Introduction:

The problem of pattern and scale is one of the central problems in ecology. Description of ecological patterns depends on the scale of observation. Moreover, the notion that the ecological patterns observed at a given spatial is scale is typically a result of mechanisms operating at different scales (Levin, 2002) makes it challenging to link the patterns to underlying processes. To confront this challenge, it becomes crucial to employ statistical metrics that examine the scale-dependency of spatial patterns, rather than commonly employed measures of aggregation tendencies between individuals (such as uniform, random or clumped dispersion) (Plotkin et al., 2002; Scanlon et al., 2007).

Most of the empirical datasets recording species occurrences in a landscape can be summarized as a two-dimensional grid of a square cells with a unit size equaling the spatial resolution of observation. Each of the cells will be either occupied (at least one individual present) or empty. With this information, a ‘cluster’, which is a contiguous group of occupied cells becomes a highly informative unit of spatial patterns. Sizes of such clusters and their distribution is determined by the total population size, spatial resolution of a grid and the underlying ecological processes that affect the aggregation patterns. Analysis of such patterns is greatly benefitted from the field of percolation theory which produces solid expectations for the patterns of cluster size distributions in the absence of any aggregation mechanism. With a random Poisson process of assembly, cluster sizes show a sudden phase shift (A figure will help here) above a characteristic population size (percolation threshold), where very large clusters appear.

Previous few analyses of rich empirical datasets of plant communities have analyzed the distribution of cluster size (refs). He and Hubbell (2006) first employed this approach on the detailed tree census carried on BCI. They first showed that the cluster size characteristics of species’ populations exhibited significant phase shift when plotted against population size and importantly, the smallest unit of measurement (spatial resolution). They tested the hypothesis of such random dispersion with clumping on an empirical data and showed that it explains the spatial patterns of many tree species. A critical observation was that the critical ‘percolation thresholds’ for the smallest spatial unit (spatial resolution) were species-specific, indicating that a species-specific mechanism of dispersion explained their spatial distribution patterns.

The relationship between cluster size distribution and the spatial resolution of the observation is particularly important one for the empiricists, since one can potentially use a snapshot data of abundances (rather than the rare time series datasets) to calculate the characteristic spatial resolution above which local effects percolate over the whole map to produce large clusters. Characteristic thresholds for a randomly distributed population sizes are well-known. However, it is important to study how these thresholds change when the underlying local mechanisms of spatial dynamics of the population influence the aggregation tendencies between neighbors.

For example, severe dispersal limitation will restrict the formation of bigger clusters when looked at with high resolution. Therefore, one may expect that the bigger clusters would appear at much lower spatial resolution in this case compared to the one with random dispersion.

We aim to understand how the cluster size distribution varies with the spatial resolution of the observation when the population is driven under different mechanisms (local processes vs. regional processes).

Method:

We simulated population growth in a 500 X 1000 grid where total population size remained constant (births/time step=deaths/time step).

We employed three mechanisms of habitat filtering, dispersal limitation and intraspecific competition with varying levels of intensity to simulate the population growth.

Parameters:

1. Spatial autocorrelation of landscape suitability:

We used Gaussian random fields over our grid to generate habitat suitability values for each cell in a grid. We adjusted the level of spatial autocorrelation to essentially create scenarios of habitat heterogeneity at different spatial grain. E.g. If the habitat are highly autocorrelated, then the suitability values are very homogeneous at very high spatial resolution.

1. Dispersal parameter:

We used a square dispersal kernel with a distance d where the recruitment in a given empty cell occurs only from the occupied cells inside the kernel with non-zero probability.

1. Crowding effect:

We created three distinct modes for the crowding effect-

1. No crowding- recruitment probability does not depend on the no. of occupied cells inside the square dispersal kernel. i.e. recruitment occurs if there is at least one occupied cell inside the kernel.
2. Positive effect- Facilitative effect (Or seed limitation effect) recruitment probability is higher if there are more occupied cell inside the kernel.
3. Negative effect- (Janzen-Connell effect) Neighboring occupied cells decrease the probability of recruitment.

Simulation:

At a given time,

1. 10% of the individuals are randomly removed from the map (death events).
2. Empty cells are randomly chosen for recruitment until the total number of recruitments reach 10% of the population.
3. Recruitment probability is determined by the product of the habitat suitability value (between 0 and 1) and the probability of recruitment under given dispersal mode.

For a no crowding effect, recruitment probability is 1 if there is at least one occupied cell inside the dispersal kernel.

For positive effect, recruitment probability is 0.5 if there is exactly one occupied cell inside the kernel. Probability increases with further increase in occupied cells as a log function with the base equal to the total area of a dispersal kernel.

For negative effect, the recruitment probability is 1 if there exactly 1 occupied cell in a dispersal kernel. The probability decreases with further increase in occupied cells as 1-log(neighbors) with the base equal to the total area of a dispersal kernel.

We simulate this dynamic for 10000 steps (the aim is that spatial structure remains relatively unchanged towards the end).

We aggregate the final abundance data at different spatial resolutions higher than the one of simulation (1 X 1). For each set of aggregated data, we counted distinct clusters using Hoshen-Kopelman algorithm.

We then

1. Plot the biggest cluster size (as a proportion of total map) against spatial resolution of ‘observation’. (Let’s call it a characteristic curve)
2. Plot the change in patch size perimeter against different spatial resolution.
3. Test whether the percolation is observed for different mechanisms. If yes, test if the percolation thresholds differ (for population size and spatial scale) for different mechanisms.

Test which species exhibit the characteristic curve closest to one of the tested mechanisms.

Results:

When the cluster size characteristics are plotted against the spatial grain of observation,

1. Random dispersion AND habitat filtering show sharp percolation thresholds i.e. the transition between the likelihood of observing small vs. big (or spanning) clusters is sharp.
2. For habitats with stronger spatial autocorrelation, the percolation threshold appears at higher spatial resolution compared to the case of random dispersion.
3. When local segregation or aggregation mechanisms i.e. crowding effect or dispersal limitation, are dominant, the onset of percolation is not as sharp, where the size of biggest clusters increases more gradually with spatial resolution compared to random dispersion or habitat filtering.

Thus, to descriminate between the signatures of local processes, metrics of how sharply the cluster size characteristics change with spatial resolution prove informative.