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Modelling of forest stand dynamics using Markov chains

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ABSTRACT

Understanding forest complexity and self-organization across multiple scales is essential for both ecology and natural resource management. In this paper, we develop a Markov chain approach for the modelling of forest stand dynamics. The aim of this work is to generalize the recently developed Perfect Plasticity Approximation (PPA) model for scaling of vegetation dynamics from individual level to the landscape level through the ecosystem hierarchical structure. Our basic assumption is that the forested ecosystem and disturbance regimes can be modelled on 3 hierarchical scales (levels): individual trees, forest stand (or patch, defined as a spatial unit about 0.5–1 ha of the same forest at one successional stage.) and landscape (collection of forest patches of different forest/soil types at different successional stages) levels. In our modelling approach the PPA model is an intermediate step for scaling from the individual level to the forest stand level (or patch level). In this paper we develop a Markov chain model for stage-structured dynamics of forest stands (patches). In order to determine the structure of the Markov chain model and estimate parameters, we analyze the patch-mosaic patterns of forest stands of the Lake States (MI, WI, and MN) recorded in the USDA FIA database as well as data for other US states and Canada. The distribution of macroscopic characteristics of a large collection of forest patches is considered as an estimate of the stationary distribution of the underlying Markov chain. The data demonstrates that this distribution is unimodal and skewed to the right. We identify the simplest Markov chain that produces such a distribution and estimate the upper bound of the probability of disaster for this Markov chain.

1. Introduction

The forest ecosystem has a complicated spatially-heterogeneous hierarchical structure emerging from numerous interdependent individual processes. The fundamental problems are to understand how macroscopic patterns of ecological systems emerge as a result of self-organization of individuals, as well as the way ecosystems respond to different types of environmental disturbances occurring at different scales (Levin, 1999, 2003). The overall goal is to develop a model capable of predicting how the disturbances occurring at local scales will propagate to the large scales of ecological hierarchy. An ideal model would present an analytically tractable model predicting landscape-level vegetation dynamics using individual ecophysiological traits as variables and available forest survey data as initial conditions. The major idea of this approach is to scale up forest heterogeneity patterns across the forest hierarchy. More than 30 years ago, Simon Levin (Levin and Paine, 1974; Levin, 1976) applied a conservation law to describe spatial stochastic dynamics in ecological systems consisting of distinct and independently evolving spatial patches and developed an idea that equilibrium spatial patterns can emerge at the patch-mosaic level (Watt, 1947). This approach has been generalized for studying patch-mosaic patterns in hierarchical ecological systems. In addition, this approach was applied in spatial ecology, particularly for modelling of vegetation dynamics in heterogeneous environment (Wu and Levin, 1994; Wu and Loucks, 1996; Moorcroft et al., 2001; Kohyama, 2005, 2006). Wu and Loucks (1996) called this framework the hierarchical patch-dynamics concept, and provided a comprehensive discussion of this concept. The major challenges in developing models within the hierarchical patch-dynamics concept are to define hierarchical levels and to develop models for each level and connections between them.

Our modelling framework, called Matreshka (after the Russian nesting doll), is a particular realization of the hierarchical patch-dynamics concept in application to forested ecosystems (Strigul, 2012). The model represents forest dynamics at the landscape level as interaction of two separated processes occurring at different spatial and temporal scales: 1) the dynamics caused by individual-level processes (growth and mortality in the given neighborhood) within forest stands, and 2) the dynamics of the mosaic of forest stands caused by large disturbances, both natural (forest fire, hurricanes etc.) and anthropogenic (silvicultural operations). The first hierarchical level, individual-tree dynamics within the forest stand, is described by the recently developed Perfect Plasticity Approximation

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(PPA) model that scales up individual-level processes to the stand level (Strigul et al., 2008; Purves et al., 2008) or by an individual-based forest simulators (for example, SORTIE). The PPA offers good predictions for stand level attributes (such as basal area, tree density, and size distributions), biomass dynamics and self-thinning, and ecological patterns (such as succession, invasion, and coexistence). This model includes the system of von Foerster partial differential equations and the PPA equation (Strigul et al., 2008). Unlike the individual-based simulator, the PPA model is both analytically tractable and computationally simple. Initially, the model was developed as an approximation of the crown plastic SORTIE model (Strigul et al., 2008), but it was also demonstrated that the PPA model captures the dynamics of temperate forests. In particular, Purves et al. (2008) estimated parameters of the PPA model by using the data collected by the Forest Inventory and Analysis (FIA) Program of the U.S. Forest Service (FIA data) for the US Lake states (Michigan, Wisconsin, and Minnesota). It was demonstrated that the PPA model accurately predicts forest dynamics and succession on different soil types (Purves et al., 2008). The Matreshka model employs the PPA model as an intermediate step of scaling from the individual level to the forest stand level (or patch level).

The goal of this paper is to develop a model for patch dynamics at the next hierarchal level (forest stand level). We propose to use a Markov chain model to describe forest stand mosaic. In case of the simplest Birth–Disaster Markov chain (see Section 3.1) the Markov chain approach is mathematically equivalent to the patch-dynamics modelling framework developed by Simon Levin (1976). This paper has two particular objectives: 1) to develop a modelling approach for forest stand dynamics, and 2) to apply this modelling approach to available forest inventory data. In this paper we use the USDA FIA data v. 4 (Forest Inventory and Analysis Program, 2010) accessed in May 2010 (FIADB is available at http://fia.fs.fed.us). To model forest stand dynamics we have adapted classical matrix models employed in life-cycle analysis (Caswell, 2001). In order to determine the structure of the Markov chain model and estimate parameters we consider the patch-mosaic patterns of forest stands for different US states and Canada. We have employed two different approaches: 1) inversion of the stationary distribution of the Markov Chain, and 2) analysis of the repeated measurement data (see Section 2.2 for the details).

We have considered distributions of different macroscopic parameters characterizing forest stands for large collections of forest stands as an estimate of the stationary distribution of the underlying Markov chain. We identify that simplest Markov chain that produces patch-mosaic patterns similar to the observed in the data and estimate upper bounds of the probability of disaster for this Markov chain.

2. Modelling of the mosaic of forest stands

2.1. Basic discrete time Markov chain model

The discrete time Markov chain developed for stand (patch) dynamics may be easily generalized to a continuous time framework by allowing times between transitions to be random (exponentially distributed). A simplified version of the Markov chain model proposed here corresponds to a conservation equation for the patch dynamics developed by Levin and Paine (1974). The advantages of the Markov chain approach are the following: the structure of the Markov chain allows us to easily define transitions of stands between stages, the stand level transition probability matrix is easy to interpret and estimate, and the forest development occurs on a relatively large time scale allowing to discretize stand states.

The matrix modelling approach employed in this section has been widely used in ecology in applications to life-cycle analysis and stage-structured population dynamics following the classical works of Leslie (1945) and Lefkovitch (1965). The Leslie model classifies individuals based on the age structure where individuals can move only to the next stage, while the Lefkovitch model classifies individuals by the stages according to the life-cycle graphs where individuals can move to different stages. A comprehensive review of these models and their application in ecology can be found in Caswell (2001). We generalize this approach to the forest stand level. In a particular case, where the transition probability matrix is a Leslie matrix, the Markov chain approach is a discrete counterpart to a reaction–advection model considered in the previous section. We propose to use a more general Markov chain with the transition probability matrix similar to the Lefkovitch matrix, as the Leslie model does not predict observed stand patch-mosaic patterns of the North-American forests (we refer to Section 3 for details). Under certain simplifying assumptions, the Lefkovitch model can be related to a reaction-advection-diffusion model as a continuous counterpart (Takada and Hara, 1994). These discrete and continuous models already have numerous applications in modelling of forest dynamics on different scales (Usher, 1969; Roberts and Hruska, 1985; Moorcroft et al., 2001; Kohyama, 2005, 2006, see also Discussion section).

The states in the Markov chain are represented by stand successional stages $\{1,2,\ldots, m\}$ characterizing the forest stand development. In certain applications, such as in forest fire models, the successional stage is characterized by the absolute stand age i.e. time since the last major fire disturbance. However, in general, the choice of the parameter characterizing stand successional stage is a challenging problem that we address in the next section. It is important to notice that the Markov chain model assumes that the development of a focal stand (patch) is a stochastic process independent of neighboring stands (patches). The $\{1,2,\ldots, m\}$ are discrete intervals of the variable characterizing stand succession (in particular, stand age or biomass). The final stage m represents a certain maturity type stage.

The evolution of one stand (patch) may be represented using a graph as in Fig. 1 and is described using a general transition probability matrix:

$$P = \begin{pmatrix} r_1 & p_1 & 0 & 0 & \cdots & 0 & 0 \\ q_{2,1} & r_2 & p_2 & 0 & \cdots & 0 & 0 \\ q_{3,1} & q_{3,2} & r_3 & p_3 & \cdots & 0 & 0 \\ \vdots & & & \ddots & \ddots & & \\ \vdots & & & & \ddots & \ddots & \\ q_{m-1,1} & q_{m-1,2} & q_{m-1,3} & q_{m-1,4} & \cdots & r_{m-1} & p_{m-1} \\ q_{m,1} & q_{m,2} & q_{m,3} & q_{m,4} & \cdots & q_{m,m-1} & r_m \end{pmatrix} \quad (1)$$

We assume that the patch is observed with high enough frequency and that the forest grows slowly enough so that it is not possible that the patch suddenly grows through two consecutive states. This may also be adjusted using wider intervals for the stages. Each time the progress is made with probability p_i.

We assume that the forest may stay in any one state i with probability r_i. This can be due to some minor disturbances or the discrete time observations. In particular, the forest succession can be such a slow process that it would be possible that the stand stays in the same range of values for two consecutive observations.

The $\{q_{ij}\}_{i\in \{2,\ldots m\}, j\in \{1,\ldots,m-1\}}$ probabilities describe disturbances at the stand level. The disturbances include disaster events that completely destroy forest stands ($q_{x,1}$, $x = 2,\ldots, m$) or smaller scale events that change the stand successional stage to one of the previous stages with certain probabilities ($q_{h,k}$, $h > k > 1$). These disturbances paint a complete picture of the development of forest as a mosaic of patches. The model makes no distinction or explanation between causes of the disturbances leading to successional stage (represented as biomass or stand age) reduction for a forest patch. However, it is obvious that intensive forest harvesting or frequent natural disturbances would lead to larger $q_{i,j}$ probabilities.