Agent-based dynamic modelling of forest ecosystems at the Warra LTER Site

W. Su[1,2*], M.J. Brown[3] and B. Mackey[1]
[1] Department of Geography, Australian National University, ACT
[2] Current address for correspondence: Department of Primary Industries, Water and Environment, GPO Box 44, Hobart, Tasmania 7001
[3] Forestry Tasmania

Abstract

A spatially explicit, dynamic simulation model of forest ecosystems at the Warra LTER Site was prepared. The advantage of this form of modelling is that one can not only explore the dynamic interactions of the sub-components of the ecosystem but also experiment with different disturbance regimes and management options.

The simulation model was built using an agent-based modelling approach. The approach builds a virtual landscape ecosystem and simulates how the various components of the forest ecosystem fit together and interact with each other. Fire is the main disturbance source in the succession of the eucalypt forest ecosystem in this area and plays a critical role in the process of patterning the forested landscape. The emergent patterns from the simulation are in accord with the succession theory for the type of the forested ecosystem being modelled. Fuel dynamics are the main contributing factors to the definition of the fire regime of the forest ecosystems, and study of fuels in relation to topographic features is needed to further improve the simulation result.

Introduction

A critical issue for native forest management is the accumulated and long-term ecological impacts of silvicultural regimes and forest management practices. Forecasting these potential impacts is very difficult for a number of interrelated reasons. Forest ecosystem processes are played out on a landscape-wide basis, whereas traditional forest survey is limited to networks of small sample field plots. Thus, we generally lack data about the larger scaled patterns and processes. Furthermore, the patterns of biodiversity and vegetation structure vary through time in response to fire regimes and ecological processes that govern forest successional pathways.

Simulation modelling provides a tool for exploring how forest pattern and process may vary through time on a landscape-wide basis. However, no suitable landscape dynamic model has been available for application in Australia. Consequently, this project aimed to develop a prototype landscape dynamic model suitable for exploring the long-term impacts of land use and global change perturbations, and to investigate the ability of the model to replicate current forest ecosystem pattern in a test landscape in the Southern Forests of Tasmania. The work reported here forms part of a PhD project undertaken by the senior author at the Australian National University.

An ecosystem is a self-organised, complex adaptive system (Brown 1994). The ecological processes acting within an ecosystem create patterns at different spatial

* Corresponding author
e-mail: mick.brown@forestrytas.gov.au
brendan.mackey@anu.edu.au
wengui@dpiwe.tas.gov.au

and temporal scales. The nature of these patterns will vary depending upon dynamic interactions among the constituent biota of the ecosystem and the environment. The complexity of ecosystem phenomena results from dynamic interactions of hierarchically structured components. Thus phenomena at one level may be the result of interactive processes among components at other levels.

Object-oriented modelling is a technology which can assist in formulating a model of a complex system in the real world. The basic elements of design in object-oriented modelling are the objects and object interactions. Objects formulated in a model are largely abstractions of the objects in the real world ecosystem. In computer programming, data and operations are grouped into a self-sufficient modular unit as a subprogram which represents an equivalent abstraction of objects in the system being modelled. A model can be formed by combining the objects into structured networks in a hierarchy. With object-oriented modelling, the nature of the interactions among the hierarchically structured components can be explored, and the emergent properties resulting from these interactions can be experimented with.

This study is based on the wet eucalypt and rainforest ecosystems at the Warra Long-Term Ecological Research (LTER) Site in southern Tasmania. The ecology of these types of forest has been well studied (e.g. Gilbert 1959; Jackson 1968; Brown and Podger 1982; Jarman and Brown 1983; Read and Hill 1988; Kirkpatrick *et al.* 1988; Hickey 1994; Read and Brown 1996; Reid *et al.* 1999) giving an empirical and theoretical base for the formulation of the simulation model. The study examines the complex ecological succession paths in response to environmental resource gradients and fire regimes, as well as the main ecological processes.

The model built in this study is an agent-based, discrete event, simulation model based on a generic object-oriented simulation framework called Swarm developed by the Santa Fe Institute (Minar *et al.* 1996). It provides a group of reusable software objects for managing, analysing, displaying and controlling simulation experiments. With Swarm, an agent-based discrete event simulation model of a complex system can be built. In this simulation model, an individual tree is the basic agent. There are also other objects representing the environments where the agents live.

Model design

The purpose of this simulation model is to observe how species diversity emerges from the interactions of individual trees with the environment and disturbances due to fire, to determine the regeneration process.

The individual tree was chosen as a key agent in this simulation because species diversity is both an emergent property from individual trees and an important feature of forest ecosystems. The model simulates the biological processes of birth, growth and death for each individual tree. These processes in turn are controlled through the interactions of each of the individual trees with their local environment.

The environmental objects are treated as a series of two-dimensional lattice objects representing the environmental conditions in which the trees live. A two-dimensional discrete lattice defines the spatial location of the tree objects. Models built in this way can be viewed as a virtual landscape inside the computer.

The objects in the simulation model are able to dynamically update their properties according to events such as regeneration, growth, death and fire during each of the simulation time steps. Each of the objects has its own life span and schedule for change through time. Some of them are static since they slowly respond to time or other events. For instance, a topographic feature is relatively static over a 100-year period, and therefore can be treated as constant during the simulation. Others such as trees grow every year and their properties need to be updated in every simulation time step. The simulation was designed to run using a yearly time step over periods of hundreds of years.

The model also incorporates the effects of regeneration, mortality and fire processes.

Model development

The ecosystem in the study area has been divided into three distinctive subsystems: the climate, the environment and the forest.

1. Climate subsystem

The climate is a broadscale phenomenon, and is treated as a constant and global constraint on the local physical environment processes in this model.

The local environment variables such as temperature, rainfall, surface hydrological dynamics and soil moisture condition etc. are interpolated from topographically related physical and ecological processes. These variables and related processes were modelled through ANUCLIM and used as inputs to the simulation model as part of the environment component.

MacArthur's (1962, 1967) forest fire danger index (FDI) is used to characterise the climate condition of the fire season in this simulation. The FDI is used as a variable for the risk of forest fire during the fire season in the study area. Under a specific weather condition, the fire occurrence and the behaviour depend on local conditions such as topographic features, fuel load, etc. The FDI is used here as a general qualification of the weather condition, it is not spatially explicit in this model.

Fire has a critical impact on the dynamic development of the wet sclerophyll forest ecosystem. It consists of four component variables: temperature, air humidity, wind speed, and drought factors in soil. The form of the FDI is:

$$FDI = 1.25 \cdot D \cdot e^{(T-H)/(30+0.234w)}$$

where FDI is the forest fire danger index, D is drought factor (1 to 10), which is a function of soil water deficit; T is air temperature; H is air humidity; and W is the wind speed in the open, 9 m above ground.

2. Environment subsystem

In the environment subsystem, four objects have been identified to act as the main controllers of species diversity in southern forests: elevation, aspect, slope and soil moisture. Each effect is discussed below.

Elevation.—Elevation gradients affect environmental variables such as temperature and rainfall, and thus may define the distribution of the different types of the vegetation community and species diversity. The elevation is represented in a three-dimensional surface in the simulation model just as a digital elevation model (DEM) does in geographic information systems (GIS).

Aspect.—Aspect is modelled as a spatially distributed, two-dimensional, passive object and has strong effects on fire and fire behaviour. The north-west aspect is drier than others because the prevailing wind is north-westerly. Three aspect directions have been sampled, based on the effects of the aspect on fuel load properties of the ecosystem in the study area. The effects of the aspect on fire behaviour through rate of spread and intensity of the fire have also been spatially explicitly modelled.

Slope.—Like the aspect object, the effect of slope is only considered on fire behaviour. It is assumed here to have little effect on the modelled species diversity of the ecosystem. There may be other complex interactions which exist between the slope and the ecosystem but the effect on fire is considered to be most important for this simulation model.

Soil moisture index.—Soil moisture affects various aspects of the ecosystem and has a significant effect on fuel moisture content (Cheney 1981). The effect of fuel moisture content on the behaviour of fire has been modelled in relation to soil moisture in this simulation model.

3. Forest subsystem

There are four objects (and two sub-objects) identified and considered the major sources to contribute to the emergence of the characteristics of the ecosystem: trees, species, forest (including young and mature subsets) and seed space. Each is discussed below.

Tree object.—The simulation model is built under the assumption that the individuals are the major source of emergent properties of the ecosystem. The species diversity or species composition at a particular site arises from the contribution of each of the individual trees.

Species object.—Each tree belongs to a species, which is also identified in the model. The species object is designed to capture the similarity of features at the species level. The separation of the features of a species from a tree is a level of abstraction since the features at species level never change on a basis of each individual tree. Examples include shade tolerance, seeding and seedling features, age to maturity, longevity and reproduction.

Forest object.—The forest object is a level of hierarchy above the tree and species. The purpose of the forest class forms a virtual forest ecosystem (Figure 1). Therefore, the forest class consists of a two-dimensional lattice, which identifies the location of each individual tree and the trees that are spatially distributed on the two-dimensional lattice.

In order to distinguish the different aspects of the age of a tree in the process of regeneration, and the process in response to fire, the forest object has been sub-classified into young forest and mature forest objects.

The young forest objects grow and get transferred to mature forest objects, leaving a space for new seedling establishment. Young forest objects are killed by fire and old forest objects eventually die, also leaving a space for a new seedling.

Seed space object.—The seed space object is designed to keep track of the seed availability for the regeneration process. It

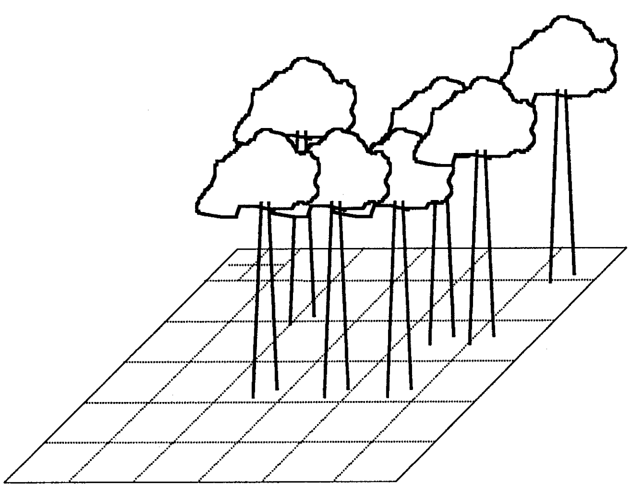

Figure 1. A visual presentation of the forest object.

is a dynamic mechanism to let species compete for available locations. Seed space associates with each of the species and interacts with regeneration processes. It also has a feedback effect from fires because fire stimulates seed germination for some species.

Ecological process related objects.—There are two main linked ecological processes which are critically important to the wet sclerophyll forest ecosystem dynamics. The first is the regeneration process and the second is fire.

The seven species chosen in this simulation model have distinctive ecological characteristics in response to the two important processes. Regeneration of *E. obliqua* and *E. delegatensis* relies on fire, whereas the rainforest species do not. Therefore two types of regeneration must be simulated differently in response to fire and non-fire events during the simulation. In terms of function, these two types of regeneration processes have distinctive differences.

The regeneration object.—The regeneration object is designed to model the regeneration process of the rainforest species in the ecosystem at each simulation time step. This object is scheduled in a yearly time step and interacts with the seed space object, species object and forest object to carry out the regeneration process. The regeneration process object gives uniform control of the regeneration process in the simulation and ensures every species gets the same opportunity to compete for regeneration space.

The responsibility of the regeneration object is to trigger the regeneration process (by sending a message or invoking an operation) of the forest object at each time step during the simulation. It is scheduled in Forest Model Swarm against the global clock each year to emulate the season for seedling establishment (spring), during which the seeds from last year will be ready for germinating if there is a spare site and the condition at that site is suitable. A suitable condition is where there is a site available for occupation by a proper species which has sufficient seeds. If more than one species is suitable for the site, other controls or rules are introduced to decide which one has the establishment advantage. Final decisions on an unresolved conflict are by random selection. However, this is not common since the species chosen in this study have distinctive ecological preferences which hardly ever conflict.

The season triggers the regeneration process. The species are checked annually one by one. If it is, for example, a eucalypt species, and there is no fire at the sites, no regeneration process occurs. If it is a non-eucalypt species, the regeneration process will start. As was discussed earlier, the competition for sites depends on the seed availability and other ecological properties of the species such as shade tolerance. A random shuffle is used to decide how many seeds for a species can be germinated if there are many sites suitable for that species.

Fire regeneration object.—The fire regeneration object is responsible for the fire-related regeneration process of the species.

Fire is a highly variable event both in space and time. The occurrence of the fire depends on ignition source, seasonal local climate and weather conditions, topographic effects and vegetation.

Fire object.—A fire object models the process of fire in relation to the development of the ecosystem. Since the occurrence of fire relies on the weather condition during the fire season, the weather condition is generated based on the distribution of the fire danger index (FDI) during the fire season from real data. The fire object serves as a spatial and temporal generator of the occurrence of random fire in the simulation. The occurrence and behaviour of fires will depend on the fuel load and time since last fire. The effects of the fire on the forest will depend on the species characteristics as well as the status of each of the individual trees.

In order to create a generic scenario of the climate condition during the fire season in the study area, two years of daily based weather data were obtained from the Bureau of Meteorology in Tasmania. These data were used to calculate the monthly spread of FDI values. This distribution of FDI values was then used to randomly generate the local weather conditions in the fire object. In future models, the distributions would incorporate more extreme events to include summers of very low FDI as well as high extreme events such as in February 1967.

Fuel load object.—The fuel load object represents the fuel accumulation dynamics. Although the occurrence of the fire depends on the local climate and weather conditions during the fire season, the behaviour of the fire will largely be decided by the fuel load of the site and topography as well as topographic-related features such as soil moisture condition. The fuel load is closely related to the intensity of the fire, while the topographic feature decides how the fire spreads across the forested landscape.

For the fuel load dynamics, there are many models to describe the fuel accumulation over time in *Eucalyptus* forest. The equation is used also in various mathematical forms such as polynomial (Hutson and Veitch 1985) and linear equations. The most commonly used form of fuel load model is as follows:

$$W_t = W_{\max} (1 - e^{-kt})$$

where W_t is the fuel load at time t, $W_{\max}$ is the maximum fuel load under the static condition, k is the fuel decomposition rate, and t is the time since last fire.

The fuel space spread of the fire is calculated using the following algorithm in the fuel space:

$$F_{(x,y)} = \sum_{(i=x-1,j=y-1)}^{x+1,y+1} F_{(i,j)}$$

where $F_{(x,y)}$ is the fire at location (x, y).

The fuel space object is a dynamic object with feedback effects from the environment objects and the fire object. Therefore, the fuel dynamics of the forest floor in the study area is not only a function of time since last fire but also of the variables describing the topographic features of the study area. Calculations are based on observations made in the Southern Forests of Tasmania. The strong influences of the topographic features, mainly slope and aspect, on fire intensity and rate of spread across the wet sclerophyll forest have been discussed by Cheney (1981).

The fuel load object is also used to calculate the rate of spread and intensity of the fire at the specific location based on the topographic features and the fuel load of that site. The rate of spread on flat ground is calculated by using Noble's equation (Noble *et al.* 1980),

$$Ros = a \cdot W_f \cdot FDI$$

where Ros is the rate of spread (m/hr), and W_f is the fuel load (t/ha), FDI is the forest fire danger index (MacArthur 1962) and a is constant (1.2).

Time since last fire object.—In the fuel load object, the fuel load is a function of time since last fire. Therefore, another object which records the variation of time since last fire has been created to indicate the elapsed time of the fire at each location in the study area. It is dynamically updated during each simulation time step.

Simulation control related objects.—Objects do not stand alone, they must be put together and interact to make a usable model. The object's interactions come into play only when we put them together in the correct way. This is the final task in simulation modelling.

At the final stage of the modelling, the Forest Model Swarm object initialises the objects created from the modelling process and schedules them in a logical order. It also establishes the overall interactions of the objects. Figure 2 describes the interaction relationship of the objects of the Forest Model Swarm object, and Figure 3 gives an overview of the overall structure of the simulation model.

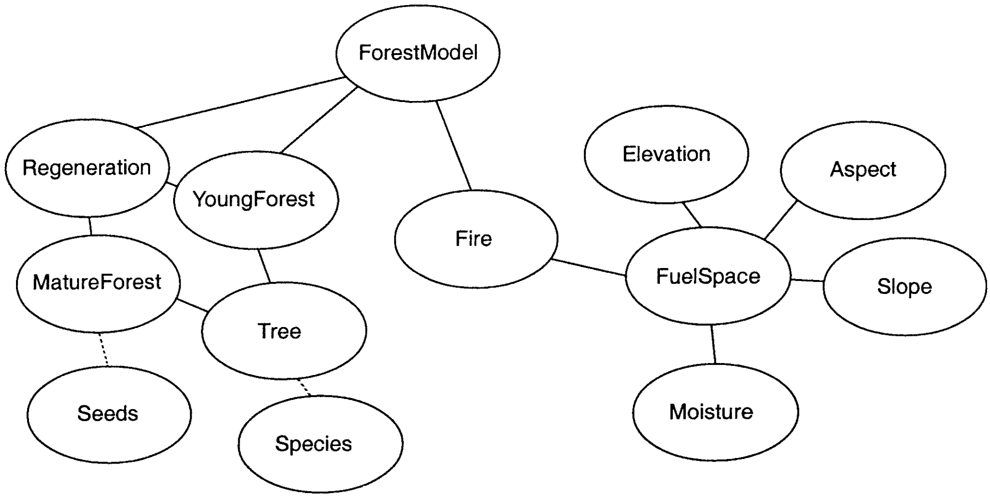

Figure 2. The relationship of the objects inside the Forest Model Swarm object. Solid lines indicate that, for example, fuel space is a function of moisture, slope etc. Dotted lines indicate an association relationship; for example, each tree and seed belong to only one species.

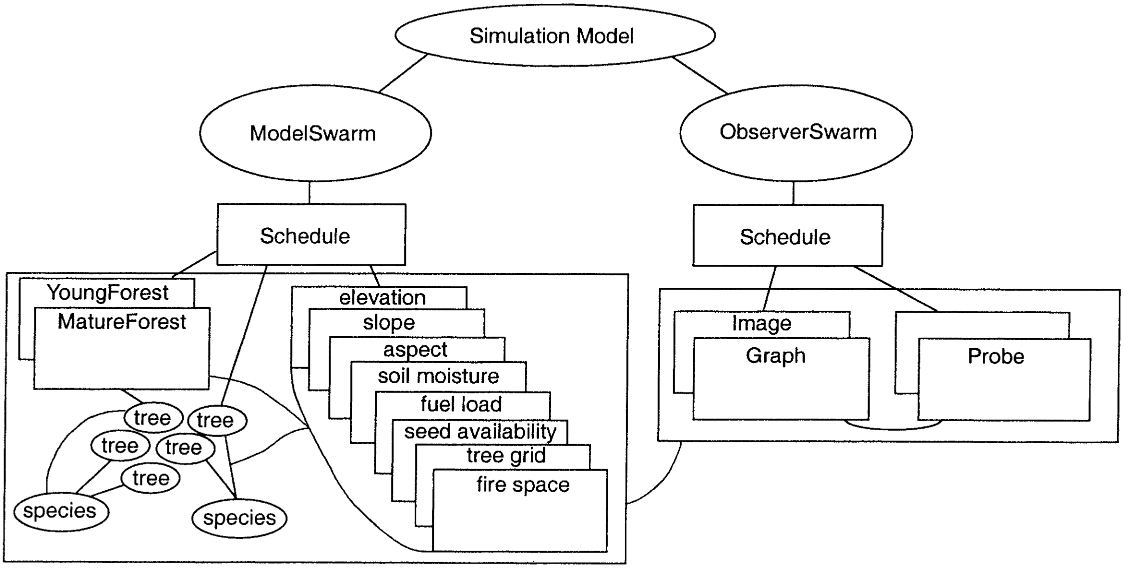

Figure 3. The overall structure of the simulation model.

Simulation

The characteristics of tree species as individual agents

The simulation is based on seven species. Each of them represents an important ecological or functional group within the ecosystem. The characteristics of the seven species are given below.

***Eucalyptus obliqua*.**—*Eucalyptus obliqua* is a widespread and dominant species in wet sclerophyll forests. It lives for 350–450 years. The site preference for *E. obliqua* is comparatively mesic, well-drained, lowland habitats on a variety of substrates and terrain associated with relatively higher fire frequency. The substrates often are dolerite, sandstone and mudstone. The altitude range is below 400 m in the study area. It represents various types of communities, from wet sclerophyll to mixed forest through combinations with other species. It displaces *E. regnans* on deep, well-drained soils on fertile sites which are relatively drier with moderate to high fire frequency, and is itself replaced by *E. delegatensis* at higher altitudes on similar sites.

Regeneration of *E. obliqua* in wet forests relies on fire (Hickey 1994). The succession pathway is decided by fire regimes, especially the interval between fires, or fire-free period after the fire. At the stage of wet sclerophyll forest, if the fire regime changes and the interval between fires becomes long enough, the succession is towards rainforest through the mixed forest stage. However, if the fire regime remains the same, wet sclerophyll forest types would be maintained. The fire intensity and season also play an important role in deciding the species composition and age structure of the forest community.

The species composition and community structure often correspond to the soil fertility and moisture gradient of the sites. Heathy understoreys are typical on siliceous soils. On fertile soils, a tall scrub understorey will be present. On moist fertile sites, a pure stand can be formed. With decrease of soil moisture, it coexists with other eucalypt species such as *E. viminalis*.

Eucalyptus obliqua has canopy-stored seeds which are available each year and are dispersed through gravity. Regeneration occurs only after fire.

***Eucalyptus delegatensis*.**—Ecologically, *E. delegatensis* is similar to *E. obliqua*, except it has a higher altitude distribution than *E. obliqua* (between 400 and 600 m). It occupies comparatively fertile, moist, well-drained sites with Jurassic dolerite soil parent material.

Eucalyptus delegatensis can dominate a range of community types. It forms pure stands but frequently associates with *E. obliqua* at lower altitudes. This species is more fire sensitive than *E. obliqua*.

***Nothofagus cunninghamii*.**—*Nothofagus cunninghamii* is a cool temperate rainforest species. It lives for 400–600 years. Rainforest can perpetuate itself without broadscale disturbance (Jarman and Brown 1983). It is fire sensitive and may be converted into *Eucalyptus* forest after fire, if there is an available seed source. The altitude range of *N. cunninghamii* is very wide. It can grow from sea level to 1500 m but grows best below about 700 m. The current distribution of rainforest in the study area is in moist, sheltered gullies along drainage lines where humidity is high, and on well-drained, moderate to steep slopes topographically protected from fire.

In the model, this species is the main representative of rainforest components and can either form a pure rainforest alone or in association with *Phyllocladus aspleniifolius*, or occur as a subordinate stratum to eucalypts within mixed forests. It is less shade tolerant than *Atherosperma moschatum*, which may replace it in small stands in wet gullies (Read and Hill 1988). We do not take this situation into account in the simulation since there is little pure *Atherosperma* forest found in the study area.

Nothofagus cunninghamii seeds every year, although mast years do occur. Seeds are ground stored with a longevity of three years. Seed dispersal is by gravity and wind. The regeneration is continuous without fire.

Phyllocladus aspleniifolius.— *Phyllocladus aspleniifolius* is another rainforest component. Its altitude range is from sea level to 800 m and it lives for more than 800 years. It has a wide topographic range and is often associated with *Nothofagus cunninghamii, Atherosperma moschatum, Eucryphia lucida* and *Acacia melanoxylon.* Also it can be present in mixed forest with *E. obliqua* and *E. delegatensis.*

In this simulation model, it acts as a species to form both rainforest and mixed forest types. It is assumed to produce good seed every year, seed longevity is between five to seven years, and seeds are dispersed by birds. Regeneration is assumed to be continuous in the absence of fire.

Acacia melanoxylon.—*Acacia melanoxylon* is a widespread species that appears in many different communities. It usually dies after 80–120 years. It ranges from sea level to 800 m on a wide range of topography, from low-lying swamps to mountain slopes. It is found in rainforests, mixed forests and wet sclerophyll forests.

In the model, *A. melanoxylon* represents species related to a range of time scales of disturbance and can associate with wet sclerophyll forests as well as rainforest. It seeds annually in huge quantities and relies on gravity and small animals for dispersal. Regeneration is rare without disturbance.

Pomaderris apetala.— *Pomaderris apetala* represents the broad-leaved shrub component associated with wet sclerophyll forests. It lives for 60–80 years. Its seeds are gravity dispersed and ground stored. Regeneration occurs after broadscale disturbance.

Gahnia grandis.—*Gahnia grandis* is an early coloniser after fire and only persists with frequent fire. It lives for 15–25 years. Its seeds are ground stored and dispersed by birds and gravity.

The simulation was carried out for an area of 9 km by 6 km in the Southern Forests at the Warra LTER Sitein Tasmania. The model was set to run for 500 years. The spatial pattern of the species diversity can be clearly viewed by converting the result into images.

Results

The result of this simulation is a series of snapshots taken from the simulation at 25-year intervals. The output of the species distribution data is put into text files and imported into a GIS and presented as a grid. The pattern of the species distribution can then be viewed in image form.

The simulation result can be viewed as a reassemblage of the species distribution in the real world. For example, classification methods can be applied to obtain a vegetation map since the vegetation type is defined by the species composition. Sometimes there are clear boundaries and sometimes boundaries are unclear and can only be defined by statistical classification techniques.

Patterns readily emerge from the simulation. Figures 4 and 5 are snapshot images taken at 100 and 500 years from commencement of the simulation. Different shades represent different species, with black being recently burnt (newly available habitat) areas.

Figure 4 is the snapshot at 100 years. From this image, there are clear patterns emerging after fire disturbance. A few fires have occurred in the area, creating patches of varying species composition and age structures. The large central grey patch is *E. delegatensis* regenerated from an early fire. The black patch on the right is a freshly burned patch. The species are in the recovery phase. The light grey colour inside the black patch is *Gahnia,* which is a pioneer species colonising the latest burned patch.

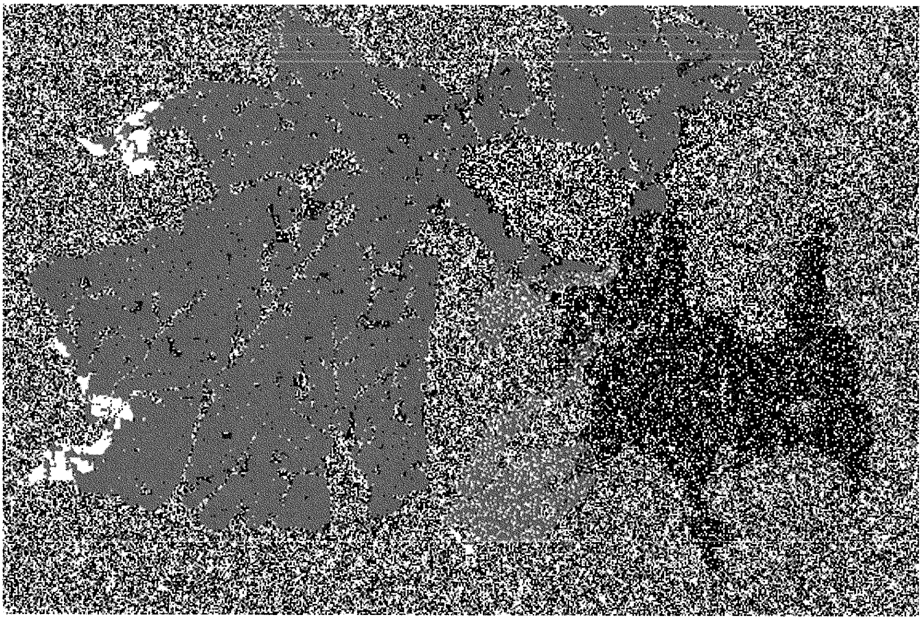

Figure 4. Simulation at 100 years.

The result at 300 years is similar to that at 100 years, but the pattern evolves at the local scale since succession is happening without major fire disturbance. The species composition in the area undergoes progressive change. More and more wet sclerophyll species invade the ecosystem. A close examination of the simulation shows that clear natural boundaries are related to sharp topographic changes and abrupt fire-disturbance events. The succession elsewhere takes the form of changes in relation to local environmental gradients and competition for resources.

The snapshot at 500 years (Figure 5) is the final stage of the simulated forest ecosystem. *Eucalyptus delegatensis* is dominant at high elevations. In the gullies, high soil moisture content and low terrain features limit fire spread and therefore provide the opportunity for rainforest species to develop. Similar trends appear in the area near the centre: as the eucalypt forests grow, the forest ecosystem follows the successional path towards rainforest, with *Acacia melanoxylon* and *Pomaderris apetala* gradually decreasing due to their relatively short life span.

Conclusions

The agent-based simulation approach provides some new insights into the dynamic aspects of the forest ecosystem. The approach enables one to build a virtual landscape ecosystem to simulate how the various components of the forest ecosystem fit together and interact with each other. It also provides a way to explore the interrelationship between patterns and ecological processes. The combination of the parameters can be used experimentally and the output can be validated with real data, or subjected to statistical analysis. Individual trees contribute to species diversity through the process of dynamic interactions with each other as well as with their environment. Fire is the main disturbance source in the succession of the eucalypt–rainforest ecosystem in this area and plays a critical role in the process of patterning the forested landscape. The simulated result demonstrates that the emergent pattern in the form of the vegetation type defined by species composition or diversity conforms with succession theory for the type of the forested

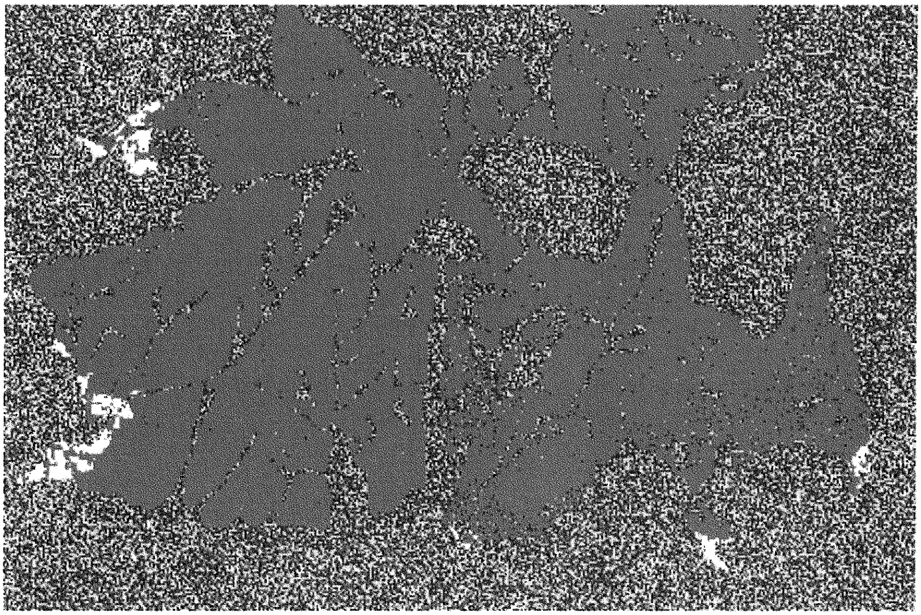

Figure 5. Simulation at 500 years.

ecosystem being modelled. The role that fire plays in the succession of wet sclerophyll forest in this area is through its direct effects on the process of species regeneration and the fire response properties of the species. The life span of species and the fire frequency will contribute to the maintenance of particular vegetation communities. The fuel dynamics of the forest ecosystem is the main contributing factor defining the fire regime of the forest ecosystem. Therefore, study of fuels in relation to topographic features is a critical aspect needed to improve the simulation result.

References

Brown, J.H. (1994). Complex ecological systems. In: *Complexity: Metaphors, Models and Reality. SFI Studies in the Sciences of Complexity. Proceedings Vol. XIX* (eds G. Cowan, D. Pines and D. Meltzer), pp. 419–443. Addison-Wesley, Massachusetts, USA.

Brown, M.J. and Podger, F.D. (1982). Floristics and fire regimes of a vegetation sequence from sedgeland-heath to rainforest at Bathurst Harbour, Tasmania. *Australian Journal of Botany* 30: 659–676.

Cheney, N.P. (1981). Fire behaviour. In: *Fire and the Australian Biota* (eds A.M. Gill, R.H. Groves and I.R. Noble), pp. 151–175. Australian Academy of Science, Canberra.

Gilbert, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 93: 129–151.

Hickey, J.E. (1994). A floristic comparison of vascular species in Tasmanian oldgrowth mixed forest with regeneration resulting from logging and wildfire. *Australian Journal of Botany* 42: 383–404.

Hutson, B.R. and Veitch, L.G. (1985). Relationships between litterfall rate, litter mass and decomposition rate in *Eucalyptus* forests in southeastern Australia. *Australian Journal of Ecology* 10: 443–450.

Jackson, W.D. (1968). Fire, air, water and earth - an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia* 3: 9–16.

Jarman, S.J and Brown, M.J. (1983). A definition of cool temperate rainforest in Tasmania. *Search* 14: 81–87.

Kirkpatrick, J.B., Peacock, R.J., Cullen, P.J. and Neyland, M.G. (1988). *The Wet Eucalypt Forests of Tasmania.* Tasmanian Conservation Trust, Hobart.

MacArthur, A.G. (1962). Control burning in eucalypt forest. *Commonwealth Forestry and Timber Bureau Leaflet* 80.
MacArthur, A.G. (1967). Fire behaviour in eucalypt forests. *Commonwealth Forestry and Timber Bureau Leaflet* 107.
Minar, N., Burkhart, R., Langton, C. and Askenazi, M. (1996). The Swarm simulation system: a toolkit for building multi-agent simulations. *Santa Fe Institute Working Paper 96-06-042*, Santa Fe, New Mexico.
Noble, I.R., Bary, G.V. and Gill, A.M. (1980). McArthur's fire danger meters expressed as equations. *Australian Journal of Ecology* 5: 201–203.
Read, J. and Brown, M.J. (1996). Ecology of Australian *Nothofagus* forests. In: *Ecology and Biogeography of* Nothofagus *Forests* (eds T.T. Veblen, R.S. Hill and J. Read), pp. 131–181. Yale University Press.
Read, J. and Hill, R.S. (1988). The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* 76: 558–584.
Reid, J.B., Hill, R.S., Brown, M.J. and Hovenden, M.J. (eds) (1999). *Vegetation of Tasmania. Flora of Australia Supplementary Series Number 8.* ABRS, Canberra.