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Testing individual-based models of forest dynamics: Issues and an example from the boreal forests of Russia

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ABSTRACT

Testing ecological models involves using independent data on model performance, which can be difficult or practically impossible to obtain. Individual based models of forest dynamics, or gap models, simulate the change of forests by computing the annual growth, birth and death of each tree at a location in a forest. The models are relatively simple and simulate results that can be translated to multiple response scales: Individual plant growth, population birth-death processes, stand environmental dynamics (*e.g.*, evapotranspiration, element cycling, heat flux, *etc.*), landscape processes, and regional and global change. This paper reviews some of the approaches applied to testing gap models. Then, it demonstrates the testing of the performance of an individual-based gap model of forest dynamics, FAREAST, through comparison against independent data from China and across Russia. As part of this model testing, biomass simulation output for 93 locations is compared to independent field-collected inventory-data from 44 Russian forests, which span a broad range of forest types across Russia. FAREAST captures biomass dynamics and stabilization at specific locations bracketing the measured values. At Changbai Mountain, the model accurately predicts the community dynamics of complex mixed forest types present along an elevational gradient, as well as the broad regional compositional patterns across China and Russia. Validation of regional detailed landscape dynamics shows the model performs with fidelity with an average R^2 value of 0.74 for 87 comparisons and an average root mean square error of 10.8 tC ha^{-1}. Performance of the model for historical conditions implies the model's applicability across a broad region and suggests the usefulness of a detailed model for evaluating forest change to management and changing climate.

1. Introduction

Ecological individual-based and agent-based models (IBMs and ABMs, respectively) have lived up to the promise of twenty-five years ago (Huston et al., 1988, see DeAngelis and Gross, 1992 for a selection of examples). There are now hundreds of IBMs of sufficient diversity to span aquatic and terrestrial ecology and to include applications in the social sciences, demography, geography and political sciences (Grimm et al., 2006; DeAngelis and Gross, 1992). Grimm and several colleagues (Grimm et al., 2006, 2010) have developed what they call the ODD (for Overview, Design, and Details) protocol, a uniform standard for describing individual- and agent-based models. In their description of the elements of the ODD protocol, Grimm et al. (2006) saw the eventual testing of IBMs models, "How are data collected from the IBM for testing, understanding, and analyzing it?" as a central model design issue. They further noted the importance of emergence in designing IBMs, "Which system-level phenomena truly emerge from individual traits, and which phenomena are merely imposed?" We see such emergence as a critical aspect of IBM testing and will illustrate this with the testing of an example from a well-developed category of IBMs, forest gap models (Shugart and West, 1980). The case we present is the testing of the FAREAST model (Yan and Shugart, 2005) across Russia at multiple scales.

Gap models simulate individual trees, specifically their growth, mortality, and decomposition into litter in a relatively small area, typically the size of a forest gap. Forest gap models (Botkin et al., 1972; Shugart and West, 1977) reflect the classical concept of "gap phase" replacement (Watt, 1947). Specifically, gap models account for competition among individuals of multiple tree species for light and other resources with the outcome determining the composition and structure of the forest through aggregation of homogenous mosaic patches through time (Shugart, 1984).

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Gap models in the model lineage originating with the FORET model (Shugart and West, 1977) often were developed with a protocol of using what was called "verification tests" of model agreement against calibration data and "validation tests" against strictly independent data (Cale et al., 1983; Mankin et al., 1977). A recent review of a range of different model tests on gap models can be found in Chapter 5 of Shugart and Woodward (2011), and an earlier review in Shugart et al. (1992). The parameters of gap models are quantifications of well-appreciated biological processes (*e.g.*, death, regeneration, and individual growth as influenced by environmental conditions) and straight-forward representations of element cycling (Hobbie et al., 1998; Pastor and Post, 1988), moisture dynamics (Yan and Shugart, 2010), and radiation fluxes in plant canopies (Gu et al., 1999).

Gap-model outputs resemble vegetation field survey data (inventories of numbers, sizes and species of the plants on a plot of land), thus making field survey data highly valuable for validation of simulation results. In the past 20 years, IBMs have been used to provide increasingly accurate simulations of forests for current and past conditions (Mladenoff, 2004). Applications of these models include investigation of forest disturbance and succession, evaluation of stand management, and for predictions of forest response to altered climate. In applying a gap model across an area as vast as Russia, one encounters a wide range of soil and climate. There has been considerable discussion on the values and forms of the specific functions used to quantify the responses of species to environmental conditions, notably climate conditions (see Bugmann, 2001 for a review of this topic). It is clear that the application of any model over a region with great differences in environments needs to be tested to the greatest extent possible against independent data representative of these differences to evaluate model performance.

We continue to endorse the importance of testing against independent data as a significant part of any model testing procedure. One of the significant points in the Grimm et al. (2006) ODD protocol is the recognition of emergent properties as an essential attribute of IBMs. While the need for procedural caution in testing complex models is a good idea that has been with us for a while (Mankin et al., 1977; Gentil and Blake, 1981; Power, 1993), we feel that testing at multiple hierarchical levels is another important dimension of testing IBMs. IBMs by definition operate at multiple hierarchical scales, certainly at least two scales: the first at the level of an individual organism and the second from the consequent responses from interactions among individuals, thus, it seems logical to test this class of models at multiple scales. In the case of gap models, the response scales are individual trees with their birth, growth and death; demography and performance of tree populations of different species on small plots, the aggregate dynamics of these plots across a landscape, and in the present case, the regional change from the behavior of multiple landscapes. Clearly successful performance at any one of these scales does not guarantee success at another.

2. Model description and justification

The individual-based gap model FAREAST (Yan and Shugart, 2005) was developed to simulate the forests of Changbai Mountain in China, an area famous for its rich tree-species and forest-type diversity. The study presented here utilizes data from across Russia with the added constraint of limiting species to their current range limits. This greatly expands the area from that previously analyzed by Yan and Shugart and confirms their qualitative results comparing simulated and observed forest types for the Russian Far East through the use of independent forest inventory biomass data for a quantitative comparison.

A general description of sub-routines and parameters from the FAREAST model is included below; a more detailed description can be found in Appendix 1 or Yan and Shugart (2005). FAREAST simulates forest structural change by tracking individual trees through time for independent sample plots at a geographic site with the input of general climate, soil and species parameters. FAREAST uses monthly climate variables derived from historical station data to compute daily temperature and update soil water. In particular, at each location, the model's climate inputs are drawn from a statistical distribution of monthly values for minimum and maximum mean temperature and mean total precipitation which is derived from 60 years of data recorded at local weather stations (NCDC, 2005a,b). Values for soil variables including field water holding capacity, soil carbon and nitrogen are derived from Stolbovoi and McCallum (2002) for each location. The birth, growth, and eventual death of individual trees are determined in response to local environmental variables. Soil conditions are initialized with site conditions for soil field capacity, soil carbon for the top two layers (Ao and humus layers) and plant available nitrogen pool, which are all updated annually in response to changing bio-environmental conditions, soil moisture and available nutrients. In gap models, individual trees compete for light and nutrients and alter their availability. The models are driven by external stochastic variation in environmental forcings and stochastic processes govern the birth and death of trees on a circular plot.

Within FAREAST, nutrient competition among individual trees determines biomass accumulation and annual leaf and fine root renewal. The effects of competition are computed annually according to a mass balance approach which tracks the movement of carbon and nitrogen from the soil layers into the individual trees for growth. The trees contribute to carbon and nitrogen to litterfall which the model tracks as returned to the soil to again be included in the available nutrient pool. Without sufficient nutrients on the plot, the growth of trees, according to the diameter increment, is scaled back accordingly. The plot size must be large enough for the effect of large trees suppressing the growth of subordinates and the death of a large tree to be manifested as an abrupt and significant change in the plot micro-environment. This size is a function of tree height, crown width and latitude (Kuuluvainen, 1992) and the one-twelfth hectare plot size used in the FAREAST model is in the size range in which both competitive suppression and stand release occur in this class of models (Shugart and West, 1979).

Fifty-seven individual tree species are included in this version of the FAREAST model, and can be grouped into ten genera (*Abies* spp., *Betula* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Populus* spp., *Tilia* spp., *Quercus* spp., *Fraxinus* spp., and *Ulmus* spp.) and two collections of less common species (other deciduous and other coniferous). These species represent the genera which dominate Northern Eurasian forests. Six genera of trees (*Pinus*, *Picea*, *Abies*, *Larix*, *Betula*, and *Populus*) cover 87.4% of the forested areas in Russia, and, of those six dominant genera, the four coniferous genera cover 71.1% of this forested area (Shvidenko and Nilsson, 2003). There is a marked contrast between the diversity of the Amur River region of the Russian Far East (RFE) near the Chinese border. When the ranges of existing tree species are mapped, the ranges of 38 individual tree species overlap in the Amur region of the RFE compared to an average of 9 overlapping ranges in the other regions across Russia. Species are included in simulation for each location, hereafter called sites, from range maps created for this study in ESRI ArcGIS (2008) using range information adapted from Nikolov and Helmisaari (1992) and Hytteborn et al. (2005). At the start of simulation all potential species whose range indicates their presence at a site are available for colonization, however individual species characteristics, including light, nutrient and water demands, define which species establish and survive during succession. For example, *Larix* spp. are strongly light demanding, and so colonize in early succession,