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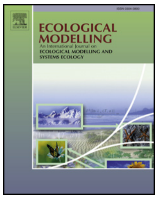

Modeling and simulation of tree spatial patterns in an oak-hickory forest with a modular, hierarchical spatial point process framework

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ABSTRACT

Modeling and simulating tree spatial distribution in complex forests is important to ecologists and applied scientists who seek to both understand pattern-creating biological processes and create realistic model forests that can be used for hypothesis testing and sampling experiments. Several patterns of tree spatial distribution can co-occur in a forest. Clustering can occur due to localized patterns of growth and mortality of larger trees and corresponding regeneration of smaller trees, while trees of medium size can exhibit more uniform patterns. Inter-tree interaction may be characterized by asymmetry of competitive strength, with larger individuals having a disproportionate influence on smaller individuals.

Many point process modeling approaches exist, but few have incorporated hierarchical principles that describe inter-tree competition. Those that do sometimes assume symmetric interaction among trees, which can be unrealistic. None of the existing models allow for the use of different model types at each level of the hierarchy, something that could provide a more realistic representation of the patterns displayed by trees of different size. In this study, we model and simulate a forest using a novel, modular, hierarchical approach that allows for the use of different model types at each hierarchy level, and incorporates asymmetrical interactions as well as the effects of environmental covariates. The forest is a mid-successional 8-ha stem-mapped oak-hickory watershed in Pennsylvania, USA. Results suggest that asymmetrical interactions based on tree size do exist, and these are mediated by the effects of topography. The hierarchical models reproduce the spatial patterns found in the original data better than non-hierarchical versions of the same models. The flexibility afforded by the modularity of our modeling framework will allow simulation of forests with varying levels of complexity as well as the testing of ecological hypotheses about drivers of spatial pattern creation.

1. Introduction

Ecologists and forest managers model spatial patterns of forest trees for two main reasons: to understand the processes that lead to forest community development, and to understand the effects of stand spatial structure on growth of individual trees. Spatial patterns can be governed by a mixture of chance events and plant-plant interactions mediated by environmental gradients (Bormann & Likens, 1994). As competition theory suggests, patterns of soil resource availability and propagules influence initial stand composition, and as plants' zones of influence begin to overlap, competitive or facilitative hierarchies develop, with interaction strength related to life history strategy, plant size, and interplant distances (Bella, 1971; Brooker et al., 2008; Schwinning & Weiner, 1998; Wu et al., 1985). In mixed deciduous northern hardwood forests, these processes are thought to be mediated by the effects of topography and its effects on light and soil conditions (Frey et al., 2007). Spatial pattern dynamics reflect these processes, with younger stands exhibiting a more clustered pattern, followed by stand homogenization as competition intensifies, followed by a different type of clustered pattern as mortality and gap dynamics become important (Larson et al., 2015; Raventos et al., 2010). Analysis of the relationship between tree size, location, and environmental gradients can thus advance the science of plant community ecology by supporting existing hypotheses or suggesting new ones in cases where observed patterns and relationships do not align with current theory.

Point process models are useful tools for studies of spatial patterns. They are particularly appealing because they can be used to describe the spatial or temporal structure of a phenomenon and to create simulated point patterns based on the spatial distribution of observed points. In point process modeling, the set of locations of events (e.g., tree locations) is seen as one realization of a stochastic event-generating process. The intensities or density functions of these processes can be

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modeled using various families of statistical models that incorporate randomness, environmental covariates, and inter-point interaction functions.

The selection of an adequate point process model depends on the system under study. For example, a homogeneous Poisson process (HPP) model is typically used as a type of null model of spatial pattern; descriptors for observed patterns are compared against those generated from an HPP model in order to diagnose a non-random spatial distribution of points (Baddeley et al., 2015; Wiegand & Moloney, 2014). In systems where environmental trends like topographic gradients affect patterns, inhomogeneous Poisson process (IPP) models will better describe the observed patterns (e.g. Getzin et al., 2008). For applications like forest ecology where clustered patterns are common (Grabarnik & Särkkä, 2009; Stoyan & Penttinen, 2000), the family of cluster models might be more appropriate. Finally, a type of Markovian model commonly referred to as a Gibbs model relies on a pair potential function that specifies a set of symmetrical inter-point interaction strengths, and is often used for patterns where individuals are dispersed.

In order to incorporate in point process models the potential for asymmetric, hierarchical relationships that commonly exist in forests, Högmander and Särkkä (1999) proposed a modeling system in which the intensity of the points in the highest level of the hierarchy is modeled first using a Gibbs point process model, then the lower levels of the hierarchy are modeled as subsequent Gibbs processes, conditional on the intensity of the higher levels. Illian et al. (2009), Genet et al. (2014), and Grabarnik and Särkkä (2009) used a similar Gibbsian approach, defining hierarchies by reproductive strategy (the former), and tree size (the two latter). Although Gibbs models have many advantages, they are not suitable for the variety of clustered patterns that occur in forests (Baddeley et al., 2015; Illian et al., 2008; Stoyan & Penttinen, 2000). In addition, multi-type Gibbs models are parameterized with information about the relative strengths of interaction between individuals of different types, something that might not be known to the researcher a priori (Baddeley et al., 2015; Illian et al., 2009; Prokešová et al., 2006; Wiegand & Moloney, 2014). These difficulties suggest that Gibbs models are not always suitable for modeling forest stands where a combination of different pattern types, hierarchical relationships, and environmental trends coexist. We argue that a more flexible approach is needed.

To address the needs for modeling and simulating complex forests where hierarchy and different spatial patterns may co-occur, we propose a modular, hierarchical point process modeling framework (MHPPF). In this approach, it is assumed that trees of different size classes may display different spatial patterns and thus that different families of point processes and environmental variables should be used to describe them. This is achieved by the modularity of our approach: at each level of the tree size-based hierarchy a different model type and covariate can be used. More specifically, a multivariate inhomogeneous Poisson or cluster process is constructed by the superposition of independent point processes that are conditioned on the cumulative point intensities of the higher levels of the hierarchy and/or environmental covariates. Although the form of the hierarchy can be constructed following different theories or hypotheses, the approach we present here assumes that trees of different size classes interact asymmetrically in the direction of decreasing size. Asymmetric competition is incorporated by adding the intensity of the higher levels in the hierarchy as covariates in the modeling of lower hierarchy levels. That is, the locations of trees lower in the hierarchy are dependent on the locations of trees at higher levels, but not vice-versa. A generalized joint probability density associated with such a framework can be expressed as

$$f(x) = \alpha \prod\nolimits_{i=1}^{j} \begin{cases} f_i(S_i|\theta_i) & if\ i = j \\ f_i(S_i|S_{i+1}...S_j,\ \theta_i) & if\ i \neq j \end{cases} \tag{1}$$

where x is the combined pattern of all levels, α is a normalizing constant, i is the hierarchy level (1 is the lowest and the smallest tree size class), j is the number of levels, S_i is the intensity of the level i pattern, and θ_i is the vector of parameters associated with the environmental covariates associated with the intensity of the level i pattern. Simulation is achieved by performing the modeling and simulation sequentially based on the hierarchy of point types, incorporating the simulated intensity surfaces from higher levels as inputs in the form of covariates to the simulation process at lower levels.

In the current study, we lay out the methods for implementing this approach, demonstrate its application by modeling a mapped stand of trees in central Pennsylvania, USA, and compare results of this new approach to a method that does not incorporate hierarchical principles. We hypothesized that trees of different size classes would exhibit different types of spatial patterns, and that these patterns would be related to not only the presence of larger trees, but also to environmental covariates. Specifically, we hypothesized that in this mid-successional forest, smaller trees would be clustered, and larger trees would show a more hyper-dispersed pattern and that the MHPPF would allow us to simulate realistic tree spatial patterns in this complex forest.

2. Methods

2.1. Study site and data

Mapped tree data for this study were obtained from the Susquehanna Shale Hills Critical Zone Observatory (SSHCZO) (Kaye et al., 2015), an approximately 8-ha watershed found in the Ridge and Valley physiographic region of central Pennsylvania, USA (Fig. 1). The watershed is oriented east-west, with predominantly north- and south-facing aspects and an elevation range of 240–300 m above sea level. Tree information for 2050 trees was collected in 2012 and included geographic location obtained using a survey-grade GPS and data logger, species, and diameter at breast height (DBH) to the nearest 0.254 cm (0.1 in) for trees greater than 20.32 cm (8 in) (Kaye et al., 2015; Naithani et al., 2013; Wubbles, 2010).

To define each hierarchy level, trees were grouped into diameter classes, with the assumption that DBH is related to competitive strength and thus different sized trees may display different spatial patterns. To create tree size groupings, the Jenks optimization procedure found in the classInt package for version 3.3.3 of the R statistical software (Bivand, 2015; Jenks & Caspall, 1971; R Core Team, 2015) was used. We chose the Jenks method because it provides a site-specific way to classify DBH into natural groups that are internally homogeneous relative to other potential groupings, making it a generic approach for conducting this type of analysis in new forest ecosystems with different DBH distributions. The four DBH class boundaries identified by this method were as follows: 20.3–29.1 ($n = 744$), 29.2–37.6 ($n = 682$), 37.7–48.5 ($n = 442$), and ≥48.6 cm ($n = 182$). The convention we use here is that large diameter classes represent higher levels in the competitive hierarchy, i.e. level 4 is the highest level of the hierarchy and level 1 is the lowest.

To evaluate the potential effect of topographic gradients on the spatial patterns of the different size-class trees, we evaluated elevation (USGS, 2010), percent slope, and transformed aspect (Beers et al., 1966), all of which were based on a 3-m pixel digital elevation model (DEM) and generated using the Spatial Analyst extension of ArcGIS Desktop software (ESRI, 2014). In addition, two topographic indices were generated using the terrain function of the raster package of R (Hijmans, 2015): topographic position index (TPI) and topographic ruggedness index (TRI) (Wilson et al., 2007). TPI represents an index of relative slope position, and TRI is an index of local topographic complexity. All DEM-based variables were smoothed using the focal mean function applied in a 5 × 5 pixel window in R's raster package (Hijmans, 2015).

To incorporate potential tree-size-mediated competition effects, fixed-bandwidth kernel estimates of the intensity surfaces of levels 1–4