Arborscapes: A Swarm-Based Multi-agent Ecological Disturbance Model

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This paper presents an agent-based, object-oriented ecological model of forest dynamics designed to examine the role of disturbance on diversity. Arborscapes is based on Swarm, an agent-based software platform that offers advantages for ecological modeling, including a suite of standardized libraries of objects, schedules, and probes, and architectural features such as inheritance, message passing, encapsulation, and hierarchical structure. Object-oriented models are more transparent, portable and more easily modified than process oriented models, and therefore promise to facilitate collaboration on computational experiments. The initial application of Arborscapes was the analysis of disturbance dynamics, but the model was designed to be modified for a variety of applications in the simulation of vegetation community dynamics.

Keywords: community assembly, ecological model, ecological disturbance, diversity, forest dynamics, Swarm.

1. Introduction

There are many unresolved theoretical questions about the nature of organization in ecological assemblage and the mechanisms that govern species abundances. Although there is a substantial literature on diversity, theoretical explanation has encountered difficulty, in part because of the wide variety of ecological and evolutionary processes, and varied historical and geographical circumstances (Huston 1979, Petraitis et al. 1989, Schluter and Ricklefs 1993).

Empirical investigation of these issues in forest systems has resulted in a substantial literature, but is hampered by problems presented by ecological study in general: 1) large numbers of species, individuals, and interactions, 2) high variability, and 3) long lifespans of individual organisms. For this reason, computer models have been successfully used for three decades to pursue general explanations in ecology. A long lineage of spatially explicit forest models has evolved to explore disturbance, competition, and the effects of climate change on forests (e.g. Bolker et al. 1995, Botkin et al. 1972, Coffin and Urban 1993, Moloney and Levin 1996, Pacala and Tilman 1994, Shugart and West 1977). These models are composed of landscapes composed of cells, each occupied by an individual tree whose fate is tracked over time. Most use species life history traits as the fundamental parameters of individual trees.

Agent-based models consist of a collection of individuals, each of which possesses the information needed to behave autonomously, according to a set of rules, and to interact locally with neighboring agents. Interactions are simple and local, yet can lead to complex patterns at the landscape or global scale (Turner and O'Neill 1995). In some models, local interaction of individuals generates landscape dynamics that respond to perturbation recursively, where, for example, the behavior of fire is governed by local forest structure, which is in turn governed by the pattern of past fires. In state variable models, spatial interactions are unimportant, individuals are assumed to be identical, and populations are treated as aggregated variables (Huston et al. 1988). In contrast, in agent-based models, as in ecological systems, space and history matter.

Here, we present a generic agent-based model, Arborscapes, designed to facilitate the exploration of the role of disturbance in structuring species and landscape diversity. Arborscapes was implemented using the Swarm modeling platform which uses a discrete-event, object-oriented approach designed to simulate systems with multiple interacting agents. Swarm offers modellers a basic design that can be adapted for a variety of uses. A Swarm-based model provides an agent template, which can be modified, and a library of tools that measure and track system behavior (Minar et al. 1996). The Swarm platform contains libraries of reusable, adaptable model components, expandable sets of agents in hierarchically-nested structures and a schedule of events over those agents. A set of windows also allows the user to observe model behavior in progress. While many models of vegetation communities exist, they tend to be community and problem-specific. Arborscapes offers a researcher a transparent, accessible, and adaptable ecological model template.

While disturbance has been found to be widespread in ecological systems, community dynamics models have yet to satisfactorily integrate disturbance (Sousa 1984). Agent-based models are ideal vehicles to explore these issues, since organisms, like agents, possess the constraints that govern interactions (Judson 1994). No emergent properties of the landscape are assumed a priori, but instead arise from local interactions. Arborscapes strives to be parsimonious (sensu Shugart and Urban 1989) with simple, local rules generating global system behavior, and is particularly apt for exploring the role of historical events in landscape development.

This paper presents Arborscapes in the context of a specific application--an exploration of how a gradient of disturbance patterns diversity. This instantiation is offered only as an illustration of a range of potential applications. Arborscapes is intended to be a generic model to be modified to address questions that pertain both to specific communities and problems, as well as theoretical issues of disturbance and community dynamics.

2. Ecological context: equilibrium or nonequilibrium

Ecologists have been struggling to understand the nature of organization in forest ecosystems for over a century. Classical explanation of ecological processes assumed that communities were equilibrium systems which rarely experienced disturbance. Recovery from disturbance was expected to proceed in an orderly, linear way toward a stable state of a uniquely adapted species assemblage--a climax community. Species diversity, productivity, and stability were assumed to increase with time to a maximum at climax (Margalef 1963).

Empirical research of the past few decades has revealed the near ubiquity of natural disturbances, such as fire, windstorm, landslide, climate events, and insect and disease outbreaks in forest ecosystems (Sousa 1984). Ecologists now suggest that most species assemblages are fundamentally nonequilibrium systems (Huston 1979, Whittaker and Levin 1977), perhaps resulting in some cases solely from endogenous dynamics (Sole and Manrubia 1995). Moreover, anthropogenic disturbances, now common, have novel and unpredictable consequences in natural communities. Although disturbance is known to be widespread, a theory of community dynamics which integrates disturbance into a nonequilibrium model has not yet been articulated (DeAngelis and Waterhouse 1987, Veblen et al. 1992).

One hypothesis that has been proposed, the intermediate disturbance hypothesis (Connell 1978, Pickett and White 1985), suggests that species diversity is highest, not at a stable endpoint of recovery from disturbance--the classical climax forest--but rather at intermediate levels of disturbance, both of frequency and intensity. In contrast to equilibrium-based theory of classical ecology, the hypothesis is based in a concept of a natural dynamic that is unstable and disorderly.

The current application of Arborscapes model examines the dynamics of abstract forests under varying levels of disturbance, investigating questions such as, how does species coexistence change under changing levels of disturbance? How does history matter in ecological dynamics? Under a designated disturbance regime, does a system trend toward a steady state? If so, can there be multiple steady state outcomes for similar parameter values? What characterizes the trajectory of a transient to a steady state?

3. Arborscapes

Arborscapes was designed to share the basic assumptions of prior individual-based spatial forest models. Most forest gap models aim to predict community-level phenomena based on idealized life history traits (e.g., JABOWA [Botkin et al. 1972], FORET [Shugart and West 1977], FOREST [Ek and Monserud 1974], SORTIE [Pacala et al. 1993]). The life history attributes (sensu Noble and Slatyer 1980) used to parameterize species in Arborscapes reflect the general grammar of many forest models. The general approach has been functional classification of species based on a suite of linked successional attributes that reflect competition for resources.

Tree species have often been categorized, both empirically (e.g., Whitmore 1989) and for modeling purposes (e.g., Acevedo et al. 1996, Shugart 1984, Shugart and Urban 1989) based on regeneration success relative to light availability. Tolerance to light conditions has been widely used in ecological studies as a benchmark by which to associate a suite of successional traits with functional types. Modelling species as one of several light-tolerant classes is consonant with the more general concept of functional groups in successional status (Smith and Huston 1989). Recent work suggests that light may be the preeminent resource in competitive interactions. Bolker et al. (1995), for example, present data that suggests that most factors, such as nutrient availability, are overwhelmed by the importance of light. Huston and Smith (1987) have shown that modeled competitive interactions based on life history traits related to light produce realistic outcomes.

Arborscapes shares this approach of functional classification with an emphasis on the role of light in controlling regeneration. The current instantiation of the model is populated by tree species with suites of traits spanning a spectrum from early to late successional adaptations. Functional species roles determine regenerational response to disturbance, with early successional species adapted to higher levels of disturbance and late successional species adapted to lower levels of disturbance. Commonly, recruitment and mortality are modeled by simple stochastic processes whereas growth rates are determined by differential equations (Coffin and Urban 1993). In Arborscapes, in contrast, traits are given discrete values, and growth is modeled by graduation of the tree through life stages of a length relative to lifespan. Model output appears reasonable and coherent with other forest model behaviors.

In the treatment of disturbance, Arborscapes differs from models where disturbance is treated as an exogenous feature. Location, size, proportion of damage, and frequency of disturbance events are commonly given fixed spatial or temporal probabilities (e.g. Moloney and Levin 1996). By contrast, in Arborscapes, the occurrence of disturbance is dependent on landscape structure, which is in turn dependent on prior disturbance history. Some recent gap models have adopted similar recursive disturbance architectures (e.g. LANDIS [Mladenoff et al. 1996]). Spatial and temporal patterns of disturbance depend on age, susceptibility, and patchiness of individuals on the landscape.

4. Model architecture

The forest landscape of Arborscapes is a mosaic of continually shifting patches, where seeds are cast onto the forest floor and germinate, and trees grow, set seed and die, either from old age or exogenous factors. The spatial landscape of Arborscapes is a two-dimensional cell grid, in which each cell may be simultaneously occupied by an adult tree and an understory successor seedling or sapling. Each individual possesses attributes of two sorts: 1) a set of fixed, species-specific life history attributes, and 2) a time-related state that varies with rules that govern changes at each time step. The landscape dynamics depend on species competitive interactions alone, since the model does not incorporate environmental heterogeneity. System behavior depends on competitive interactions for light coupled with exogenous disturbances. The decision not to make the landscape a torus was grounded in the potential for redundant magnification of contagious disturbance. Edge artifacts are minimized as the model proceeds. The model schedule proceeds on an annual step basis.

The forest is initialized with a user-specified number of trees of user-specified component species of random age and location. Unvarying species-specific traits currently include, 1) shade tolerance, 2) canopy density, 3) longevity, 4) fecundity, 5) seeding periodicity, 6) seed dispersal abilities, and 7) seed longevity in the soil. In addition, trees have traits that vary depending on age, currently, 1) the amount of heat required to burn, and 2) the amount of heat given off while burning.

In the current version, the exogenous disturbance is fire, but the model can be modified to accommodate any contagious disturbance, such as windstorm, insect infestation, or pathogens, and multiple simultaneous disturbances. Disturbance propagates according to a set of rules governing species vulnerability to disturbance. Fires are ignited by lightning, which strikes in random locations with a user-specified frequency. Lightning kills the individual struck, but fire will not spread unless heat emitted by that individual is sufficient to set a neighbor ablaze. Landscape patterns, thus, depend on the interaction of fire with local forest structure and community recovery.

Life History Attributes

The current instantiation of Arborscapes provides an illustration of parameterization of a forest populated by eight species across a successional gradient. These life history attributes are:

1) longevity

Each individual spends a species-specified time span in various life stages. Growth is achieved by graduation from each of five assigned life stages: seedling, sapling, young adult, mature adult, and senescent adult, with the length of each stage varying by species longevity. Trees reach reproductive maturity and produce seeds at the mature adult stage, and die at the end of the senescent stage.

2) seeding periodicity

Trees often do not produce prolifically seeds in every year, but on an intermittent periodicity specific to a species. Seeding periodicity in the model is expressed as an integer that describes an interval of years between seed production.

3) fecundity

Species vary by the abundance of seeds produced; this capacity is expressed as an integer that describes the number of seeds that fall into each cell to which seeds can disperse.

4) seed dispersal

Seeds are dispersed on the ground in the neighborhood of the parent depending on species dispersal capacity. Seed dispersal is expressed as a seeding radius of number of cells distant from the tree. Seeds of all species accumulate beneath the forest at a rate at which nearby mature adults shed them.

5) seed mortality

Seeds in the soil bank suffer mortality from predation and injuries. Seed mortality is expressed as a species-specific proportion of seeds of a species within a cell that die during each time step.

6) canopy density

Canopy density indicates how much light penetrates through a tree's canopy into the understory. The densities of the tree canopies varies by successional status. Canopy is designated by an integer reflecting categorization as one of three classes: sparse, intermediate, or dense. Canopy density, then, governs regeneration and overstory capture.

7) shade tolerance

All cells may be occupied by an overstory and an understory tree simultaneously. Each species has a specified shade tolerance that determines the potential of a sapling of a species to achieve the overstory. Shade tolerance is designated by an integer reflecting categorization as one of three classes: tolerant, intermediate, or intolerant. Seedlings can germinate, and sapling attain the overstory, depending on their tolerance of canopy density. If an overstory tree catches fire, seedlings, saplings and seeds in the soil are also killed.

8) heat given off by burning trees

The quantity of heat emitted by a burning tree varies by values 1) specific to its age and 2) specific to its species. Heat output depends on the amount of fuel provided by each of the five stages of life. Senescent trees burn hotter than mature adults, which burn hotter than young adults, while burning seedlings and sapling emit no sensible heat. The heat output of each burning tree can be felt by its eight immediate neighbors.

9) heat required to ignite

Every tree struck by lightning burns, but fire spreads through the landscape only when heat is propagated from tree to tree. The heat output of neighbors is sensed by an individual and it burns if the sum of total heat effect exceeds its designated ignition threshold. Susceptibility to ignition depends on 1) a value specific to its life stage, and 2) a value specific to its species. Senescent trees are most easily ignited, followed by young adult trees and then mature adult trees. Seedling and saplings are killed if any neighbor is burning.

Germination

Germination is governed by rules that depend on 1) probability and 2) species adaptations. Each cell accumulates dispersed seeds, and so can contain numerous seeds from many species. Germination occurs by weighted lottery relative to the number of seeds of each species in the cell. Remaining seeds are susceptible to mortality each year at a species-specific rate. Seeds on the forest floor either remain until they die at a species-specific mortality rate, or until they win the seed lottery. A seed can germinate 1) in a cell where there is no adult tree, or 2) under an adult tree. A site can be vacant either because a tree has died of old age or burned in a fire. If the site is vacant, the seedling captures the site. Saplings, however, become adults on a site occupied by an overstory tree only if their species-specific shade tolerance permits.

Mortality

Having captured a site, a young tree will succeed to later life stages until it dies of old age or is burned in a fire. Mortality from disturbance is dependent on 1) the susceptibility of a tree due to life stage, and 2) the intensity of the disturbance, measured by the proportion of burning neighbors and their heat output. Thus, mortality from fire is dependent on the structure of the landscape, which resulted from past fire. Burned sites will be recolonized by seeds in the soil, but preferentially by those of early successional species that disperse farther, are more fecund, and mature more rapidly. Mortality from disturbance is thus not a fixed probability, but depends on fire intensity, which depends the number and heat output of burning neighbors.

Disturbance

Lightning strikes are probabilistic in occurrence but fire is deterministically dependent on landscape structure. The frequency of lighting strikes in each year occurs with a probability between zero and a user-assigned integer. Lightning is distributed stochastically in landscape space. Youngsters burn if an overstory tree burns, but if the site has no adult tree, then seeds, seedlings and saplings survive. Since individual trees vary in their susceptibility by species and age, spatial patchiness develops. If by chance time passes with no lightning strikes in a neighborhood, shade tolerance species will regenerate and mature, and fire becomes less contagious. Stochastic patterns of disturbance in time and space, then, instantiate patchy patterns of susceptibility to disturbance in the landscape.

Visualization tools

In addition to defined agents and a schedule of events, Arborscapes provides visual tools for the observation of the model on a time step basis. Windows in the current application graphically track the abundance of seeds in the forest by species, the location of seedlings and saplings, the location of the adult trees in the forest, and the size and location of wildfires. A probe feature allows the user to query any cell on species, age, and attributes of the individual at the site. These window functions can be crucial to evaluating model behavior. There are also windows that concurrently graph 1) the abundance of each species, 2) species richness, and 3) total species entropy. Windows that allow modification of run parameters include 1) size of the landscape, 2) number of species, and 3) frequency of disturbance.

Pattern analysis

To analyze spatial and temporal pattern dynamics generated by the model, output can be linked to one of many pattern analysis packages, or pattern-analysis algorithms can be written into the code to suit the user. Arborscapes output has been linked to Fragstats (McGarigal and Marks 1995), a comprehensive pattern analysis program. The raster version, appropriate for the evaluation of the structure of cell-based models, generates metrics for area, patch density, size and variability, edge, shape, core area, diversity, contagion, interspersion, and nearest neighbor values. Mathematica, an analytical software package, was used to quantify results. Many of these analytical tools, however, including wavelet and Fourier analysis, are being integrated into Swarm.

Model objects

Arborscapes has the following objects: Tree, Forest, Species, SeedSpace, Spring, and Fire. The simplest and most common object is the Tree, the record of the state of an individual tree, including its life history attributes. Few methods are implemented in the Tree class as the species object is responsible for the actual state transitions that a tree may undergo. For example, a tree object is sent a 'step' method and then relays the message to its species object with a reference to itself as an argument.

The Forest object provides the space in which the simulation is taking place, a simple square grid where each cell represents the area required by a tree. The Forest maintains 1) a reference from every occupied cell in the grid to the tree currently growing at that location and 2) a separate list of all the trees currently growing within its boundaries. There are two subclasses of the Forest class: in the YoungForest class, seedling and sapling versions of trees graduate from the YoungForest to the MatureForest when they reach young adulthood, whereas in the MatureForest, trees at the end of their senescent phase are removed from the simulation.

The species object is the most complex participant in the model. Its role is to record all of the attributes of a species and to execute the actual simulation step on behalf of every tree belonging to the species. Attributes that differ across species include:

a. Age Levels: the [[ageLevels]] array stores the number of years a tree of a given species spends in each state.
b. Heat resistance: the [[resistance]] array holds heat resistance to ignition of different thresholds for each age level.
c. Heat: the [[heat]] array stores the amount of heat a tree of a given species will radiate while burning.
d. Canopy structure: the [[canopyStructure]] variable stores the opacity of species' canopies.
e. Seedling-related variables: [[seedPeriodicity]] governs seeding cycle. Every [[seedPeriodicity]] years it releases [[seedsPerSquare]] seeds over an enclosing square of (2*[[seedingRadius]] + 1) grid cells. Every year a fraction [[seedMortalityRate]] of the seeds per location are destroyed.

The SeedSpace object is used by the Species to keep track of the seed distribution. When a tree seeds, the resulting change in seed levels is recorded in the SeedSpace of the tree's species object. SeedSpace is also responsible for enforcing seedMortalityRate.

The Spring object implements the insertion of new trees into the model. For every empty understory cell, the spring object asks each species how many seeds of its kind are potentially able to grow in that cell in a time step. The spring object then generates a seedling in the cell and puts it in the YoungForest.

The Fire object is responsible for initiating disturbance in the model. The fire object selects grid cells randomly at a lightning strike frequency drawn from a uniform distribution between 0 and [[freqLStrikes]].

5. Swarm advantages

The Swarm modelling environment is an advantageous platform for individual-based model implementation, including object orientation, inheritance, and standardization.

Object orientation

Most languages used to implement scientific models, such as FORTRAN, C or Pascal, are procedural, where the programmer defines data-structures modified by procedures which contain the essential model logic. In a simple FORTRAN forest model, the programmer defines a multi-dimensional array where the first two dimensions represent spatial coordinates and the rest hold attributes of the tree at a given location. As more procedures are added, it becomes difficult to maintain consistency, as every new procedure can potentially alter other model data-structures.

Object-oriented languages, such as C++, Java, and Objective-C, solve this problem by providing the notion of a software object. A sortware object contains attributes, or private data-structures, and methods, or privileged procedures, which are accessible to the rest of the model by message passing.

So, for example, we might define an object called a **tree**, with an attribute called **height** and a method called **grow** which increments the height of the tree. This definition would ensure that the only way to alter the height of the tree would be to send it the message to grow. The encapsulation provided by this method is essential to the development of larger, more complex models. Swarm implements agents as software objects.

Extendibility through inheritance

Another advantage of object-oriented languages is the notion of inheritance. When a programmer defines objects, s/he defines object classes, and then creates many instances of a given class. A programmer can define sub-classes which 'inherit' the properties, or attributes and methods, of the original class, by augmenting them with attributes and methods to specialize them. We might define a sub-class of **Tree** called **Deciduous Tree** which inherits a height attribute but contains a new attribute called annual cycle, specific to **Deciduous Tree**. This strategy of specialization through inheritance makes it possible to reuse and extend objects and allows other researchers to explore variations on the basic Arborscapes model.

Standardization

An objective of Swarm is to contribute to a standardized methodology for computer-based experimentation, similar to those used in empirical research. Scientists setting up computer experiments should be able to utilize a well-defined route from the description model results, reproduction of such results, and calibration of a model experiment. To this end, Swarm provides:

1. Probes. It can be useful to inspect values stored in attributes of model objects, to look at model implementation, for example, or unexpected behavior. Probes greatly simplify the process of agent inspection.

2. Measurement tools. Swarm also provides tools which gather measurements from the objects and generate basic statistical information about them, information that can be viewed interactively or stored to a file for later processing.

3. Reproducibility. One of the greatest difficulties a scientist encounters when recreating a simulation based on written accounts is the problem of intended system dependencies. Simulations are very likely to use libraries that are specific to the target computer, thus internalizing routines which cause different behavior when implemented on another architecture. Swarm has been coded to minimizes dependency on specific architectures and maximize portability.

4. Scheduling. Another difficulty encountered in reproducing simulations is the problem of underspecified scheduling. Without a standard mechanism for scheduling the actions in a simulation, scientists must describe the exact order of events in accompanying publications. Reimplementation of the model is likely to schedule events slightly differently, generating different results. Swarm provides a standard

scheduling mechanism which requires the modeller to be explicit about event order, maximizing portablity and precision.

5. Nested hierarchies. The ability to nest clusters of objects and activities is highly appropriate for the complexity of temporal and spatial scale in ecological systems.

6. Current and future research agendas

Maynard Smith (1974) suggests that ecological systems can be approached in one of two ways, either by a detailed mathematical description of specific systems, or by a general and abstract description that aims to capture the essential properties of the system. The design of Swarm makes both approaches possible through libraries of expandable elements. The Arborscapes exploration of the role of disturbance in generating diversity took the more general approach, and initial results suggest a tendency for system behavior to be attracted to regions of state space with characteristic species abundance ratios, a tendency toward multiple steady states at intermediate levels of disturbance, and sensitivity of trajectories to early interactions.

A future research goal is the parameterization of the model using empirical data from a forest under known disturbance conditions in order to test model assumptions, including system-specific data on topography, climate, elevation, hydrology, and additional life history traits that should allow plausible predictions and the verification of historical trends. This project will be facilitated by current efforts to link GIS databases directly to Swarm models.

The Swarm platform offers distinct advantages for collaborative modeling. Swarm offers a suite of standardized libraries of objects and classes, schedules, measurement tools, and probes, that can be utilized and extended, and useful architectural features such as inheritance, message passing, encapsulation, and hierarchical structure. Object-oriented models are more transparent, intuitive, portable and more easily modified than process oriented models, and, because of this, promise to facilitate collaboration on computational experiments. The model is particularly apt for studying poorly understood aspects of complex ecosystem dynamics such as scaling phenomena and large-scale dynamics which are a consequence of individual interactions.

Code: The full, free source code of Swarm is available as V1.0 on SFI webpage at http://www.santafe.edu/projects/swarm; Arborscapes 1.0 at: http://margay.sscnet.ucla.edu/~reb/arborweb/arbormain.html; Fragstats at: http://www.fsl.orst.edu/lter/data/software/fragstat.htm.

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Figure 1. Arborscapes architecture includes agents interacting on layers of two-dimensional spatial landscapes with behaviors governed by methods on a schedule.