)$$

2. Conditional on site i being occupied, the site has an expected abundance of λ

$$N_i | z_i \sim \text{Poisson}(z_i \lambda)$$

3. Conditional on abundance at site i , the expected count is binomial with N_i trials and probability of success p

$$y_{i,j} | N_i \sim \text{Binomial}(N_i, p)$$



English translation:

1. Site i has probability ψ of being occupied

$$z_i \sim \text{Bernoulli}(\psi)$$

$$\text{logit}(\psi_i) = \alpha + \boldsymbol{\beta} \mathbf{X}_i$$

2. Conditional on site i being occupied, the site has an expected abundance of lambda

$$N_i | z_i \sim \text{Poisson}(z_i \lambda)$$

$$\log(\lambda_i) = \alpha + \boldsymbol{\beta} \mathbf{X}_i$$



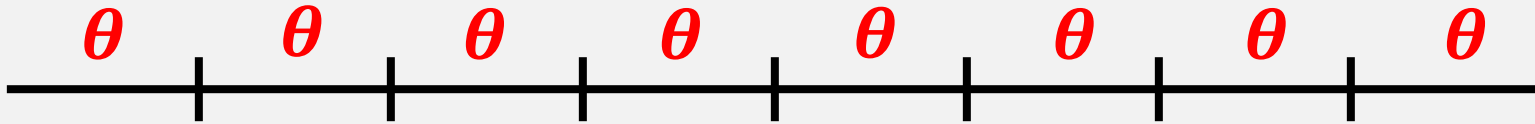
Model Formulation

ψ



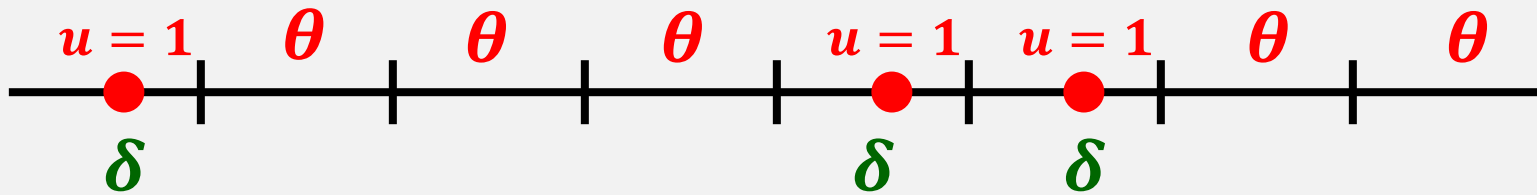
Model Formulation

$$z = 1$$



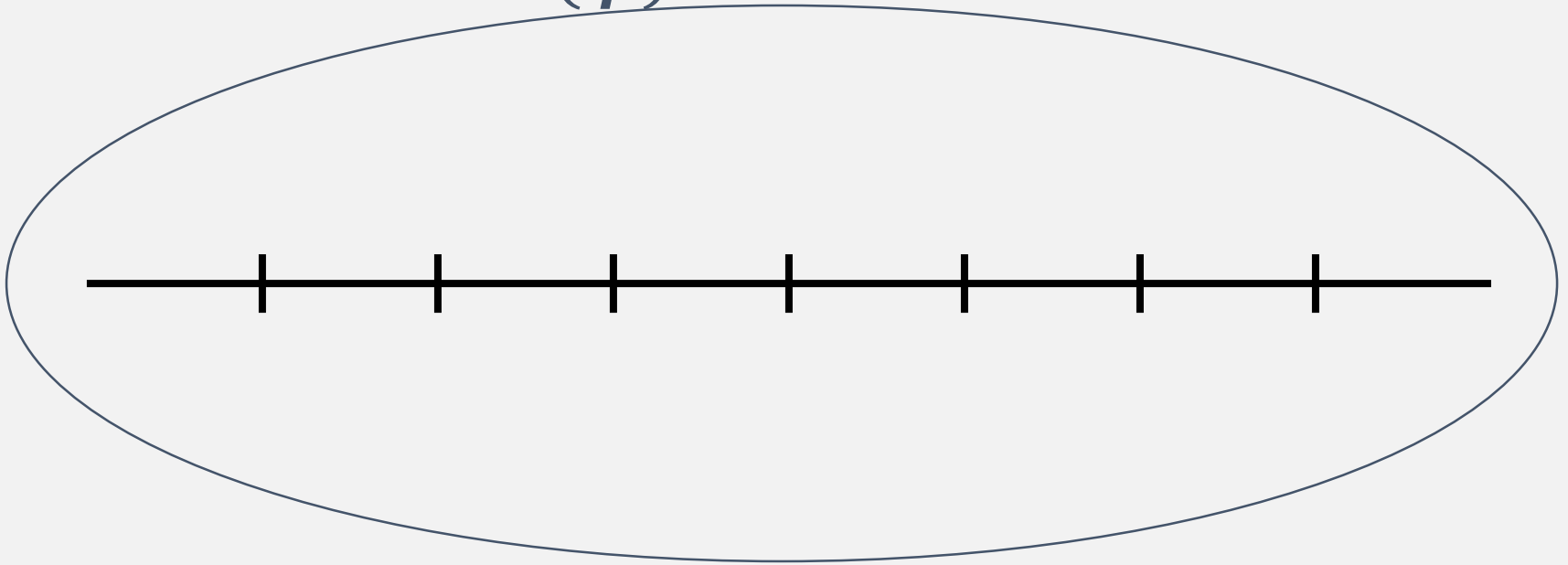
Model Formulation

$$z = 1$$



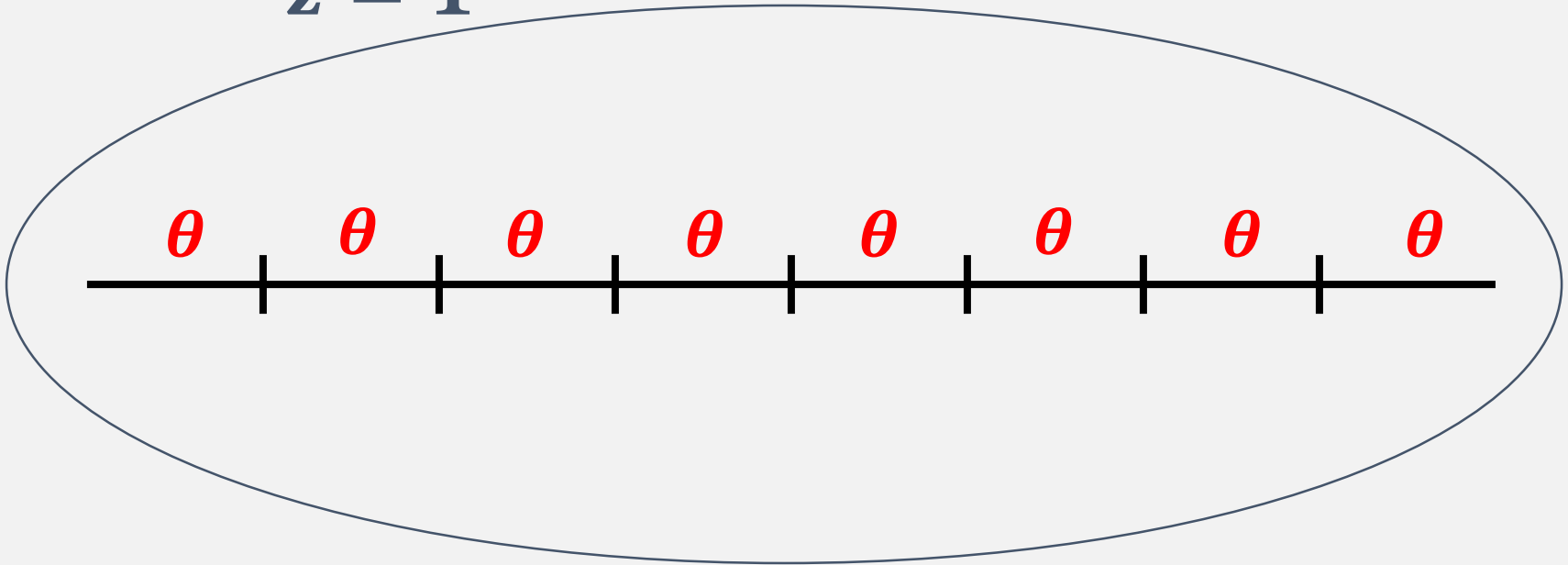
Tracking transect model

$z \sim \text{Bernoullie}(\psi)$

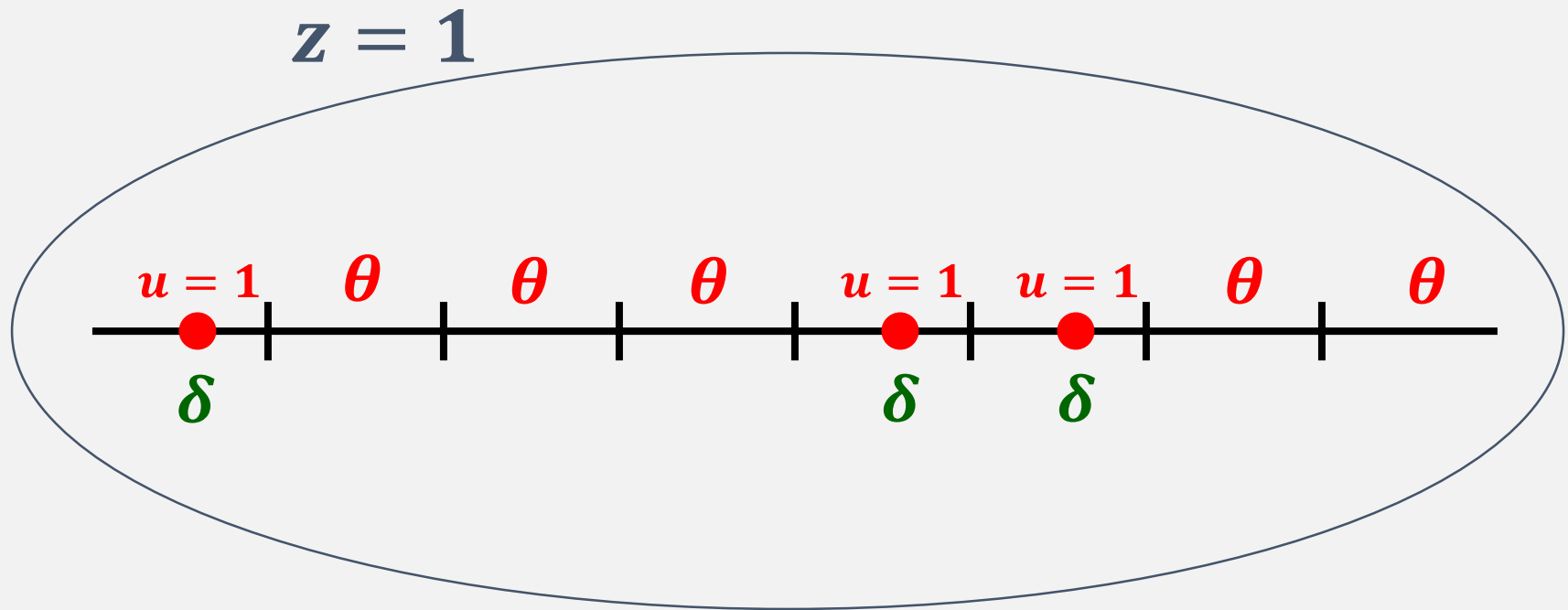


Tracking transect model

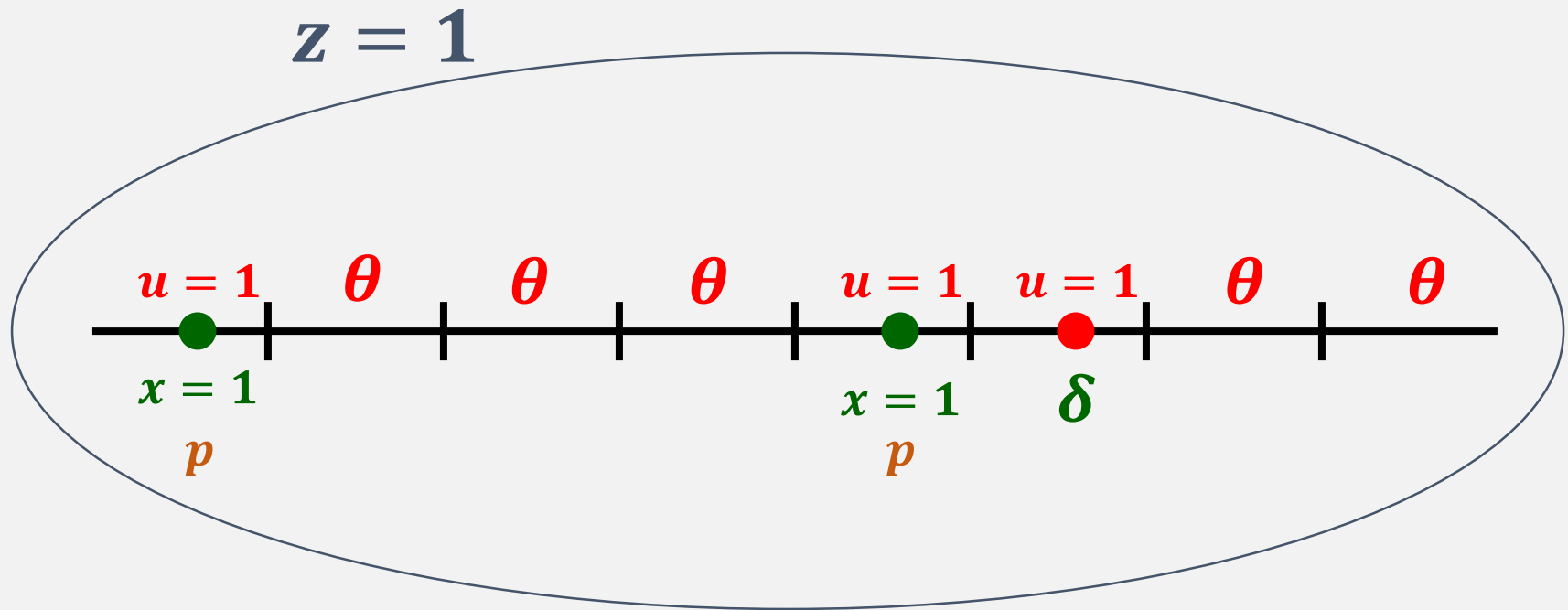
$z = 1$



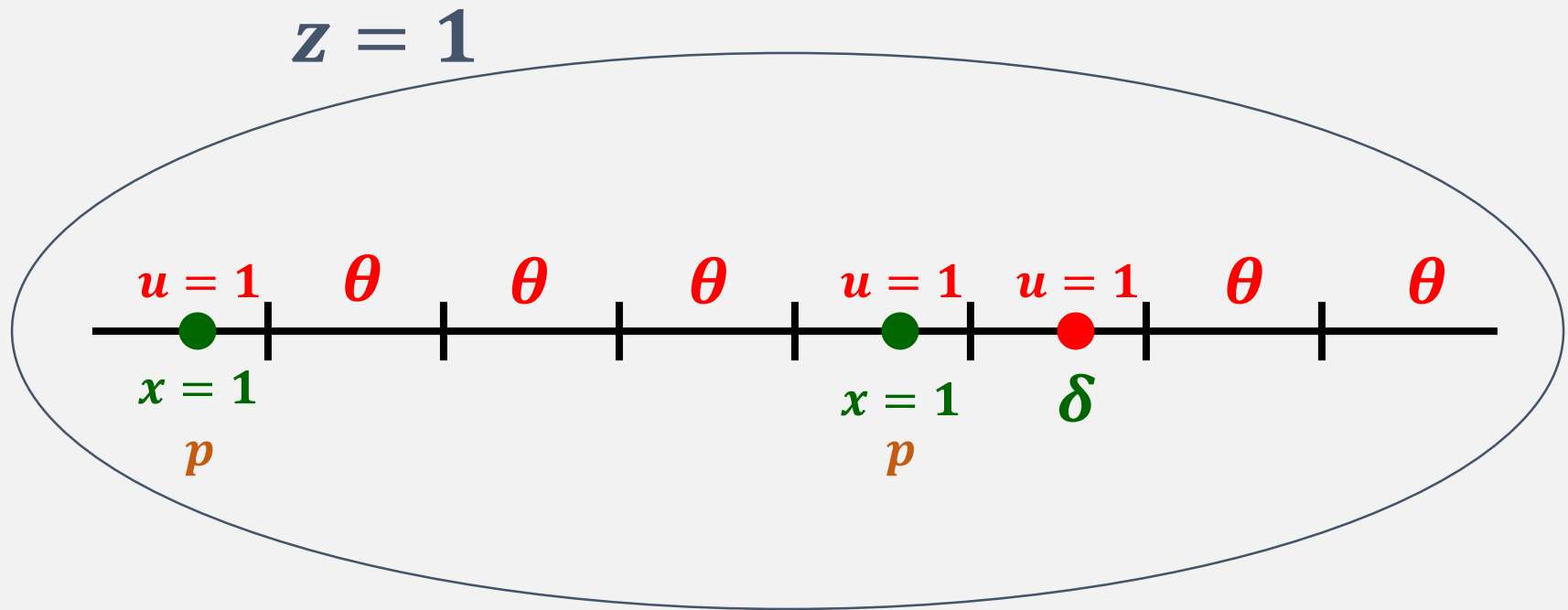
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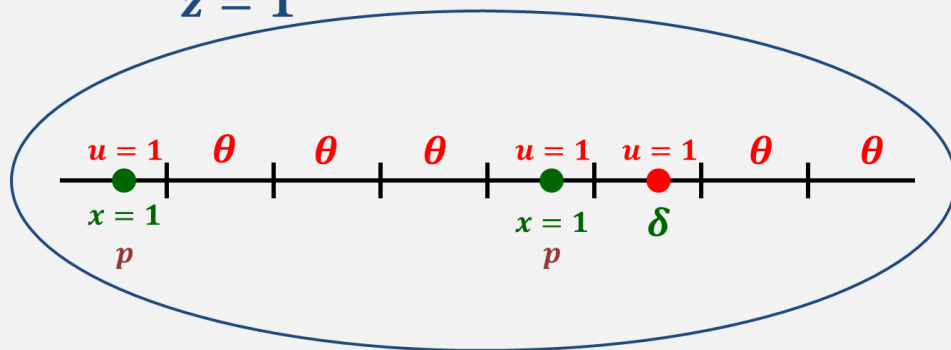


Tracking transect model



Model Formulation

$z = 1$

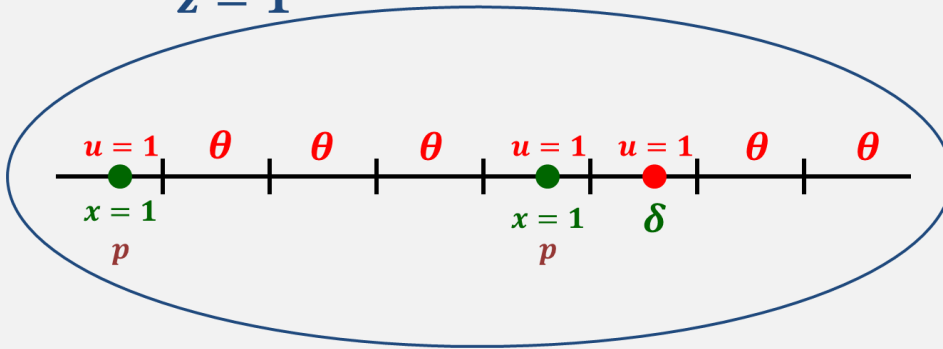


$$z_i \sim \text{Bernoulli}(\psi_i)$$



Model Formulation

$z = 1$



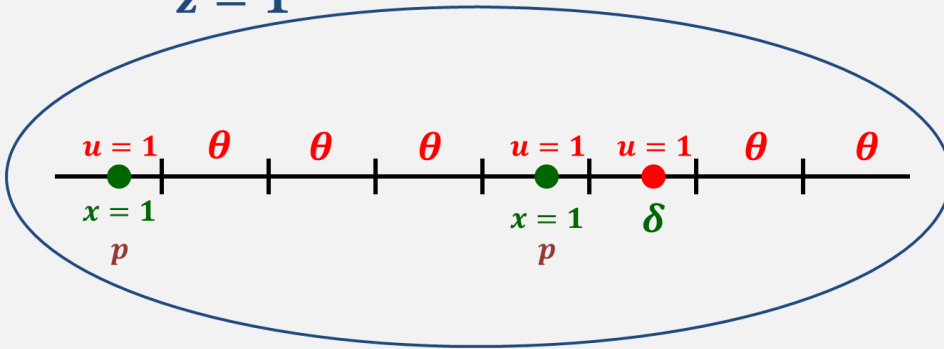
$$z_i \sim \text{Bernoulli}(\psi_i)$$

$$u_{i,j} | z_i \sim \text{Bernoulli}(\theta_{i,j})$$



Model Formulation

$z = 1$



$$z_i \sim \text{Bernoulli}(\psi_i)$$

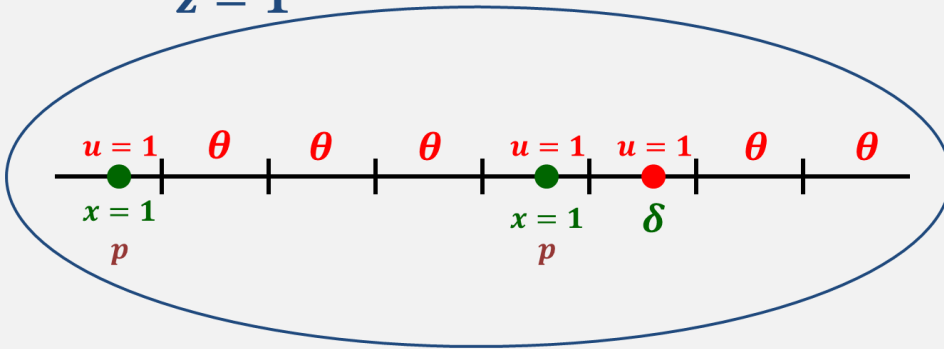
$$u_{i,j} | z_i \sim \text{Bernoulli}(\theta_{i,j})$$

$$x_{i,j,k} | u_{i,j} \sim \text{Bernoulli}(\delta_{i,j,k})$$



Model Formulation

$z = 1$



$$z_i \sim \text{Bernoulli}(\psi_i)$$

$$u_{i,j} | z_i \sim \text{Bernoulli}(\theta_{i,j})$$

$$x_{i,j,k} | u_{i,j} \sim \text{Bernoulli}(\delta_{i,j,k})$$

$$y_{i,j,k,l} | x_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k,l})$$



The Conceptual Middle Ground

- The Observation-driven View
 - e.g. Mark-recapture analysis
- The Process-driven View
 - e.g. Leslie matrix models
- The Hierarchical View
 - Accounts for both; includes all uncertainty



Bayesian vs. Frequentist

- I use Bayesian methods because:
 1. Limits on MLE complexity
 2. Intuitively easier to understand models
 3. Freedom to develop more specific models



BUGS model formulation

```
for(i in 1:sites){  
  z[i] ~ dbern(psi)  
  for(j in 1:surveys){  
    y[i,j] ~ dbern(z[i]*p)  
  }  
}
```



BUGS model with covariates

```
for(i in 1:sites){  
  psi[i] <- alpha + beta*x[i]  
  z[i] ~ dbern(psi[i])  
  for(j in 1:surveys){  
    p [i] <- alpha.p + beta.p*x[i]  
    y[i,j] ~ dbern(z[i]*p[i])  
  }  
}
```

