

An aerial photograph of a savanna landscape. The foreground and middle ground consist of rolling, golden-brown hills dotted with numerous dark green, rounded trees. The background shows more distant, hazy hills under a clear sky. The text is overlaid on the upper half of the image.

Hierarchical models for distribution and abundance

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Fundamental questions in population/community ecology



- How many are there ? -> abundance
- Where are they ? -> species distribution/abundance
- Spatial, temporal and spatiotemporal patterns in Dist&Abu ? -> Trends, maps
- What environmental drivers determine Dist&Abu ? -> niche modeling
- What demographic drivers determine Dist&Abu ? -> survival/recruitment, colonization/extinction
- Statistical associations in Dist&Abu of multiple species ? -> Species interactions, ...

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- spOccupancy/spAbundance let you to tackle these questions via the fitting of hierarchical statistical models (HMs)

=> what are HMs and what is distribution and abundance ?

Overview



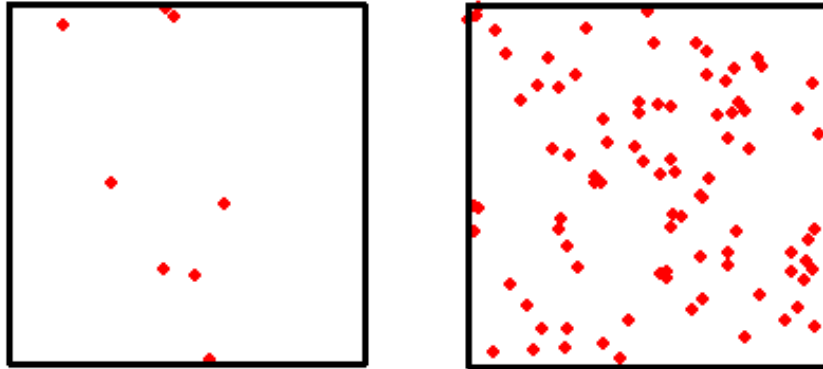
- What are hierarchical models ?
- What is distribution (z) ? abundance (N) ? ... relationship between the two ?
 - Point patterns (PPs) and measurement errors in PPs
 - Discretization of space & summarization of PPs: yields Dist and Abu
 - Deterministic relationship between Dist and Abu
 - Measurement errors when assessing Dist&Abu
 - HMs for Dist&Abu

(Use of "*Experimental Statistics*": simulate stuff to "*see how things are*")

Fundamental model for animal/plant pops: point patterns



- PP: Outcome of point process, random process that produces "points" in 1D, 2D, 3D, ...
- Both number of points and locations are random
- PP described in terms of intensity: limiting expected density of points
- e.g. Homogeneous PP (HPP)

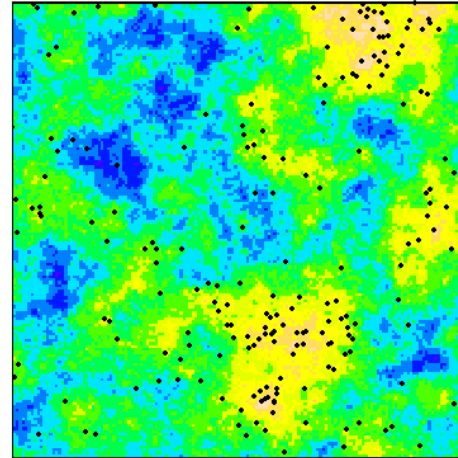
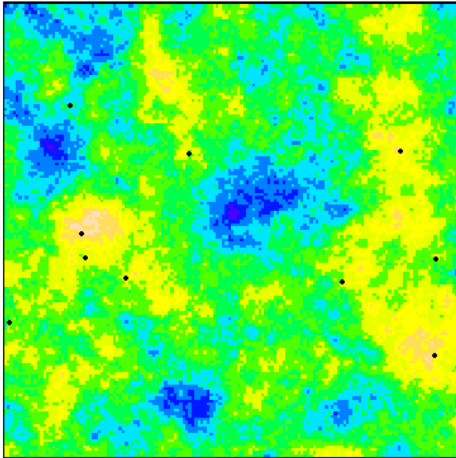


AHMbook::sim.fn()

Fundamental model for animal/plant pops: point patterns



- e.g. Inhomogeneous PP (IPP)

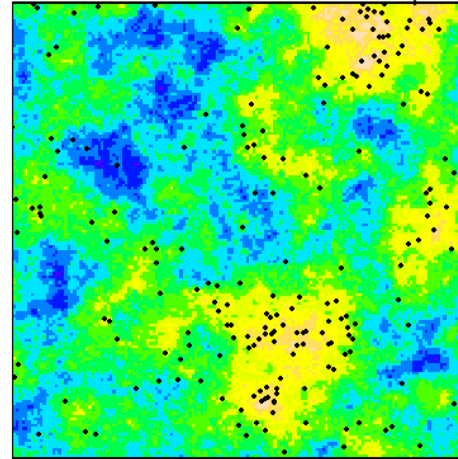
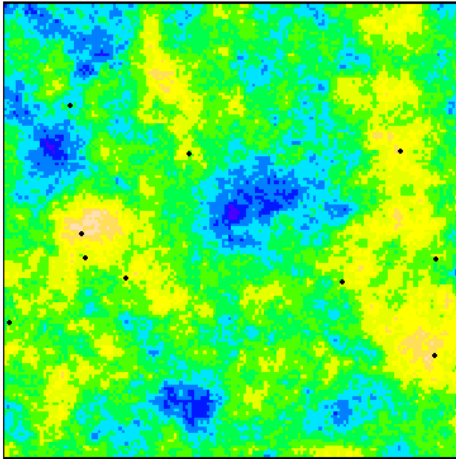


AHMbook::simPp()

Fundamental model for animal/plant pops: point patterns



- Three types of measurement errors for PPs
- ?, ?, ?

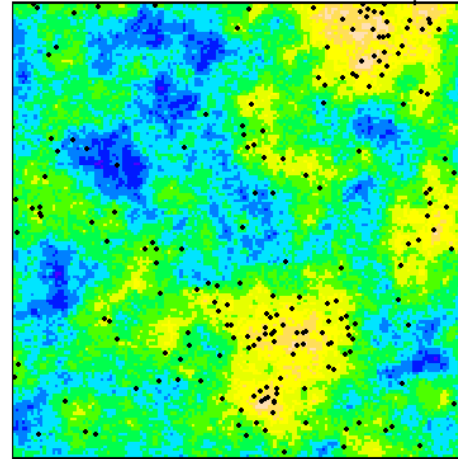
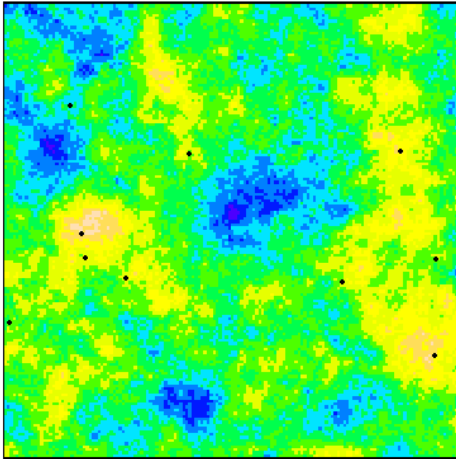


AHMbook::simPp()

Fundamental model for animal/plant pops: point patterns



- Three types of measurement errors for PPs
- Location error, false negatives, false positives (also mark errors)



AHMbook::simPPe()

Why don't we do all pop./comm. ecology with PPs ?



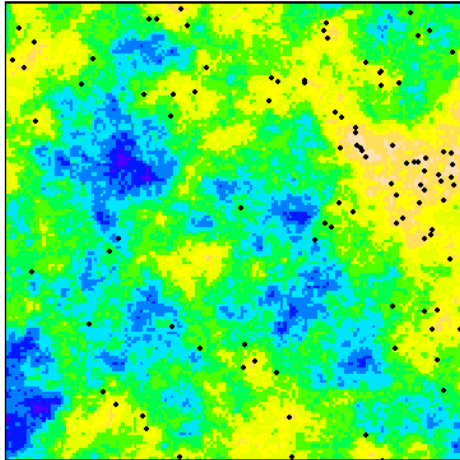
- Location may be hard to measure precisely for every individual
- PPs defined in continuous space: conceptually harder, especially for non-statisticians, e.g., contain integrals, and biologists hate integrals
- Plus, humans like to put things into boxes
- Data may already come in some aggregated form (e.g., administrative units)

=> most times we work with data for discretized space

What happens when we discretize space ?



Point pattern with
core and buffer area



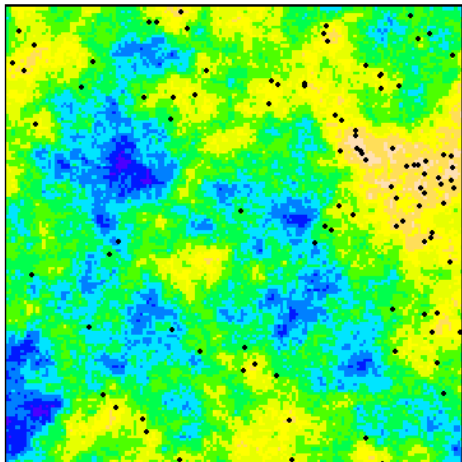
Mean intensity (λ) = 0.00444

What happens when we discretize space ?



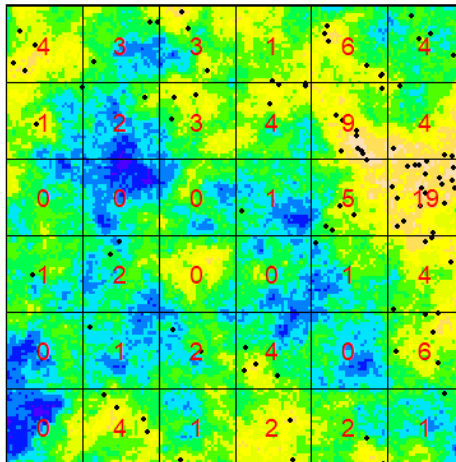
- Abundance and Distribution/Occurrence/Pres-Abs: discrete-space summaries of PPs

Point pattern with
core and buffer area



Mean intensity (λ) = 0.00444

Abundance, N



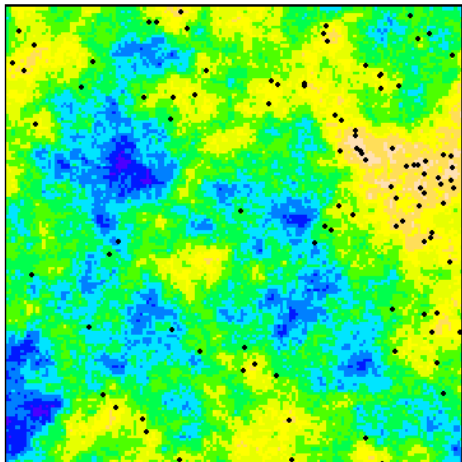
Mean(N) = 2.78, var(N) = 12.23

What happens when we discretize space ?



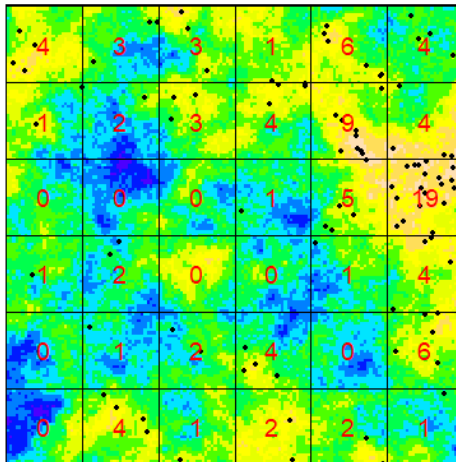
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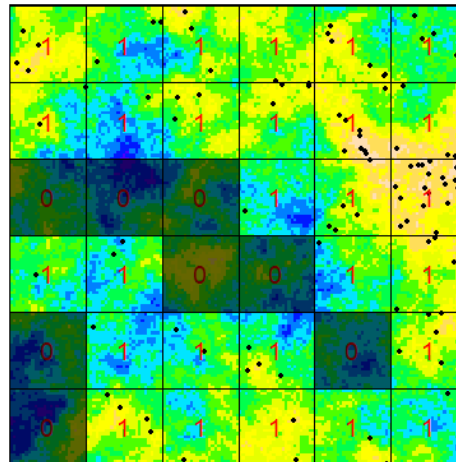
Mean intensity (λ) = 0.00444

Abundance, N



Mean(N) = 2.78, var(N) = 12.23

Occurrence, z



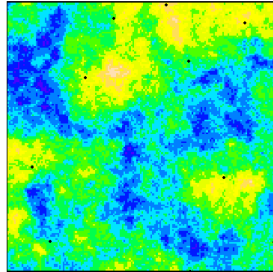
Mean(z) = 0.78

Dist&Abu depend on PP intensity and spatial scale



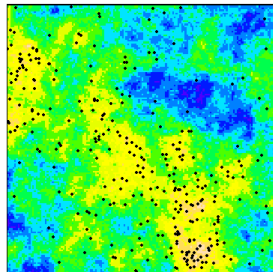
- Dependence on intensity

Point pattern with
core and buffer area



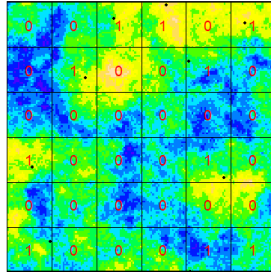
Mean intensity (λ) = 0.00044

Point pattern with
core and buffer area



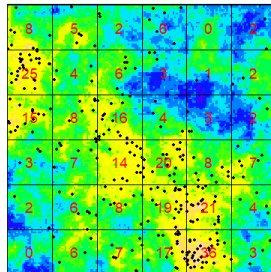
Mean intensity (λ) = 0.01333

Abundance, N



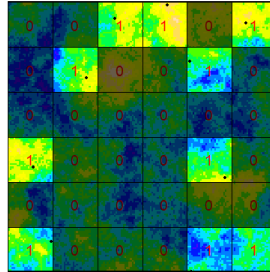
Mean(N) = 0.28, var(N) = 0.21

Abundance, N



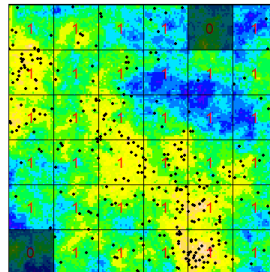
Mean(N) = 8.33, var(N) = 64.74

Occurrence, z



Mean(z) = 0.28

Occurrence, z



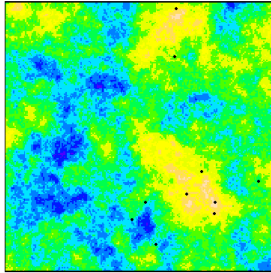
Mean(z) = 0.94

Dist&Abu depend on PP intensity and spatial scale



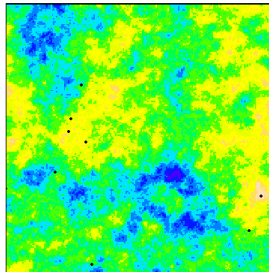
- Dependence on spatial scale

Point pattern with
core and buffer area



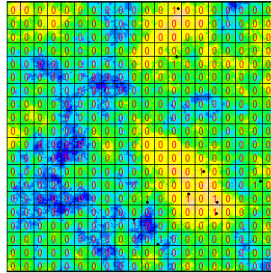
Mean intensity (λ) = 0.00025

Point pattern with
core and buffer area



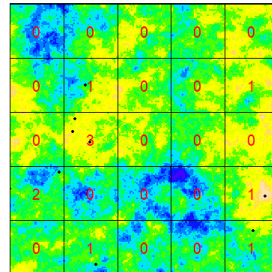
Mean intensity (λ) = 0.00025

Abundance, N



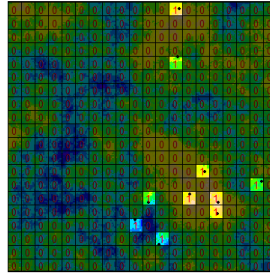
Mean(N) = 0.03, var(N) = 0.02

Abundance, N



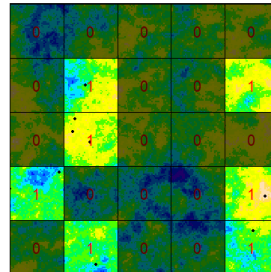
Mean(N) = 0.4, var(N) = 0.58

Occurrence, z



Mean(z) = 0.03

Occurrence, z



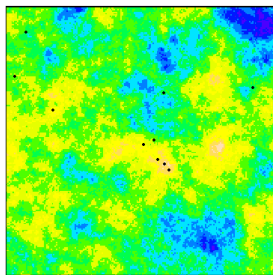
Mean(z) = 0.28

Dist&Abu depend on PP intensity and spatial scale



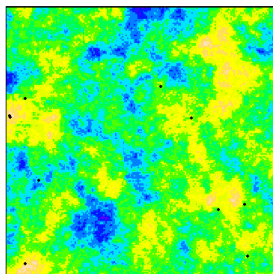
- Dependence on spatial scale

Point pattern with
core and buffer area



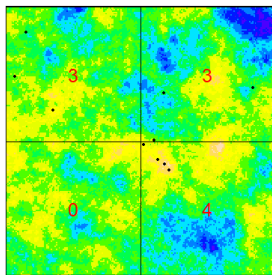
Mean intensity (λ) = 0.00025

Point pattern with
core and buffer area



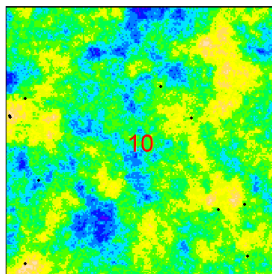
Mean intensity (λ) = 0.00025

Abundance, N



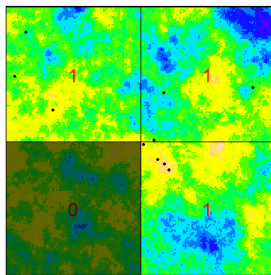
Mean(N) = 2.5, var(N) = 3

Abundance, N



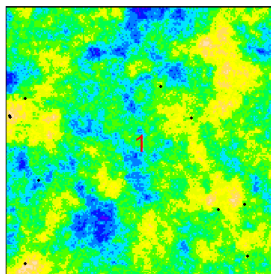
Mean(N) = 10, var(N) = NA

Occurrence, z



Mean(z) = 0.75

Occurrence, z



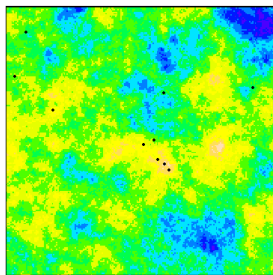
Mean(z) = 1

Dist&Abu depend on PP intensity and spatial scale



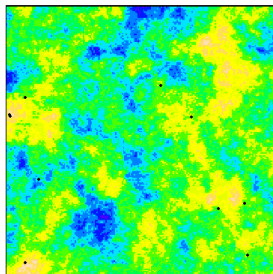
- Dependence on spatial scale

Point pattern with
core and buffer area



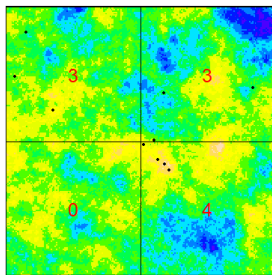
Mean intensity (λ) = 0.00025

Point pattern with
core and buffer area



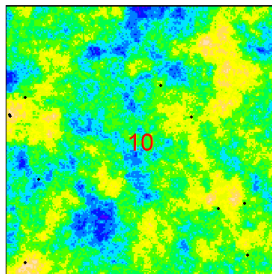
Mean intensity (λ) = 0.00025

Abundance, N



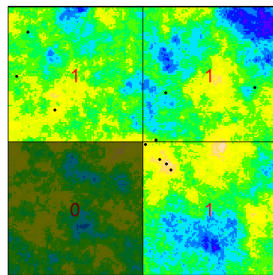
Mean(N) = 2.5, var(N) = 3

Abundance, N



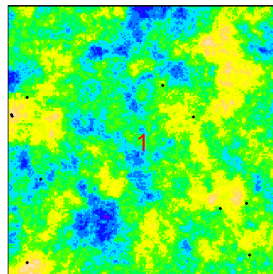
Mean(N) = 10, var(N) = NA

Occurrence, z



Mean(z) = 0.75

Occurrence, z



Mean(z) = 1

Therefore,

- If you need an occupancy prob. of ~ 0 , just make your sites the size of a stamp
- If you need an occupancy prob. of 1 for every occurring species, just make your entire study area a single site

Side comment on "Distribution"



- Here, mostly use "distribution" synonymous with presence/absence, occurrence, or occupancy probability
- But can use "distribution" more generally and indeed use all of the following as a characterization of "species distribution":
 - Point pattern (i.e., realization of a point process) or intensity of point process (i.e., its expectation)
 - Realized or expected abundance
 - Realized or expected presence/absence (latter is occupancy probability or prob. of presence)
- Thus, a species distribution model (SDM), or a map based on it, may depict any of these

More on scale dependence of Dist & Abu



- Can't directly compare occupancy and abundance when spatial scale differs
- Downscaling/upscaling, "modifiable area unit problem", "change of support", "areal disaggregation regression"
- 4 important (and undercited) papers by Keil *et al.*, 2013-2014
- Great paper by Pacifici *et al.*, *Ecology*, 2019
- Also recent paper by Murphy *et al.*, *Eco. Apps*, 2023

Relationship between distribution and abundance

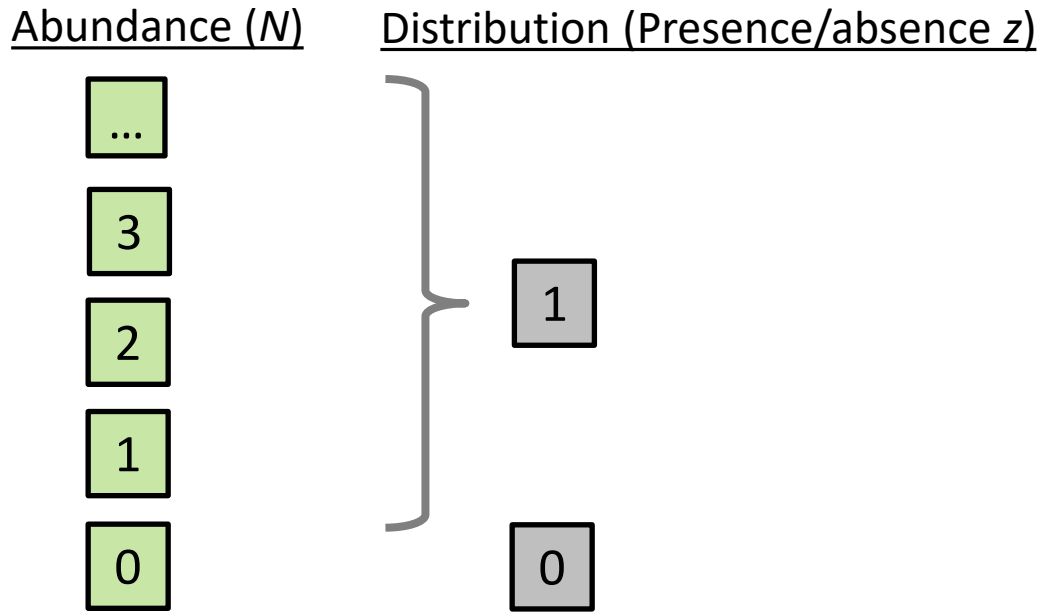


- Not independent things: distribution is deterministic function of abundance
- Dist: Information-poor summary of abundance; *"the poor man's abundance"*

Relationship between distribution and abundance



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Relationship between distribution and abundance



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Abundance (N)

...

3

2

1

0

Distribution (Presence/absence z)



1

0

Thus:

$$p(z = 1) = 1 - p(N = 0)$$

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Abundance (N)

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Distribution (Presence/absence z)



1

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Thus:

$$p(z = 1) = 1 - p(N = 0)$$

with Poisson abu. model:

$$N \sim \text{Poisson}(\lambda)$$

$$P(N = 0) = e^{-\lambda}$$

$$\Rightarrow \text{occ. prob. } \Psi = 1 - e^{-\lambda}$$

Relationship between distribution and abundance



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Abundance (N)

...

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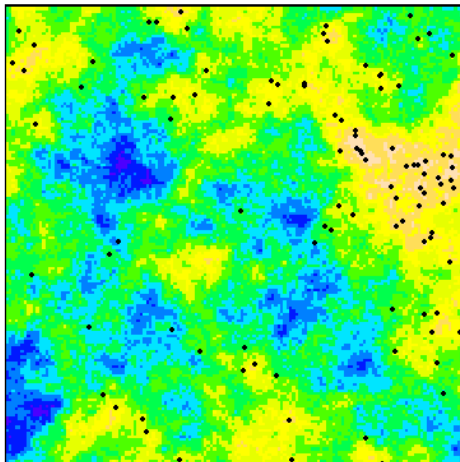
- (Hence, typically, zero-inflated abundance model is a cheap modeling trick only)

Measurement errors in distribution and abundance



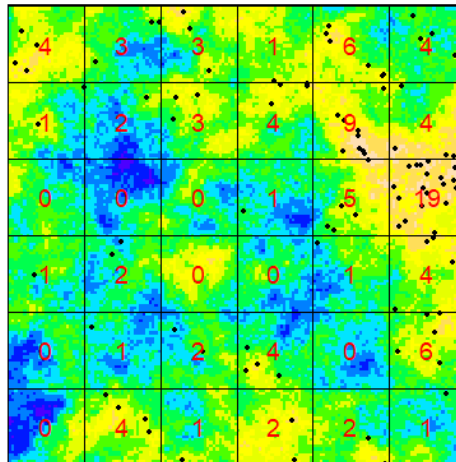
- We had 3 for the PP How many do we have for Dist&Abu ?

Point pattern with
core and buffer area



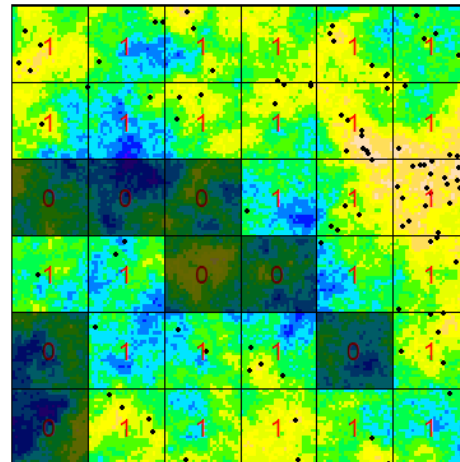
Mean intensity (λ) = 0.00444

Abundance, N



Mean(N) = 2.78, var(N) = 12.23

Occurrence, z



Mean(z) = 0.78

Why may it be a good idea to account for measurement errors ?

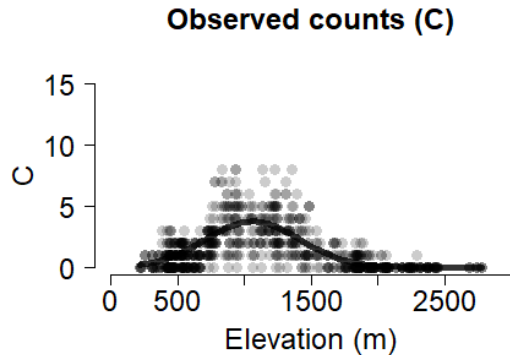
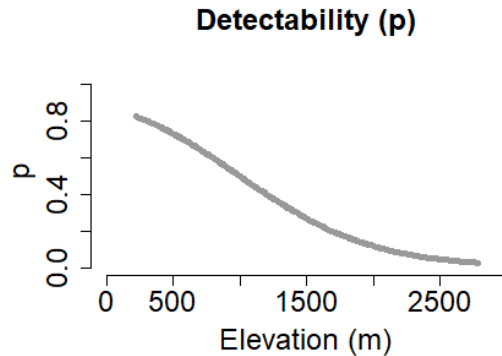
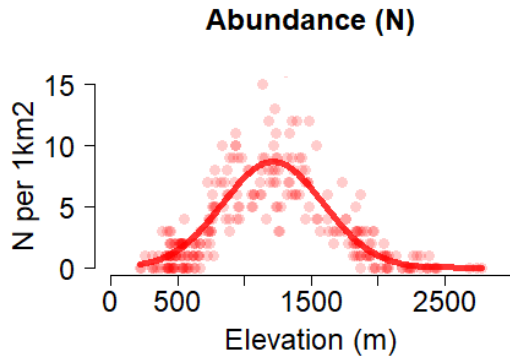


- Depends on the goal of model: e.g., do we need absolute quantities (true N) or are we happy with mere patterns ("relative N ") ?
- Two examples where it would matter (simulated data)

Spatially variable detection probability



- Elevation gradient of abundance and of measurement error

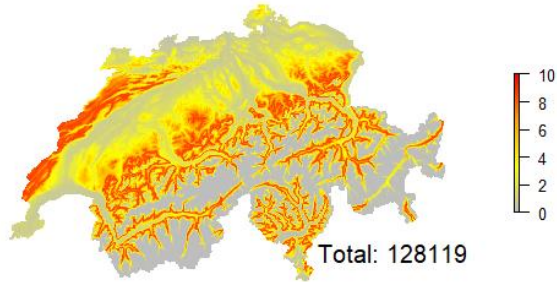


Spatially variable detection probability

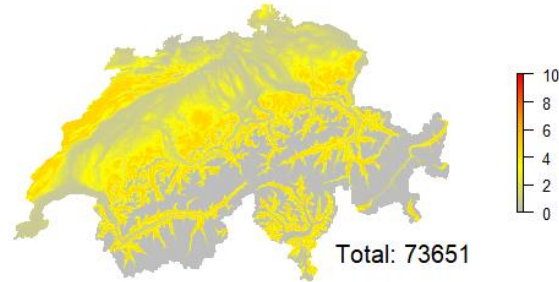


- Spatial predictions and national population size

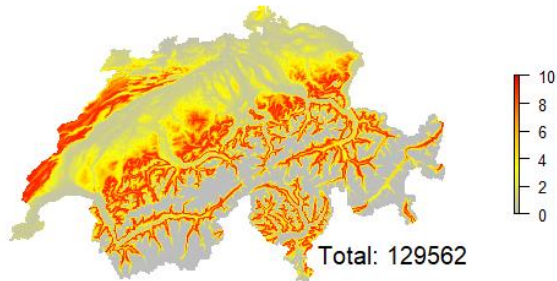
**Bullfinch density
(simulated truth)**



**Estimated bullfinch density
(ignoring detection error)**



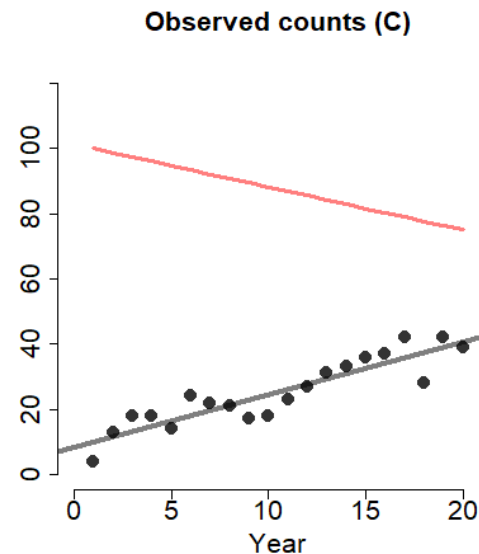
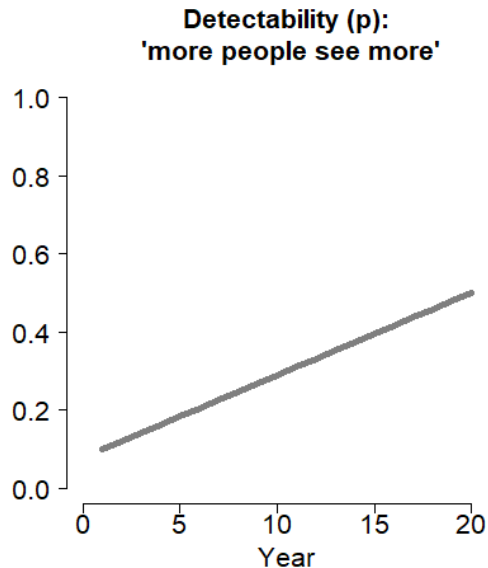
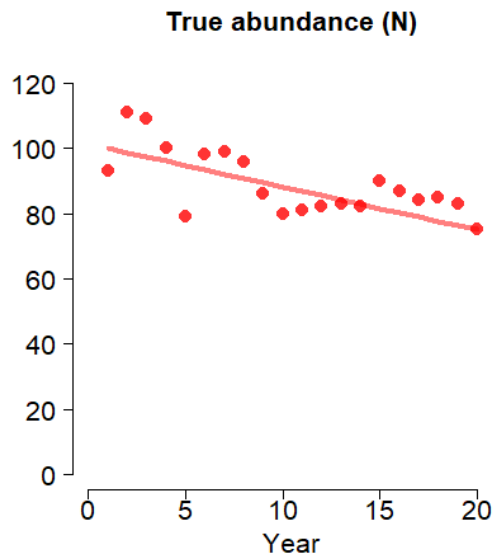
**Estimated bullfinch density
(correcting for detection error)**



Temporally variable detection probability



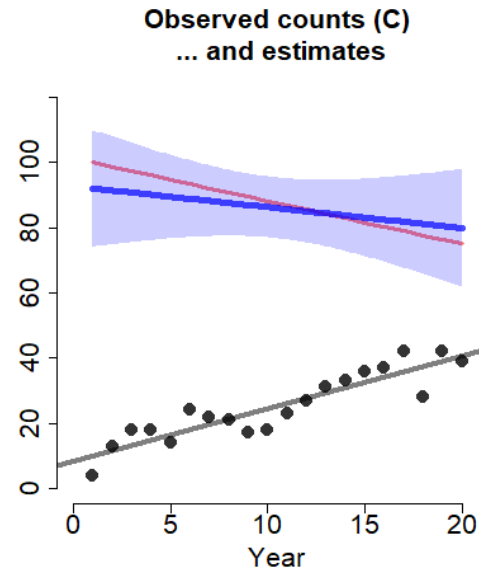
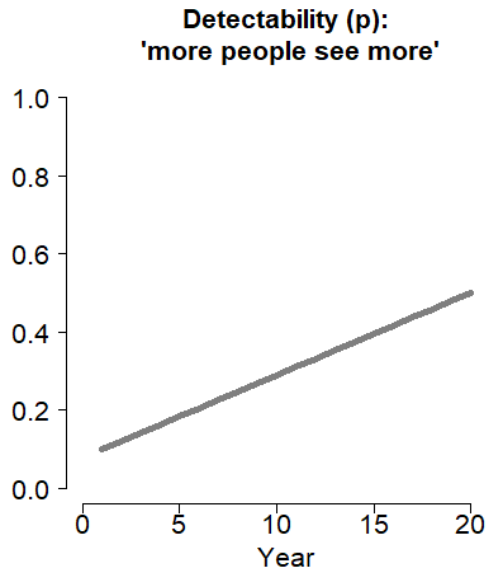
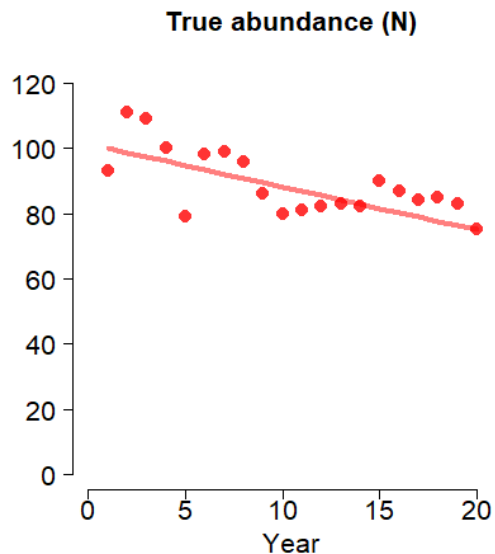
- Time trends in abundance and of measurement error



Temporally variable detection probability



- Time trends in abundance and of measurement error



Hierarchical models, or HMs



- Describe sequence (or hierarchy) of random processes, or random variables (RVs)

$$\begin{array}{l} x \sim f(\omega) \\ y \sim g(x, \theta) \end{array}$$

- Factorization of joint distribution $[x, y]$ into marginal ($[x]$) and conditional distribution, $[y|x]$:
 $[x, y] = [x] [y|x]$
- Estimands: parameters ω and θ ; latent variables x
- x : latent variables = unobserved RVs = random effects**
- Many advantages: e.g., modeling correlations, also enforcing clarity of thought
- Typically one submodel for each process underlying observed (or raw) data
- Plenty of statistical models can be formulated as HMs

Most common example of HM: mixed models



- MMs always have random effects that are continuous and drawn from normal distribution, appear additively in linear predictor of a LM or GLM

$$y_{ij} \sim \text{Normal}(\alpha_i, \sigma_{res}^2)$$

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

Most common example of HM: mixed models



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$$y_{ij} \sim \text{Normal}(\alpha_i, \sigma_{res}^2)$$

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

or

$$y_{ij} \sim \text{Normal}(\alpha_i + \beta_i x_i, \sigma_{res}^2)$$

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta^2)$$

Most common example of HM: mixed models



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More general hierarchical models



- NOTE: random effects can be discrete even binary (i.e. 0/1)
- ... and can follow distribution other than normal ... e.g., Poisson or Bernoulli
- Two examples of such more general HMs, where one describes state and other observation

$$y_{ij} \sim \text{Binomial}(N_i, p_{ij})$$

$$N_i \sim \text{Poisson}(\lambda_i)$$

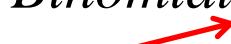
$$y_{ij} \sim \text{Bernoulli}(z_i p_{ij})$$


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

More general hierarchical models



- NOTE: random effects can be discrete even binary (i.e. 0/1)
- ... and can follow distribution other than normal ... e.g., Poisson or Bernoulli
- Two examples of such more general HMs, where one describes state and other observation

$$y_{ij} \sim \text{Binomial}(\textcircled{N_i}, p_{ij})$$
$$\textcircled{N_i} \sim \text{Poisson}(\lambda_i)$$


$$y_{ij} \sim \text{Bernoulli}(\textcircled{z_i} p_{ij})$$
$$\textcircled{z_i} \sim \text{Bernoulli}(\psi_i)$$


HMs can be thought of as linked GLMs !



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- And we can add effects of covariates

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_2 x_{2,ij}$$

$$\log(\lambda_i) = \beta_0 + \beta_1 x_i$$

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_2 x_{2,ij}$$

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_i$$

HMs can be thought of as linked GLMs !



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

- ... and spatial effects !

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_2 x_{2,ij}$$

$$\log(\lambda_i) = \beta_0 + \beta_1 x_i + \mathbf{w}_i$$

$$\mathbf{w}_i \sim \text{MVN}(\mathbf{0}, \Sigma)$$

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_2 x_{2,ij}$$

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_i + \mathbf{w}_i$$

$$\mathbf{w}_i \sim \text{MVN}(\mathbf{0}, \Sigma)$$

Summary: What are Distribution and abundance ?



- Dist is z/ψ and abundance is N/λ
- Dist&Abu are summaries of a point pattern → get a feel for PPs with `simPPE()`
- [PP: the fundamental demographic model of animals and plants]
- Dist&Abu depend on underlying intensity of PP ... and on scale of spatial discretization!
- ... they are scale dependent
- Dist is deterministic function of abundance
- Dist&Abu are the same when intensity and/or scale small
- Otherwise, Dist is information-poor summary of abundance
- Beyond some density, Dist becomes uninformative about abundance
(when all quads occupied)

Summary: Measurement errors



- 3 for point patterns, only 2 for Dist&Abu
- Abundance measurements: counts
- Distribution (or presence/absence) Measurements: detection/nondetection data
- Can screw things when unaccounted for
- Accommodation requires repeated measurements

Summary: Hierarchical models for Dist&Abu



- HM: statistical models that are a linked sequence (or hierarchy) of submodels, typically one for each process that underlie observed data
- Typical processes in Dist/Abu : state process (e.g., abundance or pres./abs.) & observation process (e.g., false negatives, false positives)
- Thus, with such HMs we can model Dist/Abu as random effects, while correcting for ubiquitous measurement errors in all field data on plant and animal distribution and abundance

Thank you.

