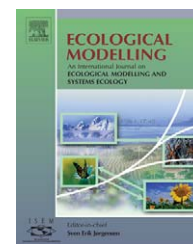


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Deviation from power law, spatial data of forest canopy gaps, and three lattice models

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ARTICLE INFO

Article history:

Received 15 August 2005

Received in revised form 18 May 2006

Accepted 19 May 2006

Published on line 20 July 2006

Keywords:

Forest canopy gaps

Stochastic lattice model

Two-state model

Three-state model

Propagating-wave model

Power law

ABSTRACT

Forest canopy gaps are important for tree regeneration and species diversity. We develop a method to analyze the spatial patterns of forest canopy gaps, focusing on the relative importance of different scales in spatial variation. We apply this method to forest data, and to spatial patterns generated by three spatial Markov chains in which the transition rate of each site depends on the nearest neighbors: (1) two-state model, in which each site is either a gap or a canopy site, (2) three-state model, which considers gaps, occupied, and disturbed sites. This was originally proposed as a model for mussel bed spatial dynamics, and (3) propagating-wave model, which is derived from the model for wave regenerating fir forest, by considering stochastic transition and neglecting the directionality of wind. For a given spatial pattern, the variance of the fraction of area covered by gaps decreases with the size of the area considered. We introduce a method to quantify the deviation from a power law (i.e. from a line in a logarithmic plot). A characteristic spatial scale of the patterns is most clearly visible for the propagating-wave model. The spatial gap data from a neotropical forest (BCI) and a cool temperate forest (Ogawa Forest Reserve) are consistent with the two-state model and three-state model, but not with the propagating-wave model.

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In recent years, stochastic lattice models have found a wide range of applications in theoretical ecology. This can be explained partly by the greatly enhanced availability of spatial data on ecosystems. Fig. 1 shows the canopy height in a 450 m × 550 m forest plot in the Ogawa Forest Reserve, Japan (Tanaka and Nakashizuka, 1997). Each small square corresponds to a 5 m × 5 m area and is classified according to vegetation height. Canopy gaps, or the parts of the forest where the vegetation height is lower than a 19 m threshold, are shaded in gray. There are many canopy gaps differing in size and shape. By providing a variety of local microenvironments, these gaps have an important influence on the regeneration of different species (Poulson and Platt, 1989).

The spatial patterns and dynamics of the gaps in the forest depend on diverse processes that influence tree growth and gap formation. Gaps once generated tend to expand at their

edges due to tree mortality and local disturbance caused by wind. In addition, the spatial pattern of the forest is affected by environmental conditions such as climate, topography, or soil quality (Lertzman et al., 1996) as well as disturbances by fires, landslides and storms, or land use in the past (Nakashizuka, 2002; Suzuki, 2002).

The influence of disturbance by wind is most clearly seen in wave regeneration in subalpine fir forests (Shimagare). Both in Japan and in the northeastern United States, a strong wind generates waves of disturbance and recovery, as illustrated in Fig. 2 (Sprugel, 1976; Kohyama and Fujita, 1981). To explain these patterns, lattice-based models were introduced by Iwasa et al. (1991) and Sato and Iwasa (1993), and the stochastic versions were studied by Satake et al. (1998). In these models a cohort of trees much taller than their windward neighbors is exposed to strong wind and experiences dieback.

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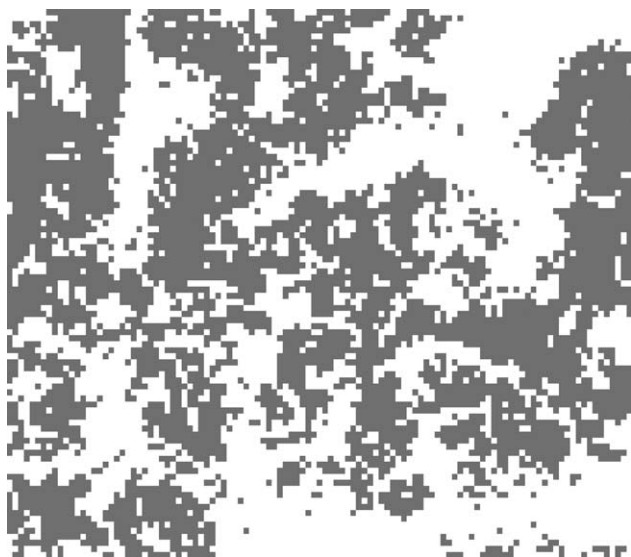


Fig. 1 – Gaps (white) and high canopy (gray) in the Ogawa forest plot, 1986. Gap sites are defined as sites with a vegetation height below a 19.2 m threshold, which corresponds to the median and average height.

Lattice models have also been applied to forests without strong directionality. Kubo et al. (1996) introduced a lattice model of canopy disturbance and recovery, and applied this to spatial data by Hubbell and Foster (1986). Lattice sites are classified as gap and canopy sites, and the rate of transition between the two states depends on the neighboring sites. A canopy site (with high vegetation) experiences dieback faster if the average height of its neighboring sites is low, which is similar to the wave regenerating model but has no directionality. This interaction causes clumping and positive correlation between neighboring sites. Bias correction in parameter estimation was developed by Satake et al. (2004). The equivalence of the spatial patterns generated by the lattice dynamics model of Kubo et al. to the Ising model in statistical physics was discovered by Katori et al. (1998).

More complex lattice models for forest dynamics were studied by Jeltsch and Wissel (1994), who considered the physiological ageing of trees and interaction in an extended neighborhood. Rademacher et al. (2004) studied a model for beech forest regeneration in central Europe. A “forest game model” was analyzed by Manrubia and Solé (1997) and Alonso and Solé (2000). Lattice models for forest dynamics have also been studied in the context of forest fires (Drossel and Schwabl, 1992;

Pennanen and Kuuluvainen, 2002). Pascual and Levin (1999) compared approximation methods for stochastic lattice models of disturbance and recovery. The methods developed to analyze forest spatial patterns are useful in the analysis of spatial patterns of ecosystems other than forests, such as mussel beds in the intertidal rocky shore (Guichard et al., 2003) or sea-grass (Bell et al., 1999).

In classical lattice models of statistical mechanics, important quantities describing the global behavior of a system often show a power law dependence of one or more observables on the spatial scale, when the parameters are near critical values (Binney et al., 1992). Variables measured on different spatial scales, such as density or cluster size, appear as a line when they are plotted on a logarithmic scale, i.e. they follow a power function of the spatial scale. Complex natural systems show similar properties, and often they do not require specific parameter values, a phenomenon referred to as self-organized criticality (Bak, 1997). Even if the spatial scale is changed, the system shows similar statistical properties (Pascual and Guichard, 2005). Hence, the power law is interpreted as the absence of a characteristic spatial scale and is thus termed “scale-free”. Investigating scale-free properties of different statistics, both for critical and non-critical parameters, might be a useful step in analyzing processes that generate spatial patterns.

Hubbell and Foster (1986) found that the gap size distribution of a neotropical forest on Barro Colorado Island, Panama, is near a line in a log–log plot. This means that it can be approximated by a power law. In their analysis, gap sites are those with a canopy below a threshold, which they chose as 2, 5, or 10 m. Similar results were obtained for a temperate forest in the Ogawa Forest Reserve, Japan (Tanaka and Nakashizuka, 1997). For both forests, the distribution fits quite well to the gap size distribution observed for the Ising model with near critical parameters, which is near a power law (Katori et al., 1998; Kizaki and Katori, 1999). A power law gap size distribution has also been reported in models with more complex structures (Manrubia and Solé, 1996). A power law behavior for the clusters of occupied sites was detected by Guichard et al. (2003) in their three-state model.

In this paper, we propose a new method, based on the variance of the fraction of gap sites, to measure the deviation from the power law. The application of this method is illustrated for three stochastic lattice models used in ecology, and for the data from two forests. The results of this analysis can be used to compare models and data. We introduce a statistical test that allows us to check whether the forest patterns can be regarded as typical for a given model.

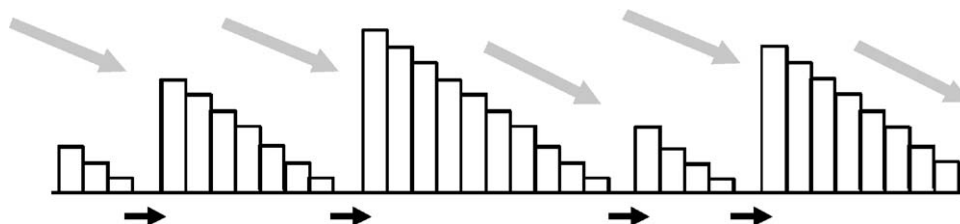


Fig. 2 – Waves of disturbance caused by wind in wave regenerating fir forests. Wind hits the high front trees and causes them to die. At the same time the smaller trees which are protected from wind continue growing. The wave pattern retains its shape and moves slowly in the direction of the wind.

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