Spatial Ecology

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Special Feature

Space: The Final Frontier for Ecological Theory[1]

Most ecologists realize that the interplay of dispersal, disturbance, and spatial mosaics can profoundly alter the outcome of species interactions. Indeed, an appreciation of the spatial dimension and spatial heterogeneity is well established in natural history. Nonetheless, for many ecologists, "spatial complications" are used as a catch-all for explaining away surprising results, or as a condemnation of ecological theory that is accused of oversimplification because of its neglect of spatial variation. What is missing are serious experiments that explicitly test major hypotheses emerging from recent theoretical explorations of spatial effects. The purposes of this Special Feature are to alert ecologists to the general insights emerging from spatial models, and to show how these concepts apply to the natural world.

Ecology 75(1) (1994)

Why space matters? – ecological reasons

1. Space plays fundamental roles in affecting the genetic structure and evolution of species, in regulating population dynamics, and in determining patterns and functions of communities.

2. Genetics – The milestone of genetics and evolution is the Hardy-Weinberg Equilibrium which predicts genotypic frequencies in the offspring from the allele frequencies of the parents. A key assumption for the HWE is random mating. Geography can prevent random mating if individuals are more likely to mate with neighbors than with mates chosen at random from the entire population.

3. Speciation – A branching process by which different kinds of organisms originate from a single ancestral population. (Allopatric speciation: geographically isolated species diverge and evolve into different species.)

Darwin's finches

- **The Galapagos lie 800-1100 km west of Ecuador**
- **45 islands, islets & rocks**
- **0.7 to 5 millions years old**

Allopatric speciation: The proximity of the various islands has permitted enough migration of the finches among them to enable distinct island populations to arise. But the distances between the islands is great enough to limit interbreeding between populations on different islands. This has made possible the formation of distinctive species on the various islands.
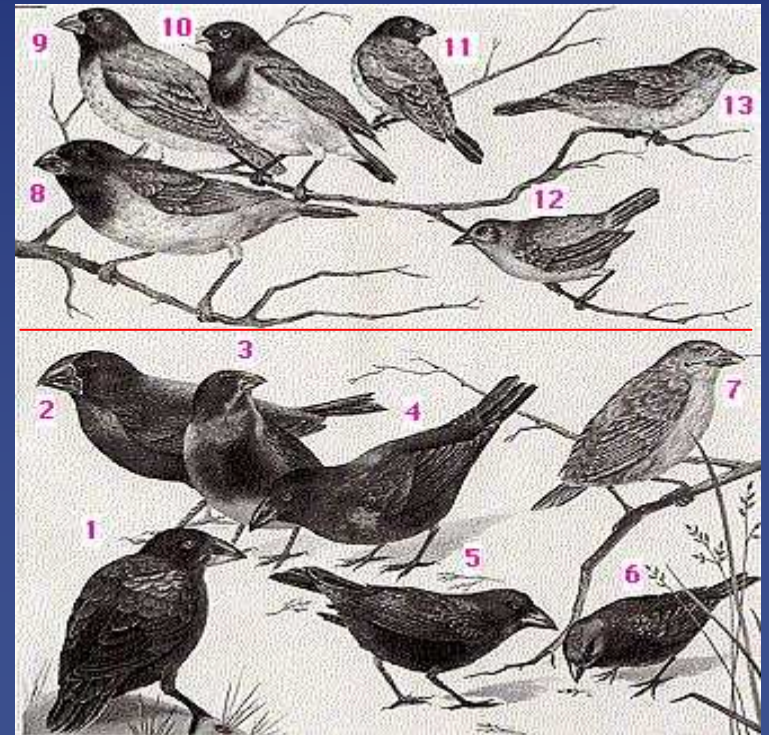
4. **Population dynamics – is fundamentally determined by: birth, death, immigration and emigration. Migration is a spatial process defined by spatial parameters such as dispersal distance, dispersal mode, and environmental heterogeneity/barriers, etc. These parameters are ultimately responsible for the numerous observed spatial patterns of distribution.**

5. **Population interactions – Prey-predator and competition are the basic interactions. Huffaker's mite experiment is a classic study showing how spatial barriers would promote cyclic coexistence of two prey-predator mites raised in a microcosm. One is herbivorous mite feeding on oranges, the other is predatory mite feeding on the herbivorous mite. Huffaker separated oranges by creating barriers using vaseline. The heterogeneity he created made the dispersal of the prey between patches relatively easy but difficult for the predator.**
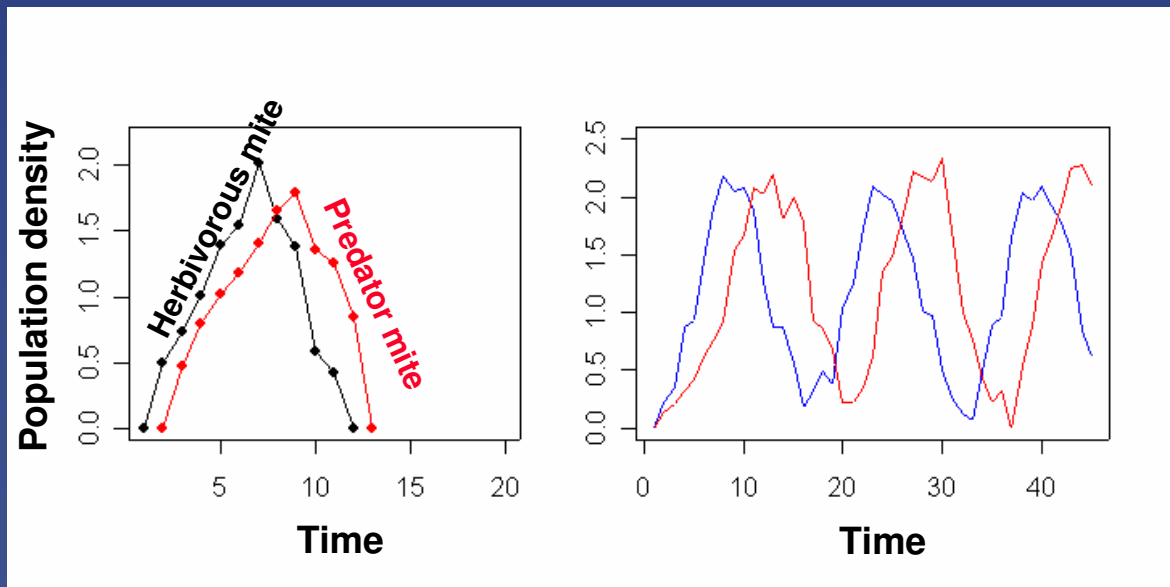
6. **Community theories and patterns** – Many community theories in essence are developed to describe the distribution of species in space (e.g., the theory of island biogeography, niche theory, the neutral theory of Hubbell). So are the many community patterns such as species-area curves, beta diversity (describing spatial structure of communities in space).

7. Many ecological applications are spatially based (spatially referenced), e.g., identification of biodiversity hotspots/coldspots.

8. **Modeling species distributions:**
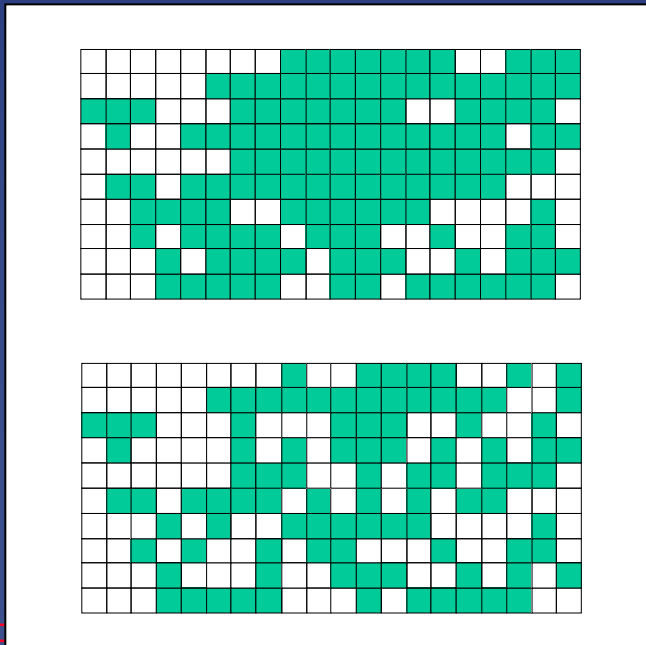
Issue 1 – Map agreement/thematic classification accuracy

Issue 2 – Image restoration (Ising model, Bayesian method)

Issue 3 – Interpreting occurrence using external variables (autologistic regression)

Why space matters? – statistical reasons

Identical and Independently-Distributed (*iid*) data model

1. **One of the most fundamental assumptions in statistics is that observations (samples) must be taken under identical conditions and each sample is taken independent of any others.**

2. **Such a set of data forms a random sample. Typical scenarios that generate a random sample include: (1) Sampling with replacement, (2) observations as the result of repeated, independent trials of an experiment, under conditions that are identical w.r.t. those factors that can be controlled. Observations in a random sample are identical and independently distributed.**

3. **Standard statistical techniques (e.g., mle, test statistic) can then be applied to the data to build a statistical model, to estimate the model's parameters and to draw inferences/conclusions.**

Spatial data are commonly correlated

iid is a very convenient assumption that makes much of mathematic-statistical theory tractable. However, spatial data are commonly correlated.

Typical situations – Data closer together, in space (or time), are more likely to be similar than data far apart. Such data cannot be modeled as statistically independent.

Examples –

1). Soil pH value is typically positively correlated over space.

2). A big tree is less likely to live in the proximity of another big tree of the same species because of competition for limiting resources (e.g., light, nutrients).

Ecological applications of spatial statistics

Some typical applications include:

1. **Measuring, detecting and testing spatial patterns (random, regular, aggregated) in order to gain insights about the possible mechanisms that generate and control the phenomena of interest,**

2. **Quantifying spatial correlation (autocorrelation), spatial structures and scaling effect on the structure,**

3. **Modeling species dispersal/movement, estimating dispersal modes and rates,**

4. **Modeling species distribution in terms of external variables (soil properties, climate variables) in order to interpret and predict species distribution,**

5. **Estimating population parameters (e.g., the abundance of a wildlife),**

6. **Developing efficient sampling schemes and experiment designs,**

7. **Spatial prediction/interpolation: to estimate the volume of variables of interest (biomass) in the unsampled locations in terms of the neighboring information and other covariates.**

Inferring competition from tree distribution

1. **Intraspecific competition – Individual trees become regularly spaced.**

2. **Interspecific competition – Different species become spatially repulsed.**
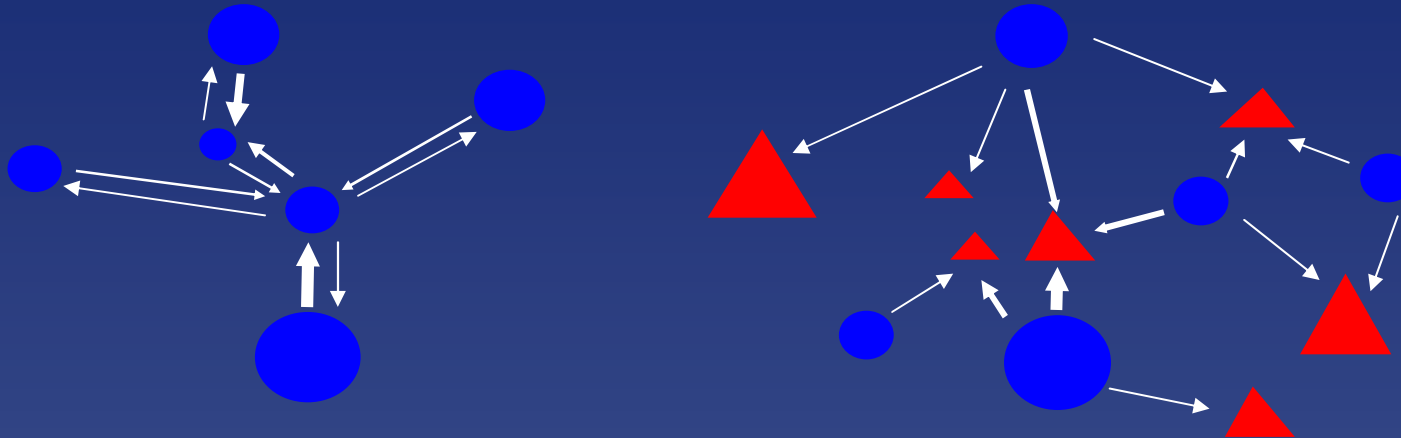
So it is reasonable to assume:

- **If there is no selective mortality (random mortality), spatial distributions of pre-mortality and post-mortality remain the same.**

- **If the post-mortality pattern is more regular (or repulsed) than the pattern of pre-mortality, there is evidence of competition.**

- **If the post-mortality pattern is more aggregated than the pattern of pre-mortality, there is evidence of attraction.**

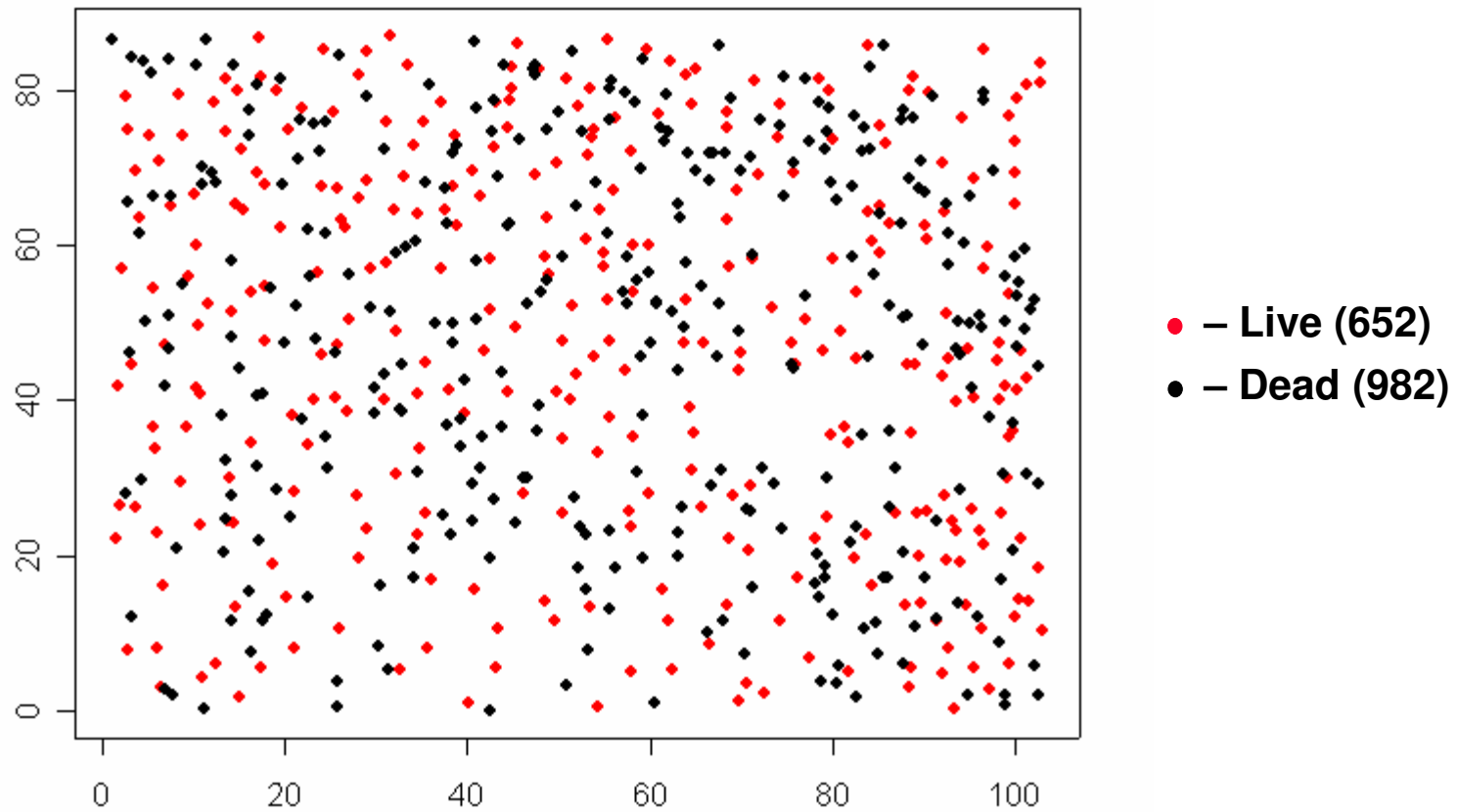# Tree distributions in an old-growth forest in the Victoria Watershed (> 250 years)
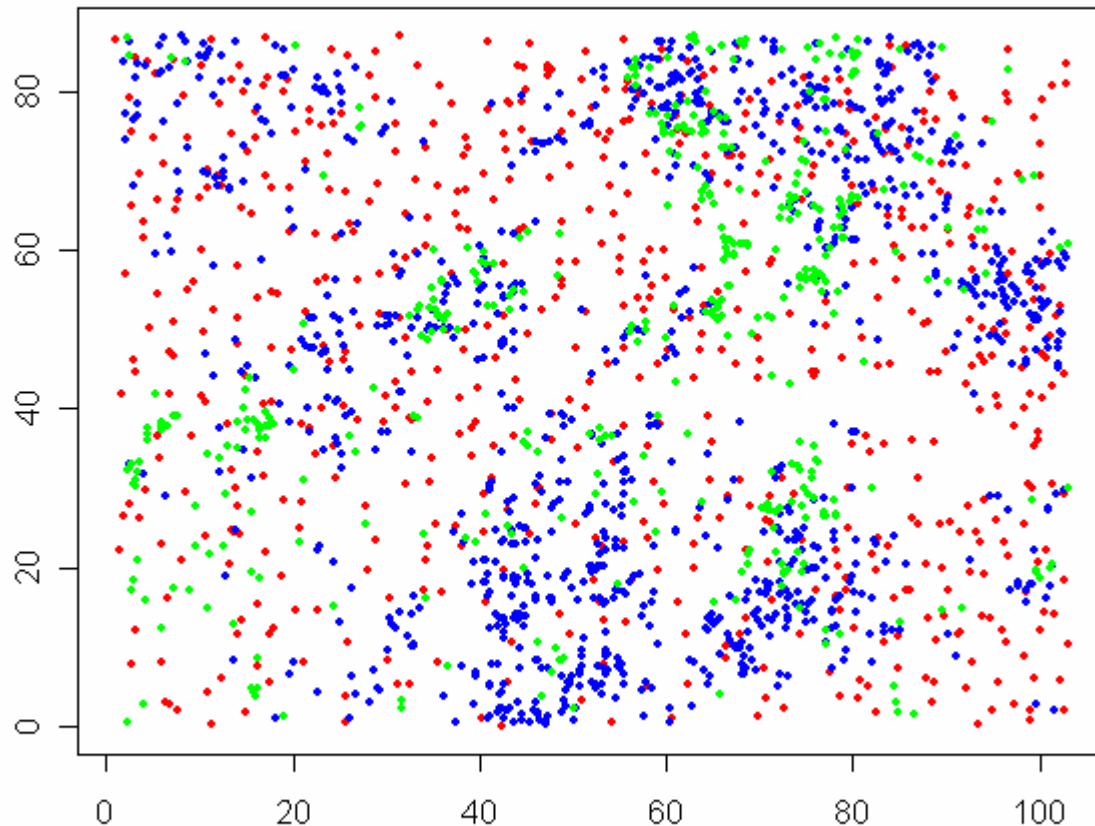
- – Douglas-fir (652)
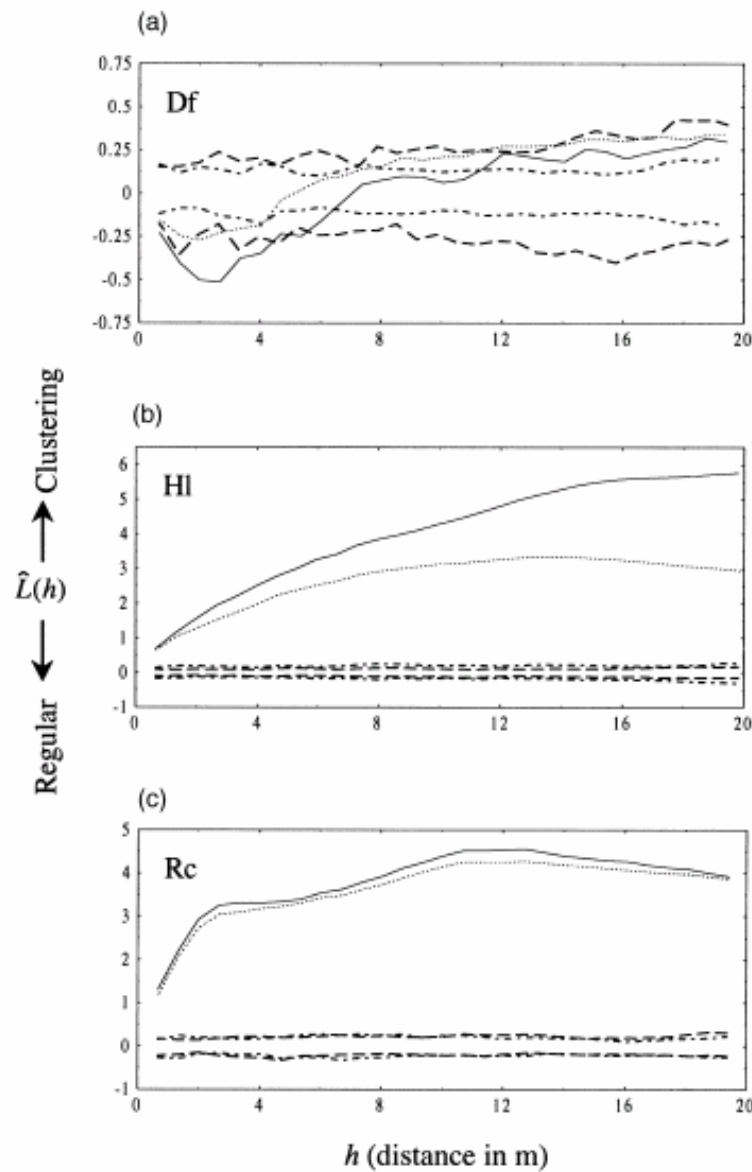- – Western Hemlock (982)
- – Western Redcedar (416)

Total number of trees: 2050

Plot size: 102×87 m

Live and dead Douglas-fir trees

- ● – Live (652)
- ● – Dead (982)

Intraspecific distributions of live trees and live + dead trees for Df, Hl and Rc

Confidence envelopes were generated from 25 simulations

——— Observed distribution for live trees
---- 95% confidence envelope for live trees
········· Observed distribution for dead + live trees
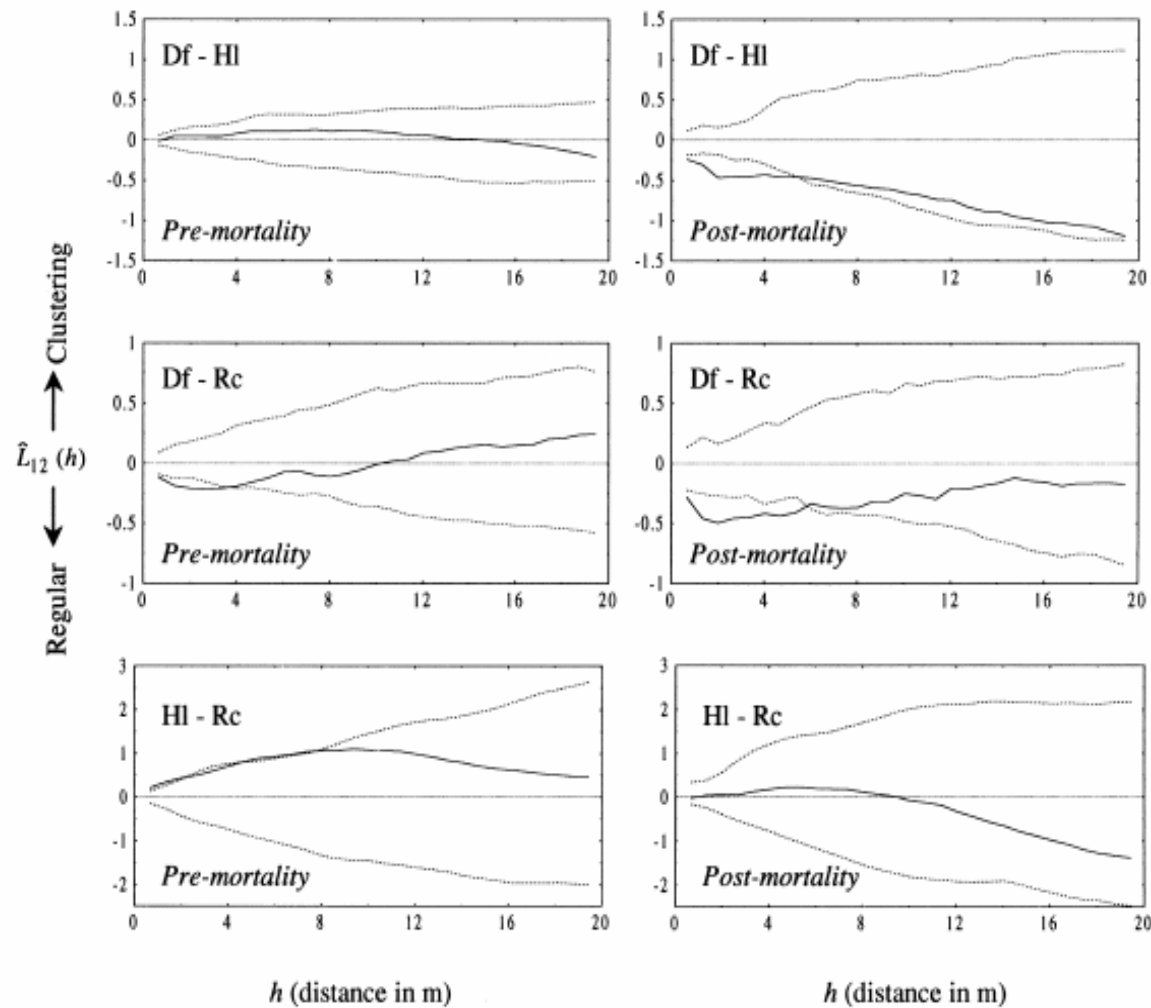------ 95% confidence envelope for dead + live trees

Results:

Df – more regular after dead
Hl – more aggregated
Rc – no change

Interspecific distributions of Df, Hl and Rc: pre-mortality versus post-mortality


Results:

The post-mortality patterns for all the species pairs become more repulse than the pre-mortality patterns, suggesting strong interspecific competition among the species.

	Early successional species	**Late successional species**
Species	Douglas-fir	Western hemlock Western redcedar
Spatial pattern	Regular	Clustered (under gaps created by the death of Douglas-firs)
Competition	Intraspecific competition	Interspecific competition
Mortality	Caused by intraspecific competition	Caused by interspecific competition

- **Are these findings applicable to younger forests?**
- **How spatial pattern, competition, and mortality change with age?**

Open questions

1. **Separate biological mechanisms from habitat heterogeneity – Aggregation can be produced from dispersal limitation and habitat heterogeneity. How we may design sampling schemes/field experiments to separate these two types of aggregation?**

2. **Modeling spatial heterogeneity – Most spatial theories and techniques require stationary and isotropic assumptions. Few real data meet these assumptions, and applications usually requires predicting anisotropic or nonstationary patterns.**

Neyman-Scott pattern

Observed   **Simulated**
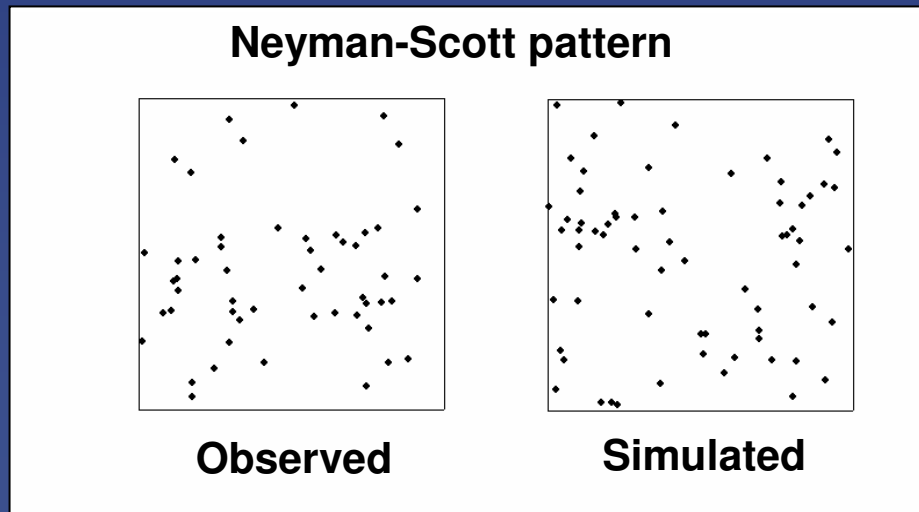
3. Scaling effect: Few spatial data can avoid the problem of the size of sample area (called support in geostat, or modifiable areal unit in geography, or grain size in landscape ecology). In many applications, the support of the samples is not the same as the support of the estimates we calculate.

Additive variable:
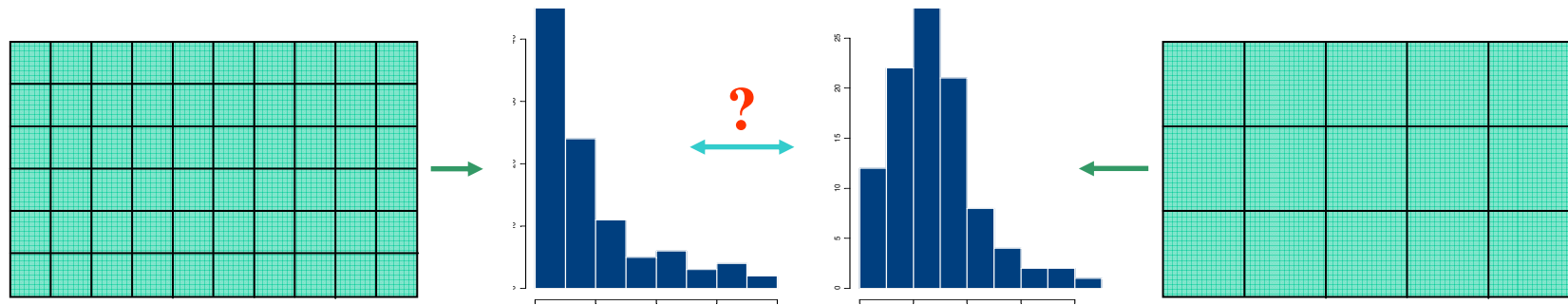**(# of trees in a quadrat)**

5 balls	3
7	4

scaled up →

8
11

Nonadditive variable:
(# of species in a quadrat
# of cars per city block)

3 colors (1b, 2r, 2 w)	3 colors (1b, 1g, 1y)
3 colors (3b, 2r, 2 w)	1 color (4g)

scaled up →

5 colors
4 colors

Can we scale down or up a spatial process?

Spatial estimation: scale effect

Number of stems and number of species per m^2 at different sampling scales (grain size) in a 1000×500 m rain forest of Malaysia. The entire plot has 335,356 trees belonging to 814 species. The densities at each grain size were computed as follows: (1) divide the plot into a grid system using a given scale (e.g., 5×5 m), (2) count the total number of stems and the number of species in each cells, respectively, (3) average these two quantities across all the cells, and (4) then divide the averages by the scale.

The results clearly show how sampling scale affects the species diversity. They suggest that diversity based on per unit area (the last column) is a misleading measurement for comparing diversity between two ecosystems.

Grain size (m)	No. stems/m^2 (std. error)	No. species/m^2 (std. error)
5×5	0.671 (0.244)	0.585 (0.197)
10×10	0.671 (0.167)	0.475 (0.095)
20×20	0.671(0.130)	0.318 (0.038)
25×25	0.671 (0.121)	0.267 (0.026)
50×50	0.671 (0.100)	0.129 (0.008)
100×100	0.671 (0.085)	0.049 (0.001)
250×250	0.671 (0.048)	0.011 (0.0004)
500×500	0.671 (0.041)	0.003 (< 0.001)
500×1000	0.671	0.0016