

Modelling Plant Spread in Forest Ecology using Cellular Automata

Sergio. A. Cannas^{†*}, Sergio A. Páez [‡] and Diana E. Marco[‡]

[†]Facultad de Matemática, Astronomía y Física,

Universidad Nacional de Córdoba,

Ciudad Universitaria, 5000 Córdoba, Argentina

[‡]Centro de Ecología y Recursos Naturales Renovables,

Facultad de Ciencias Exactas, Físicas y Naturales,

Universidad Nacional de Córdoba,

Velez Sarsfield 299, 5000 Córdoba, Argentina

Abstract

Cellular automata models are increasingly used in ecology, since they permit integrate space, ecological processes and stochasticity in a single predictive framework. We constructed a cellular automaton model to analyze the regeneration of Alerce (*Fitzroya Cupressoides*), a long-lived tree species (3,600 years) endemic of Southern Argentina and Chile. This species regenerates in open areas produced by large disturbances like landslides and volcanic events. Regeneration in gaps produced by fallen trees is probably less important on large time scales. Using a stochastic dynamic rule and the Monte Carlo method we simulate the long term population dynamics of Alerce in competition with other species, to determine the possible extinction risk of this species of great economic and conservation importance.

In cellular automata models information from different sources can be translated into a set of transition rules which define the behaviour of the system[1]. Thus, factors central to the explanation of plant spread, such as biological interactions and stochasticity, and the explicit consideration of space are easily incorporated in these models, increasing their ecological realism. In this work we constructed a cellular automaton model to analyse the regeneration of Alerce (*Fitzroya cupressoides*), a long-lived tree species

*Member of the National Research Council, CONICET (Argentina)

endemic of Southern Argentina and Chile. This species is considered a relict in the sense that it is better adapted to past climate conditions than to the present ones; consequently, it cannot compete effectively with other tree species better adapted to the present climate (e.g. *Nothofagus spp.*), and it is now restricted to adverse habitats at high altitude, on infertile soils, or on poorly drained sites[2, 3].

It has been observed that this species regenerates well in open areas produced by large disturbances like landslides and volcanic events (hereafter generically referred as “catastrophes”) frequent in the Andean Cordillera[3, 4], leading to the hypothesis that, on large space and time scales, these events may be important to the survival of the species in the area[3]. In order to check such hypothesis we implemented a cellular automaton model which simulates the dynamics of *F. cupressoides* in mixed forests with *Nothofagus spp.* and in the presence of random catastrophes. The model is based on the following assumptions: a) the periodic catastrophic disturbances provide favourable conditions for regeneration of *F. cupressoides* in high altitudes [4, 6, 8, 9, 10]; b) *F. cupressoides* is slow-growing, shade-intolerant, and survives on sites where competition with other tree species is low, where form pure or mixed forests with *Nothofagus spp.* spp.[12, 4, 7]; c) significant seed production occurs every ten or twenty year for *F. cupressoides* and every two year for *Nothofagus spp.*[7]; d) age of reproductive maturity (seed production) is about seventy year for *F. cupressoides* and twenty year for *Nothofagus spp.*[7, 10]; e) *F. cupressoides* establishment on a disturbed site accelerates soil development[12].

The model consist of a square lattice of N sites with open boundary conditions, where each site represents a forest fragment patch with an area of 6 Km^2 , which is the average size observed in the present forest patch distribution[6]. Therefore, each sites does not represent a single tree, but a full forest patch that can contain both *F. cupressoides* and *Nothofagus spp.*. This approach is based on the assumption that the large scale dynamics of the forest is dominated by its observed patched structure, differing from the “individual-based models” approach[11] of recent application in forest ecology[13]. Each site has associated three discrete dynamical variables a_i , b_i and s_i ; a_i and b_i represent the reproductive maturity of the populations of *F. cupressoides* and *Nothofagus spp.* at site i respectively, with $0 \leq a_i \leq a_{max}$ and $0 \leq b_i \leq b_{max}$; $a_i = b_i = 0$ represents an unoccupied site; $s_i = 0, 1$ represents the soil state at site i : $s_i = 0$ is a recently site that can only be colonised by *F. cupressoides*, while $s_i = 1$ means a rich soil that can be colonised both by *F. cupressoides* and *Nothofagus spp.*.

We consider a random initial site occupation, with a fraction of sites $f_A = 0.3$ and $f_B = 0.5$ occupied by *F. cupressoides* and *Nothofagus spp.* respectively, estimated from the present patch distribution[7]. States of variables a_i , b_i and s_i are also chosen randomly. We use a parallel dynamics, with a time unit representing a period of ten years, based on the following dynamical rules: once a site is colonised, the population maturity increases by a unit at every time step. We don't allow self-regeneration of *F. cupressoides* sites, that means, the population of a pure *F. cupressoides* site dies when $a_i = a_{max}$. Once established, *F. cupressoides* updates site state to $s_i = 1$ after $t_B = 15$ time steps. After that, *Nothofagus spp.* can also colonise the same site. When *Nothofagus spp.* reaches its maximum maturity at a mixed site, *F. cupressoides* suffers a local extinction, that is, a_i is updated to zero. We take $a_{max} = 60$ and $b_{max} = 30$. We consider a colonisation probability that depends only on the occupation of nearest-neighbour sites whose population maturity exceed a minimum value $t_f^a = 7$ for *F. cupressoides*, and $t_f^b = 2$ for *Nothofagus spp.*.

Then, the updating rule for a single site i at time t can be summarized as follows:

1) A catastrophe occurs with probability p , which we assume for simplicity independent of the site. In this case $s_i(t) = a_i(t) = b_i(t) = 0$; otherwise:

2) if $s_i(t-1) = 0$ then $s_i(t) = b_i(t) = 0$ and

$$a_i(t) = \begin{cases} 1 & \text{with probability } p_i^a(t) & \text{if } a_i(t-1) = 0 \\ b_i(t-1) + 1 & & \text{if } 0 < a_i(t-1) < a_{max} \\ 0 & & \text{if } a_i(t-1) = a_{max} \end{cases} \quad (1)$$

3) if $s_i(t-1) = 1$ then

$$b_i(t) = \begin{cases} 1 & \text{with probability } p_i^b(t) & \text{if } b_i(t-1) = 0 \\ b_i(t-1) + 1 & & \text{if } 0 < b_i(t-1) < b_{max} \\ b_{max} & & \text{if } b_i(t-1) \geq b_{max} \end{cases} \quad (2)$$

$$a_i(t) = \begin{cases} 1 & \text{with prob. } p_i^a(t) & \text{if } a_i(t-1) = 0 \text{ and } b_i(t-1) = 0 \\ a_i(t-1) + 1 & & \text{if } 0 < a_i(t-1) < a_{max} \text{ and } b_i(t-1) < b_{max} \\ 0 & & \text{if } a_i(t-1) = a_{max} \text{ or } b_i(t-1) = b_{max} \end{cases} \quad (3)$$

4) if $a_i(t) = t_B$ then $s_i(t) = 1$.

We assume for the colonisation probability p_i^α ($\alpha = a, b$) of site i the simple model $p_i^\alpha(t) = \frac{1}{4} \sum_{j \text{ nn } i} \Theta(\alpha_j(t-1) - t_f^\alpha)$, where the sum $\sum_{j \text{ nn } i}$

runs over all nearest-neighbour sites of i and $\Theta(x)$ is the Heaviside step function.

Using Monte Carlo simulations we analyzed the temporal behaviour of the mean occupation densities of *F. cupressoides* and *Nothofagus spp.* $\rho_A(t) \equiv (1/N) \sum_i \langle n_i^a(t) \rangle$ and $\rho_B(t) \equiv (1/N) \sum_i \langle n_i^b(t) \rangle$ respectively, where the occupation variables are defined as $n_i^\alpha(t) \equiv \Theta(\alpha_i(t))$ ($\alpha = a, b$) and $\langle \dots \rangle$ means an average over different samples of the stochastic noise (typically 400). We repeated the simulations for several systems sizes up to $N = 1200$, verifying that the results becomes almost independent of N for $N \geq 400$.

We observed that, after some transient period τ , where ρ_A and ρ_B typically exhibit damped oscillations, they always relax asymptotically to a stationary state that we call the equilibrium, that is, $\rho_A(t) \rightarrow \rho_A^{eq}$ and $\rho_B(t) \rightarrow \rho_B^{eq}$ when $t \rightarrow \infty$. While τ depends on the initial distributions f_A and f_B , we verified in all the simulations that ρ_A^{eq} and ρ_B^{eq} are independent of the initial conditions but depends strongly on the catastrophe probability p . In Fig. 1 we show the equilibrium densities as a function of p for $N = 400$. We see that the long time behaviour presents four different regimes or dynamical phases: a) there exists a value $p = p_1$ such that for $p < p_1$ we have a total extinction state, that is, $\rho_A^{eq} = \rho_B^{eq} = 0$; b) there exists a value $p = p_2$ such that for $p_1 < p < p_2$ we have a coexistence state where populations of both species stabilize at finite values; c) there exists a value $p = p_3$ such that for $p_2 < p < p_3$ only *F. cupressoides* survives and d) for $p > p_3$ we have again a total extinction situation.

The first case is the most interesting one. Here the catastrophe probability is not enough to allow the regeneration of *F. cupressoides*. Since there is a small but finite catastrophe probability, once *F. cupressoides* is extinct, disturbed sites cannot be regenerated and also *Nothofagus spp.* becomes extinct for large enough times. The behaviour of the equilibrium densities around this transition point strongly reminds that of the order parameter of a critical phenomena. In order to check this possibility we analyzed two other quantities.

First, we calculated the relaxation time τ , defined as the time such that $|\rho_A(t) - \rho_A^{eq}| < \epsilon$ and $|\rho_B(t) - \rho_B^{eq}| < \epsilon$ for all times $t > \tau$, where ϵ is some arbitrarily chosen small number (we take $\epsilon = 0.001$). In Fig. 2 we show a numerical calculation of τ for fixed initial conditions, as a function of p , in the neighbourhood of $p = p_1$. We see that τ presents a sharp peak around p_1 , that is, the system presents something like a critical slowing down.

Second, we calculated the autocorrelation functions

$$C_{\alpha\beta}(t, t') \equiv (1/N) \sum_i \langle n_i^\alpha(t) n_i^\beta(t') \rangle - \langle n_i^\alpha(t) \rangle \langle n_i^\beta(t') \rangle$$

where $\alpha, \beta = a, b$. In the equilibrium $t, t' \gg \tau$ we have that $C_{\alpha\beta}(t, t') = C_{\alpha\beta}(t - t')$ and $C_{\alpha\beta}(t'') \sim (1/N) \sum_i \langle n_i^\alpha(t'') n_i^\beta(0) \rangle - \rho_A^{eq} \rho_B^{eq}$. In Fig. 3 we show a log-log plot of $C_{aa}(t)$. The other correlation functions behave in a similar manner. The linear dependence exhibited by $C_{aa}(t)$, as p approaches p_1 from above, shows that it develops a power law tail for long times, in the neighbourhood of the transition point. This behaviour is another signature of a critical phenomena. Critical behaviour implies strong fluctuations and an extreme sensitivity to external perturbations that we expect will rise the *extinction probability*. In Fig. 4 we can see a calculation of the extinction probability during the first t years of the evolution, as a function of p . For low values of t this probability depends on the initial conditions, but for longer times it converges to a single curve that is independent of the initial conditions. We see that this probability is very high around the critical point, even in the coexistence state, taken a value about 40% at $p = p_1$.

Finally, we checked the above calculations for different sets of values of b_{max} , a_{max} , t_B , t_f^a and t_f^b . The general behaviour showed to be qualitatively independent on such variations and also the quantitative differences were almost negligible, evidencing the robustness of the model to uncertainties in these parameters.

Summarizing, we showed that a long term stationary state in which the average population density of forest patches occupied by *F. cupressoides* remains constant is possible areas where colonisation and coexistence with other species are mediated by catastrophe occurrence. Such state is highly sensitive to the catastrophe rate p , showing several regimes or dynamical phases as p is varied. In particular, at low values of p the system presents a transition between a *total extinction* and a *coexistence* state at $p = p_1$, with characteristics of a *critical phenomena*, such as very large relaxation times and power law temporal correlations. Such critical behaviour lead to a high *extinction probability* in the neighbourhood of p_1 , even in the coexistence state. Since the probability of disturbances per unit area and unit time p depends on the total area of the *F. cupressoides* forest, the stretching of such area, either by human action or modification of climatic variables due to global change, could enhance the extinction probability of *F. cupressoides*.

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References

- [1] G. B. Ermentrout and L. Edelstein-Keshet, *J. Theor. Biol.* **160**, 97 (1993).
- [2] J. Schmithüsen, *Vegetatio. Edic.* **10**, 313 (1960).
- [3] A. Lara, *The dynamics and disturbance regimes of Fitzroya cupressoides forest in south-central Andes of Chile* [Thesis]. Dep. of Geography of Colorado (1991).
- [4] T. T. Veblen and D.H. Asthon, *Biol. Conserv. Edic.* **23**, 141 (1982).
- [5] T. T. Veblen, F. M. Schlegel and J. V. Oltremari, *Temperate Broad-Leaved Evergreen Forests*, J. D. Ovington (Ed.), Elsevier, Amsterdam (1983).
- [6] C. Donoso, V. Sandoval, R. Grez, and J. Rodriguez, *J. Veg. Sci. Edic.* **4**, 303 (1993).
- [7] C. Donoso, *Bosques Templados de Chile y Argentina - Variación, Estructura y Dinámica - Ecología Forestal*, Editorial Universitaria S.A. Santiago de Chile, (1993).
- [8] L. Casertano, *Bull Seismol. Soc. Amer. Edic.* **53**, 1415 (1963).
- [9] H. Illies, *Geología de los alrededores de Valdivia y volcanismo y tectónica en márgenes del Pacífico en Chile meridional*, Instituto de Geología y Geografía, Universidad Austral de Chile, Valdivia (1970).
- [10] A. Lara and R. A. Villalba, *Science* **260**, 1104 (1993).
- [11] M. Huston, D. De Angelis and W. Post, *BioScience* **38**, 682 (1988).
- [12] T. T. Veblen, R. J. Delmastro and J. E. Schlatter, *Environ. Conserv. Edic.* **3**, 291 (1976).
- [13] S. I. Higgins, D. M. Richardson and R. M. Cowling, *Ecology* **77**, 2043 (1996).

Figure Captions

Figure 1: Equilibrium densities of occupied sites by *F. cupressoides* ρ_A^{eq} and *Nothofagus spp.* ρ_B^{eq} vs. the catastrophe probability p , for $N = 400$ (the error bars are smaller than the symbol sizes).

Figure 2: Relaxation time τ vs. the catastrophe probability p (the error bars are smaller than the symbol sizes).

Figure 3: Log-log plot of the equilibrium autocorrelation function for alerce sites $C_{aa}(t)$ for different values of the catastrophe probability p around the critical point $p_1 \approx 0.0033$. The results were obtained by averaging over 2000 samples of the stochastic noise (the error bars are smaller than the symbol sizes).

Figure 4: Extinction probability for *F. cupressoides* during the first t years vs. the catastrophe probability p , starting from $f_A = 0.3$ and $f_B = 0.5$ and averaging over 2000 samples of the stochastic noise (the error bars are smaller than the symbol sizes).

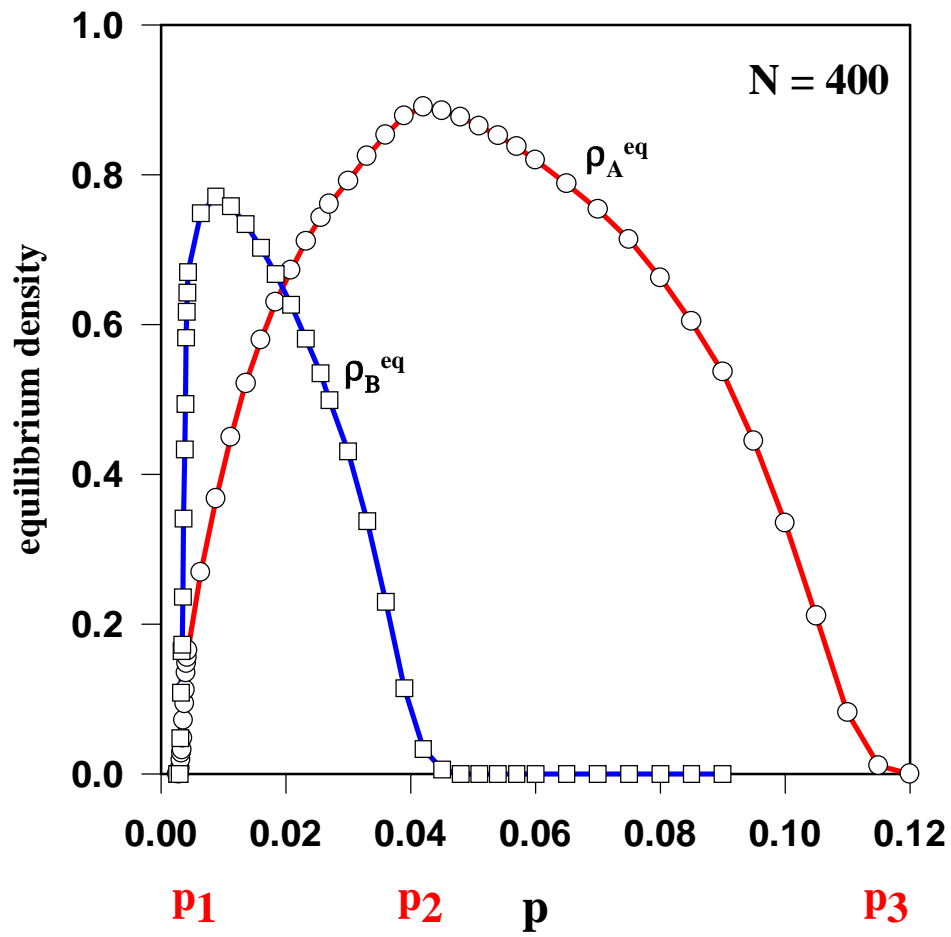


Figure 1: "Modelling Plant spread in Forest Ecology..."

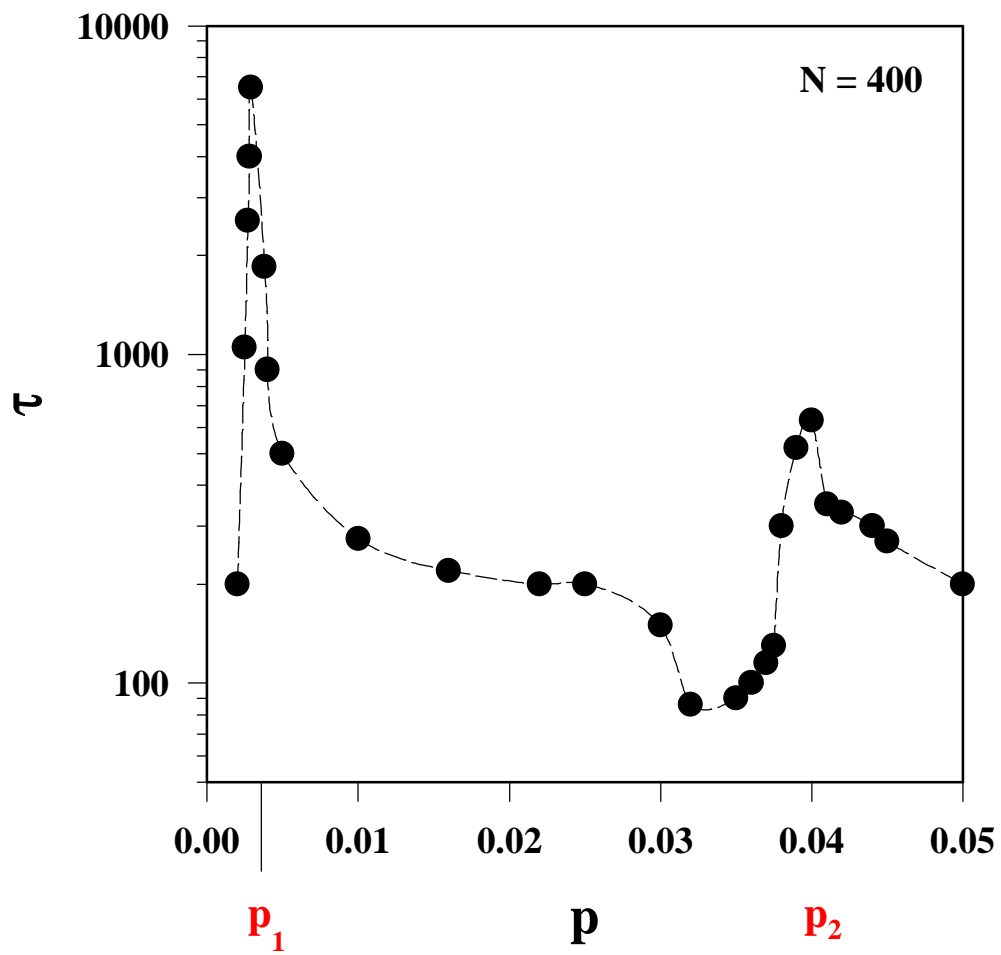


Figure 2: "Modelling Plant Spread in Forest Ecology..."

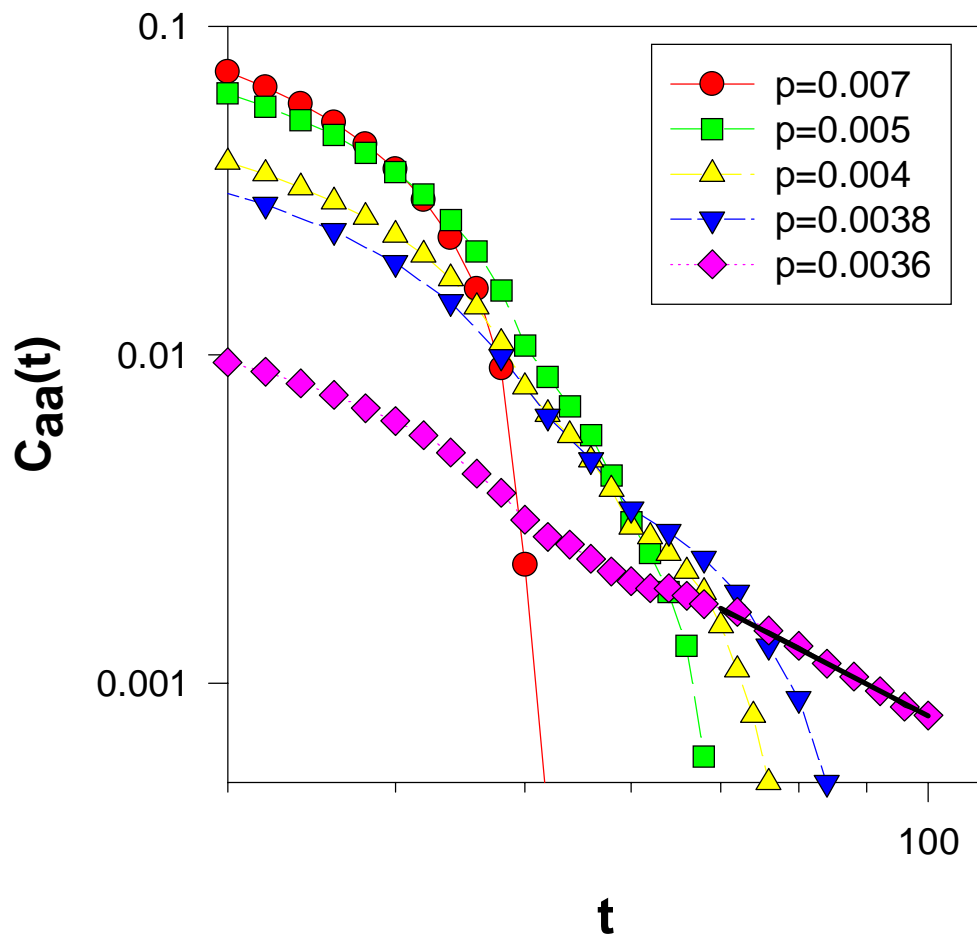


Figure 3: "Modelling Plant Spread in Forest Ecology..."

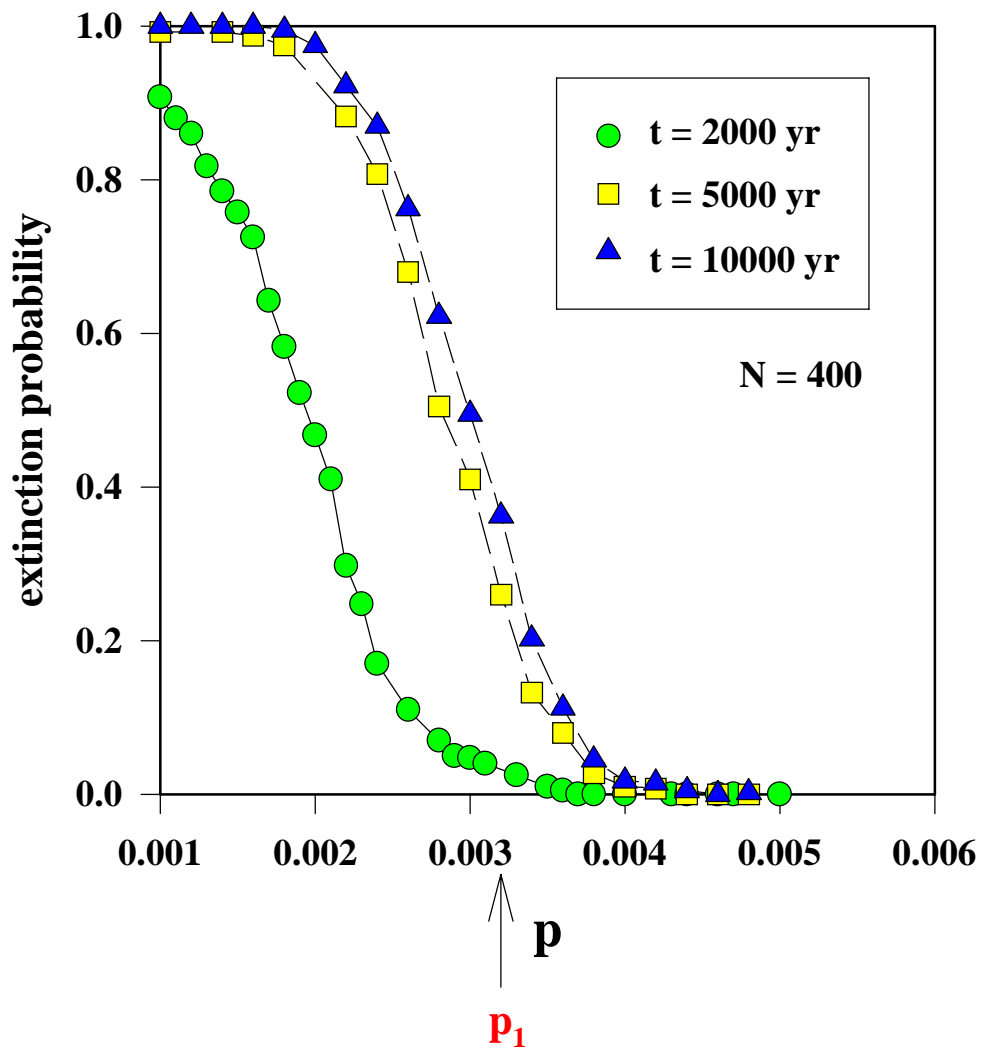


Figure 4: "Modelling Plant Spread in Forest Ecology..."