Ecological and evolutionary impacts of disturbance regimes on vegetation structures

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Goal

To investigate the demographic and evolutionary consequences of different disturbance regimes on vegetation structures using an individual-based spatially explicit dynamical model.

Background and motivation

Understanding vegetation dynamics and worldwide vegetation structures is crucial for predicting how plants respond to climate change and how their response feeds back into the atmosphere. The latter occurs through changes in the carbon cycle and in the albedo of the terrestrial vegetation cover. Acquiring a detailed understanding of vegetation dynamics is challenging, however, due to the many diverse processes that drive the ecology and evolution of vegetation structures. At the physiological level, light, moisture, temperature, and nitrogen availability are the key factors to which plants have to adapt. At the level of an individual tree, the neighborhood interactions that arise from competition for light and from soil processes influence the local conditions that in turn affect tree development. At the level of a stand or forest, natural and anthropogenic disturbances such as fire, disease spread, or logging greatly influence the size distribution and species composition of vegetation structures. In addition to the direct impact on forests, disturbance processes also affect the demographics and life-history strategies of trees, although little is known about those effects.

Disturbance regimes vary greatly from woodland to woodland. In tropical forests, for example, the typical disturbance is a single large tree toppling over, leaving a gap in the canopy for other trees to exploit. In contrast, disturbances in temperate forests are usually associated with fire and wind that sweep through large areas, destroying trees along their path. Human activities are also increasingly altering the natural disturbance patterns of forests, through logging or the prevention of forest fires. A better understanding of the ecological and evolutionary impacts of different disturbance regimes may not only help explain patterns in worldwide vegetation, but also elucidate the long-term implications of anthropogenic impacts. Field studies have attempted to observe the adaptive response of plants to disturbances, but interpreting such data is difficult when neighborhood interactions and disturbance regimes lead to antagonistic selection pressures. As an alternative to field studies, theoretical investigations based on dynamical forest models have the potential to yield insights into the impacts of disturbance regimes on phenotypically plastic and evolutionary processes of plants. Numerical analyses of disturbed forest dynamics may furthermore help craft policies that will support nature conservation and sustainable exploitation.

While dynamical forest models have the potential to yield important insights into the impacts of different disturbance regimes, the complex mechanisms involved in forest dynamics are difficult to reproduce. Multiple temporal and spatial scales, ranging from those of tree-to-tree interactions to those of global environmental change, make forest modeling a challenging task: should the focus be on individual trees, on patches of significant scale, or on vegetation landscapes? Forest dynamics have been modeled at all three levels: gap models (JABOWA, Botkin et al. 1972; FORET, Shugart and West 1979) describe forest growth on a coarse grid, representing patches of trees. Horizontally, patch properties are homogeneous; yet, a patch's vertical structure accounts for each tree the patch contains. Patches change independently of one another, because inter-tree distances are ignored. The lack of horizontal interactions in gap models motivated the developments of models with refined grid resolution that explicitly account for exact tree locations (SORTIE, Pacala et al. 1993). In such models, grid points are either empty or occupied by individual trees, and interactions among trees occur over influence zones defined according to tree morphology. The spatially-implicit Perfect Plasticity Approximation (PPA, Purves et al. 2008) is based on the assumption that projected tree crown area can completely cover the canopy. Strigul et al. (2008) showed that the simplified dynamics described by the PPA agree well with those of a more detailed spatially explicit individual-based model. The LANDIS model by Mladenoff (2004) was developed during the 1990s in an effort to study forests at a landscape scale. LANDIS runs on a mesoscale grid, with each cell representing a forest stand in terms of age classes of different tree species. While providing the necessary tools for studying a forest's interactions with natural and anthropogenic disturbances, the LANDIS model lacks the mechanistic complexity of individual-based models. In summary, spatially explicit models of the dynamics among individual trees are promising tools for studying forest dynamics, but remain under-explored because of the associated high computational cost (Levin et al. 1997; Busing and Mailly 2004). Even so, individual-based models are likely to offer the best choice for simulating disturbed forests, as they avoid unrealistic assumptions about the horizontal homogenization of disturbances that have to be made in patch-based models.

The aim of this project is to explore the ecological and evolutionary impacts of different disturbance regimes on forests. We will develop an individual-based spatially explicit model of forest dynamics with trees characterized by two salient functional traits: leaf mass per area and height at onset of reproductive investment. For different disturbance regimes, we will explore the short-term ecological impacts and the longer-term evolutionary impacts of disturbances. The anticipated results will be critically compared with earlier findings obtained by Falster et al. (in preparation) for a spatially implicit size-structured metapopulation model with disturbances.

Research questions

The present effort will address the challenge of elucidating impacts of different disturbance regimes from three complementary angles: demographic consequences, evolutionary consequences, and methodological requirements.

- How do different disturbance regimes affect salient aggregate statistics of forest structure, such as leaf area index and standing biomass? How do disturbance regimes influence the ecological coexistence of different tree species?
- Can different disturbance regimes cause changes in the predicted range of trait values?
- How do the results obtained for the proposed individual-based spatially explicit model differ from those obtained by Falster et al. (in preparation)? In particular, will our individual-based model lead to trait distributions that markedly differ from those obtained by Falster et al.?

Finally, if time permits, we will analyze multiscale aspects of forest dynamics using a coarse-graining approach. We will first try to obtain statistical information about tree-to-tree interactions and use those statistics to characterize a coarse-grained process. If successful, we will attempt to use these results to simplify aspects of the full model to reduce the associated computational costs.

Methods and work plan

Spatial representation

Forests will be represented as a spatio-temporal point process (Särkkä and Renshaw 2006; Comas and Mateu 2008) in continuous two-dimensional space. To avoid boundary effects, we will use periodic boundary conditions, i.e. the spatial domain will be the two-dimensional torus obtained by identifying the opposite sides of the unit square. The state of a forest at a given time is therefore represented by a configuration of (marked) points on the unit torus.

Physiological model

The life cycle of a tree is characterized by dispersal, establishment, growth, reproduction, and death and is driven by the tree's energy budget. The available light determines the amount of carbon dioxide that the tree can assimilate at the leaf level via photosynthesis. The assimilated energy is then redistributed and used for the respiration of the living tissues supporting the tree, dry matter production, and reproduction. We follow the physiological model developed by Falster et al. (in preparation). For this project, two functional traits are considered: *leaf mass per area* (LMA) and *height at maturation.* Well-supported empirical scaling relationships link the size of a tree with the masses of its various structural tissues. The level of shading induced by neighborhood competition defines the leaf assimilation rate, which we multiply by the leaf density to obtain the assimilation rate for each tree. Respiration is defined to be proportional to the total mass of the living tissues. Net production, which is partially allocated to growth of the various tissues and partially to reproduction, is obtained by subtracting the expenses for respiration and leaf turnover from a tree's total carbon dioxide assimilation. Allocation to reproduction depends on the height at maturation of the tree and determines the rate of offspring production.

Neighborhood competition

In our model, competition between trees is exclusively based on light availability. This process is asymmetric in the sense that taller trees shade smaller trees. We assume that the extent to which one tree shades another depends on their sizes and horizontal distance. Shading among trees will be computed by assuming that trees have 'flat tops', i.e., have crown composed of a single layer of leaves at the top of the tree (Strigul et al. 2008). Higher layers shade the layers beneath if they overlap horizontally. The shading intensity will be weighted with opacity coefficients to account for the vertical separation between tree crowns. As a potential future extension, we may add one or more layers of foliage to better reflect the true vertical structure of tree crowns.

Environmental stochasticity

Tree configurations are driven by a birth-death-growth-interaction model. Following a continuous-time Markov process, changes in the pattern of tree locations are determined by birth and death events. New individuals are recruited into the population at a rate that depends on the reproductive rate of each tree and on seedling survival, and are removed from the population at a rate that depends on wood density and a shade-tolerance factor as well as on disturbances.

Disturbance regimes

Disturbance processes cause the death of individuals. We assume that the time between disturbances is exponentially distributed and that the center of a disturbance occurs at a random point in space (corresponding to a spatially homogeneous Poisson process). A disturbance destroys a fraction of all trees located within a given distance from its center. A disturbance regime can thus be characterized by three parameters:

- The rate of occurrence of the disturbance.
- The extent of the disturbed area.
- The probability that any given tree within the disturbed area dies.

By taking the product of these three parameters, we obtain the intensity at which the forest is disturbed. In this way, we can represent a wide array of disturbances, ranging from a single tree fall (small area with a high probability of tree death) to wind disturbing large forested regions (large area with a low probability of tree death).

Evolutionary dynamics

To assess evolutionary effects on a tree population, we introduce mutations in the two considered functional traits (LMA and height at maturation). The resultant evolution of the distribution of those trait values is then observed through time.

Model implementation

We plan to implement the model in C++. Because individual-based models can be computationally burdensome, it is imperative to store the forest's state efficiently. One possibility is to divide the torus into m^2 coarse cells such that it suffices to compute the interactions between same-cell and neighbor-cell trees. This representation will reduce the determination of all vital rates from quadratic to linear complexity in the total number of trees. Initial forest configurations will be generated randomly. At each fixed time step, we must compute the energy budget and update the state of every tree in the forest. While it is unnecessary to store the point configurations in time, it is important to store the distributions of traits, sizes, and locations. To visualize the results, we intend to use R or Matlab.

Relevance and link to EEP's research plan

The analyses described here are relevant to evolutionary studies of biological populations under global change and human interventions. This project therefore contributes to EEP's research project on *Evolving Biodiversity* by addressing the selection pressures exerted on ecological systems through local interactions and different disturbance regimes.

Expected output and publications

This research is intended for publication as a co-authored article in an international scientific journal.

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