The origin of spatial structures in ecology

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Setting the stage

Landscape ecology studies the spatial variation of species composition throughout landscapes. That variation is called beta diversity.

Likewise, landscape genetics studies the spatial variation of the genetic structure of individuals or local populations throughout landscapes.
Setting the stage

Ecologists want to understand and model spatial [or temporal] community structures through the analysis of species assemblages observed at georeferenced sampling sites.

• For an ecologist, species assemblages are the best response variable available to estimate the impact of [anthropogenic] changes in ecosystems.

• Difficulty: species assemblages form multivariate data tables (sites x species).
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- For an ecologist, species assemblages are the best response variable available to estimate the impact of [anthropogenic] changes in ecosystems.
- Difficulty: species assemblages form multivariate data tables (sites x species).

Likewise, landscape geneticists analyse multivariate genetic data describing individuals or local populations observed at georeferenced sampling sites.
**Spatial variation**

In ecology, **beta diversity** is the variation in species composition among sites.

**Temporal beta diversity** is the variation in species composition among observations of a site through time.

Likewise, **genetic beta diversity** describes the genetic variation among sites on the map.

Beta diversity is not random; it is organized in natural communities. It displays **spatial structures**.
Ile Callot, Finistère.

Photo P. Legendre
Stonehenge, Wiltshire, southern England. Photo P. Legendre
Two types of spatial processes

Spatial structures in communities indicate that some process has been at work to create them. Two families of mechanisms can generate spatial structures in communities.
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Spatial structures in communities indicate that some process has been at work to create them. Two families of mechanisms can generate spatial structures in communities:

- **Induced spatial dependence:** forcing (explanatory) variables are responsible for the spatial structures found in the species assemblage. They represent environmental or biotic control of the species assemblages, or historical dynamics. The spatial structures are generally broad-scaled.

- **Community dynamics:** the spatial structures are generated by the species assemblage themselves, creating autocorrelation\(^1\) in the response variables (species). Mechanisms: *neutral processes* such as ecological drift and limited dispersal, *interactions* among species. Spatial structures are generally fine-scaled.

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\(^1\) *Spatial autocorrelation* (SA) is technically defined as the dependence, due to geographic proximity, present in *the residuals* of a [regression-type] model of a response variable \(y\) which takes into account all deterministic effects due to forcing variables. Model: \(y_i = f(X_i) + SA_i + \varepsilon_i\).
Five cases illustrating the origin of spatial structures through different types of relationships between an explanatory variable $x$ and a response variable $y$ observed across space.

Modified from Fortin & Dale (2005)

Case 1: Null situation

Four ponds (large circles) connected by a stream. A light current is flowing from left to right in some cases.
Case 1: Null situation

\[ x_{j-2} \quad w_x = 0 \quad x_{j-1} \quad w_x = 0 \quad x_j \quad w_x = 0 \quad x_{j+1} \]

\[ y_{j-2} \quad w_y = 0 \quad y_{j-1} \quad w_y = 0 \quad y_j \quad w_y = 0 \quad y_{j+1} \]

Representation of this process in a simulation program:
\[ y_j = \varepsilon_j \] where the \( \varepsilon_j \) are iid random normal deviates

\text{iid} : \text{independent and identically distributed}
Case 1: Null situation

\[ y_j = \varepsilon_j \]

Case 2: \( y \) depends on \( x \)

\[ y_j = \beta_0 + \beta_x x_j + \varepsilon_j \]
Case 1: Null situation

\[ x_{j-2} \quad w_x = 0 \quad x_{j-1} \quad w_x = 0 \quad x_j \quad w_x = 0 \quad x_{j+1} \]

\[ y_{j-2} \quad w_y = 0 \quad y_{j-1} \quad w_y = 0 \quad y_j \quad w_y = 0 \quad y_{j+1} \]

Case 2: \( y \) depends on \( x \)

\[ x_{j-2} \quad w_x = 0 \quad x_{j-1} \quad w_x = 0 \quad x_j \quad w_x = 0 \quad x_{j+1} \]

\[ x_{j-2} \quad \beta \quad x_{j-1} \quad \beta \quad x_j \quad \beta \quad x_{j+1} \]

\[ y_{j-2} \quad w_y = 0 \quad y_{j-1} \quad w_y = 0 \quad y_j \quad w_y = 0 \quad y_{j+1} \]

Case 3: SA in \( y \)

\[ x_{j-2} \quad w_x = 0 \quad x_{j-1} \quad w_x = 0 \quad x_j \quad w_x = 0 \quad x_{j+1} \]

\[ y_{j-2} \quad w_y \quad y_{j-1} \quad w_y \quad y_j \quad w_y \quad y_{j+1} \]

Case 4: Induced spatial dependence

\[ x_{j-2} \quad w_x \quad x_{j-1} \quad w_x \quad x_j \quad w_x \quad x_{j+1} \]

\[ x_{j-2} \quad \beta \quad x_{j-1} \quad \beta \quad x_j \quad \beta \quad x_{j+1} \]

\[ y_{j-2} \quad w_y = 0 \quad y_{j-1} \quad w_y = 0 \quad y_j \quad w_y = 0 \quad y_{j+1} \]

Case 5: SA in \( x \) and \( y \), \( y \) depends on \( x \)

\[ x_{j-2} \quad w_x = 0 \quad x_{j-1} \quad w_x = 0 \quad x_j \quad w_x = 0 \quad x_{j+1} \]

Water flow

\[ y_j = w_y y_{j-1} + \varepsilon_j \]

\[ x_j = w_x x_{j-1} + \zeta_j \quad \text{spatial autocorrelation in } x \]

\[ y_j = \beta_0 + \beta_x x_j + \varepsilon_j \quad \text{spatial dependence of } y \text{ on } x \]
Case 5: SA in x and y, y depends on x

\[ x_j = w_x x_{j-1} + \zeta_j \quad \text{spatial autocorrelation in x} \]
\[ y_j = \beta_0 + \beta_x x_j + w_y y_{j-1} + \epsilon_j \quad \text{spatial dependence and autocorrelation in y} \]
Construction of the environmental surface

Deterministic structure:
binormal patch $[0, 9.39]$

SA in environmental variable
$[-2.15, 2.58]$

Normal error $N(0,1)$
$[-2.72, 2.58]$

Environmental surface
$[-4.46, 10.60]$

Construction of the response surface

Environmental surface $x 0.3$
$[-1.34, 3.18]$

SA in response variable
$[-2.40, 3.19]$

Normal error $N(0,1)$
$[-3.07, 3.77]$

Response surface
$[-3.79, 5.60]$

The End