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Simulation and quantification of the fine-scale spatial pattern and heterogeneity of forest canopy structure: A lacunarity-based method designed for analysis of continuous canopy heights

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Abstract

Forests canopies are dynamic, continuously varying, three-dimensional structures that display substantial heterogeneity in their spatial arrangement at many scales. At the stand-level, fine-scale spatial heterogeneity influences key canopy processes and contributes to the diversity of niche space and maintenance of forest biodiversity. We present a quantitative method that we developed based on a novel application of two well-established statistical techniques – lacunarity analysis and principal component analysis (PCA) – to determine the fine-scale (0.5–33 m) spatial heterogeneity found in the outer surface of a forest canopy. This method was specifically designed for the analysis of continuous canopy height data generated by airborne LiDAR systems or digital photogrammetry; however, in this study we demonstrate our method using a large, well-documented dataset composed of simulated canopy surfaces only. We found that the magnitude of the lacunarity statistic was strongly associated with canopy cover ($R^2 = 0.85$) and gap volume ($R^2 = 0.84$), while the pattern of decline in lacunarity across discrete measurement scales was related to many size- and density-related attributes of stand and canopy structure ($0.27 \leq R^2 \leq 0.58$) and their diverse vertical and horizontal spatial distributions. PCA uncovered two major gradients of spatial heterogeneity from the 10 dimensions of our original lacunarity dataset. The stronger of these two gradients reflected the continuous variation in canopy cover and gap volume, while a second, more subtle gradient was associated with the array of possible vertical and horizontal spatial configurations that might define any one measure of canopy cover. We expect that this quantitative method can be used to support a broad range of practical applications in sustainable forest management, long-term ecological monitoring, and forest science. Further research is required to understand how these statistical estimates and gradients of measured spatial heterogeneity relate to other ecologically relevant patterns of forest composition, structure, and function.

Keywords: Canopy height models; Canopy structure; Forest structure; Lacunarity analysis; Laser remote sensing; LiDAR; Principal component analysis; Spatial heterogeneity; Spatial pattern analysis

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Nomenclature

BA	basal area (m^2) per hectare (ha)
CC	canopy cover (%)
CD	quadratic mean crown diameter (m)
CHM	canopy height model
CW	quadratic mean crown width (m)
DBH	diameter at breast height (cm)
GAP	gap volume (%)
H_L	Lorey's mean stand height (m)
LiDAR	light detection and ranging
PC1	first principal component
PC2	second principal component
PCA	principal component analysis
P_O	modified Pollard's nearest-neighbour statistic
QMD	quadratic mean diameter (cm)
r	box size of gliding window (grid-cell units)
RD	Curtis' relative density
s	box size of gliding window (m)
SD	stand density (n/ha)
SHDI	Shannon's Height Diversity Index
VOL	stand volume (m^3/ha)
$\Lambda(r)$	lacunarity statistic measured at box size r
Λ_{TOTAL}	normalized lacunarity statistic integrated across all scales r

1. Introduction

Heterogeneity is an inherent, ubiquitous, and critical property of ecological systems, and is thought to sustain many aspects of ecosystem function and biodiversity across space and through time (Kolasa and Pickett, 1991; Caldwell and Pearcy, 1994; Pickett et al., 1997). Heterogeneity, as an ecological concept and system property, has many definitions, occurs in many forms (Kolasa and Rollo, 1991), and is strongly dependent on the spatiotemporal scales of observation and methods of measurement (Legendre and Fortin, 1989; Gardner, 1998; Gustafson, 1998; Dale, 1999). Forest ecosystems are often described by attributes of composition, structure, and function (Franklin et al., 2002), and heterogeneity arises when any or all of these attributes vary in space, time, or both (Dutilleul and Legendre, 1993; Li and Reynolds, 1995; Franklin and Van Pelt, 2004).

A precise definition of spatial heterogeneity depends upon the nature of the ecological pattern and entities of interest (Dutilleul and Legendre, 1993; Gustafson, 1998). For example, discontinuous spatial phenomena (e.g., individual tree locations, nest sites, etc.) form distinctive point patterns that are a result of their distribution throughout a region of space (Dale, 1999). In this case, spatial heterogeneity is defined by variability in density of the discrete objects or entities (referred to as events in point pattern literature) in space, and by their degree of departure from complete spatial randomness (CSR) towards aggregation or overdispersion (regularity or uniformity). CSR occurs when discrete events are dispersed both randomly and independently of one another (Diggle, 2003). Many ecological processes and system attributes, on the other hand, occur more continuously over space or time (e.g., photosynthesis, temperature, humidity, canopy density, etc.). Continuous spatial phenomena are considered to be heterogeneous when one or more ecosystem attributes vary across discrete subregions of space in an irregular or non-random manner (Dutilleul and Legendre, 1993). Measures of spatial heterogeneity are almost always tied to variability in time, because ecosystems are by definition inherently dynamic in both space and time (Gustafson, 1998).

Forest canopies are dynamic, continuously varying, three-dimensional (3-D) spatial structures composed mostly of leaves, twigs, branches, and the open spaces (gaps) among them (Parker, 1995). Canopies are shaped by all components of stand structure including live tree-size and age distributions, stem density, species composition, crown widths and depths, leaf area and density, growth form, and the spatial arrangement of individual boles (Spies, 1998). The fine-scale spatial structure of forest canopies is often conceptualized within a hierarchical framework (Fournier et al., 1997), where individual leaves are organized into increasingly coarser-scale structures, such as shoots or twigs, branches, whorls, crowns, and finally into spatial neighbourhoods of individual crowns (Parker, 1995; Song et al., 1997; Cescatti, 1998). At coarser spatial scales, discrete neighbour-