Use of an object-based model to represent complex features of ecosystems

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Abstract:

In this article, an ecosystem model that has been developed as an engineering tool is briefly described. Sample results from two simulations are then presented, and the model is examined with regards to its usefulness and applicability vis à vis the representation of complex features of ecosystems. The model is in many ways unique: First, its scope (i.e., the number of different types of ecosystem components that are included) is much broader than that of most other ecosystem models, and key processes are represented at relatively high spatial and temporal resolutions (10 metres and 10 minutes, respectively). Second, it is entirely object-based: every abiotic and biotic component in the system is represented as a distinct entity. Thus, each organism, or small group of organisms, is treated as an individual object that lives in a spatially explicit environment composed of cells arranged in a 2-D lattice. Third, the model is completely configurable, so that a wide range of ecosystem configurations and their corresponding initial conditions can be specified for simulation. Thus, both the biological composition (i.e., number and type of species, initial population sizes, etc.) and the environment (i.e., terrain and atmosphere) of an ecosystem can be specified. When implemented in simulation, configurations based on simple food webs exhibit sustained material cycling, non-random spatial variation and distribution of organisms over the terrain, and persistent, multi-trophic level population dynamics. It is argued that these phenomena are emergent, and are indicative of spatial and temporal self-organisation in the modelled ecosystems.

1. Introduction

Natural ecosystems have been shown to exhibit a wide variety of structural and dynamical features that are commonly attributed to the complex system, including self-organization, emergence of spatial and temporal patterns, efficient information processing, and effectively unpredictable behaviour. The description, and prediction, of these features pose special challenges in ecosystem modelling, since the underlying processes and relationships that give rise to these phenomenon tend to span multiple levels of organisation (e.g., organism to community) and involve intricate feedback loops. As a result, there has recently been a shift away from the use of conventional "top-down" analytical models to "bottom-up" object-based approaches, in which ecosystems are portrayed at a high level of resolution as networks of many interacting components (Grimm 1999, Judson 1994, Kawata and Toquenaga 1994). This has given rise to the proliferation of the use of individual or agent-based models, cellular automata, and Boolean networks to represent ecosystems. In these, the state of each component is usually described by a set of variable values, or attributes, and its mode of operation is described by one or more rule-based expressions. With this approach, the global level dynamics of a system is not prespecified, and is, rather, approximated in simulation as the aggregate behaviour of many low level components.

Ecosystem models created with an object-based approach have been very successful in demonstrating the role of individual components on global level behaviour (and the subsequent influence of higher level phenomena on the functioning of the lower level components), and in reproducing a wide variety of complex features (see for example Beecham and Farnsworth 1998, Booth 1997, Letcher et al. 1998, Lett et al. 1999). The approach, however, has not gained widespread use by research teams creating large-scale ecosystem models. Instead, most of the object-based ecosystem models that have been developed are either: a) single-species models that are strongly empirically based, or, b) abstract, general models that illustrate theoretical principles but lack real-world descriptive capacity. In contrast, the authors have developed an object-based ecosystem model that is of a wide scope, including all of the major biotic and abiotic components of an ecosystem, while at the same time being intended for use in real-world resource management and ecosystem design projects.

The model includes representations of up to 1000 species (represented by individual plants and animals), a spatially explicit terrain (soil and water), and an atmosphere. The dynamics of these are driven by climate (rainfall, temperature and radiation). All of the major material and energetic flows that occur in natural ecosystems arise as the result of the combined activities and functioning of the modelled components. The system is time-driven, with the state of each component being updated in regular 10 minute intervals. In addition, the model is completely configurable via the use of an ancillary set of definition and specification programs: the complete constitution and initial state of an ecosystem can be specified, including the types and numbers of objects, the rules that describe their interactions, and the variable values that describe their states. The model is written in C and is currently being executed on Pentium-based computers running Windows 98.

The model has been written as part of an engineering research program, called the EcoCyborg Project, the overall objective of which is to learn to design all types of loosely aggregated, complex biological networks, or biosystems. An important emphasis of the research program is that of *cyborging*, and the potential benefits and applications of the approach with regards to ecosystem engineering. This is the origin of the name “EcoCyborg”, which is the term we use to describe an ecosystem that has been enhanced through the addition of technological control components. We perceive cyborging to be an appropriate strategy by which to: 1) compensate for otherwise unviable or unstable ecosystem designs (this is the approach used in all agro-ecosystems, space-based life support systems, etc.); 2) provide increased autonomy and viability to natural ecosystems; and 3) achieve certain functional requirements in an engineered ecosystem (e.g., water purification, biomass production, etc.). In the short term, the objective of the EcoCyborg Project is to model and simulate a hypothetical ecocyborg, as a means of exploring how such a system might be engineered, and to thereby establish some theoretical design principles and methods.

Complexity, and the characteristic features of complex systems, play an important role in ecocyborg engineering for two main reasons. First, by acknowledging the natural tendency of an ecosystem to self-regenerate and self-organise into a meta-stable state (Holling 1996), engineers may be able to design and construct systems that are inherently more viable and resilient than those that have been haphasardly assembled. Second, any control system that interacts with a complex system must be able to respond and adapt appropriately to complex inputs, i.e., those that are highly correlated in space and time, yet effectively unpredictable.

The ecosystem model described here was, therefore, written to fit within the scope of this larger project, while at the same time having a general applicability to the representation of all types of ecological systems, be they natural or artificial in origin. It should be noted that this version of the model has been developed as a preliminary engineering study, the intent of which was to test the effectiveness of the modelling approach. Thus, not all of components or their functions are portrayed in an entirely realistic manner, nor have the model’s results been validated against data from a physical system. The primary goal at this time has been solely to incorporate at least a rudimentary version of each component in the model. In future versions, the functionality of the components can be improved and modified, as can the thousands of parameter values used to describe their states, in order to obtain a realistic representation of a given physical system.

In this paper, a brief overview of the model is given, and the results of two simulations are discussed with respect to a few examples of complex features that have been observed.

2. Model description

In the model, an ecosystem is represented as being made up of three realms: biological components (all of the living plants and animals), encompassment (soil, water and atmosphere), and material storage (large mass reserves that "buffer" material cycling in the system). Each realm is modelled with a collection of associated objects, whose states are described by properties (values of variables), and whose behaviour is described by rule-based expressions (functions). The model is time-driven; during each time increment, the states of the objects in each realm are updated sequentially. The behaviours of many of the objects (e.g., plants, soil, etc.) are affected by climate-related forcing functions (rain, temperature and solar radiation). A detailed description of the model's architecture and implementation, as well as the rules that determine the behaviour of each object type is given in Parrott (2000).

As previously mentioned, the model is completely configurable. First, all of the different object types that might exist in a system can be defined. Next, for a given simulation, the objects to be included at start-up can be selected from those that have been defined, and their initial states can be specified. This approach facilitates the specification of a wide range of different ecosystem configurations and their corresponding initial conditions, making the model suitable as an engineering research tool.

Our approach is unique in that a complete mass accounting is done for the system. Most object functions (e.g., decomposition, respiration, food consumption, etc.) involve exchanges of mass with other objects, and each exchange is tracked, no matter how small the amount. To facilitate the tracking of mass, the entire system is assumed to be made up of five elements from which nine basic compounds can be formed: carbohydrate, carbon dioxide, dirt (inert soil substrate), fat, inorganic nitrogen, molecular nitrogen, molecular oxygen, protein, and water. All objects are composed solely of some combination of these nine compounds.

2.1. Representation of biological components

In the model, a number of different species types are defined, and each biological component is an instance of one of these. In current configurations, there are primary producers (plants: herbs, bushes and trees) and consumers (animals: herbivorous and carnivorous mammals are currently included; bird and insect species, as well as less selective mammal consumers will be added in future versions). Each biological component object represents either an individual organism, in the case of trees, bushes, and animals, or a small "lump" of organisms, in the case of herbaceous species. The life cycles of all producers and consumers mimic those of real organisms, and are of a finite length. Biological components reproduce (currently by seed or gestation), but offspring do not inherit the attributes of their parents (i.e., evolution of species is not accommodated in the model). Instead, each new organism is created with attribute values that are typical of juvenile individuals of its species.

2.1.1. Plants

Plant objects of all species are modelled in essentially the same way. The body of each plant object is made of carbohydrate, protein and water, and this mass is apportioned into six parts: leaf, stem, seed, root, organic storage and inorganic storage. Each plant is located in one of the grid cells on the terrain, and cannot grow beyond the bounds of this grid cell. For each grid cell, the vegetation canopy is vertically differentiated into three layers, the boundaries of which correspond roughly to the heights of trees, bushes, and grass. A plant photosynthesizes as a function of incident irradiance on its leaf surface, which depends upon leaf area and the plant's position in the canopy. Plants proceed through the usual life cycle of seed, seedling, mature and reproductive phases, etc., with perennial plants repeating these year after year. Both deciduous and evergreen species are modelled.

2.1.2. Animals

Like plants, animals of different species are all modelled similarly. Every animal's body is composed of fat, water, and protein, which is apportioned into fatty mass and lean mass. Animals also have stomachs, in which they hold food that has recently been consumed but not "digested". A very simple energy accounting scheme is used for animals in order to estimate their feeding requirements; during each time step, an animal must metabolize a sufficient amount of fat to meet its basal metabolic rate, plus any costs of growth, reproduction, movement, etc. Metabolized fat is replaced by food that is absorbed from the stomach. Thus, an animal must continually eat in order to stay alive; an animal that does not do so will die of starvation. Animals are mobile; they move about the terrain in order to find food, and to seek out a mate with which to reproduce. If an animal does not first die of other causes, it will die of old age.

All animals are related by means of a food preferences matrix, which defines the relatively "delectability" of one species to another. It is via this food matrix that an animal's eating habits are defined; a herbivorous animal, for example, will have fairly high food preferences for a number of plants, and food preferences of zero for other animals. At the moment, behavioural routines are fairly minimal, and prey do not flee from approaching predators.

2.2. Representation of the encompassment and material storage realms

All organisms live in a spatially explicit world that consists of a terrain and an atmosphere. The terrain is modelled as a regular array of rectangular cells, each of which has a number of properties, such as mass of saturated and unsaturated water, mass of organic matter, etc. Terrain routines include subsurface water flow, decomposition, nitrogen fixation, etc. Organisms interact with grid cells in a number of ways, for example, a plant absorbs water and nitrogen for growth from the terrain, and when a plant or animal dies, its corpse is added to the decomposing material in its current grid cell. Each organism "knows" its location on the terrain at any moment.

The atmosphere is assumed to be a perfectly mixed gas. Its pressure and composition (water, molecular nitrogen, molecular oxygen and carbon dioxide) are controlled by means of material transfer between the storage and the atmosphere. Organisms exchange material with the atmosphere via respiration and photosynthesis.

The material storage realm is simply a large mass of material in the solid state that is present in imitation of the various buffers that exist for natural ecosystems on Earth (e.g., the ocean, atmosphere, etc.). It consists of four chambers that contain water, molecular nitrogen, carbon dioxide, and molecular oxygen. These are accessed as required for various “control” purposes.

3. Examination of the modelling approach with regards to the representation of complex features of ecosystems

For testing and demonstration purposes, the model has been configured to represent a materially closed ecosystem of fairly small size, such as would be enclosed in a space station or other similar structure. The total volume of this hypothetical system is 13.4 x 10^6 m^3, with 33% allocated to material storage, and the remaining portion being used for the encompassment and biological component realms. The terrain has a surface area of 500 x 500m, and is subdivided into 2500, 10 x 10m grid cells. It has a gently rolling topography that slopes towards a central pond.

Sample results from two simulations based on this general configuration are presented and discussed here. Each experiment was run for 50 simulated years, at a time increment of 10 simulated minutes per cycle. The ecosystems in both simulations were configured with identical encompassment and material storage realms (i.e., the same initial atmospheric composition, soil properties, etc.), but with different biological communities. The first, EcoSim1, was configured to represent a “grassland” ecosystem, composed of only herbaceous species, and no consumers. The second, EcoSim2, was configured with a community of both plants and animals (herbivores only). Each ecosystem was subjected to the same series of weather inputs, corresponding to a mild, temperate climate.

3.1. Autopoiesis: Persistence of species, regeneration of the biological community after a trauma

The concept of autopoiesis, or self-regeneration, has often been used as a defining characteristic of complex living systems (Maturana and Varela, 1980) and has been discussed in the literature with reference to the ability of biological systems to regenerate damaged components, thereby maintaining global level structures. Ecosystems, as well, are autopoietic systems: In an established ecosystem, the structure of the biological community and the distribution of biomass amongst the components of the system, is maintained in the presence of continuous environmental “noise”. An ecosystem that undergoes a severe trauma, such as a forest fire or the loss of a keystone species, for example, will regenerate, resulting in a new, meta-stable state (Green, 1994). Similarly, in EcoSim1 and EcoSim2, both the persistence of species, and the regeneration of the biological community after a trauma, can be

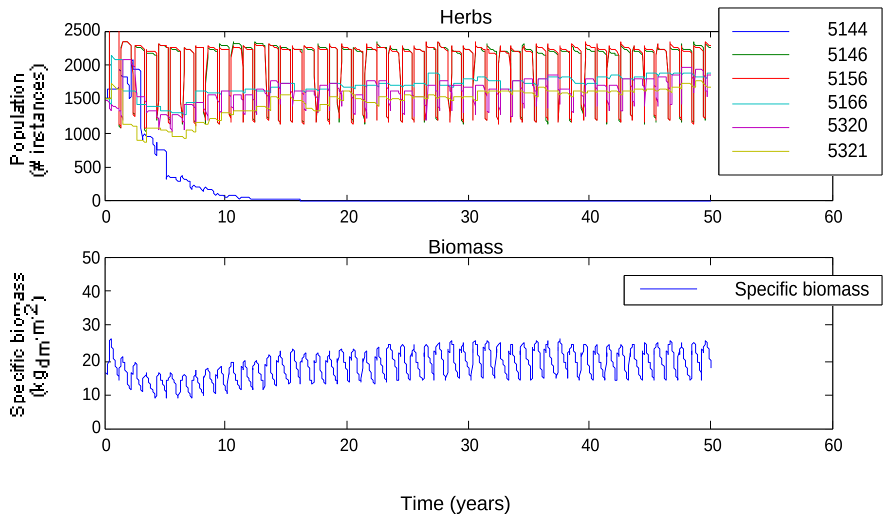

Figure 1: Population dynamics and specific biomass versus time for EcoSim1. Numbers in the legend refer to different species.

observed. These two phenomena in an ecosystem may be interpreted as examples of autopoiesis at the population and system levels, respectively.

In EcoSim1 (Figure 1), a grassland ecosystem is established and persists over the long-term, reaching a relatively stable specific biomass. Annual cycles in total population numbers and biomass are apparent; these arise due to the seasonal cycles of growth and dormancy experienced by many of the plant species. In this case, autopoiesis is exemplified by the system's ability to maintain a persistent meta-stable state at the global level, while at the same time undergoing continual replacement of lower level components (individual organisms).

In EcoSim2 (Figure 2), the resultant global dynamics are quite different from those of EcoSim1, due to the presence of herbivores. In the first few years of the simulation, most of the herbaceous species in the system are grazed to extinction. Two species (#5146 & #5321), however, undergo initial population crashes and then regenerate. The herbs are consumed by three species of herbivores, one of which (#5011) becomes extinct in the first year of simulation. The others, supported by the two remaining herb species, fall into a pattern of persistent, annual population cycles that mirror those of their food source. In addition to annual cycling, a completely emergent, multi-year cycle of predator-prey dynamics can be observed. Thus, in this case, the plant and animal species, and the ecosystem as a whole, exhibit the autopoietic ability to regenerate, with the ecosystem evolving to a two trophic-level meta-stable state characterized by persistent cycles of predator-prey dynamics.

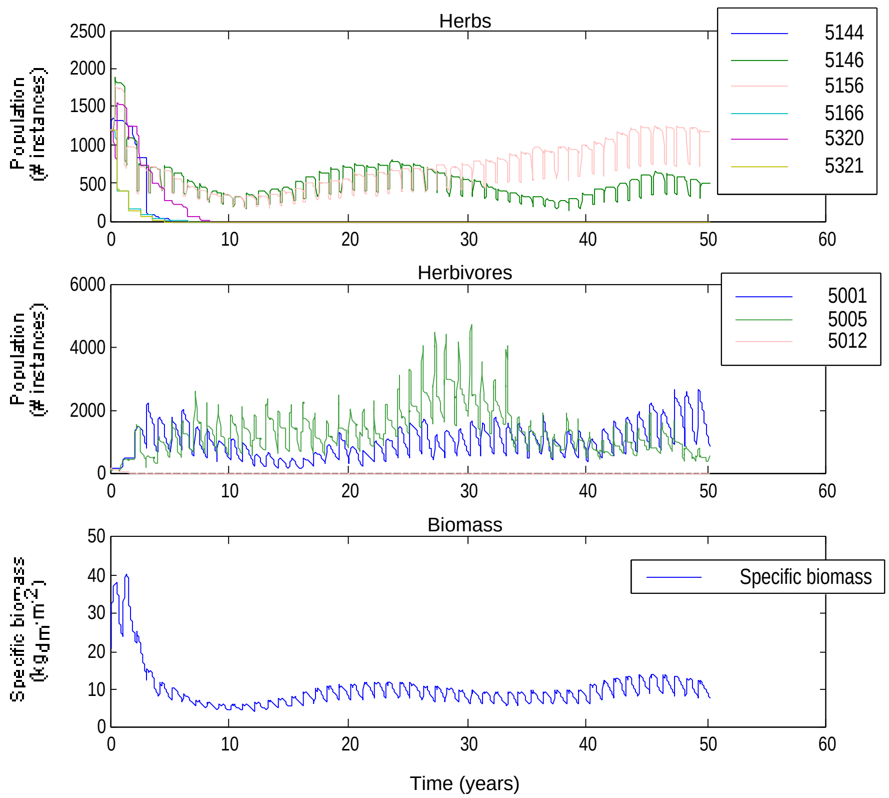

Figure 2: Population dynamics and specific biomass versus time for EcoSim2. Numbers in the legends refer to different species.

3.2. Spatial self-organisation: Emergent patterns of species distribution

Spatial self-organisation, i.e., the development of spatial patterns in the ecosystem, was observed in many instances, with respect to the distribution of species about the terrain. One example of this is shown in Figure 3 for species #5146 of EcoSim2. This herbaceous species withstood initial, very high levels of grazing, causing its population to be decimated. Its relative abundance (in terms of mass) and the number of instances in the population later increases, although the species distribution remains patchy. This patchy distribution is maintained throughout the simulation as a result of grazing by herbivorous species. This distribution pattern was persistent, and also entirely emergent, i.e., its development was not pre-specified, nor was it readily deducible from the initial model specification. This type of spatial dynamics, in which a heterogeneous distribution is seen to emerge from an initial homogeneous distribution, was typical for all simulated plant species subjected to predation by herbivores.

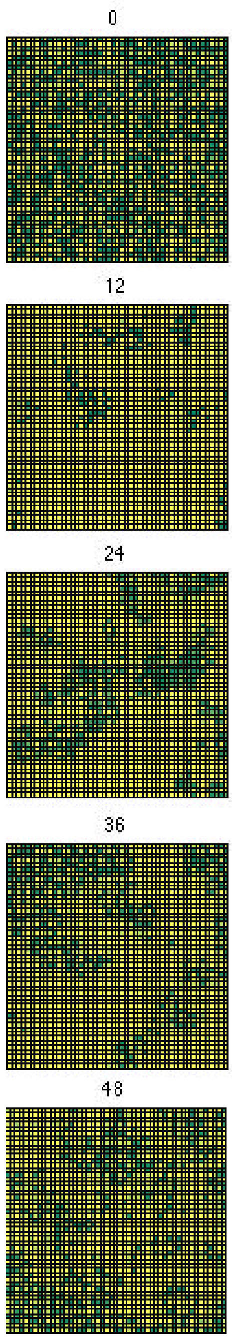

Figure 3: Spatial distribution of a sample grass species (#5146) in EcoSim2, at 12 year intervals. Each square represents a grid cell on the terrain; colouring of squares indicates presence of the species, darker coloured squares are more densely covered.

4. Conclusions

One of the most salient characteristics of a complex system is the presence of dissimilar spatial and temporal features at different scales. This makes a complex system difficult to describe since, for each observable regularity or feature at a particular scale, a different descriptive model can be written. Thus, one of the challenges in modelling and simulating such systems is to find a means by which as many of these features can be represented as possible. The object-based modelling approach that has been used for the development of this ecosystem model has been explored as a way to depict many of the features of a complex system over a range of scales.

With this approach, an ecosystem was represented at a variety of different levels of resolution: the level of the organism in the case of some species, and of the small lump of organisms for others; the level of the grid cell in the case of the terrain, etc. In addition, for each component that was represented as an object, some higher resolution information regarding the object's composition was retained (e.g., masses of the different parts of a plant, animal, or grid cell, and the corresponding compositions of these in terms of the various mass forms that are tracked in the system, etc.). Through this representation of the states of lower level components, and the subsequent implementation of these in simulation, many interesting features have emerged at all scales, particularly those corresponding to the population and ecosystem levels.

The object-based modelling approach, as used in the development of the ecosystem model described here, has proven to be an effective way to represent ecosystems and to simulate their behaviour.

The approach has enabled a relatively complete depiction of an ecosystem, including material cycling, food web relationships, and the presence of many different types of organisms. Simulation results have been achieved that exhibit phenomenological similarities to physical ecosystems (e.g., trends in biomass accumulation, and population dynamics), as well as features typical of complex systems (e.g., autopoiesis, spatial and temporal self-organisation). Overall, the approach has enabled the development of a model that is a novel contribution to the field, both with regards to the scope and resolution with which an ecosystem is represented, and the type of comportment that is elicited in simulations.

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