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A framework for agent-based modeling of community assembly and succession

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Abstract
Ecological communities are self-adaptive systems. Community assembly and succession is a self-organizing process. It is generated from multiple species invasions, selection, adaptation and optimization. A framework for agent-based modeling of community assembly and succession was presented in this paper. Species agents, space agents, functional agents and their behaviors were defined. Major procedures for agent-based modeling of community assembly and succession were proposed.

Keywords agent-based modeling; framework; ecological community; assembly; succession.

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1 Introduction

Community assembly and succession is in essence a self-organizing process, which is generated from multiple species invasions, selection, adaptation and optimization (Wang et al., 2009; Nedorezov, 2012; Zhang, 2012a, 2013a, 2013b). Understanding the mechanism of community assembly and succession is always the focus of ecologists (May, 1973; Cohen et al. 1993; Hraber and Milne, 1997; Zhang, 2012a, 2012c). Classical explanation of ecological processes assumed that communities were balanced systems that have rarely experienced disturbances. Recovery from disturbance was expected to proceed in an orderly and linear way towards a stable state of a uniquely adapted species assemblage, i.e., a climax community. Species diversity, productivity, and stability were assumed to increase with time to a maximum at climax. One hypothesis, the intermediate disturbance hypothesis suggests that species diversity is highest, not at a stable endpoint but rather at intermediate levels of disturbance (i.e., frequency and intensity). External disturbances, for example species invasion, might produce unpredictable and significant influence. Up till now, some processes or mechanisms governing community succession have been confirmed (Case, 1990; Hraber and Milne, 1997; Zhang, 2012a): (1) Niche partition/Competitive exclusion. One of two species that utilizes similar resources would be replaced by another due to their competitive interaction. This is resulted from adaptive evolution that selectively utilizes resources, or the competitive exclusion between species. (2) Multiple attractors. A community could have multiple distinct steady distributions or alternative steady states. They represent different species assemblages occurred at possible similar conditions. History of community succession determines which steady state will occur. (3) Spatial range. Biological communities possess four orderliness, number of species, number of individuals per species, space occupied by each species, and space occupied by each individual. Spatial heterogeneity, like resource aggregation or resource gradient, may reduce competition or predation effect by providing local refugee or fine adaptive mechanism. Environmental variation is indispensable to species richness, which results in different succession rules. However, spatial heterogeneity of species and individuals is always ignored. (4) Open systems. Communities are self-adaptive systems. They can respond to continuous fluctuations of the environment and population.

So far, to develop and use assembly models for describing communities is a major tool in community ecology (Morton et al., 1996). However, assembly models of multispecies ecosystems with trophic structure have been less developed, starting from the early works (Pimm and Lawton, 1978, Pimm, 1979, 1980, Lockwood et al. 1997; Bastolla et al. 2001; Bonabeau, 2001).

As mentioned, communities are complex systems. They coincide with the characteristics of agents. Hence Agent-based Modeling (ABM) can be used to modeling spatial-temporal dynamics of ecosystems and biological communities (Jennings, 2000; Mellouli et al., 2003).

So far there are only a few of studies on how use ABM in ecology. Hraber and Milne (1997) developed an ABM model on the basis of a self-adaptive system, Echo. It can be used to simulate the dynamic process of species assemblage. In this model, there are behaviors like predation, competition and mating between individuals of different species or the same species. Different species and individuals have different genotypes and hence possess different fecundity and survival capacity. Fecundity and survival capacity might enhance by learning process. Genotypes of the species or individuals with greater fecundity and survival capacity are more easily multiplied. Spatial heterogeneity, however, is not considered in the model. Topping et al (2003) proposed an ABM model, ALMaSS, which was used to simulate the growth and spread of multiple species in the heterogeneous environment. This model does not consider the self-adaptive learning process of individuals, and there are only a few of between-species interaction types. The ABM model of Savage and Askenazi (1999), Arborscapes, can be used to describe competition, growth and spread processes of multiple tree species. Each individual in the model possesses some biological attributes and behavioral rules, and some disturbances like logging are also considered. As for between-species interactions, however, this model includes competition only. And self-adaptive learning process of individuals is ignored in the model.

The present study aims to present a framework of agent-based modeling for community assembly and succession.

2 Agent-based Modeling Framework for Community Assembly and Succession

ABM framework of community assembly and succession consists of three parts, obtaining dynamic data on community assembly and succession, agent-based modeling, analyzing mechanism of species establishment. Major procedures include

(1) Define agents, and specify agents' behaviors.
(2) Identify relationship between agents, and construct interaction types between agents.
(3) Choose the platforms and environments for ABM, and set the strategies of ABM.
(4) Obtain necessary data for ABM. In the experiment and investigation of community dynamics, obtain spatial-temporal data of every species in the community. Use artificial recapture method to simulate species invasion and diffusion. In addition, obtain some data from references and internet.

(5) Test the patterns of agents' behaviors and system's behaviors.
(6) Run ABM model, and analyze the output from the standpoint of linking the micro-scale behaviors of the agents to the macro-scale behaviors of the system.
(7) Analyze the mechanism of community assembly and succession using ABM model.

Some definitions and methods for ABM of community assembly and succession are described as follows.

2.1 Agents and behaviors

ABM can be based on existing modeling platforms, like Swarm, Echo, NetLogo (NetLogo, 2004). Other platforms or methods can also be used, such as ALMaSS, Arborscapes, etc (Repast, 2004). Java is a pure object-oriented, distributed, robust, structure-neutral, platform-independent and dynamic programming language. We may perform systematic modeling and program using Java. Computation-extensive objects and methods can be realized as DLL (Dynamic Link Library). The available modeling environments include Windows and Linux operation systems. Modeling languages are UML, Java (JBuilder), Delphi (Borland Delphi), and C (Visual C++).

In a community, functional groups, species, individuals, etc., can be treated as agents at various levels. Several types of agents can be defined as follows (Zhang, 2012c)

(1) Species agents. Species agents include predator agents, parasitoid agents, neutral agents, herbivore agents; or include agents that individuals of different species are just labeled with between-species coordination (positive or negative coordination, or neutral interaction (non coordination), magnitude of coordination). Between-species coordination can be derived from sampling species assemblages, expressed as partial correlation, coordination coefficient (Zhang, 2011, 2012b), etc.
(2) Space agents. They are represented by two-dimensional cells.
(3) Functional agents. They include interactive agents (user-model interactions), inductive agents (user induction of spatial dynamics, by such mechanisms as the change of distribution of plant resources (changing landscape structure)), data collection and analysis agents. Of these agents, some agents may be designed as Java classes or DLLs using Java, Delphi, or C++.

In the ABM model, the invasive species agent is treated as a common species agent in the community. Location and proportion of invasive species agent and frequency of invasive events are given fixed spatial or temporal probabilities.

The community is initialized with random specified number and location of individuals of every species, or initialized by investigated community data. The model proceeds on a month or annual or daily step basis.

The model includes plant resource input (herbivorous species agents must interact with plant resources). Herbivorous species agents are given an initial supply of each plant resource in its plant resource reservoir. A species agent may acquire resources from the environment or form the interactions with other species agents. Once enough resources are gathered, species agents can reproduce themselves.

Genetically-mediated behavior determines whether two species agents can interact. The species agent genome has two main regions, each with several attributes that code for a particular interaction. The *tag* region of the genome codes for attributes which are visible to other species agents. The *conditions* region represents attributes representing internal states, known only to the species agent itself. Matching a condition attribute against a tag attribute allows the interaction coded by those attributes to occur. Whether two species agents will interact is determined by comparing tag and condition attributes for that interaction. In the model, matching alleles in tag and condition attributes allows the interaction coded by those attributes. Tests for interactions are conducted sequentially: first for predation and competition, then for mutualism, and finally for mating.

Each species agent possesses some attributes: (1) a set of fixed, species-specific life history attributes, which include longevity, fecundity, age level, and others; (2) a time-relevant state (age, etc.). Species agents are autonomous and have adaptive behaviors, i.e., they adapt their behaviors (growth, feeding, habitat selection, mate choice, etc.) according to their state and the environment, to seek higher fitness by using learning algorithms, e.g., ANNs (BP, Hebbian learning, etc.) (Zhang and Barrion, 2006; Zhang, 2007, 2010; Zhang et al., 2007; Zhang and Wei, 2009; Zhang and Zhang, 2008; Zhang et al., 2008a, 2008b)

Modeling adaptive system dynamics via individualistic mechanisms of adaptation is a fundamentally different approach than modeling with differential equations.

There are many behavioral models for agents. They include if-then rule and threshold model, artificial neural network and genetic algorithm rules, differential or difference equations (Zhang and Gu, 2001), optimization rules, multivariable decision-making, etc.

The landscape dynamics depend on species agent interactions (competition, mutualism, predation, etc.) and dynamic landscape structure (plant resources distribution, landscape structure, etc.). System behavior depends on species agent interactions coupled with exogenous species agent. The spatial landscape of the model is a two-dimensional cell grid, in which each cell may be simultaneously occupied by many species (invasive species, indigenous species).

A space agent has major attributes including: (1) plant resources availability; (2) number of individual agents of each species; (3) landscape structure and space available for species, etc. Landscape structure is driven by weather and other factors. Species agents migrate between grid cells according to the states of adjacent spatial cells.

In general, the state transition method and differential/ difference equations can be used to model the dynamics of species agents and/or landscape structure (Zhang and Gu, 2001).

2.2 Model objects

On ABM platform, agents are implemented as objects. The model is expected to include these objects: Species, GridCell, Individual, Invasion, LandStruc, etc. The simplest and most common object is the Individual, the record of the state of an individual of species, including its life history attributes. Few methods are implemented in the Individual class as the Species object is responsible for the actual state transitions that an individual may undergo. For example, an individual object is sent a method and then relays the message to its species object with a reference to itself as an argument. The GridCell object provides the space in which the simulation is taking place, a simple square grid where each cell represents the area required by some individuals. The GridCell have:

(1) A reference from every occupied cell in the grid to the individual currently residing at that location.
(2) A separate list of all the individuals currently residing within its boundaries.
(3) Current landscape structure and food availability. LandStruc generates dynamic landscape structure based on state transition method (or difference equation method), or just load it from GIS.

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 individual belonging to the species. Attributes that differ across species include age levels, longevity, fecundity, trophic level, etc. The Invasion object is responsible for species invasion events in the model. Species invasions occur in space with uniform, random or aggregated distributions at pulse way. Other objects are designed to make user -model interactions, user induction, and data collection and analysis, etc.

2.3 Visualization tools

In addition to define agents and a schedule of events, the model should provide visual tools for the observation of the model on a time step basis. Windows will graphically track the abundance and spatial distribution of each species including invasive species, etc. 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. Windows allow modification of parameters include size and structure of the landscape, number of species, frequency of invasion, etc.

2.4 Pattern analysis

A pattern is anything above random variation and thus indicates some kind of internal organization. Pattern-oriented ABM starts with identifying a variety of observed patterns, at different scales and at both individual and system levels, that characterize the system’s dynamics and mechanisms. These patterns, along with the problem being addressed and conceptual models of the system, provide the basis for designing and testing our ABM. To analyze spatial and temporal pattern dynamics generated by the model, output can be linked to one of many pattern analysis packages. We may also write pattern analysis algorithms (spatial distribution patterns, topological structures, etc.) into the code. The model output may be linked to Fragstats (a comprehensive pattern analysis program). Its raster version is 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. On the other hand, we may design pattern analysis algorithms (spatial distribution pattern, topological structure (shape, size, mosaic density, boundary, connectedness, etc.)).

Identifying the critical invasion strength for community may help develop ways to manage landscapes to maintain a particular ecological function, or to make comparisons between different communities. The critical invasion strength for community can be determined by the method of spatial phase transitions.

2.5 Parameterization

A major problem of ABM of real systems is parameterization. Parameters are acquired from community investigation or experiments or internet. Many parameters would be uncertain or even unknown. Consequently, model results are uncertain and predictions and insights from the model become questionable. Sensitivity analysis with limited available parameter values will provide a partial solution.

2.6 Model application

The completed model will be used to approach patterns and mechanisms of community succession.

Usually, the steps of the ABM have to be repeated several times because this will lead to new theories, additional patterns, or modification of the entire ABM.

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