# Spatial Modeling in Ecology


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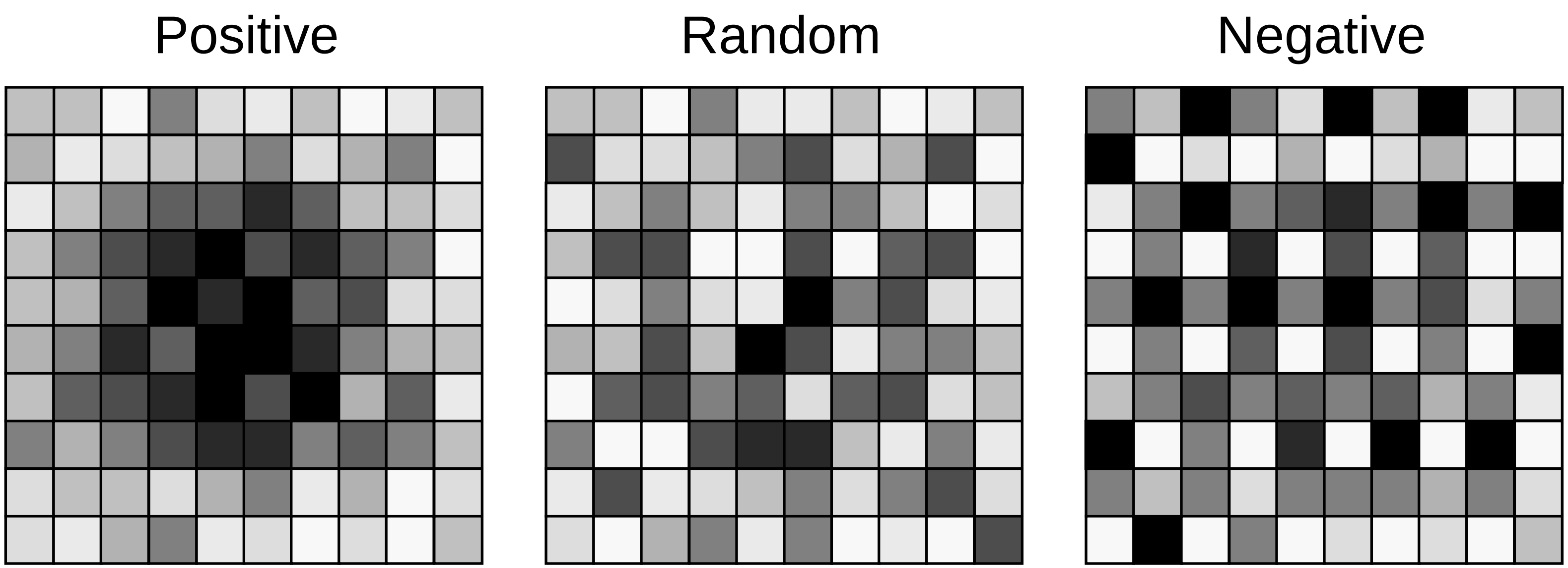
# Dependencies in Data due to Space

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

# Dependencies in Data due to Space

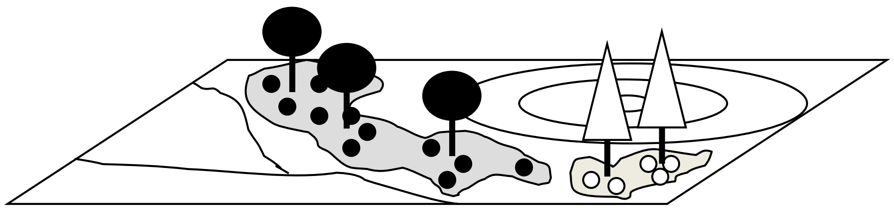
Spatial Autocorrelation

Correlation of the values of a variable according to distance

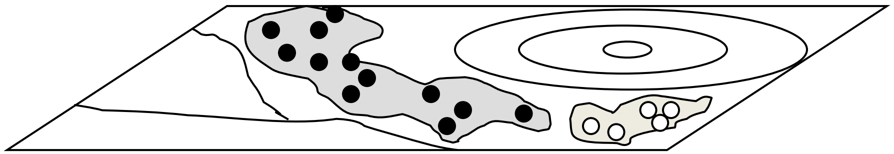



Fortin & Dale 2009

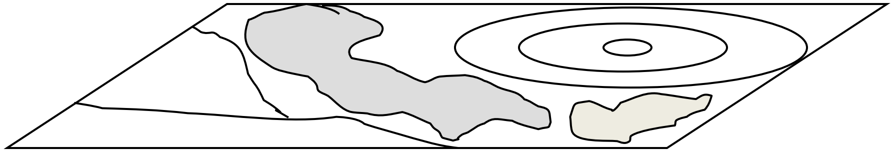
# Spatial Structure = Autocorrelation + Dependence



Spatially Distributed Seeds Due to Dispersal Processes from the Trees and the Spatially Distributed Environmental Factors



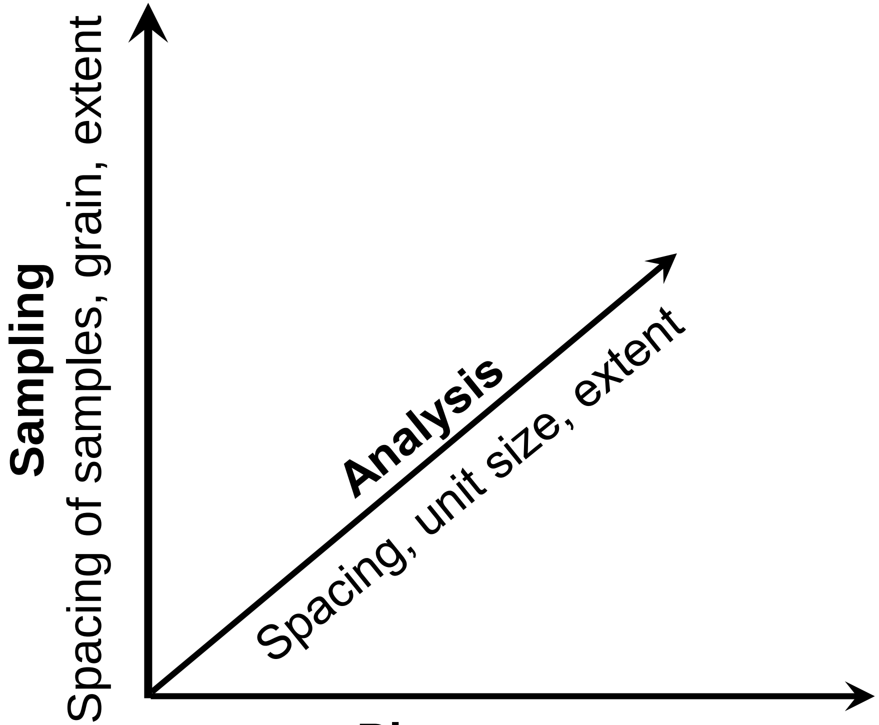
Spatially Distributed Seeds Due to the Spatially Distributed Environmental Factors



Spatially Distributed Environmental Factors

Fortin & Dale 2009

# Other Dependencies: Processes and Analysis

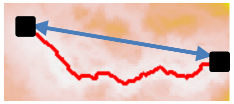



**Phenomenon**
Structure: size and spacing
Process: range of action and scale of effect

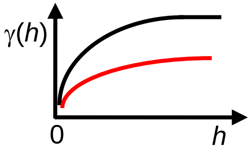
Fletcher & Fortin 2019

# Spatial Aspects

*x-y* Coordinates
Euclidean Distances
Least-cost Distances

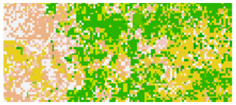


Spatial Autocorrelation
Spatial Dependence



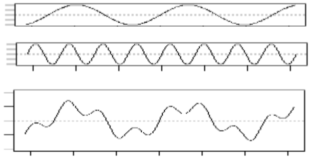

Spatial Relationship

Spatial Legacy
Spatial Contingency

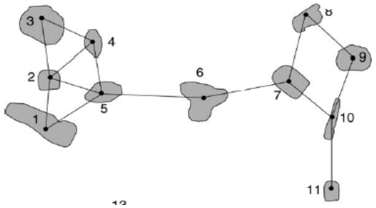


Spatial Perception

Multiscale Analysis



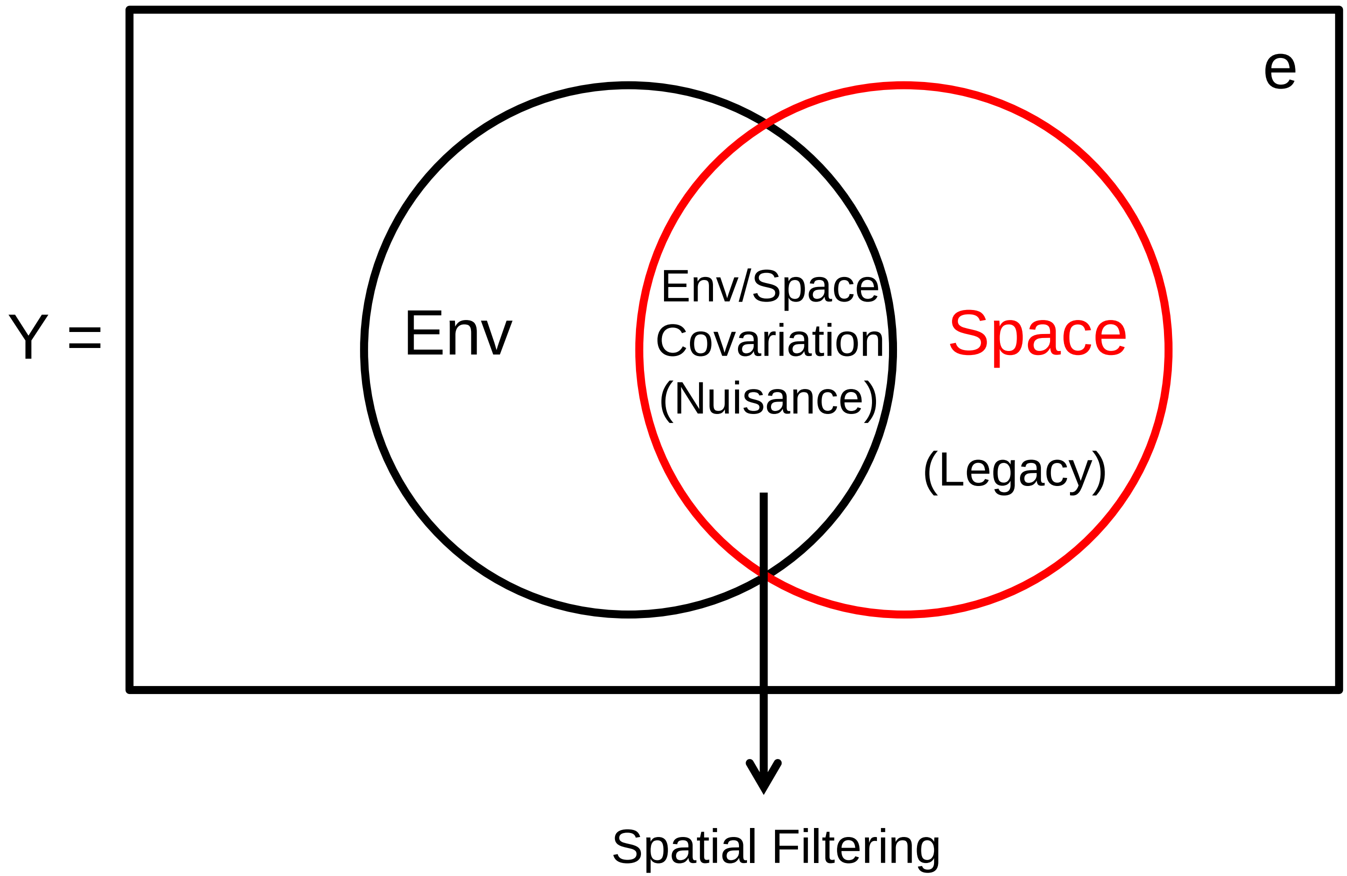
Metapopulation
Metacommunity
Metaecosystem
Metanetwork




Fortin et al 2012

# Spatial Dependence + Spatial Autocorrelation

## Environmental and Spatial Contributions




Dale & Fortin 2014

# Spatial Structure

SPATIAL NUISANCE (Space is your Enemy)
Space as a weight: Spatial autocorrelation as part of residual variation

| **G** | **D** | **C/W** | **E** |
|---|---|---|---|
| *x-y* | Euclidean Distance | Connectivity | Environment |

SPATIAL LEGACY (Space is your Friend)

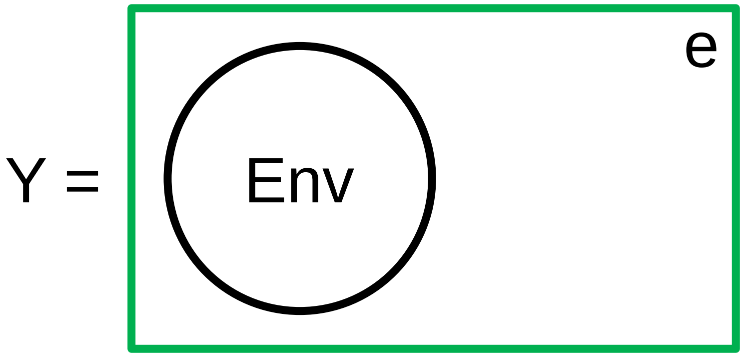
Space as a term: Spatial autocorrelation as a function

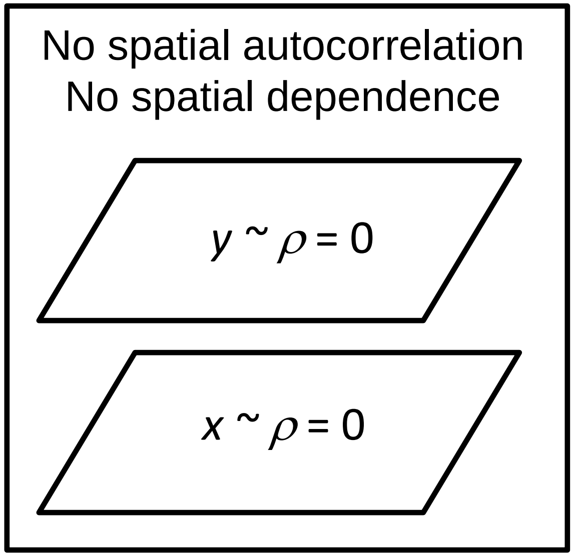
C/W = Spatial Matrix

Peres-Neto & Legendre 2010

# Regression

| Name | Model |
|---|---|
| Independent Errors (no spatial dependence) | $\mathbf{Y} = \mathbf{X}\beta + \varepsilon$ |

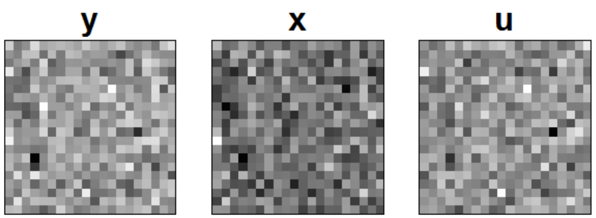



Dale & Fortin 2014

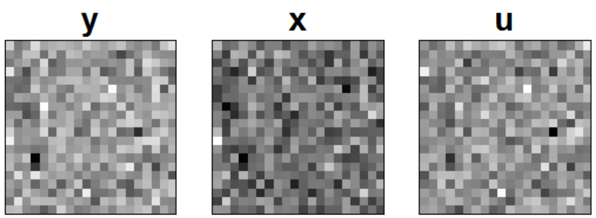
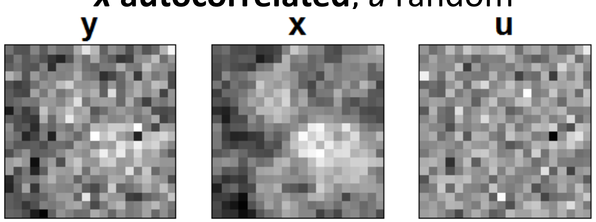
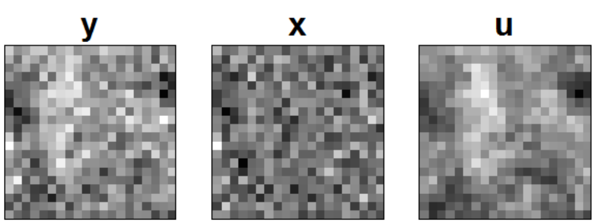
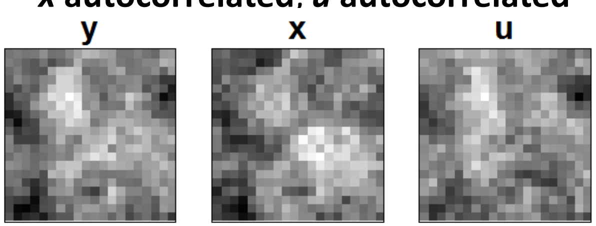
# Linear Regression

$$y = 0.5x + 0.5u$$

| *x* random, *u* random | Predictor & Response: spatially independent<br>Regression is ***correct***:<br>• Moran's *I* of residuals = -0.002<br>• Slope estimate ($b$ ± SE) = 0.500 ± 0.025<br>• True SE of slope: 0.025<br>• Type I error rate: 0.050 |
|---|---|
|  | |

Wagner & Fortin 2016

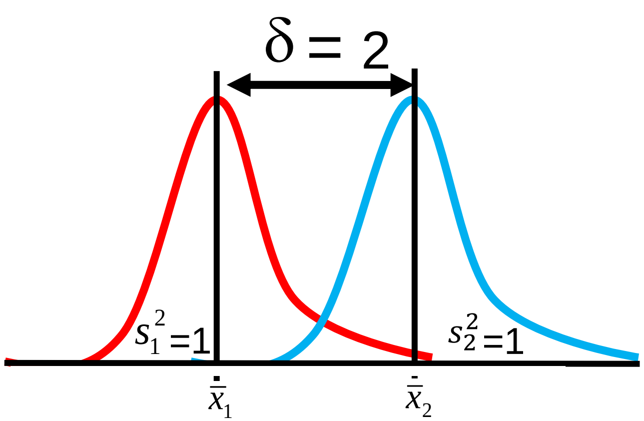
# Linear Regression

| | |
|---|---|
| *x* random, <u>u</u> random<br><br> | Predictor random, Response random<br>Regression is ***correct***:<br>• Moran's *I* of residuals = -0.002<br>• Slope estimate (b ± SE) = 0.500 ± 0.025<br>• True SE of slope: 0.025<br>• Type I error rate: 0.050 |
| ***x* autocorrelated**, *u* random<br><br> | **Predictor autocorrelated**, Response random<br>Regression is ***correct***:<br>• Moran's *I* of residuals = -0.003<br>• Slope estimate (b ± SE) = 0.500 ± 0.025<br>• True SE of slope: 0.025<br>• Type I error rate: 0.048 |
| *x* random, ***u* autocorrelated**<br><br> | Predictor random, **Response autocorrelated**<br>Regression is ***correct***, but residuals spatially autocorrelated:<br>• Moran's *I* of residuals = 0.640<br>• Slope estimate (b ± SE) = 0.501 ± 0.025<br>• True SE of slope: 0.025<br>• Type I error rate: 0.054 |
| ***x* autocorrelated**, ***u* autocorrelated**<br><br> | **Predictor autocorrelated**, **Response autocorrelated**<br>Regression is ***incorrect***:<br>• Moran's *I* of residuals = 0.629<br>• Slope estimate (b ± SE) = 0.501 ± 0.025<br>• True SE of slope: 0.071<br>• Type I error rate: 0.504 |

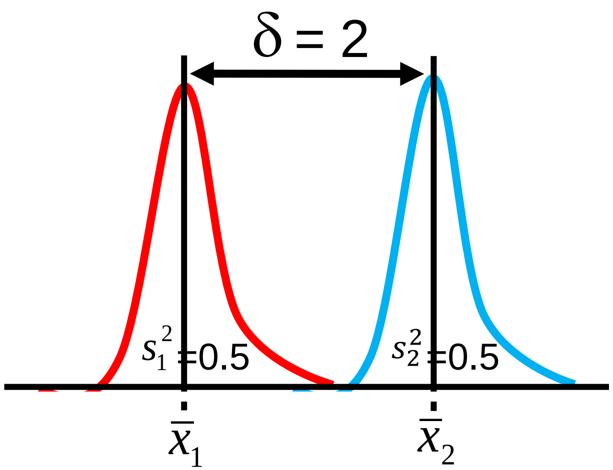
Wagner & Fortin 2016

# Spatial Autocorrelation

| Spatial Autocorrelation may: | *What does this mean?* |
|---|---|
| Inflate type I error rates | *Risk of false positives* |
| Bias parameter estimates | *Effect size may be over-estimated* |
| Inflate variability of parameter estimates | *Confidence intervals are calculated too small* |



Without Autocorrelation

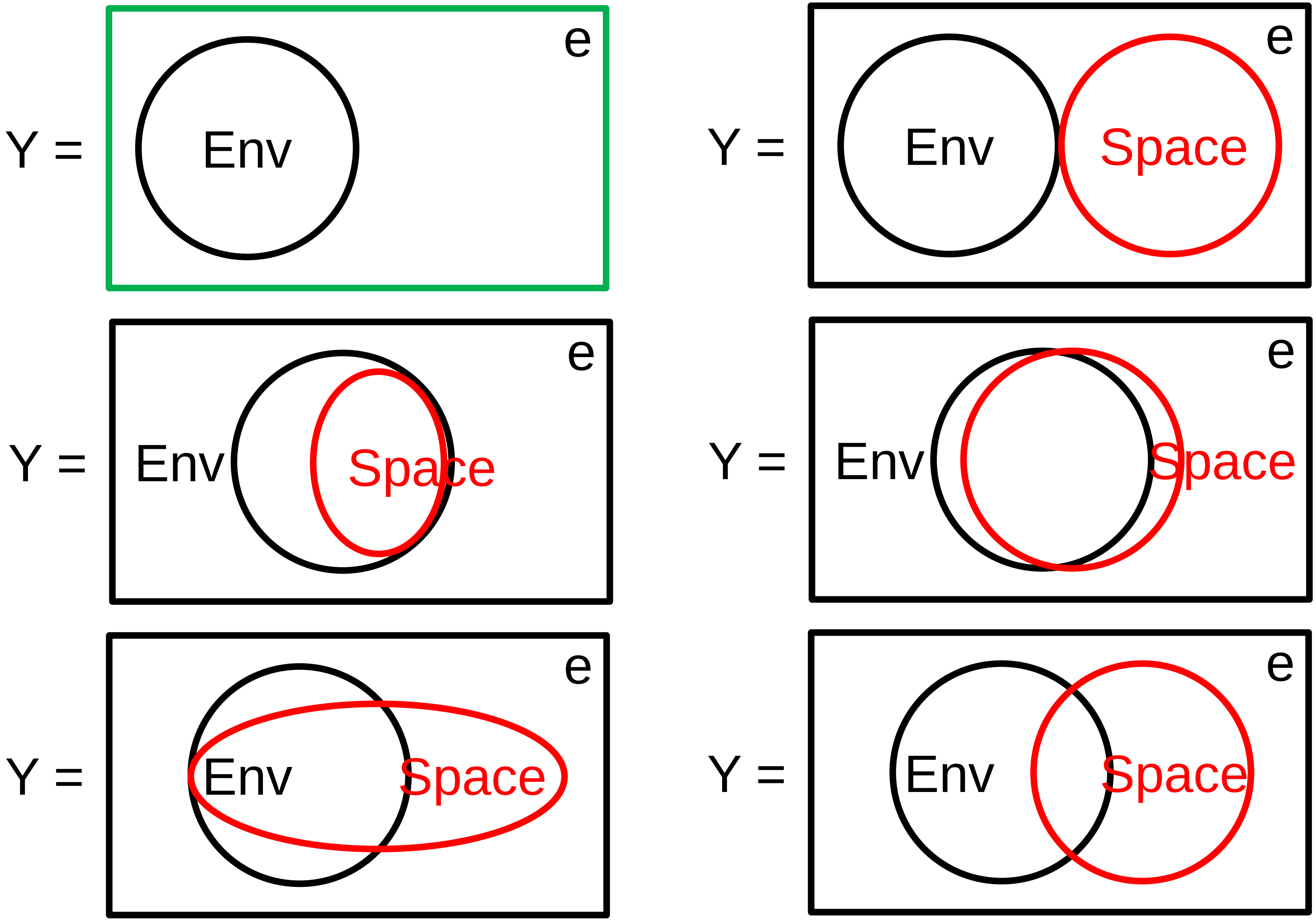


With Autocorrelation

Wagner & Fortin 2016

# Spatial Dependence + Spatial Autocorrelation

## Environmental and Spatial Contributions



# Spatial Regression

Spatial Regression (GLMM, Error, Lag)

Spatial process creates spatial autocorrelation

→Need to account for spatial autocorrelation

Spatial Regression (Spatial Filtering)

Multiple processes at different spatial scales

→Need to partial out spatial variations at all scales

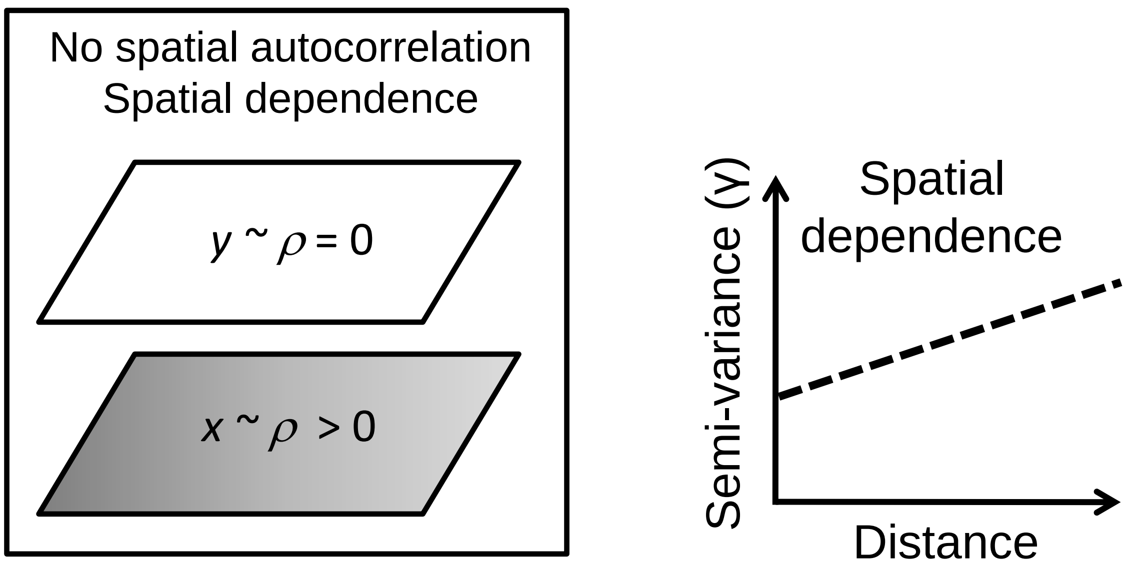
# Spatial Regression: Trend Surface Analysis

Linear regression (e.g., OLS):

$$\{x_1(s), \ldots x_m(s)\} \longrightarrow y(s) \longleftarrow \varepsilon$$

Linear regression adding spatial coordinates as predictors using OLS:

$$\{x_1(s), \ldots x_m(s), \text{lat}, \text{long}\} \longrightarrow y(s) \longleftarrow \varepsilon$$




Dale & Fortin 2014

# Spatial Regression: Trend Surface Analysis

Regression including *x*-*y* coordinates

Polynomial regression

→ Only explanatory variables are powers and cross products of the *x*-*y* coordinates

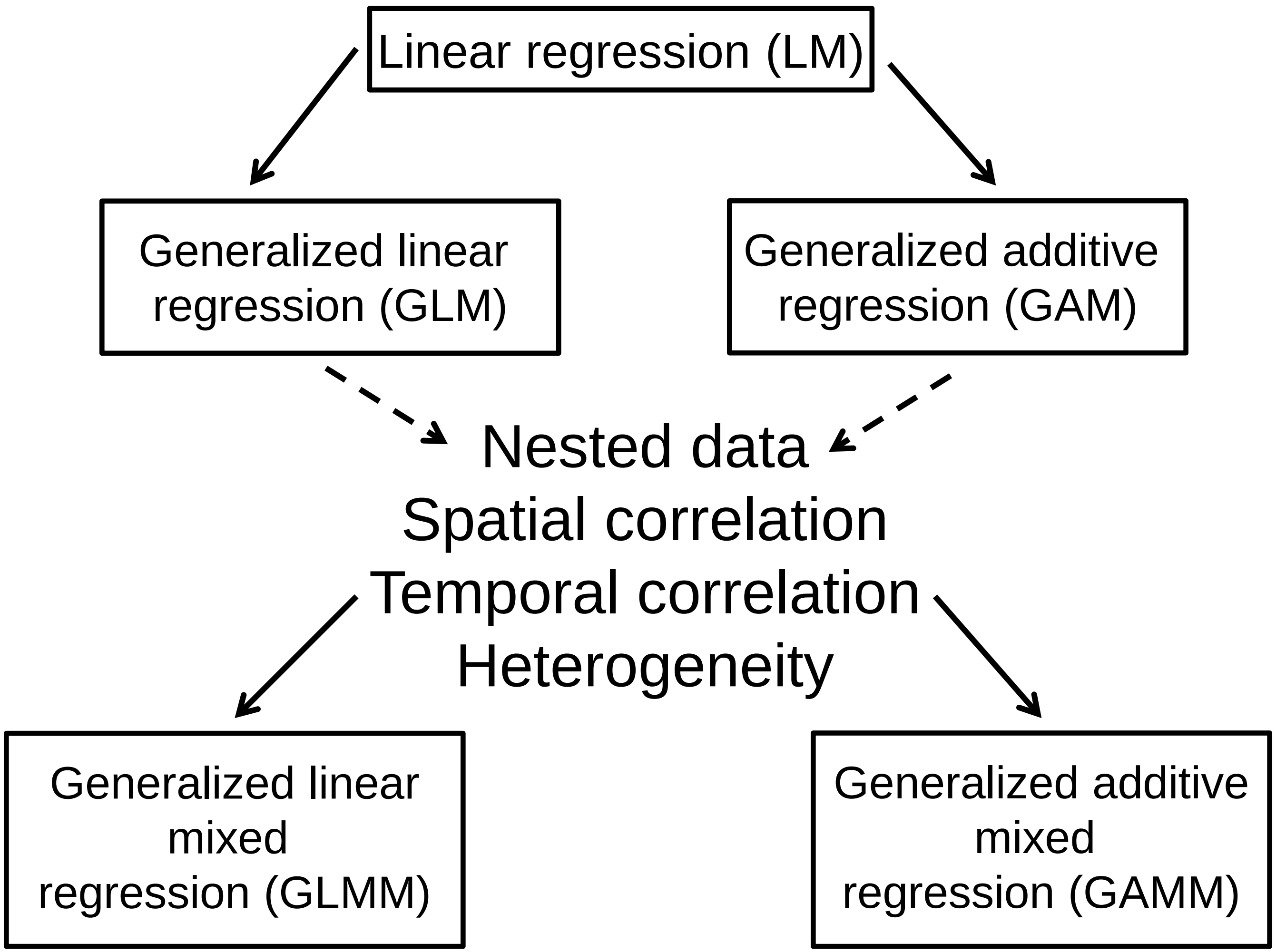
→ Power of the polynomial

→Linear, quadratic, cubic, etc.

$$Y = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \beta_3 x_i^3 + \ldots + \beta_m x_i^m + \varepsilon$$

Dale & Fortin 2014

# Regression




Adapted from Zuur et al (2009)

# Linear Regression

Linear regression (e.g., OLS):

$\{x_1(s), \ldots x_m(s)\} \longrightarrow y(s) \longleftarrow \varepsilon$

Linear regression adding spatial coordinates as predictors using OLS:

$\{x_1(s), \ldots x_m(s), lat, long\} \longrightarrow y(s) \longleftarrow \varepsilon$

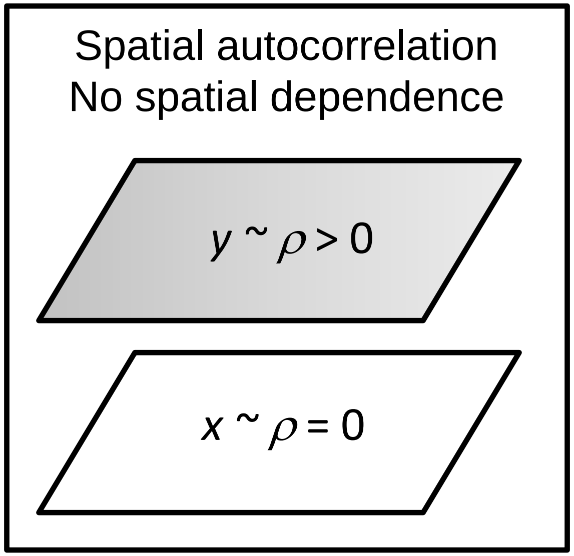
Linear regression adding spatial coordinates as random effects using Generalised Linear Mixed Model (GLMM):

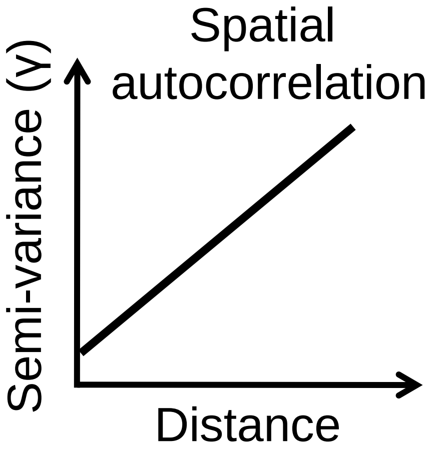
$\{x_1(s_i), \ldots x_m(s_i), z_i\} \longrightarrow y(s_i) \longleftarrow \varepsilon$

Dale & Fortin 2014

# Spatial Regression

| Name | Model |
| --- | --- |
| Independent Errors (no spatial dependence) | $Y = X\beta + \varepsilon$ |
| Autoregressive (AR) | $Y = X\beta + \rho WY + \varepsilon$ |




Dale & Fortin 2014

# Spatial Regression

| Name | Model |
|---|---|
| Independent Errors (no spatial dependence) | $Y = X\beta + \varepsilon$ |
| Autoregressive (AR) | $Y = X\beta + \rho WY + \varepsilon$ |
| Simultaneous Autoregressive (SAR) Predict from error at neighboring locations | $Y = X\beta + \rho W(Y - X\beta) + \varepsilon$ |
| Conditional Autoregressive (CAR) Predict from response at neighboring locations | $Y = X\beta + \rho C(Y - X\beta) + \varepsilon$ |

Spatial filtering regression add lagged covariates using conditional autoregressive (CAR) or simultaneous autoregressive (SAR):

$$\{x_1(s), \ldots x_m(s), x_1(s \pm h), \ldots x_m(s \pm h)\} \longrightarrow y(s) \longleftarrow \varepsilon$$

where $(s \pm h)$ is the neibourhood of s

Dale & Fortin 2014

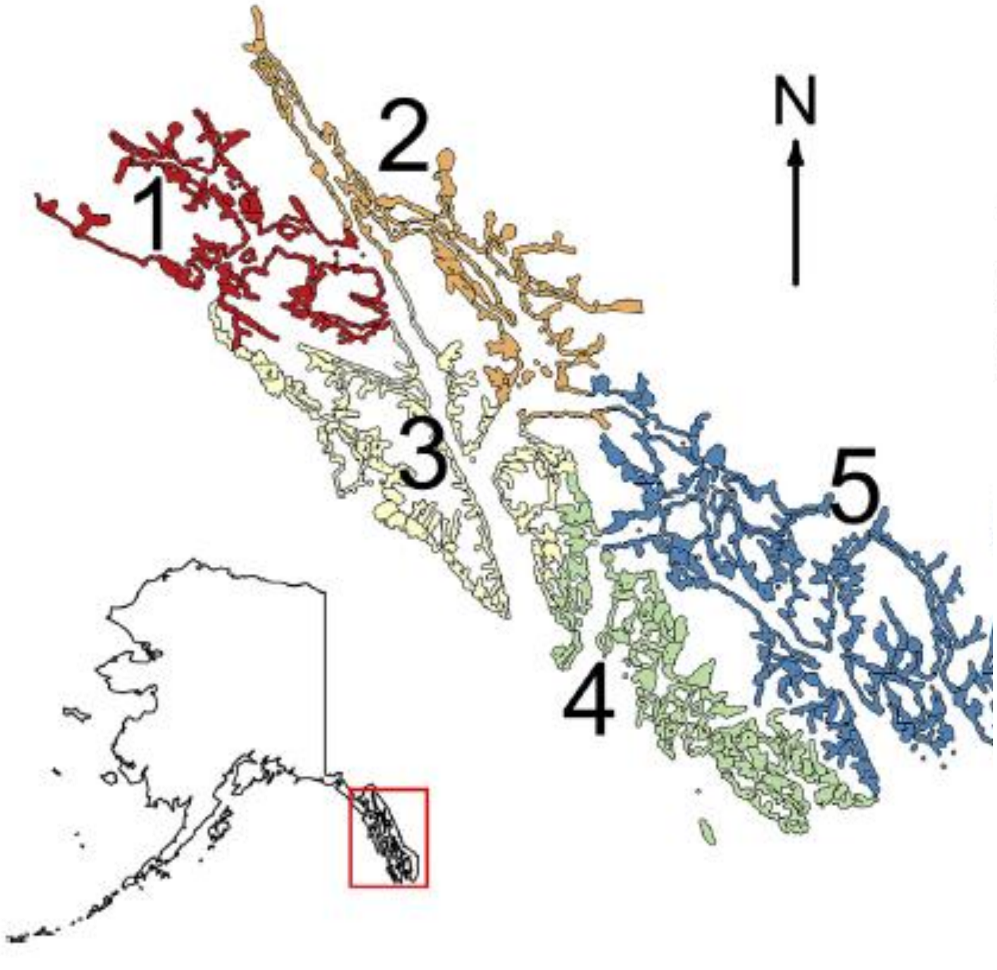
# Common Objectives of Spatial Autoregressive Models

| | |
|---|---|
| **Model Comparison & Selection** | CAR and SAR models are often part of a spatial (generalized) linear model. Prior to inference, one may compare models, and then choose one. |
| **Regression** | Estimate the spatial regression coefficients that quantify how an explanatory variable affects the response variable. |
| **Auto-correlation** | Estimate the strength of autocorrelation (or spatial connectivity) that quantifies how similarly sites change in the residual errors, after accounting for regression effects. |
| **Connectivity** | Estimate covariate effects on connectivity (neighborhood) structure. |
| **Prediction** | Goal of geostatistics (but rarely used in CAR and SAR).<br>If sites have missing data, prediction is possible. |
| **Smoothing** | Create values at spatial sites that smooth over observed data by using values from nearby locations to provide better estimates. |

Ver Hoef et al 2018 *Ecological Monographs*

# Conditional Autoregressive Models

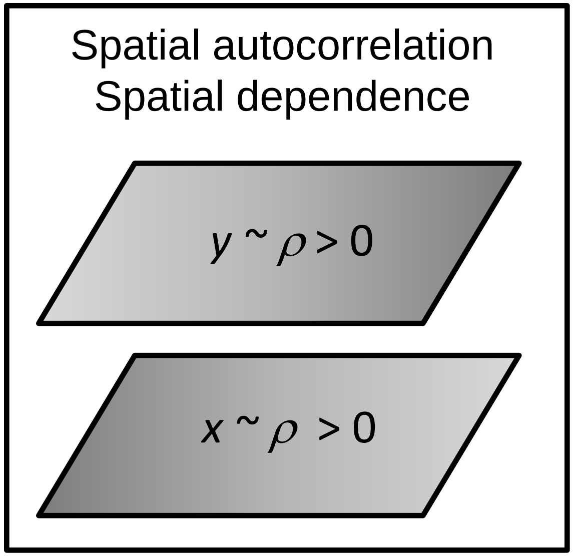
Harbor seals in Alaska: 463 polygons



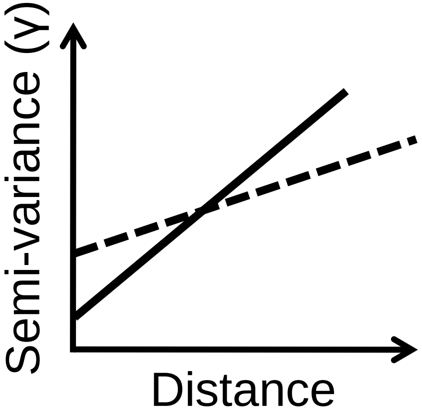

First-Neighbors

Ver Hoef et al 2018 *Ecological Monographs*

# Spatial Regression




Spatial autocorrelation
and Spatial dependence




Dale & Fortin 2014

# Generalized Least Square (GLS) Spatial Error Model (SEM)

$$y_i = \beta_0 + \beta_i x_i + \varepsilon_i + \boxed{\gamma\varepsilon_k}$$

**Model Spatial Error Covariance**

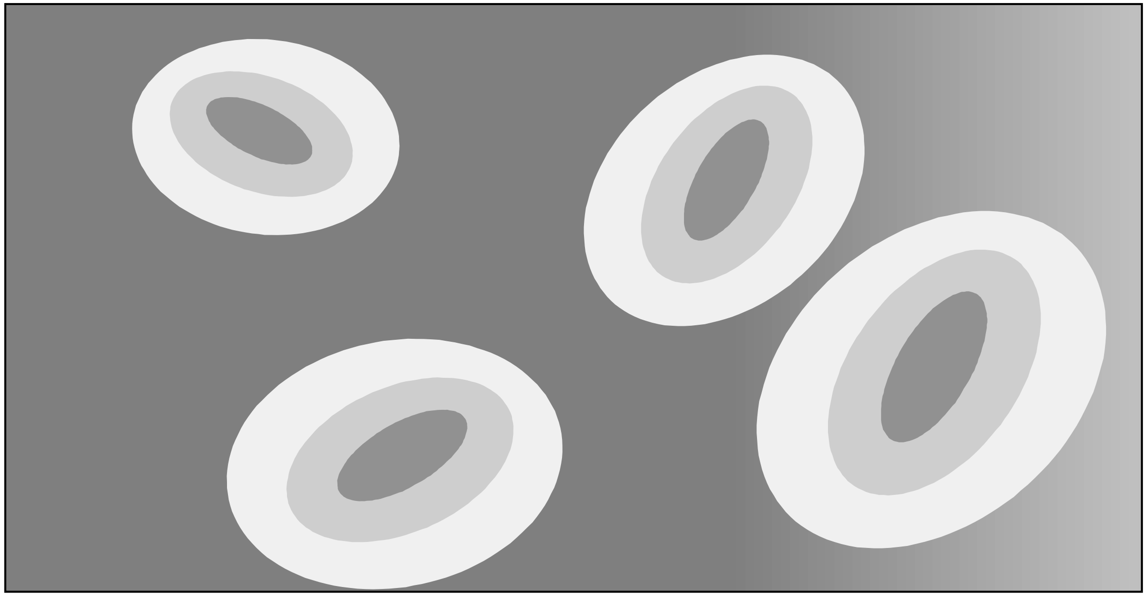
◦ Accounts for spatial autocorrelation that depends on distance only

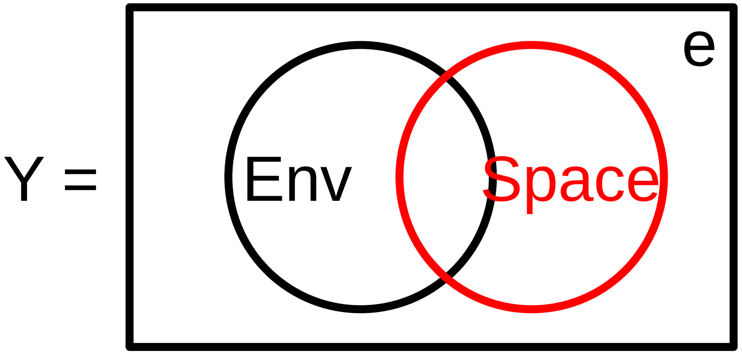
◦ Fits a geostatistical variogram model to errors

Estimating GLS residuals is an iterative process that first involves parameter estimation by OLS because before the regression is performed, the residuals are unknown.

Dale & Fortin 2014

# Several Processes → Several Scales



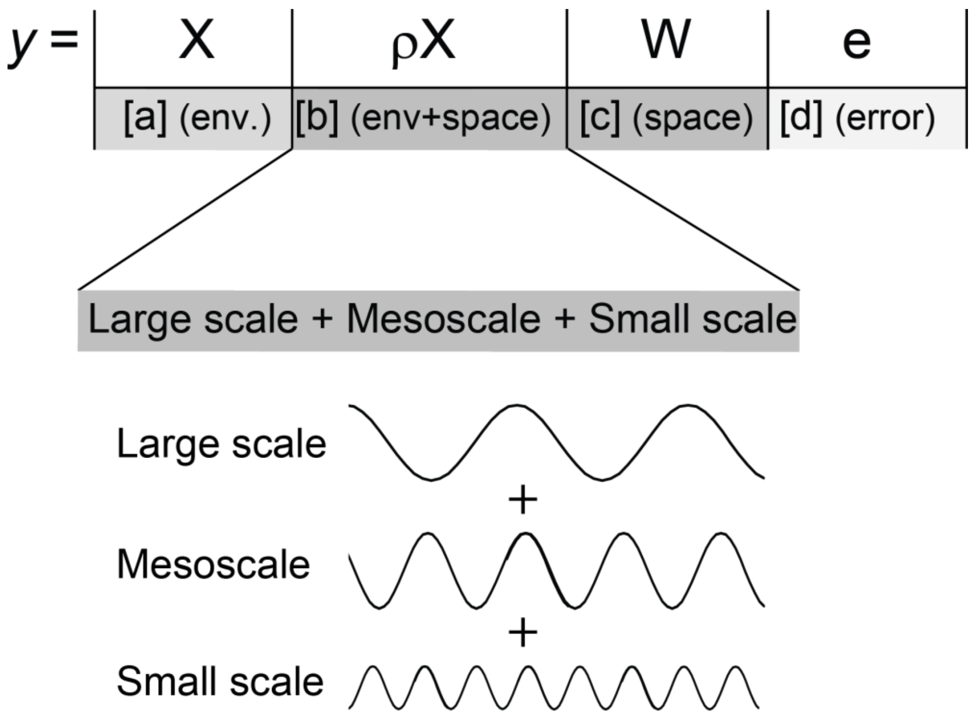



Dale & Fortin 2014

# Spatial Filtering Regression

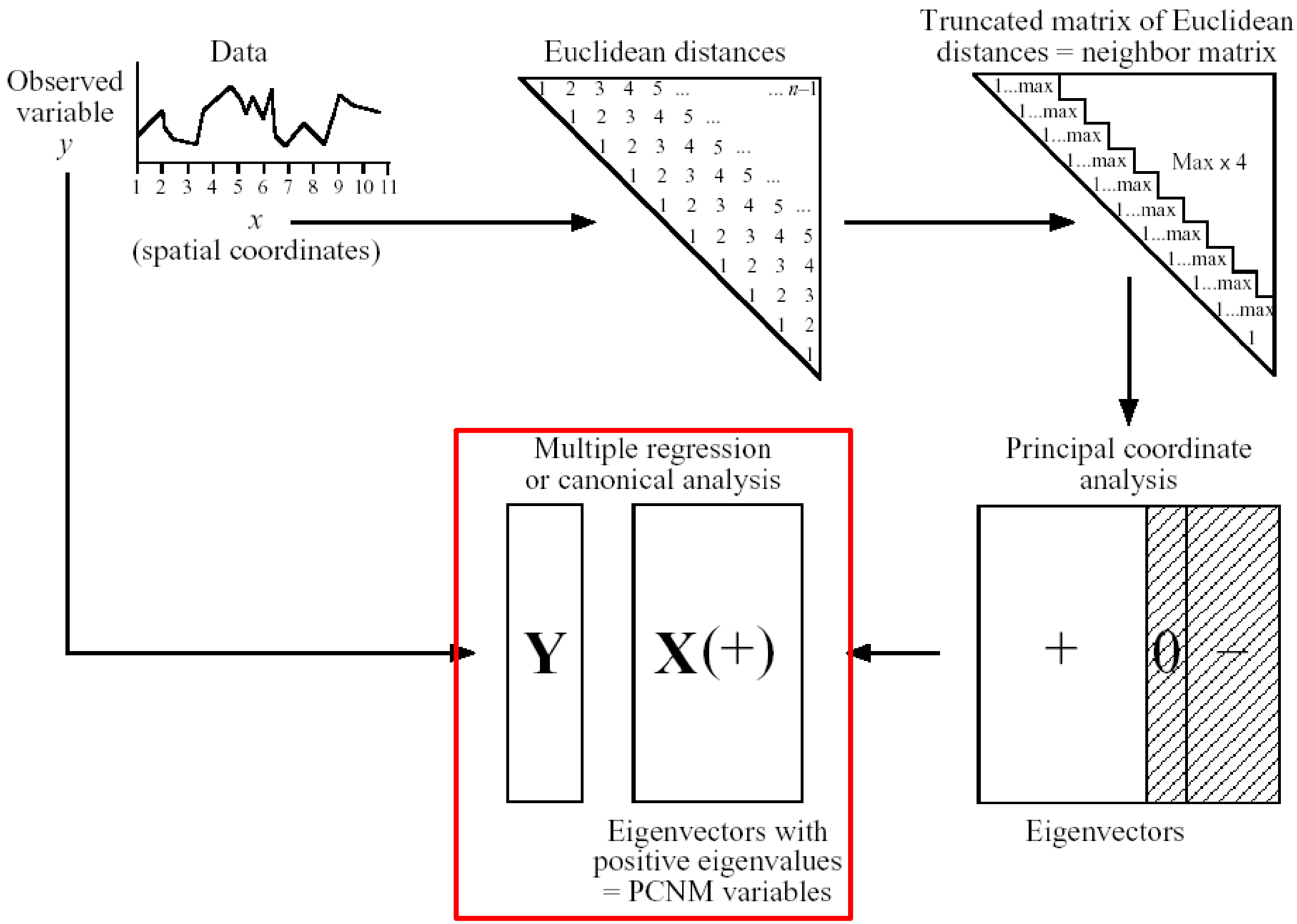
Spatial filteringregression: add spatial predictors (e.g. Moran's Eigenvector Maps):

$$\{x_1(s), \ldots x_m(s), MEM_i, MEM_k\} \longrightarrow y(s) \longleftarrow \varepsilon$$




Dale & Fortin 2014

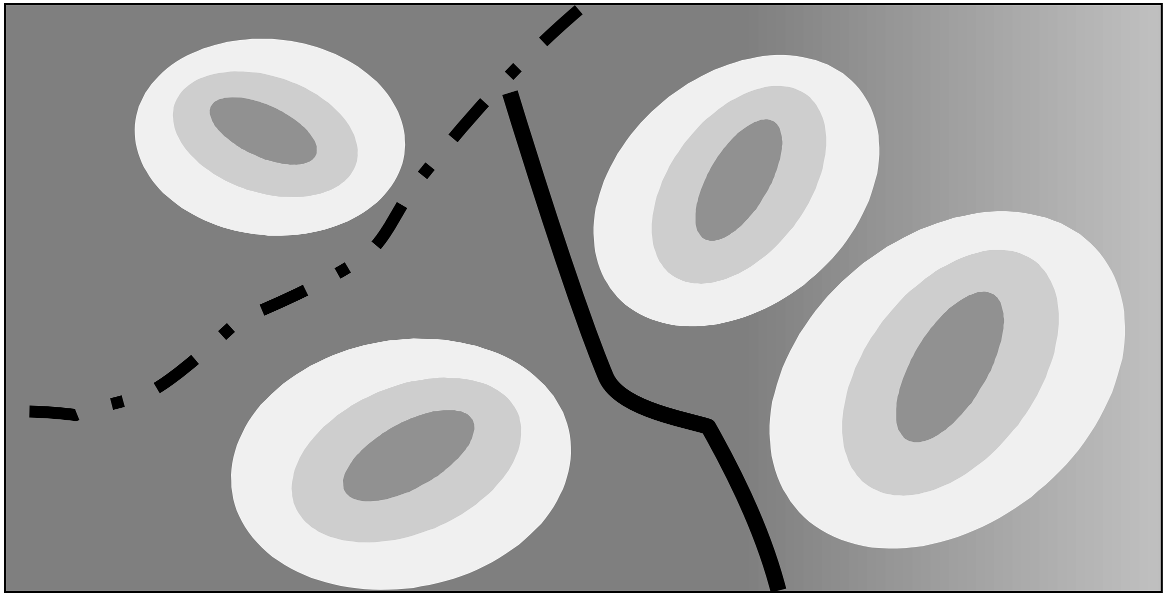
# Principal Coordinate Neighbor Matrix (PCNM/dbMEM)




Truncate the matrix of geographic distances
Decompose **D** by Principal Coordinate Analysis (PCoA)
Centre **D** and then compute eigenvalues and eigenvectors

Borcard & Legendre 2002

# Several Processes + Several Regions



Dale & Fortin 2014

# Geographically Weighted Regression

Geographically Weighted Regression (GWR) using neighbourhood to compute a linear regression at each sampling location *i*

$\{x_1(s_i), \ldots x_m(s_i)\} \longrightarrow y(s_i) \longleftarrow \varepsilon_i$

## Account for localized spatial heterogeneity

$$y_i = \beta_0(i) + \beta_1(i)x_{1i} + \beta_2(i)x_{21i} + \ldots + \beta_n(i)x_{ni} + \varepsilon_i$$

Weights specific to each location *i*
such that observations nearer to *i* are given
greater weight in the regression
than observations further away.

Fotheringham et al 2003

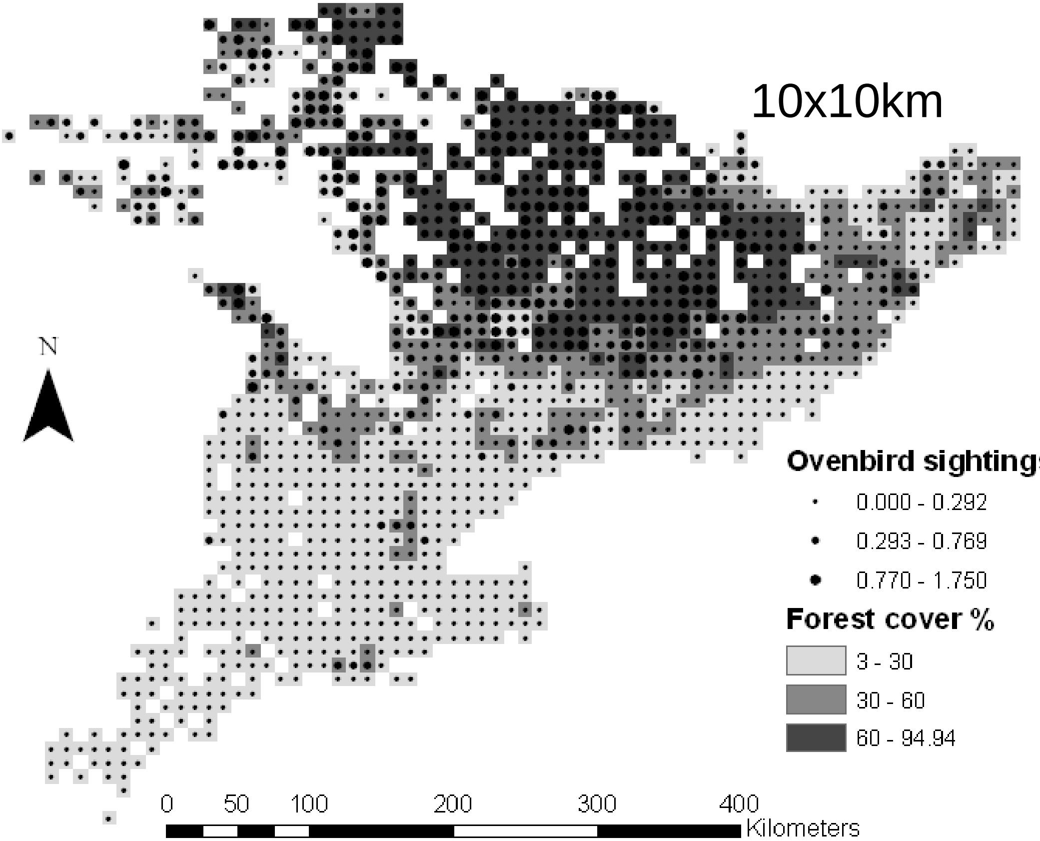
# Geographically Weighted Regression

Residuals from GWR are much lower and are less spatially autocorrelated than those of linear regression

GWR gives a much better fits even accounting for increases in the number of parameters
→ Because it is overfitting

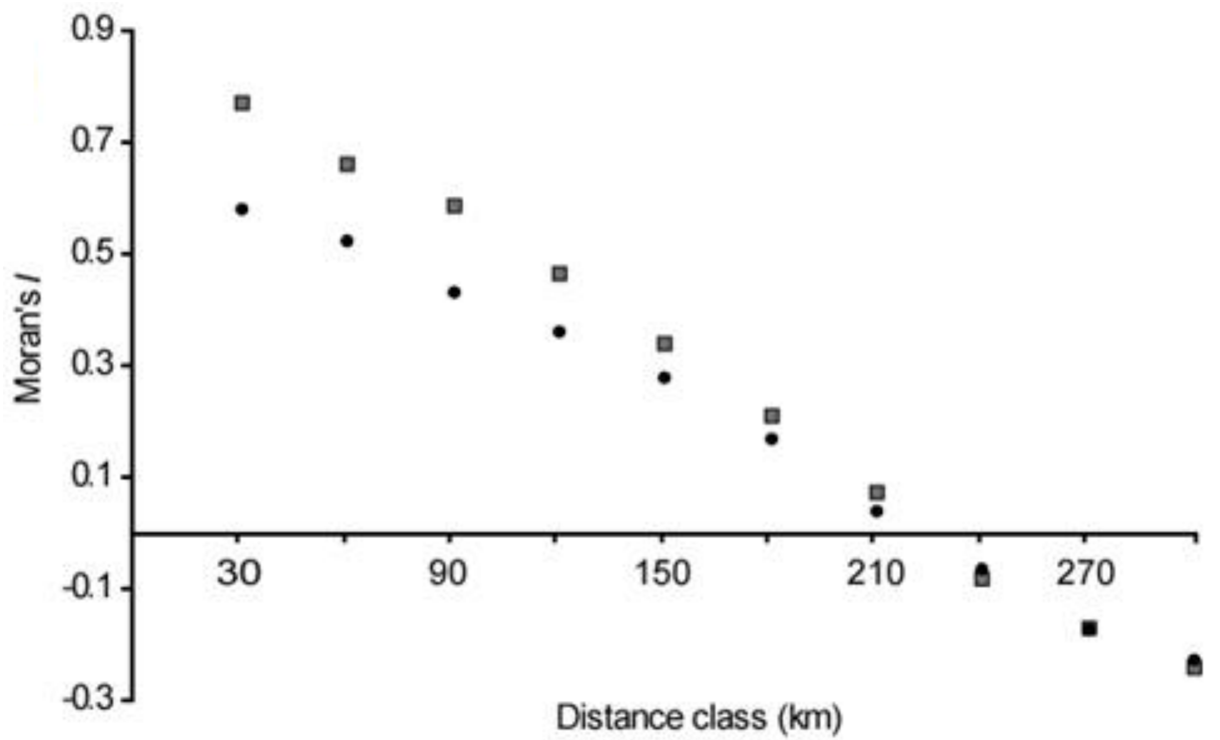
Fotheringham et al 2003

# Ovenbird Sightings ~ Forest Cover


Fortin & Melles 2009

# Ovenbird Sightings ~ Forest Cover

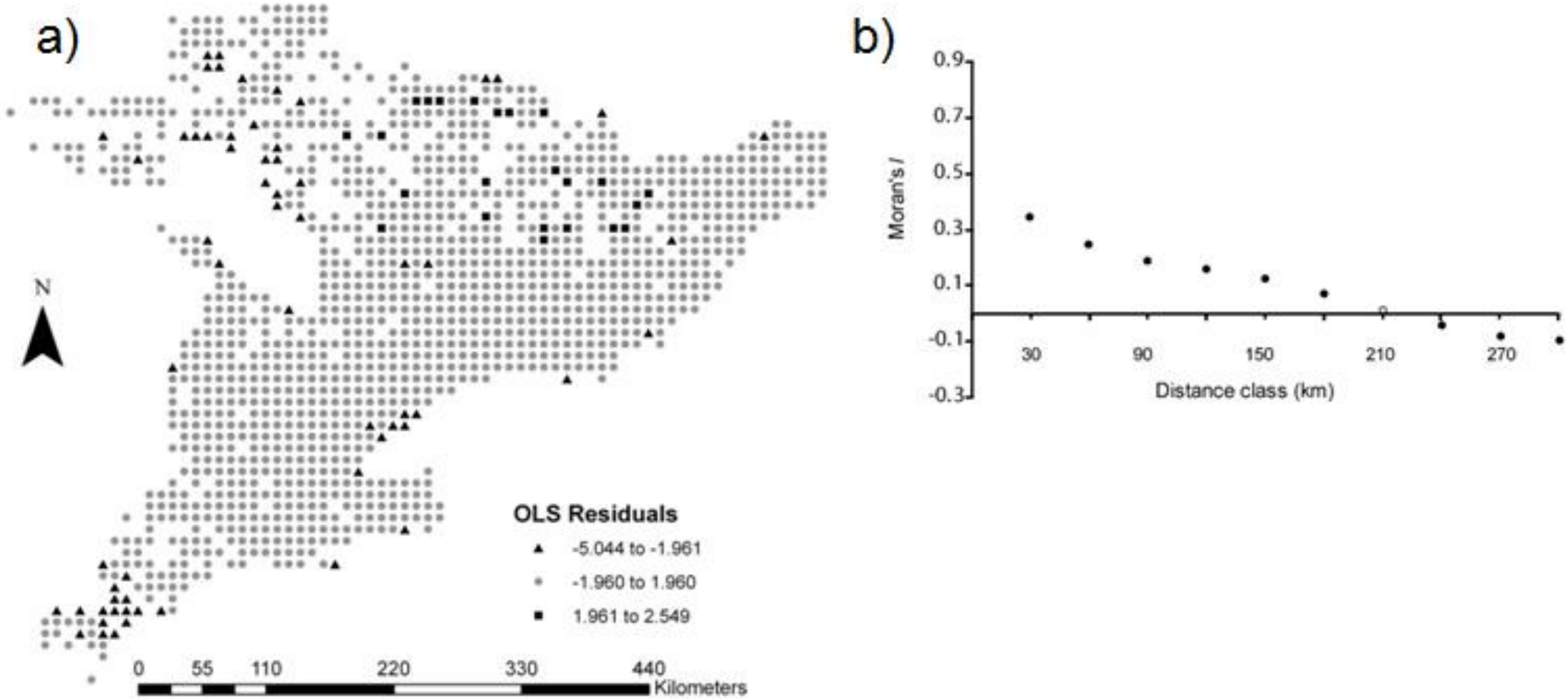



Forest cover (squares), Mean number of ovenbirds (circles)
in an Atlas square 10×10 km (*n*=1359).
Solid symbols indicate significant Moran's *I* ($p \le 0.05$)

Fortin & Melles 2009

# Ovenbird Sightings ~ Forest Cover

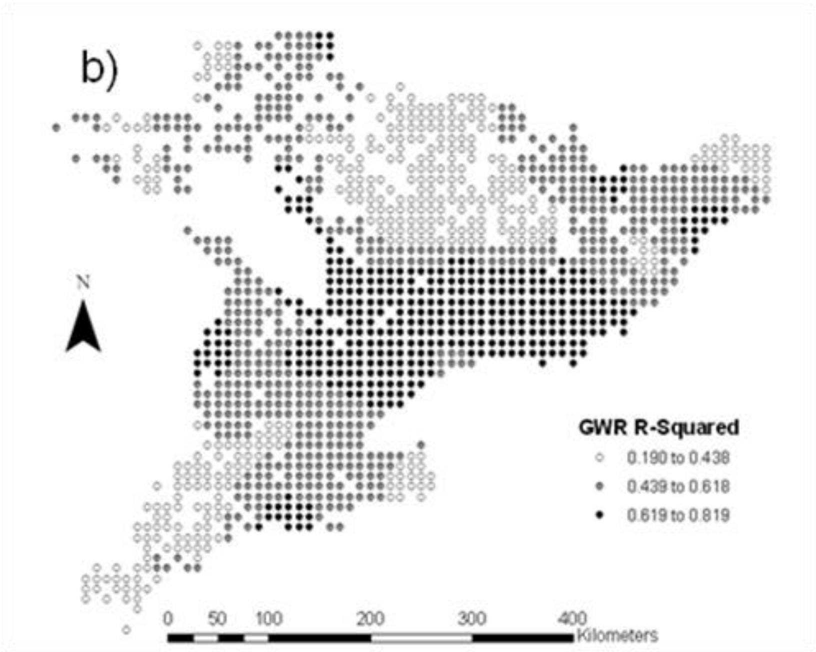
Ordinary Least Square Regression $R^2 = 0.43$

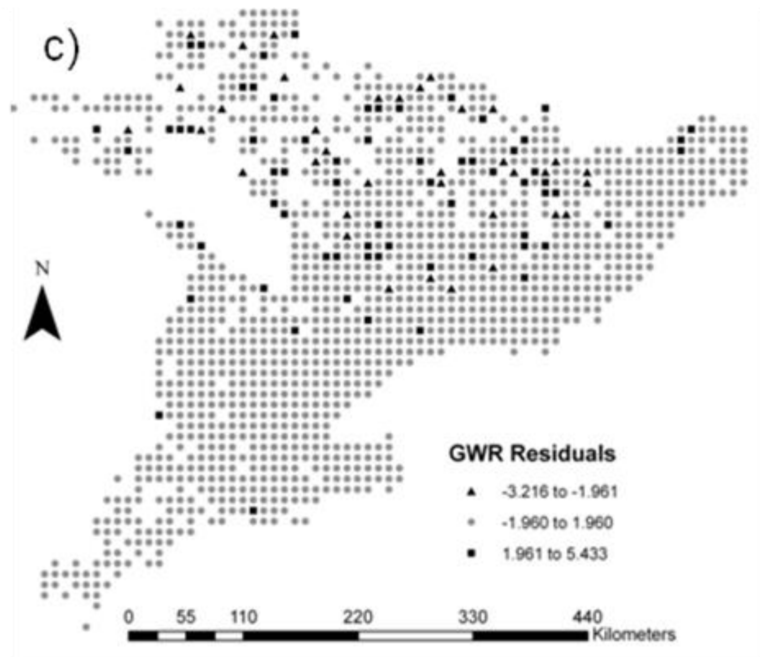



Fortin & Melles 2009

# Ovenbird Sightings ~ Forest Cover

Geographically Weighted Regression $R^2 = 0.19$ to $0.82$

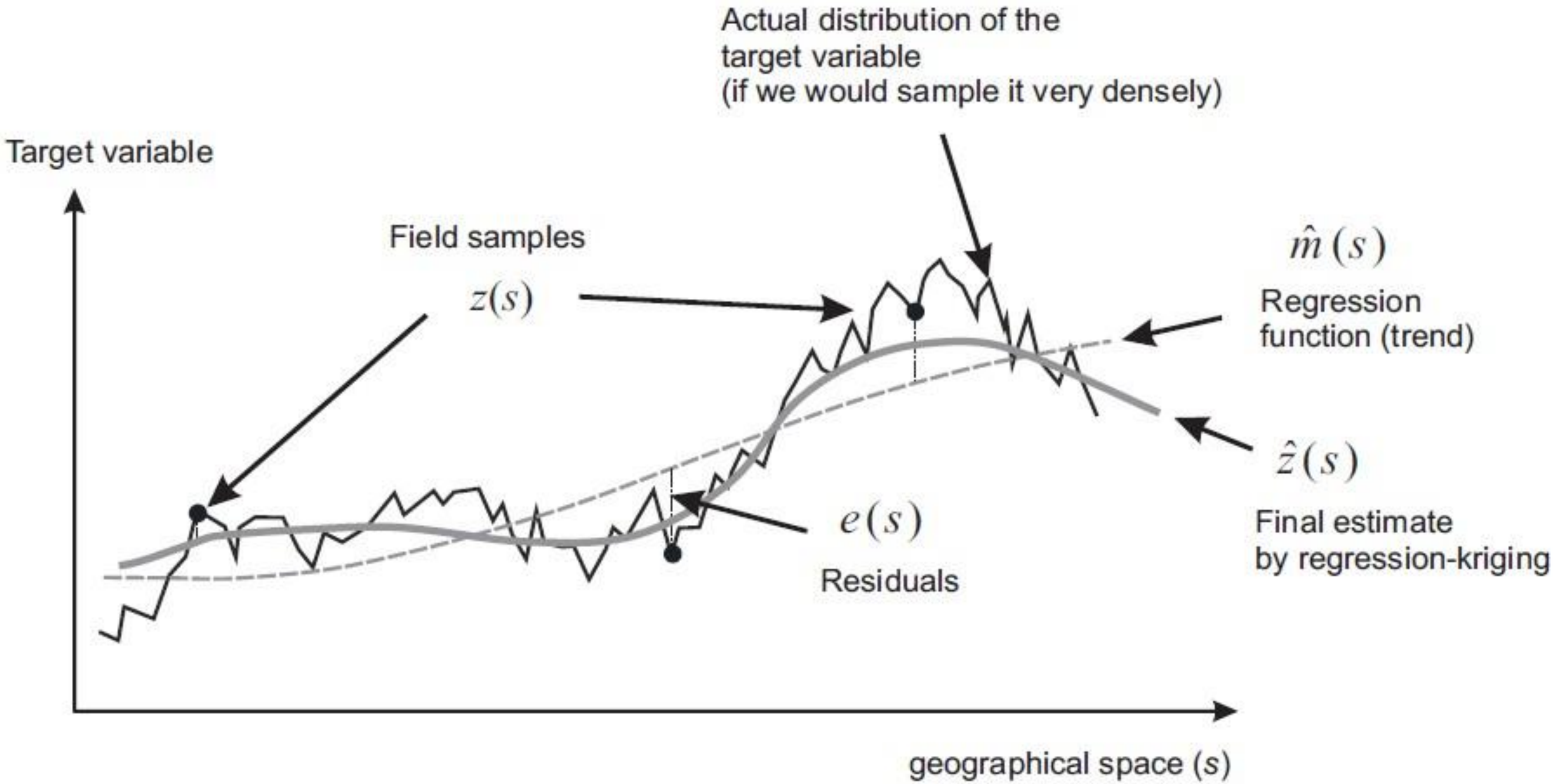



Ordinary Least Square Regression $R^2 = 0.43$

Fortin & Melles 2009

# Regression Kriging ≈ GLS



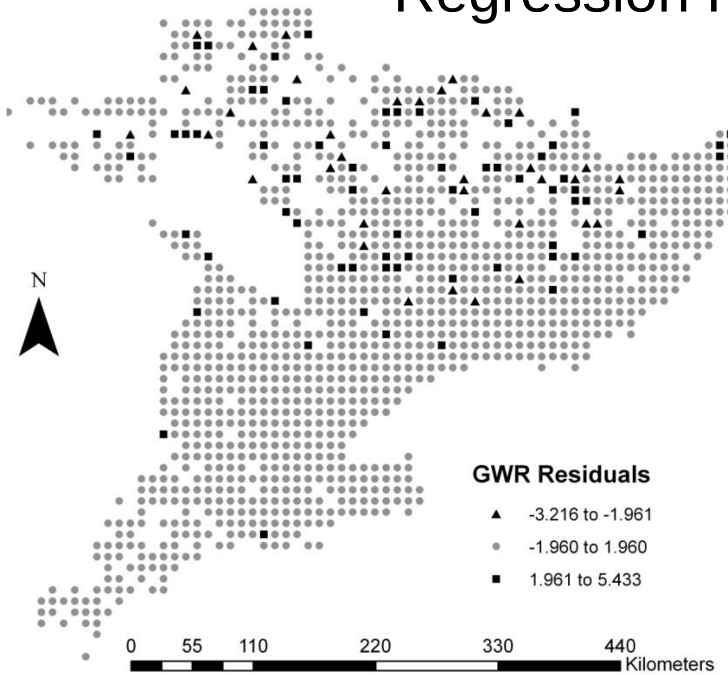

Regression kriging on residuals of linear regression

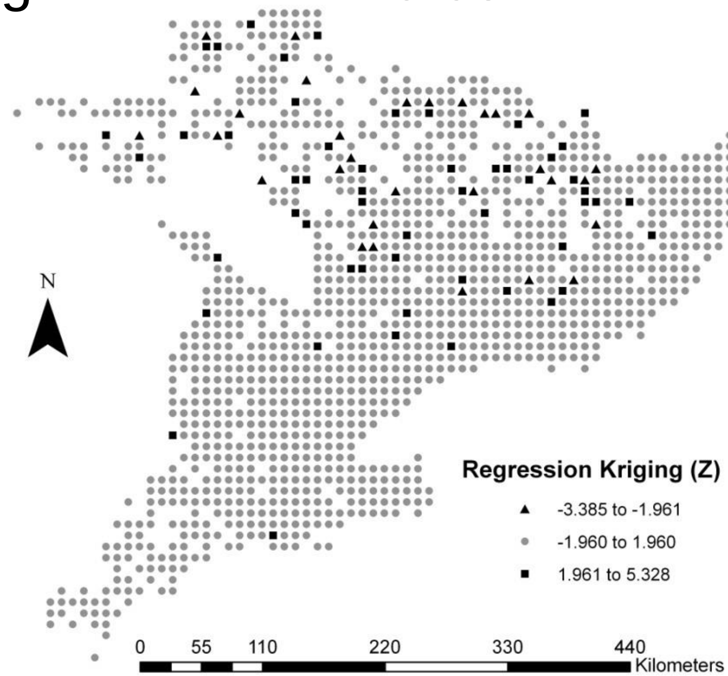
Fortin & Melles 2009

# Ovenbird Sightings ~ Forest Cover

Geographical Weighted Regression $R^2 = 0.19$ to $0.82$

Regression Kriging $R^2 = 0.68$



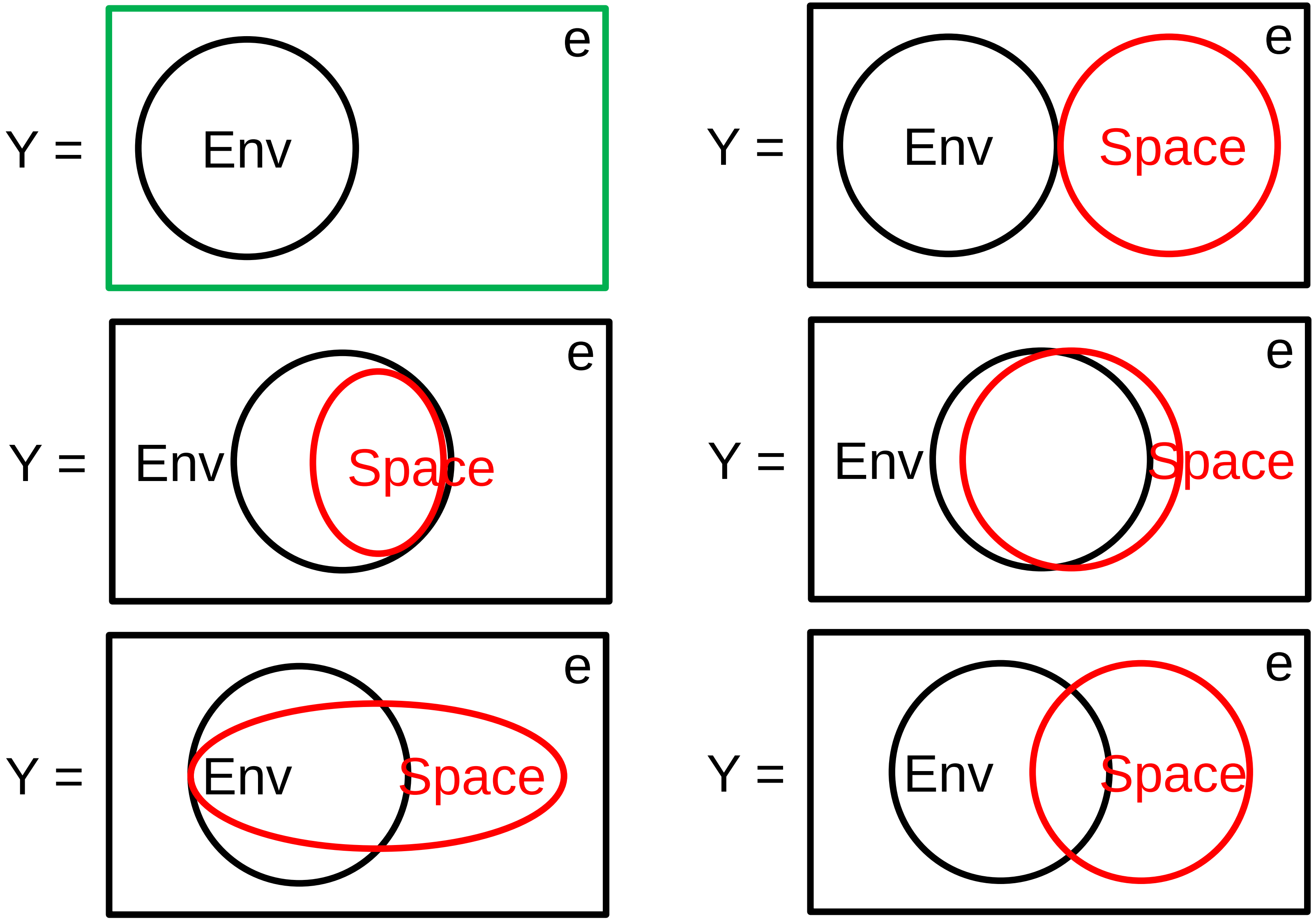




Ordinary Least Square Regression $R^2 = 0.43$

Fortin & Melles 2009

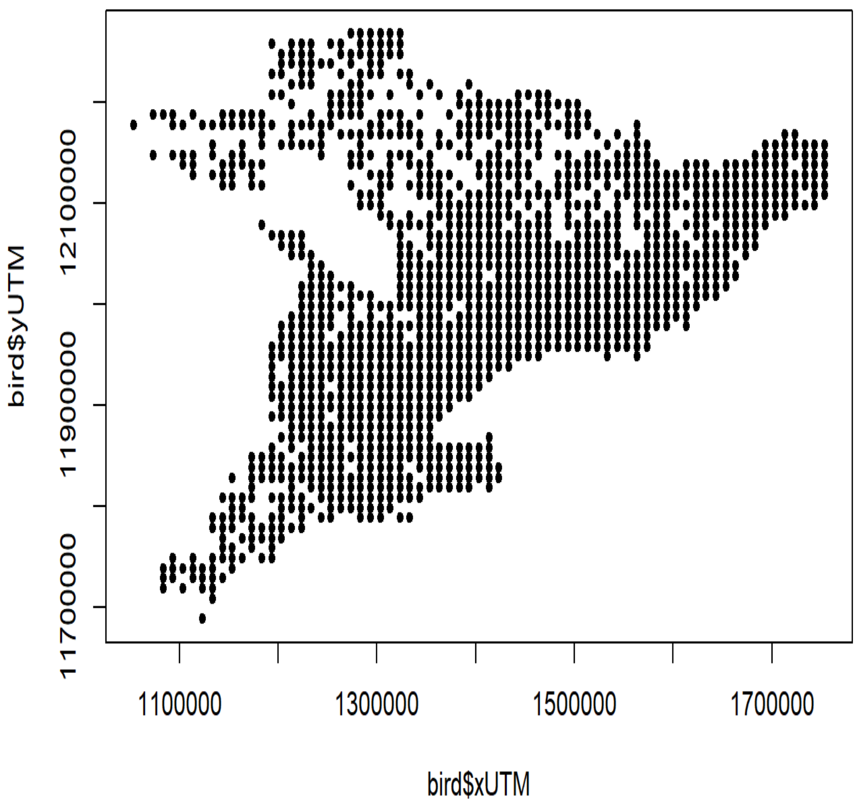
# Spatial Dependence + Spatial Autocorrelation

## Environmental and Spatial Contributions

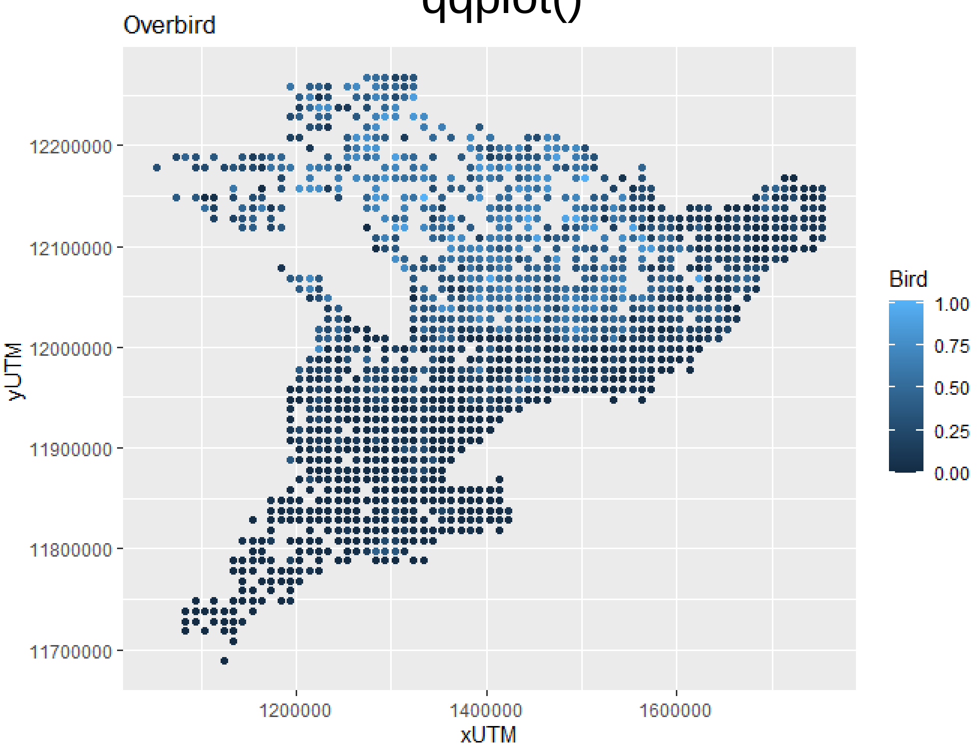


# Ovenbird Sightings ~ Forest Cover
# bird_forest.csv

plot()




qqplot()



# Spatial Regression

```
library(lme4)          # GLMM
library(MuMIn)         # r.squaredGLMM

library(nlme)          # GSL

library(spdep)         # GSL (SAR-err), SAR-lag
library(spgwr)         # Geographically Weighted Regression
library(vegan)         # spatial filtering using MEM
```

*library(care)          # CAR*
*library(spatialreg)  # spatial filtering using MEM*

```
## OSL - Linear Regression
Call: lm(formula = Bird ~ Forest)
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 1.268e-02  8.054e-03   1.575    0.115
Forest      6.322e-05  1.748e-06  36.168   <2e-16 ***

R-squared: 0.4908, Adjusted R-squared:0.4905
F-statistic: 1308 on 1 and 1357 DF,
p-value: < 2.2e-16
```

```
## OSL - Linear Regression
Call: lm(formula = Bird ~ Forest)
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 1.268e-02  8.054e-03   1.575    0.115
Forest      6.322e-05  1.748e-06  36.168   <2e-16 ***

R-squared: 0.4908, Adjusted R-squared:0.4905
F-statistic: 1308 on 1 and 1357 DF,
p-value: < 2.2e-16

## Linear regression – Trend Surface (x-y coordinates)
Call: lm(formula = Bird ~ Forest + xUTM + yUTM)
Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -8.179e+00  4.913e-01  -16.65   <2e-16 ***
Forest       4.968e-05  1.971e-06   25.21   <2e-16 ***
xUTM        -3.672e-07  2.882e-08  -12.74   <2e-16 ***
yUTM         7.282e-07  4.169e-08   17.47   <2e-16 ***
R-squared:  0.607,     Adjusted R-squared:  0.6061
F-statistic: 697.6 on 3 and 1355 DF
p-value: < 2.2e-16
```

# Spatial Regression

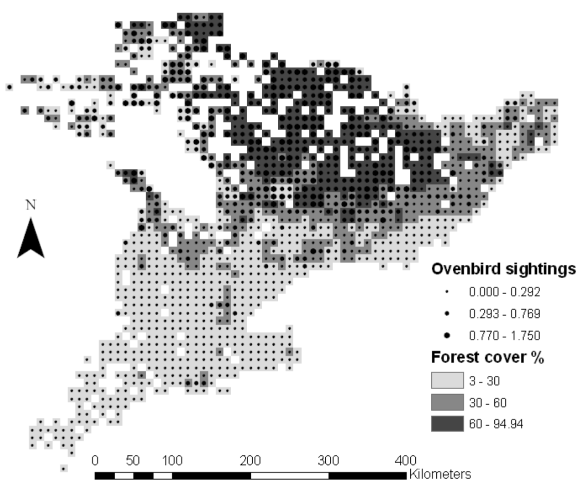
| | AIC | Adj $R^2$ | |
|---|---|---|---|
| Bird.lm | -900.3632 | 0.4908 | |
| Bird.lm.xy | -1248.2828 | 0.6061 | |
| Bird.random | -836.0008 | | 0.4816 |
| Bird.GLMM | -898.5819 | 0.4859 | 0.4880 |

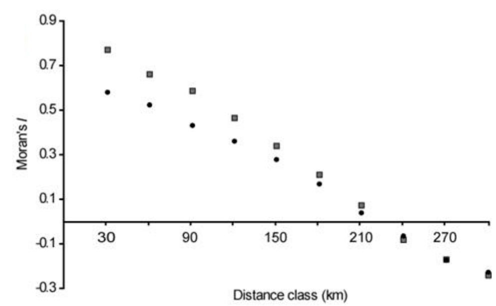
# Spatial Regression: GLS

```
Bird.GLSx = gls(Bird ~ Forest,
   correlation = corAR1(form = ~ 1 | xUTM))

Bird.GLSy = gls(Bird ~ Forest,
   correlation = corAR1(form = ~ 1 | yUTM))

Bird.corLin <- gls(Bird ~ Forest, correlation =
   corLin(form = ~ xUTM + yUTM))

Bird.corSpher <- gls(Bird ~ Forest, correlation =
   corSpher(form = ~ xUTM + yUTM, nugget = TRUE))
```

# Spatial Regression

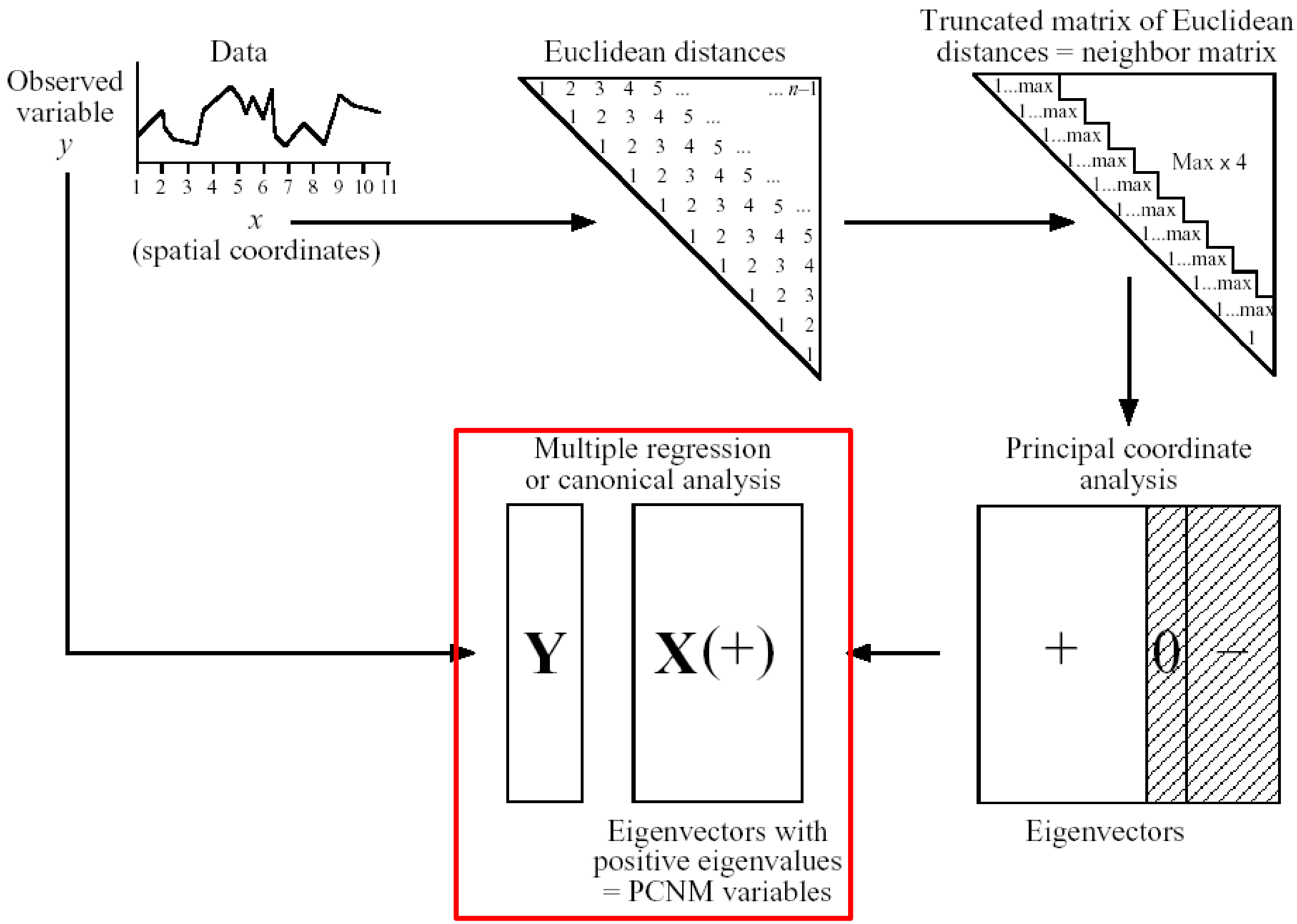
| | AIC | Adj$R^2$ | |
|---|---|---|---|
| Bird.lm | -900.3632 | 0.4908 | |
| Bird.lm.xy | -1248.2828 | 0.6061 | |
| Bird.random | -836.0008 | | 0.4816 |
| Bird.GLMM | -898.5819 | 0.4859 | 0.4880 |
| Bird.GLSx | -885.3516 | | |
| Bird.GLSy | -930.9072 | | |
| Bird.corLin | -1219.8813 | | |
| Bird.corSpher | -1449.1100 | | |




Forest (squares), Ovenbirds (circles)
10×10 km ($n$=1359)

# Principal Coordinate Neighbor Matrix (PCNM/dbMEM)




Truncate the matrix of geographic distances
Decompose **D** by Principal Coordinate Analysis (PCoA)
Centre **D** and then compute eigenvalues and eigenvectors

Borcard & Legendre 2002

# Spatial Regression

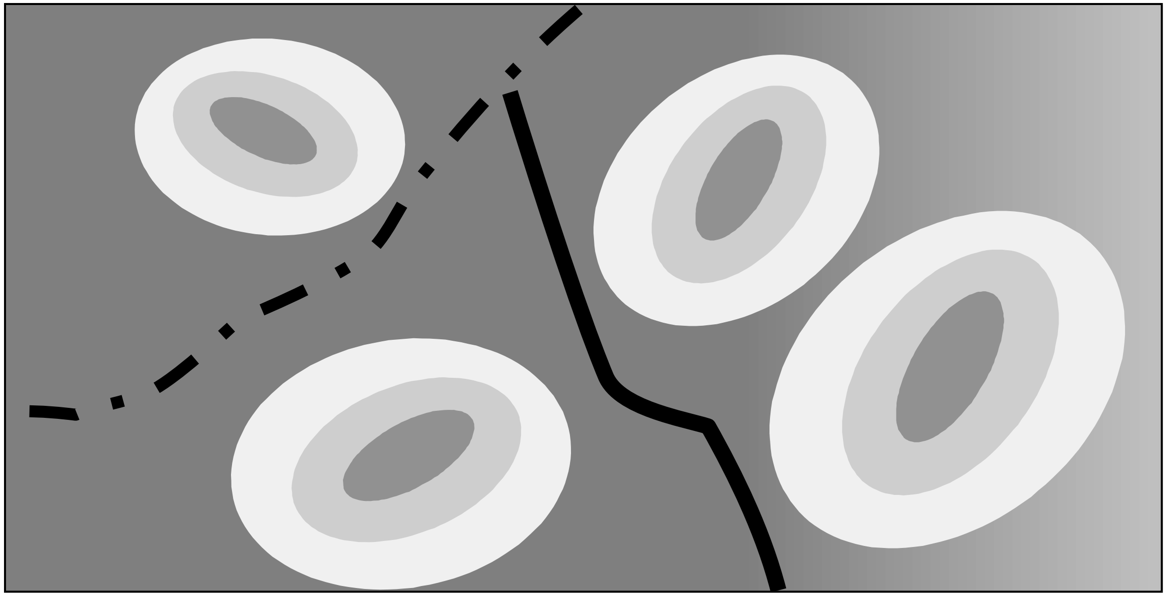
| | AIC | Adj$R^2$ | |
|---|---|---|---|
| Bird.lm | -900.3632 | 0.4908 | |
| Bird.lm.xy | -1248.2828 | 0.6061 | |
| Bird.random | -836.0008 | | 0.4816 |
| Bird.GLMM | -898.5819 | 0.4859 | 0.4880 |
| Bird.GLSx | -885.3516 | | |
| Bird.GLSy | -930.9072 | | |
| Bird.corLin | -1219.8813 | | |
| Bird.corSpher | -1449.1100 | | |

**Spatial Filtering (PCNM/dbMEM)**

**dbMEM711 (out of 1359): Adj$R^2$: 0.7168**

**dbMEM10 (out of 1359): Adj$R^2$: 0.5374**

# Several Processes + Several Regions

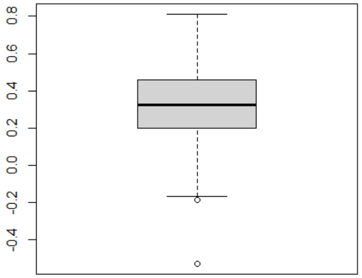


Dale & Fortin 2014

# Spatial Regression: GWR

```
> Bird.gwr
Call:
gwr(formula = Bird ~ Forest, data = bird,
    coords = cbind(bird$xUTM,
    bird$yUTM), adapt = BirdGWRbandwidth,
    hatmatrix = TRUE, se.fit = TRUE)
Kernel function: gwr.Gauss
Summary of GWR coefficient estimates at data points:
                     Min.     Median        Max.    Global
X.Intercept. -2.6903e-01 2.1842e-02  1.4355e+00  0.0127
Forest       -1.1257e-04 3.5399e-05  1.2214e-04  0.0001
Number of data points: 1359
Quasi-global R2: 0.7676538
```

```
> summary(bird$grw.R2)
   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
-0.5295  0.2005  0.3261  0.3394  0.4585  0.8126
```



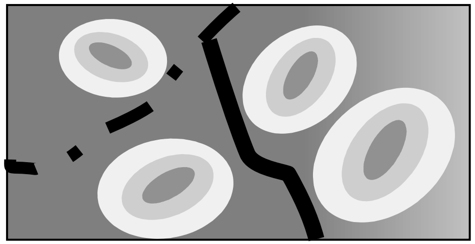
# Spatial Regression

| | AIC | Adj$R^2$ | |
|---|---|---|---|
| Bird.lm | -900.3632 | 0.4908 | |
| Bird.lm.xy | -1248.2828 | 0.6061 | |
| Bird.random | -836.0008 | | 0.4816 |
| Bird.GLMM | -898.5819 | 0.4859 | 0.4880 |
| Bird.GLSx | -885.3516 | | |
| Bird.GLSy | -930.9072 | | |
| Bird.corLin | -1219.8813 | | |
| Bird.corSpher | -1449.1100 | | |

**Spatial Filtering (PCNM/dbMEM)**

dbMEM711: Adj$R^2$: 0.7168

dbMEM10: Adj$R^2$: 0.5374

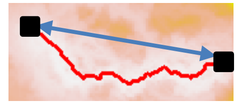


**Geographically Weighted Regression $R^2$**

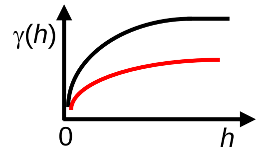
| Min. | Median | Mean | Max. |
|---|---|---|---|
| -0.5295 | 0.3261 | 0.3394 | 0.8126 |

# Spatial Aspects

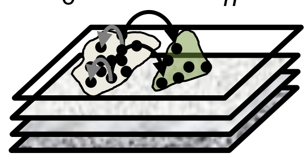
*x*-*y* Coordinates
Euclidean Distances
Least-cost Distances



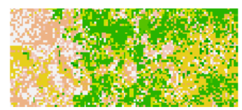
Spatial Autocorrelation
Spatial Dependence



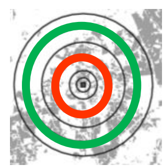

Spatial Relationship



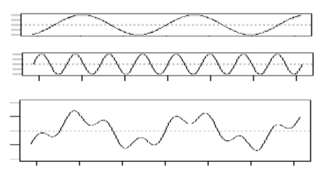
Spatial Legacy
Spatial Contingency



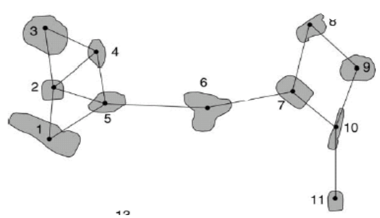
Spatial Perception



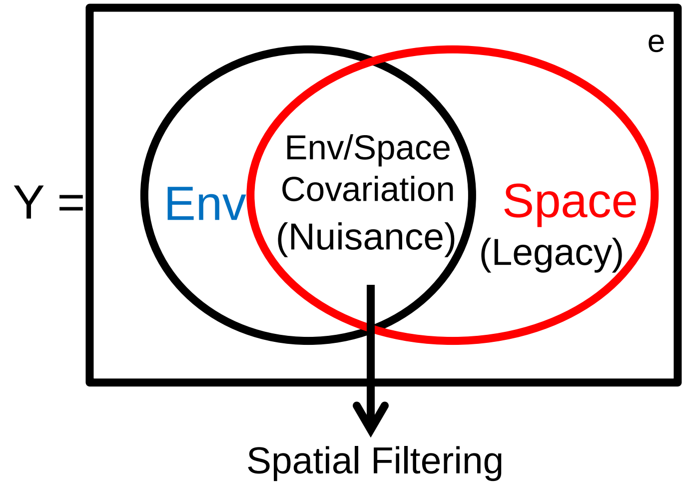
Multiscale Analysis



Metapopulation
Metacommunity
Metaecosystem
Metanetwork




Space does not replace Environmental Factors




**Better Fit**: Include Space

**Better Prediction/Knowledge**:
Include Processes & Factors