Species invasiveness in biological invasions: A modelling approach

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Abstract

The study of invasiveness, the traits that enable a species to invade a habitat, and invasibility, the habitat characteristics that determine its susceptibility to the establishment and spread of an invasive species, provide a useful conceptual framework to formulate the biological invasion problem in a modelling context. Another important aspect is the complex interaction emerging among the invader species, the non-invader species already present in the habitat, and the habitat itself.

Following a modelling approach to the biological invasion problem, we present a spatially explicit cellular automaton model (Interacting Multiple Cellular Automata, IMCA). We use field parameters from the invader *Gleditsia triacanthos* and the native *Lithraea ternifolia* in montane forests of central Argentina as a case study to compare outputs and performance of different models. We use field parameters from another invader, *Ligustrum lucidum*, and the native *Fagara coco* from the same system to run the cellular automaton model. We compare model predictions with invasion values from aerial photographs. We discuss in detail the importance of factors affecting species invasiveness, and give some insights about habitat invasibility and the role of interactions between them. Finally, we discuss the relevance of mathematical modelling for studying and predicting biological invasions.

The IMCA model provided a suitable context for integrating invasiveness, invasibility and the interactions. In the invasion system studied, the presence of an invaders´ juvenile bank not only accelerated the rate of invasion but was essential to ensure invasion. Using the IMCA model we were able to determine that not only adult survival but particularly longevity of the native species influenced spread velocity of the invader, at least when a juvenile bank is present. Other factors determining velocity of invasion detected by the IMCA model were the seed dispersal distance and age of reproductive maturity. We derived relationships between species´ adult survival, fecundity and longevity of both theoretical and applied relevance for biological invasions. Invasion velocities calculated from the aerial photographs agreed well with predictions of the IMCA model.

Key words: biological invasion, habitat invasibility, mathematical modelling, species interactions, species invasiveness.

Abbreviations: IMCA – Interacting Cellular Automata Model

Introduction

Defining biological invasion is still a difficult task, due in part to the proliferation of terms to describe various concepts used by different authors (Richardson et al. 2000). However, consensus is growing around at least two main aspects involved in the invasion process: the traits that enable a species to invade a habitat, termed as invasiveness, and the habitat characteristics that determine its susceptibility to the establishment and spread of an invasive species, termed as invasibility (Lonsdale 1999; Alpert et al. 2000). Other important aspect involved in biological invasions linking invasiveness and invasibility is the complex interaction emerging among the invader species, the non-invader species already present in the habitat, and the habitat itself (Higgins and Richardson 1996; 1998). These aspects provide a useful conceptual framework, even if somewhat simplified, to formulate the biological invasion problem in a modelling context. Model formulation has been pointed out as a suitable approach for studying and predicting biological invasions, compared with the empiric study of cases alone (Higgins and Richardson 1996).

In a schematic view (Fig. 1), main elements of the biological invasion process can be organised allowing a formulation of the model inputs (species and habitat information), and outputs (predicted patterns and rates of invasion). For example, information needed for determining woody species invasiveness is related to seed mass, age of first reproduction, and interval between masting seed crops (Rejmánek and Richardson 1996). Habitat invasibility is highly influenced by disturbance and resource availability (Burke and Grime 1996) among other factors (Lonsdale 1999; Alpert et al. 2000), and invaders themselves can have an effect on the disturbance regimes of the invaded system (Mack and D´Antonio 1998). Ecological interactions between invaders and non-invader species can be complex. For example, the invader can cause inhibition of the establishment in native species (Walker and Vitousek 1991). Respect to the model outputs, patterns of invader spread are as important as velocity for understanding the processes and mechanisms behind the biological invasions (Higgins and Richardson 1996; Higgins et al. 1996). This theoretical understanding is important for improving prediction and control of biological invasions.

Following a modelling approach to the biological invasion problem, we present a spatially explicit cellular automaton model. We first parameterise the model using field parameters from a *Gleditsia triacanthos* (Leguminosae) and *Lithraea ternifolia* (Anacardiaceae) invasion system in montane forests as a case study. We then use field parameters from *Ligustrum lucidum* (Oleaceae) and *Fagara coco* (Rutaceae) from the same system to run the cellular automaton model. We compare model predictions with invasion values from aerial photographs. We discuss in detail the importance of factors affecting species invasiveness, and give some insights about habitat invasibility and the role of interactions between them. Finally, we discuss the relevance of mathematical modelling for studying and predicting biological invasions.

Methodology

The invasion system

The montane forests taken as a case study covered most of the mountains of central Argentina up to 1400 m in the past. Native dominants are *L. ternifolia* and *F. coco* (Luti et al. 1979). At present, native forest areas are diminished by clear-cutting, grazing and urbanization, and invasion by many woody alien species is common (Marco and Páez 2000). Most frequent invaders are *G. triacanthos*, *L. lucidum, Morus* spp. (Moraceae), *Melia azederach* (Meliaceae), and *Crataegus* spp. (Rosaceae). *L. ternifolia* and *F. coco* are trees up to 15 m, able of germinating and establishing in shallow soils and rock crevices (Luti et al. 1979). *L. ternifolia* presents events of masting seed crops every two years, while *F. coco* produces seeds every year. Both species produce small dry drupes that fall and remain near the parental tree. The species do no have vegetative reproduction, and germination and seedling establishment need full sunlight and moderate moisture conditions (Keegan 1984; Bianco 1989).

The North American *G. triacanthos* and the Chinese *L. lucidum* invaders are trees up to 15 m. Both species present vegetative reproduction. The big, indehiscent pods produced by *G. triacanthos* are locally dispersed (Schnabel and Hamrick 1995), while the small fleshy drupes of *L. lucidum* are bird dispersed (Aragón 2000). Both species produce fruits in high numbers every year, and present a dense juvenile bank, both of sexual and vegetative origin (Grau and Aragón 2000; Marco and Páez 2000). The juvenile bank is defined as the collection of seedlings that germinate and establish under the canopy, surviving in the shade, until a gap in the canopy appears and seedlings can resume their growth and eventually reproduce (Silvertown and Lovett-Doust 1993). Values for life history traits considered determinants of plant spread (Higgins et al. 1996, Rejmánek et al. 1996; Marco and Páez 2000) were estimated for the species. Data were obtained from field surveys (Marco and Páez 2000), and from previous works (sources cited in Marco and Páez 2000).

The modelling approach

In the modelling context, we will use an operational definition of invasive species, as a species that spreads in space, either occupying new habitats, or increasing its cover in areas previously occupied. Thus, the main distinction is made between invasive or non-invasive species, rather than native or non-native species (Alpert et al. 2000). This approach allows for a more general treatment of the invasion problem, since cases in which native species become invaders after some habitat or climatic change (for example, shrub encroachment, Jeltsch et al. 1997) can also be considered.

Cellular automaton model

Many complex biological processes, like the spread of invasive species, are often numerically intractable. One way of simplifying these systems is using cellular automata models. A cellular automaton consists of a simulation that is discrete in time, space, and state (Ermentrout and Edelstein-Keshet 1993). The spatial domain of the model is divided into a fixed grid and each cell in the grid has a state associated with it. The state at the next time step is determined from earlier states of the cell and its neighbours, through transition rules based on different kinds of information about the system being modelled. As a model advantage, random events and habitat heterogeneity can be easily incorporated (Higgins and Richardson 1996). Cellular automata models have been widely applied to different plant ecology problems (e.g. Barkham and Hance 1982; Crawley and May 1987; Czarán 1989; Silvertown et al. 1992; Moloney and Levin 1996), although direct applications dealing with invasion problems are scarce (Auld and Coote 1980, 1990; Wallinga 1995; Collingham et al. 1996; Higgins et al. 1996; Jeltsch et al. 1997).

We developed a cellular automaton to model explicitly and in an integrated way the main factors suggested by previous works as involved in the plant invasion processes, related to species invasiveness, habitat invasibility, and interaction between species (Higgins and Richardson 1996; Higgins et al. 1996; Rejmánek and Richardson 1996; Reichard and Hamilton 1997; Marco and Páez 2000). Factors related to species invasiveness included are life history traits (mean maximum longevity of the species, mean seed dispersal distance, age of reproductive maturity, and interval between masting seed crops), and demographic traits (annual adult survival probability, mean seed production, mean germination probability, juvenile survival probability, and mean age of saplings in the juvenile bank, if present). Habitat invasibility was incorporated into the model through the main factor affecting species establishment in the system studied, heterogeneity of soil condition (deep soil or rocky ground) (Marco and Páez 2000). Interaction between the invader and the non-invader species was included as competition for suitable sites allowing germination and establishment (competition for space, Silvertown et al. 1992; Marco and Páez 2000). . Table 1 shows the parameters included in the model: d, mean seed dispersal distance (in grid units); t_{max}, mean maximum longevity of the species (in years); q, annual adult survival probability; t_m, age of reproductive maturity (in years); n, mean seed production (seeds/plant); t_s, interval between masting seed crops (in years); f_g, mean germination probability; P_s, juvenile survival probability; and t_J, average age of saplings in the juvenile bank (in years). Spatial scale (cell size) is given by the maximum canopy cover of adults (5 x 5 m), and time scale is one year. Each cell is occupied by a single individual that survives every year with probability q, and dies with probability $1-q$. The annual adult survival probability q is directly related to the longevity (t_{max}) of the species through a geometrical distribution for the probability P of dying at age t, in such a way that $P(t > t_{max}) < 0.05$. A dead individual is replaced by another individual of age equal to the mean age of saplings in the juvenile bank (t_j). Since density-dependence can occur in plants at recruitment level (Gillman et al. 1993), we incorporated it in the IMCA model as part of the site occupancy rules (only one individual is allowed to occupy a site, and a juvenile from the juvenile bank has to wait until an adult dies to reproduce). If the species does not have juvenile bank the cell becomes empty.

Colonisation probability of an empty cell depends on the number of seeds s_i coming from the rest of the cells into the cell i at time t. Colonisation of the cell occurs when at least one seed germinates and the emerged individual survives the seedling stage. Considering two independent events, f_g, the mean germination probability of the species, and Ps, the probability that a seedling survives more than two years to become a juvenile, the colonization probability (p_i) is:

$$p_i = 1 - (1 - P_s \ f_g)^{s_i} \qquad (1)$$

Total number of seeds s_i received by the cell i from individuals located at a distance z of the cell, is calculated as a density function $nf(z)$ over all cells in the grid containing a mature individual at time t, where n is the mean number of seeds produced per plant and $z = \sqrt{x^2 + y^2}$ is the distance to the parental tree. If the interval between masting seed crops is greater than one year every mature individual contributes to the counting of seeds every t_s years starting from the age of reproductive maturity, t_m.

To work with several species we developed a cellular automaton for each species, coupling the cellular automata through dynamical interacting rules to incorporate interactions. This results in a model with great power of generalisation, that we called Interacting Multiple Cellular Automata, hereafter IMCA model.

The interacting rules are the following:

The model is individual-based (Huston et al. 1988), each cell being occupied by only one individual at each time *t*.

In an empty cell we compute the probability of colonisation by different species from Eq. (1) and compare them with independent random numbers sorted for each one. If more than one species colonises the cell the final occupant is sorted with a probability that depends on the state and use of the resources in the cell. For instance, in the case study, *L. ternifolia* establishes either in shallow soil or rock crevices as well in deep soil, compared with *G. triacanthos,* that needs deep soil. Soil parameter in each cell take values of 0 or 1, representing a rocky ground and a deep soil, and are sorted with some spatial distribution at the beginning of the simulation and kept fixed through it. Cell occupancy is then defined by soil state and species characteristics: if soil value = 1, the occupants are sorted with equal probability but, if soil value = 0, then *L. ternifolia* occupies the cell. In this way, any kind of interactions between species (competition, predation, facilitation, inhibition, etc.), can be easily incorporated in the model.

Simulation Methods

We performed computer simulations of the spread of different species. First we simulated the behaviour of isolated species and then we analised the interacting situation for different combinations of pairs of species Particular parameter values used in the simulations are in Table 1.

In most of the cases the results were obtained over an average of 200 samples of random initial conditions and also over different sets of the random numbers used in the dynamics. We considered open boundary conditions (Haefner et al. 1991), that is, cells do not receive seeds from outside the grid area.

We simulated the isolated spread of *L. ternifolia* and *G. triacanthos* in an empty rectangular area, starting from a row of individuals randomly aged between 1 and t_m, along a line $y = 0$ at the bottom of the rectangle. Seed dispersal distribution was modelled as a negative exponential function

$$f(r) = \frac{2}{\pi d^2} e^{-2r/d} \qquad (2)$$

The spread front $y = h(x)$ for each species was defined as the farthest occupied cell y from the starting point for every coordinate x (Fig. 2). We defined the mean front position as

$$\bar{h} = \frac{1}{L_x} \sum_{x=1}^{L_x} h(x) \qquad (3)$$

To estimate the velocity of the spread process we use the asymptotic speed V of the averaged spread front. We averaged $\bar{h}$ over different initial conditions and different sets of random numbers, for all species, for an area of different widths, typically $L_x = 80$. Several tests performed for different area widths showed that the results did not change significatively for widths over 80 cells. We also performed simulations starting from a single located tree in the center of the area.

We first used the IMCA model to study the invasion system constituted by the alien species *G. triacanthos*, *Ligustrum lucidum* and the native dominant *L. ternifolia*. We simulated the spread of *G. triacanthos* on a rectangular area, starting from an initial distribution of individuals with random ages along a line $y = 0$ at the bottom of the rectangle. We filled the rectangle with a dense forest of *L. ternifolia* individuals of random ages. We performed another set of simulations, starting from a single *G. triacanthos* tree located in the centre of a square area covered by a dense forest of *L. ternifolia*. In the same manner, we studied the spread of *Ligustrum lucidum* into *L. ternifolia* forests.

Comparison of model performance with field data

Model fit to field data were tested using aerial photographs from the area studied, provided by the Dirección de Catastro (Córdoba Province). Black and white photographs were taken in 1970 (1:5000), 1987 (1:20000), and 1996 (1:5000). Photographs were interpreted using image processor software to enlarge them, helping in species identification at individual level. An estimation of error in the photograph interpretation was made, by identifying individual trees in the photograph and then checking if they were correctly assigned to the species. Sites where invasion after disturbances has been apparent were selected to estimate velocity of area covered by invaders, but also less disturbed areas covered by native forest were examined. The area mapped surveyed in detail and then checked at field covered 5 km^2 of a low mountainous system (about 1100 m), with predominantly deep soils and few rocky outcrops. Rate of spread was calculated estimating the square root of the area successively covered in 1970, 1987 and 1996. Calculations were made for *G. triacanthos* and *L. lucidum*.

As another mean of assessing the internal consistency of the IMCA model, we simulated the spread of the subdominant *F. coco* into *L. ternifolia* dominated forest. If the IMCA model had captured the essential features of the invasion process, and since both species are non-invader, native species, we expected populations of *F. coco* and *L. ternifolia* reaching stable coexistence in the long term. As both species have similar site preferences for germination and seedling establishment, no soil variables were introduced in this case. As in the previous simulations we started considering the spread in a rectangular area from an initial linear distribution of individuals randomly aged of *F. coco* at the bottom of the area. We filled the area with a dense forest of *L. ternifolia*. We performed another set of simulations, by initially filling the grid with a randomly interspersed distribution of individuals of *F. coco* and *L. ternifolia*, in different percentages.

Results

Cellular automaton model

In all the simulations performed, the mean spread front showed a transient period, after that a well defined asymptotic velocity *V* was reached, with a linear behaviour close to *Vt*. In the case of simulations for single species starting from a single tree located in the center of the area, the spread front developed a circular shape (not shown), with *V* similar for the simulations starting from a line of trees. *V* predicted by the cellular automaton were 9.6 ± 0.1 m/y for *G. triacanthos* and 0.6 ± 0.1 m/y for *L. ternifolia*. In all cases, the spread front *h (x)* was relatively smooth (not shown). When using the IMCA model for interacting species both *V* and the smoothness of the spread front changed. In this case, *V* tended to be lower, and the smooth spread front was replaced by a wide spread band area of rough borders, as the result of the patch formation generated by species introgression into the *L. ternifolia* forest. In the case of *G. triacanthos* interacting with *L. ternifolia,* as the spread front moved along the simulation area many patches of *L. ternifolia* were replaced by the invader, and after some time the whole area was invaded. In 300 years, the dense *L. ternifolia* forest was replaced by a pure and dense *G. triacanthos* forest. Fig. 3 shows the temporal behaviour of the mean spread front for *G. triacanthos* invading *L. ternifolia* forest in two different areas that differ in soil type, deep or rocky. A linear asymptotic *V* was developed, and although on rocky ground the invasion *V* was much more lower, *G. triacanthos* invaded and replaced the native forest anyway. We also performed simulations with a random distribution of deep soil and rocky ground in different proportions in each simulating area. The results (not shown), were qualitatively the same as in Fig. 3, with velocities that vary between the two values shown in the figure.

In simulations using field values for *Ligustrum lucidum*, the general pattern of spread was similar to *G. triacanthos* spread, although invasion velocity into the *L. ternifolia* forest was much faster, 13.6 ± 0.1 m/y. The spread front *h (x)* was highly indented (Fig. 4), and patch formation behind it was less dense compared to the forest invaded by *G. triacanthos*.

Comparison of model performance with field data

To investigate the sensitivity of the spread velocity to the main life history traits detected as important in a previous study using simple matrix and reaction-diffusion models (Marco and Páez 2000), we performed several simulations using the IMCA model, changing values of these traits for *G. triacanthos* and *L. ternifolia,* while keeping the rest of them fixed. Results from population projection matrices showed that growth stages from seedlings to adults made the greatest contribution to population growth in *G. triacanthos*. Thus, to elucidate the influence of the juvenile bank in the invasion process, we performed simulations with the IMCA model of the spreading of *G. triacanthos* into the *L. ternifolia* forest, but withdrawing the juvenile bank of the invader. In this case, the simulations led to a final stationary state with populations of *G. triacanthos* and *L. ternifolia* coexisting in the long term, because the invader was not able of replacing the native species completely. Another important trait influencing population growth detected by the matrix model was the survival of the adult stage, especially for the native *L. ternifolia*. Results from the IMCA simulations stated that, for an invader with juvenile bank, the invasion velocity into a native forest was almost independent on all the life history traits of the native except the longevity. Further simulations were performed using a simplified, random version of the one species cellular automaton model, in which the colonization probability becomes $p_i = 1$, independently of the cell *i* population. In these simulations, the dynamics of the native depended only on the survival adult probability *q* (not shown), which is related to longevity. This result holds for the simulation conditions if the invader has a juvenile bank. As fecundity was apparently of no high importance in determining population growth in the matrix model, we investigated, using the IMCA model, the variation of *V* with the mean seed production while keeping *d* and t_m fixed, for *G. triacanthos* values. Spread velocity grew logarithmically with *n*, the number of seeds, at least for large values of *n* (Cannas, Marco and Páez, submitted). We then investigated the influence of dispersal distance *d* on *V*, using the IMCA model with *G. triacanthos* parameter values. We found that *d* was one of the main factors influencing *V*, and that *V* depended linearly on dispersal distance (not shown). Using the same parameter values we investigated the relationship between *V* and t_m, the age of reproductive maturity. V decreased logarithmically with t_m for small values ($t_m <$ 7 years), and for greater values behaved as $V \sim 1/ t_m$.

Results of aerial photographs interpretation showed that invasion both by *G. triacanthos* and *L. lucidum* is very recent. By 1970, the area was still covered by native forests, dominated by *L. ternifolia* and *F. coco*. As an example, Fig. 5 shows a small disturbed stream surrounded by native forests. Although the forests had been suffering some degree of clear-cutting from past decades, a well defined tree cover was still present. By 1996, most of the area had been invaded by *G. triacanthos* and *L. lucidum*. The spread of the invaders was facilitated by disturbances like clear-cutting, fires and urbanisation, but once a new focus was established, the invaders were able to spread into the less disturbed native forest. In Fig. 6 the same area shown in Fig. 5 is presented, with the spread of *L. lucidum* marked schematically. The invader had covered the stream with a dense, almost monospecific forest (in black in the photograph), and had propagated through the watershed into the native forest (dark gray in the photograph). Light gray areas in the photograph indicate relatively less invaded native forest. Intermediate stages of the invasion process were detected in 1987 photographs (not shown). Error in species identification from aerial photographs was about 10 %. Spread velocities of the invaders calculated from the aerial photographs were in agreement with predictions of the IMCA model. For *G. triacanthos*, field calculated spread velocity ranged between 2.5 to 4 m/y, which is consistent with the velocity range predicted by the IMCA model for different habitat conditions (1.9 ± 0.1 m/y for purely deep soils to 4.4 ± 0.1 m/y for purely rocky ground, Fig. 3). For *L. lucidum*, field calculated spread velocity ranged between 11 to 12.5 m/y, slightly lower than the 13.6 ± 0.1 m/y predicted by the IMCA model.

Finally, when considering the interacting case between the two natives, non-invader species using the IMCA model, the spread of *F. coco* into *L. ternifolia* forests rendered a stable stationary situation of a mixed forest with a distribution of patches of both species. This pattern was produced because cells behind the spread of *F. coco* front can be re-occupied by *L. ternifolia* (Fig. 7). The spatial pattern is similar to that found at field (Bertrán de Solís 1986). Starting from an initial random mixing of both species, the stationary state showed fixed values of the average population densities of both species. Such values did not depend on the initial population values (Fig. 8). The predicted proportion between the stationary densities taken as number of individuals of *L. ternifolia*/number of individuals of *F. coco* = 0.67/0.29 = 2.3, compares well with the field data value (between 1.1 and 2.8 depending on habitat characteristics, Bertrán de Solís 1986).

Discussion

Results from this work showed that the modelling approach is indeed useful to understand and predict biological invasions. The IMCA model was a suitable way of integrating the main aspects of the invasion process, i.e., species invasiveness, habitat invasibility and the interactions among them.

With respect to species invasiveness, trends in life history and demographic traits detected by elasticity analyses in a matrix model previously applied to the same invasion system (Marco and Páez 2000), were easily modelled and tested for robustness using the IMCA model. For example, key factors like the growth of juveniles to the adult stage and survival of the adults were incorporated and tested into the IMCA model using a simple population structure, helping to determine their mathematical relationship with invasion success and spread velocity. The presence of a collection of juveniles waiting to grow to the adult stage not only accelerated the rate of invasion but was determinant to ensure invasion accompanied by displacement of the native species, both in *G. triacanthos* and *L. lucidum* cases. The juvenile bank is important for other forest species regeneration, like *Aglaia* spp. of the Meliaceae family (Becker and Wong 1985), and is also characteristic of the invasion pattern of *Melia azederach* (D. Marco, unpublished observation), belonging to the same family. In the matrix model previously applied, survival of adults was especially important in the case of the native *L. ternifolia*, as is typical for declining populations (Horvitz and Schemske 1995; Oostermeijer et al. 1996; Valverde and Silvertown 1998). Using the IMCA model we were able to determine that not only adult survival but mainly longevity of the native species influenced spread velocity of the invader, at least when a juvenile bank is present. Survival elasticities were also high for the invader *G. triacanthos*. Interestingly, a sensitivity analysis performed on population matrices of the toad *Bufo marinus* invading Australia showed that adult survival influenced population dynamics over any other parameter at high densities (Lampo and De Leo 1998). Also, in a non-spatial model developed for the invasion by the long-lived snail *Batillaria attramentaria* in California, the invader´s adult mortality was determinant for invasion success and displacement of the native snail *Cerithidea californica* (Byers and Goldwasser 2001).

We were able to explore the role of fecundity in the invasion process, by separating in the IMCA model the seed production and the germination probability. Although the elasticity analysis previously performed showed that fecundity was not important in determining population growth, the IMCA model stated that a relationship between seed production and velocity of spread existed, and was logarithmic. This indicates that invasiveness is not linearly influenced by seed production, in accordance to findings for pines and *Eucalyptus* species (Higgins et al. 1996; Rejmánek and Richardson 1996; Richardson 1998). Then, high propagule production is not necessarily a trait indicating high invasiveness, as it has commonly been considered (e.g., Rejmánek 1996). In the same *Bufo marinus* example given above, population sensitivity to variations in female fecundity was low (Lampo and De Leo 1998).

Importance of survival and fecundity on population growth of invaders could be conditioned by adult life expectancy (longevity). As is evident, when longevity and yearly adult survival are high, the generations overlap and individuals accumulate in this stage, increasing population sensitivity to adult survival. At the same time, the importance of the number of seeds or eggs produced to determine population growth may be lower, because of density-dependent regulation of recruitment in further stages. In *Bufo marinus,* a density-dependent mechanism at the larval stage regulates the number of individuals surviving to metamorphosis (Lampo and De Leo 1998). It is interesting to note that longevity of adult *Bufo marinus* is higher in the invading Australian populations compared to South American native populations, where predicted survival sensitivity is lower and female fecundity is higher (Lampo and De Leo 1998). An elasticity analysis of populations of the invader *Senecio jacobea* with biennial or short perennial life histories showed that fecundity was determinant for population growth in biennial populations compared to perennials (McEvoy and Coombs 1999). This relationship between adult survival, fecundity and longevity has important consequences for controlling biological invasions: short-lived invaders are more probably limited by propagule availability compared to long-lived invaders, for which probably the adult survival is the key stage to control them. Reduction of adult survival was proposed as the most effective strategy to control invasion by *Bufo marinus* in Australia (Lampo and De Leo 1998). In plants, the presence of juvenile banks as in the case of *G. triacanthos* or *L. lucidum* could difficult the implementation of this control strategy. In a simulation using the SEIBS model, Higgins et al. (2000) showed that the most rapid and cost-effective strategy for clearing invading populations of *Pinus pinaster* and *Acacia cyclops* in Cape peninsula fynbos was to clear stands of juveniles first.

The IMCA model detected a linear relationship between *V* and dispersal distance, influenced by the age of reproductive maturity in such a way that a lower age of reproductive maturity accelerated velocity of invasion even with shorter dispersal distances. A similar interaction between age of reproductive maturity and dispersal distance influencing velocity of invasion was found by Higgins et al. (1996), using the SEIBS model. These authors offered the following explanation for this interaction: slow-maturing, short-dispersing species are unlikely to have many adult trees on the edge of an invasion focus when recruitment opportunities occur. This explanation is based on the demographic structure resulting from the spatial model outputs, as we found in the IMCA model simulations, where demographic structure of invaded areas is heterogeneous. The oldest, reproductive individuals occupied the center of invading patches, while the younger, non-reproductive individuals were located in the patch borders (not shown). Thus, at least when no long-distance dispersal is considered, the spatial demographic structure of the invader is important in determining velocity of invasion. This could hold for cases where long-distance events occur, since age of reproductive maturity still affects invasion rate and interacts with dispersal distance (Higgins and Richardson 1999). Thus, even when the spread rate is defined as the expected velocity for the location of the furthest-forward individual in the population (carried by long-distance dispersion, Clark et al. 2001), spatial demographic structure could still be influencing the invasion velocity.

With respect to habitat invasibility, habitat heterogeneity was easily included. In the IMCA model simulations presented in this paper, habitat invasibility was considered as different resource availability for the species. Inclusion of habitat heterogeneity did not lead to a failure of the invasion success, but lowered the spread velocity of the invader. Other factors influencing habitat invasibility such as disturbance can be easily added to the IMCA model. Defining disturbance as any destructive event that is discrete in space and time (White and Pickett 1985), distinct disturbances involving different number of cells can be incorporated directly as site individual mortality and occupancy rules, or through modifications in fecundity and seed dispersal parameters. Thus, fire, clear-cutting, grazing or other disturbances can be easily incorporated into the IMCA model. If known, interactions between species and disturbance can also been incorporated in an explicit way. For example, non-invader and invader species may not respond in the same manner to clear-cutting. In the study case reported in this paper, the percentage of canopy cover remaining after clear-cutting is important in determining seed germination and seedling establishment. While small amounts of tree canopy removal are necessary for the native, non-invader *L. ternifolia* to recruit, the invader *G. triacanthos* needs moderate to high canopy removal (Marco and Páez 2000). If not known, possible responses of the species to disturbance can be inferred from existing basic knowledge about life history and demographic traits of the species, and from known disturbance effects on resource availability. For example, it is known that seedlings of *Ligustrum lucidum* and other species of *Ligustrum* are very shadow-tolerant (Lavergne et al. 1999; Grau and Aragón 2000). Thus, it can be expected that species of *Ligustrum* will be able to invade low-disturbed habitats, native dominated forests with closed canopies. In agreement with this, we have shown that *L. lucidum* is invading the less disturbed native forests. Also, *L. robustum* is invading non-disturbed, native forests in La Réunion island (Lavergne et al. 1999).

Interactions between species and disturbance has been pointed out as a factor precluding the usefulness of general models and motivating the necessity of context-specific model formulation (Higgins and Richardson 1998). However, we believe that this is not necessarily true. If model structure is flexible enough, as is the case of the IMCA model, a trade-off between predictive power and model generality no longer holds. Using the results obtained in this work and from other modelling efforts is possible to re-formulate the factors and precision of data needed to mechanistically understand and predict biological invasions. For example, when dealing with long-lived invaders, precise estimates of fecundity are not necessary but other factors like the dispersal distance and age of reproductive maturity should be included with the greatest precision possible in the model.

When interaction (competition) between species was considered in the IMCA model, velocity of invader´s spread was much lower compared with its spread as single species, and the native species went locally extinct. This is in agreement with results from other invasion models considering species interaction. In the study above cited, Byers and Goldwasser (2001) found that the introduced snail *B. attramentaria* displaced the native snail *C. californica* through exploitative competition. Interference competition can also be important in determining the invasion outcome. Allelopathy effects from the weed *Acroptilon repens* were conclusive in reaching plot dominance only if the native species showed some degree of sensitivity to allelochemicals produced by the weed, as simulated by Goslee et al. (2001) in a model based in field parameters. Competition with native species has not been frequently addressed in invasion studies, and at present is difficult to know in what extent this kind of species interaction is involved in invasion processes. Further field studies are required to gather suitable data for parameterising invasion models.

The present version of the IMCA model is suitable for dealing with invasions by sessile organisms like plants, bivalves like the zebra mussel (Roberts 1990), or invaders that use sessile hosts, like the fruit fly invading cultivars (Carey 1996). However, with few modifications the model can be adapted to deal with mobile invaders, from viruses to animals, by simply including an appropriate algorithm for individual displacement (Van den Bosch and Metz 1996, Yoshimura et al. 1999). Other important trait of the IMCA model is its modular design, where the building blocks are relatively simple one species cellular automata models (Cannas et al. 1999). This allows for inclusion of several species interacting between them in an explicit way, including dynamics of the invaders and native species in a single model. This trait is considered highly desirable in modelling biological invasions (Higgins et al. 2000), although has rarely been included in invasion models (but see Okubo et al. (1989), Byers and Goldwasser (2001), and Goslee et al.(2001)). Future applications of the IMCA model will be directed to a deeper exploration of habitat invasibility and interactions, both as theoretical and applied aspects of the biological invasion problem.

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Table 1. Values for the parameters used in the IMCA model. See text for parameter explanations.

Parameter	*Gleditsia triacanthos*	*Lithraea ternifolia*	*Ligustrum lucidum*	*Fagara coco*
d (grid units)	3	1	6	1
t_{max} (years)	75	140	75	40
q	0.96	0.98	0.96	0.93
t_m (years)	7	20	6	5
n (seeds/plant)	14000	6000	15000	6000
t_s (year)	1	2	1	1
f_g	0.2	0.01	0.4	0.2
P_s	0.4	0.3	0.8	0.5
t_j (years)	5	0	5	0

Figure captions

Figure 1. Schematic organisation of the main elements in a generic biological invasion process formulated as model inputs (species and habitat information), and outputs (predicted patterns and rates of invasion).

Figure 2. Schematic representation of the simulation area of the cellular automaton model. Each cell in the grid represents a site available for individual occupancy (black rhombs). Population is spreading from a line of individuals located in the bottom of the simulation area. The spread front position is indicated (irregular bold line), as well as the averaged spread front (straight bold line).

Figure 3. Average front position of *Gleditsia triacanthos* in the dense forest of *Lithraea. ternifolia* as a function of time. Velocity of the invasion front (*V*, measured as asymptotic speed of the averaged spread front) is shown, for two different habitat conditions, homogeneously deep soil (continuous line), and homogeneously rocky ground (dashed line).

Figure 4. *Ligustrum lucidum* invasion (black cells) into a dense *Lithraea ternifolia* forest (gray cells), starting from a line of trees located at the bottom of the simulation area of 80 x 160 cells. White cells correspond to empty cells. The spread front position *h (x)* is indicated.

Figure 5. Aerial photograph of the area taken as study case, corresponding to 1970. A small disturbed stream and its associated watershed is shown, surrounded by native forests dominated by *Lithraea ternifolia* and *Fagara coco* (different gray intensities correspond to slope aspect).

Figure 6. Aerial photograph of the same area shown in Fig. 5, corresponding to 1996. The watershed was almost entirely invaded by *Ligustrum lucidum*, and the native forest (light gray) has been replaced by dense forests of the invader (black area, covering the stream), and by mixed forests of the invader and native species (dark gray areas).

Figure 7. *Fagara coco* spread (black cells) into a dense forest of *Lithraea ternifolia* forest (gray cells), starting from a line of trees located at the bottom of the simulation area. White cells correspond to empty cells. Different snapshots show consecutive stages of the spreading process, from t = 20 years to t = 200 years.

Figure 8. Average population densities for the spread of *Fagara coco* and *Lithraea ternifolia* as a function of time, starting from different random spatial distributions of both species. The lower and upper curves (black lines) corresponded to an initial forest composition of 90 % and 10 % of *L. ternifolia* and *F. coco*, respectively, while middle curves (gray lines) corresponded to 40 % and 60 % respectively.

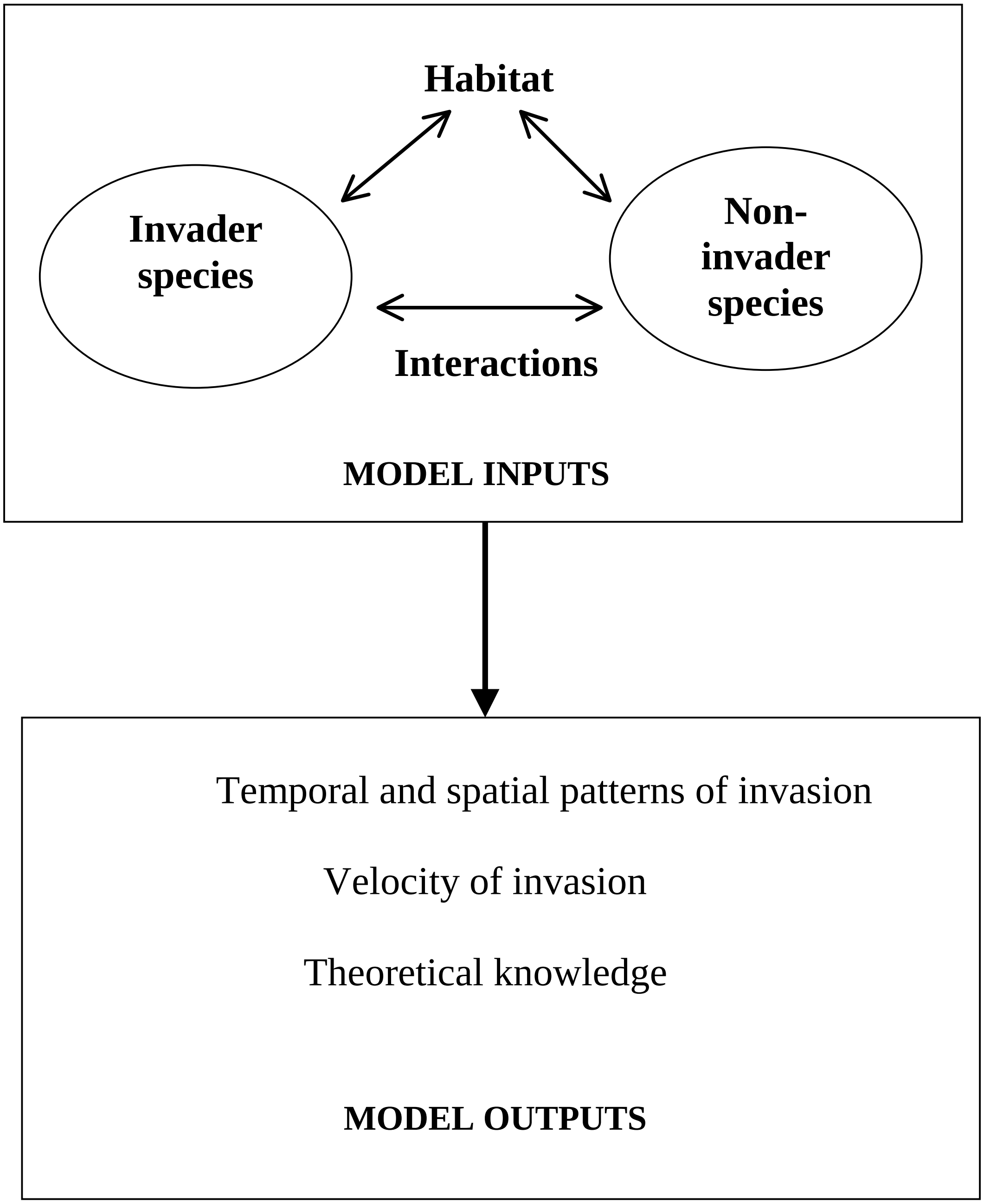

Habitat
Invader species
Non-invader species
Interactions
MODEL INPUTS
Temporal and spatial patterns of invasion
Velocity of invasion
Theoretical knowledge
MODEL OUTPUTS

Figure 1

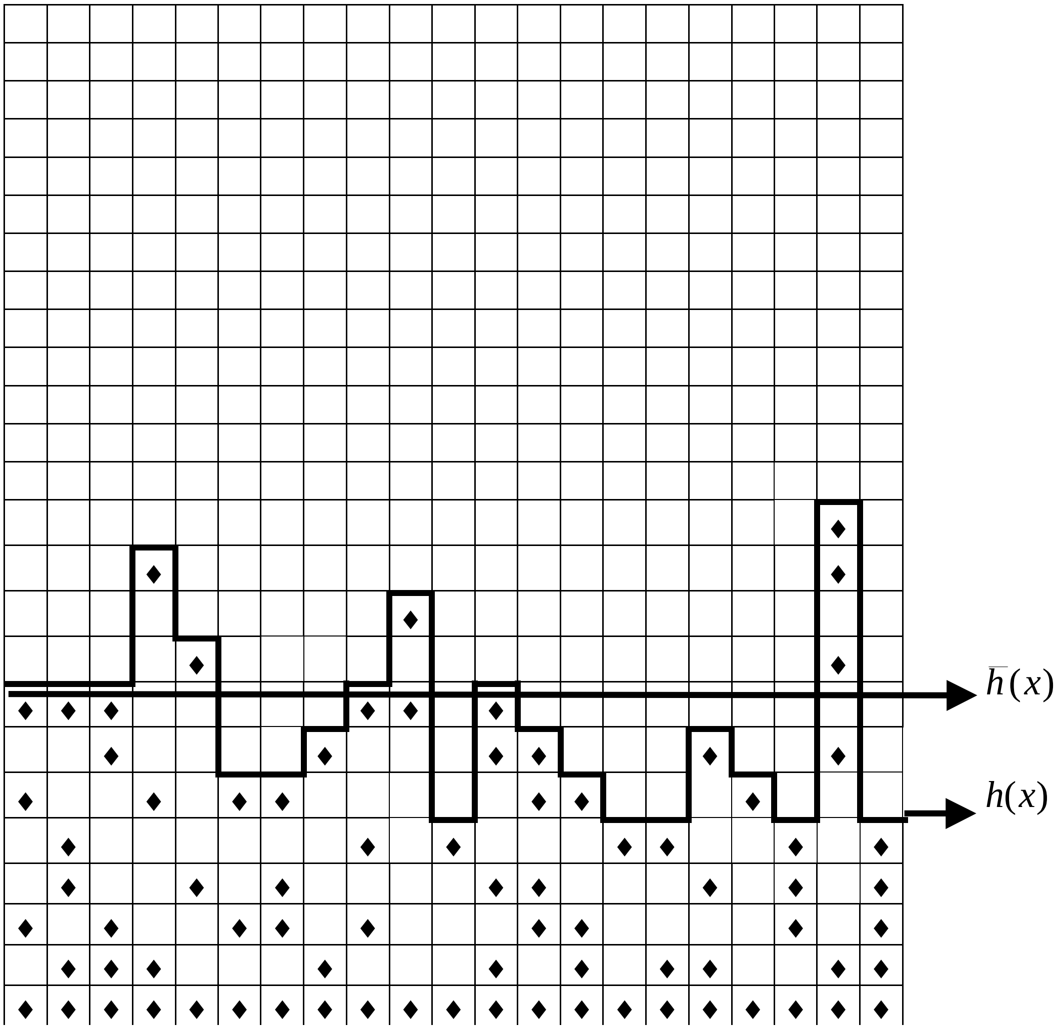
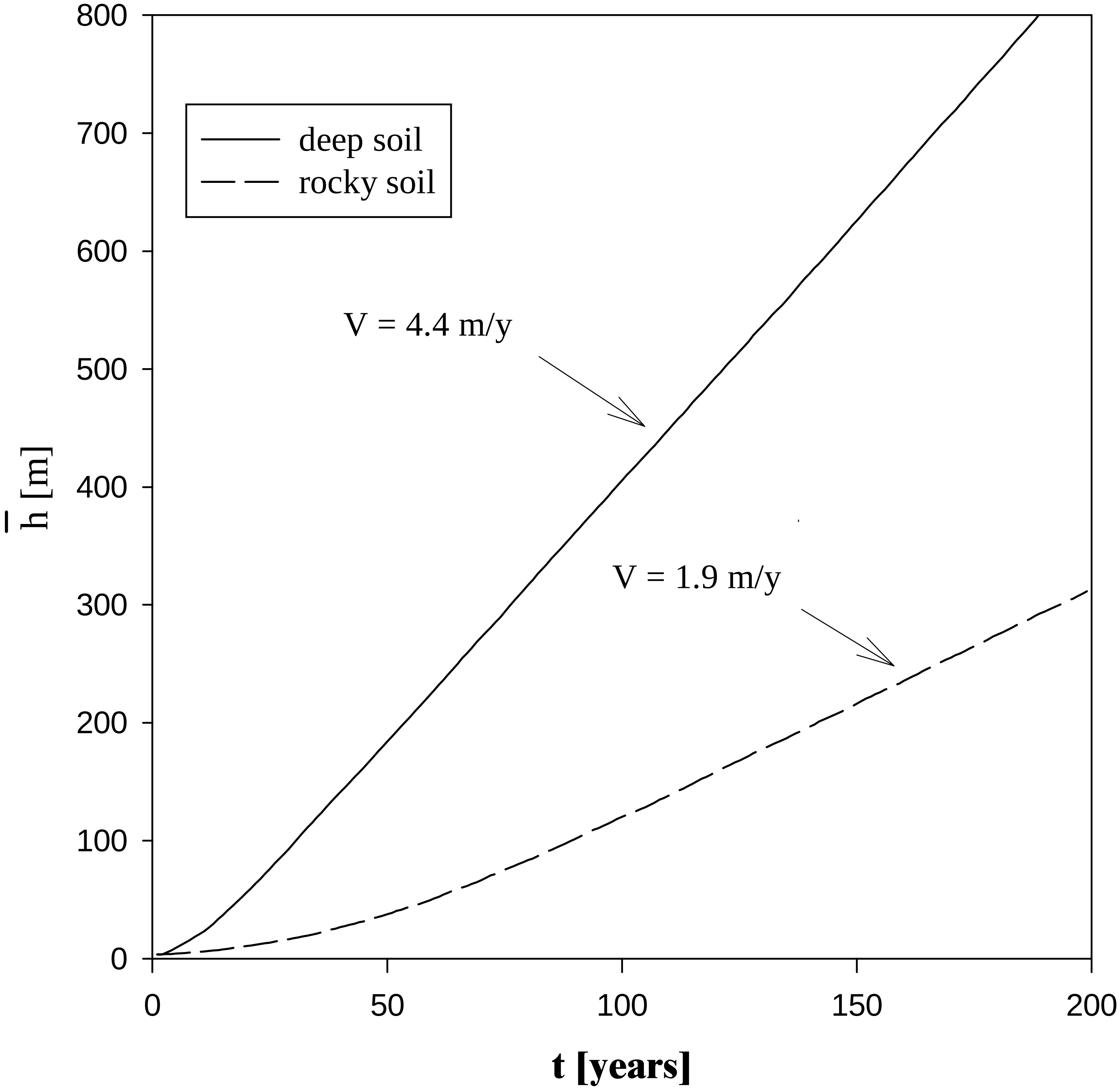


Figure 2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deep soil
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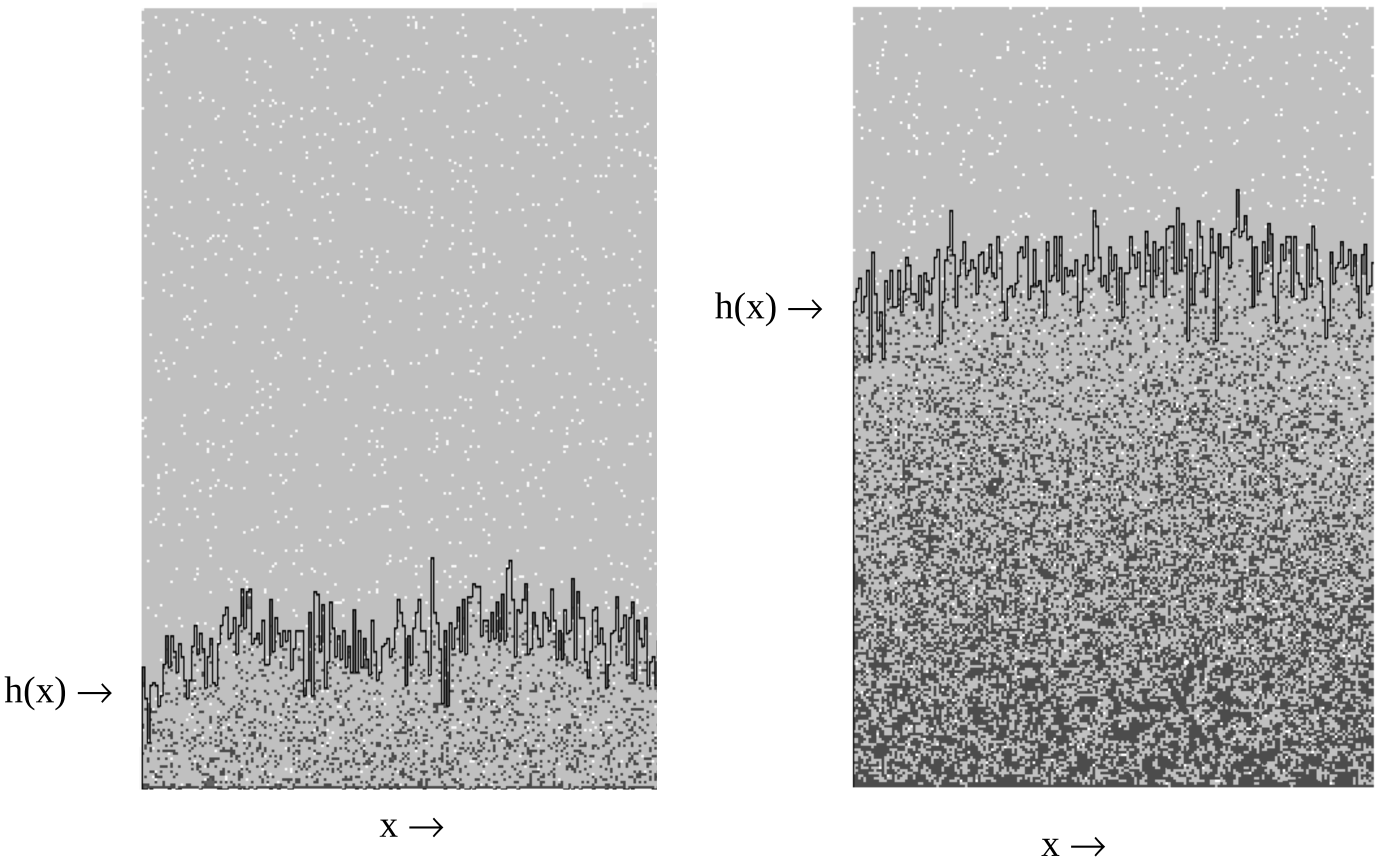
V = 4.4 m/y
V = 1.9 m/y

Figure 3



25 years

75 years

Figure 4

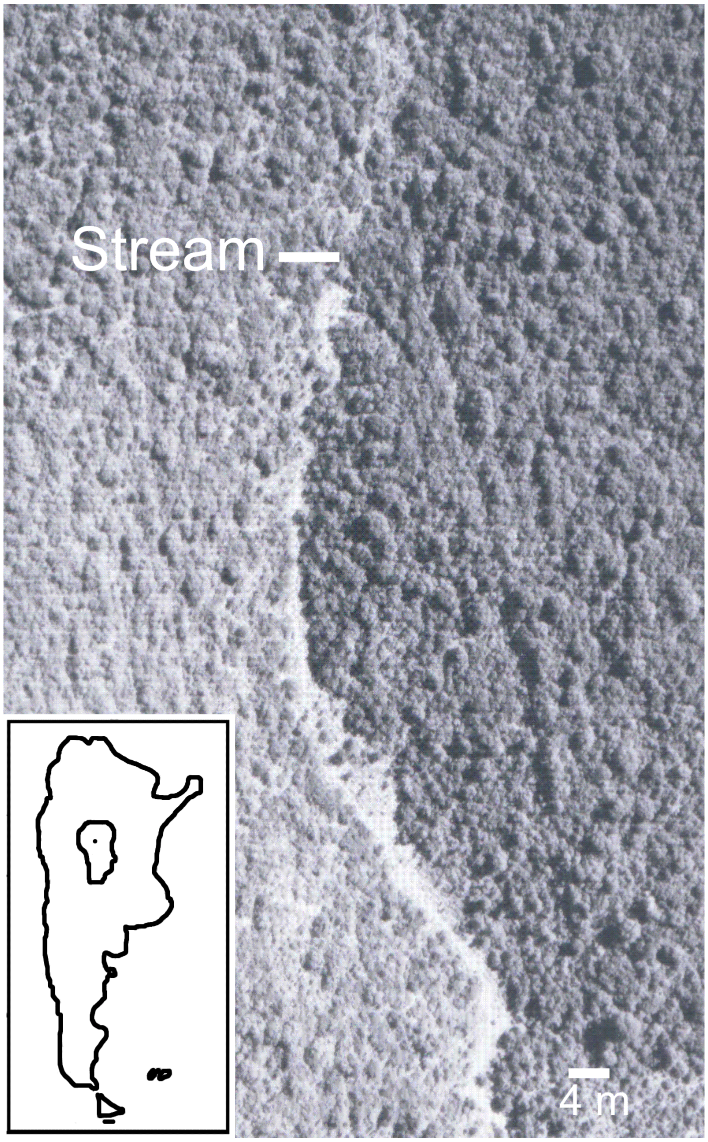


Figure 5

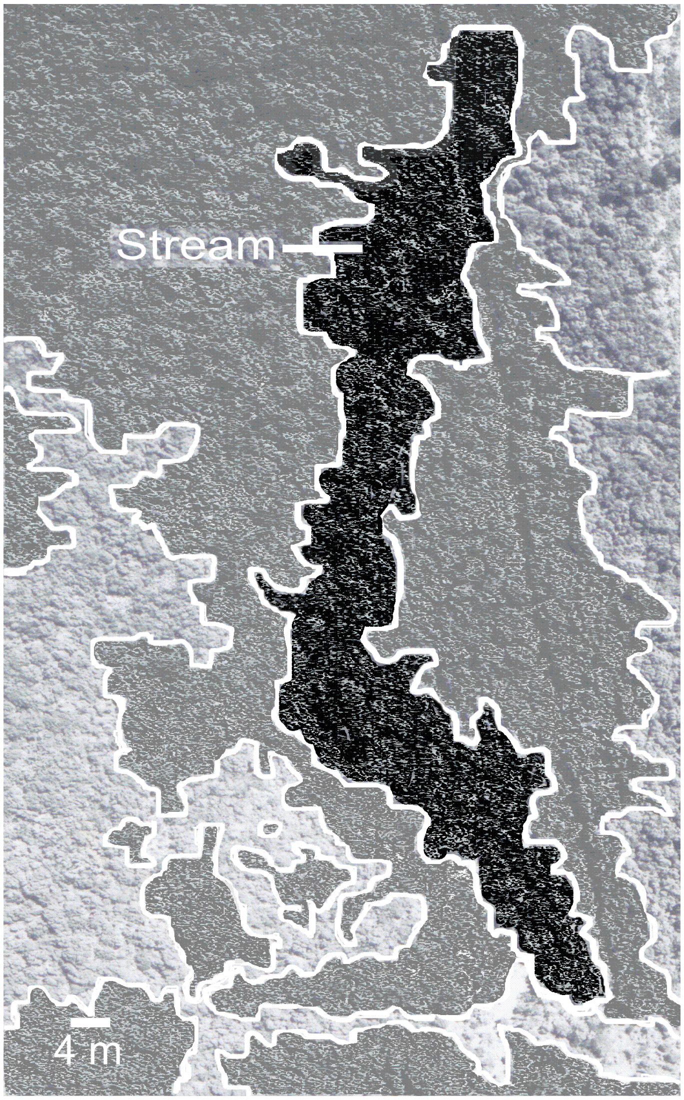
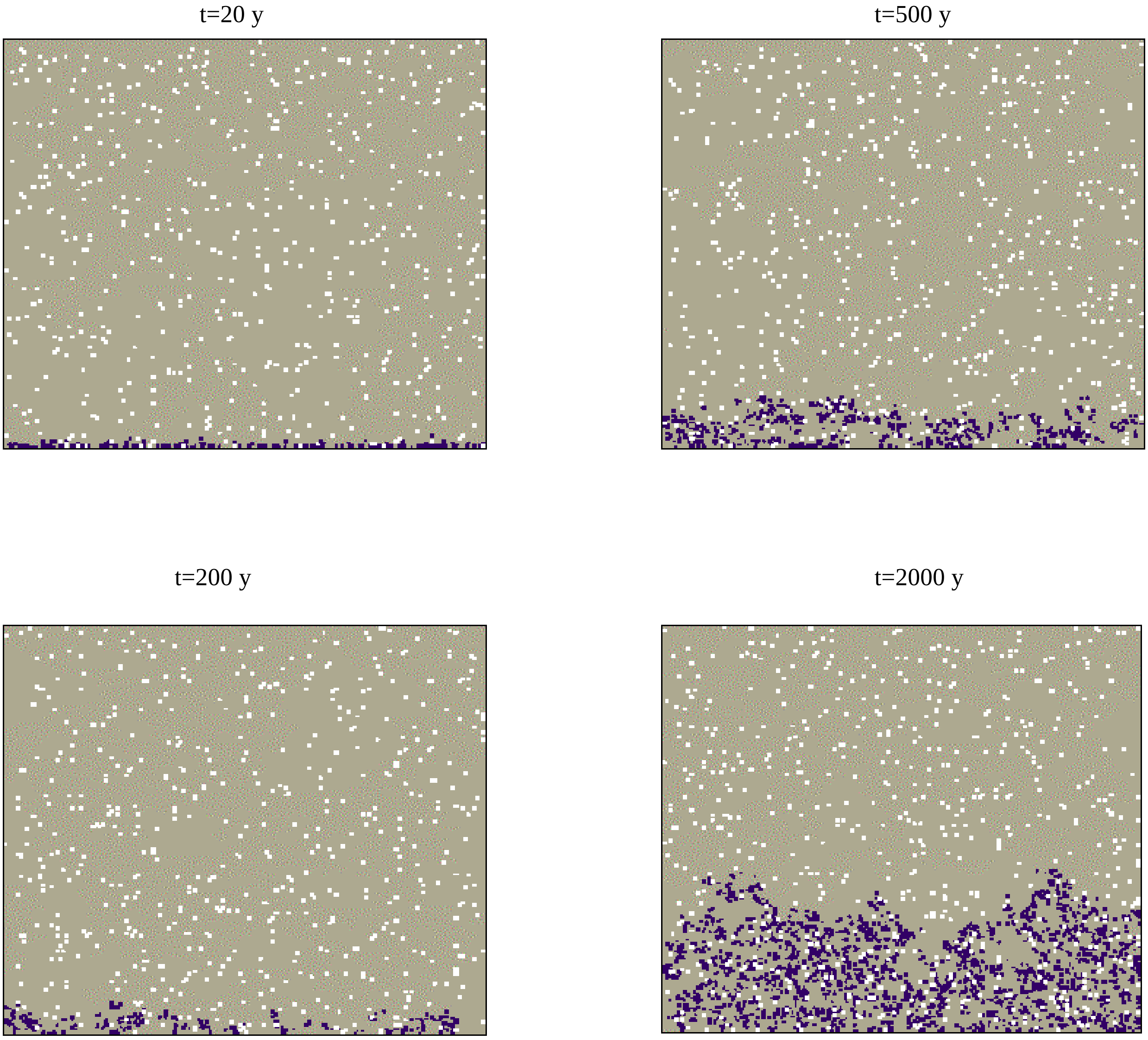


Figure 6



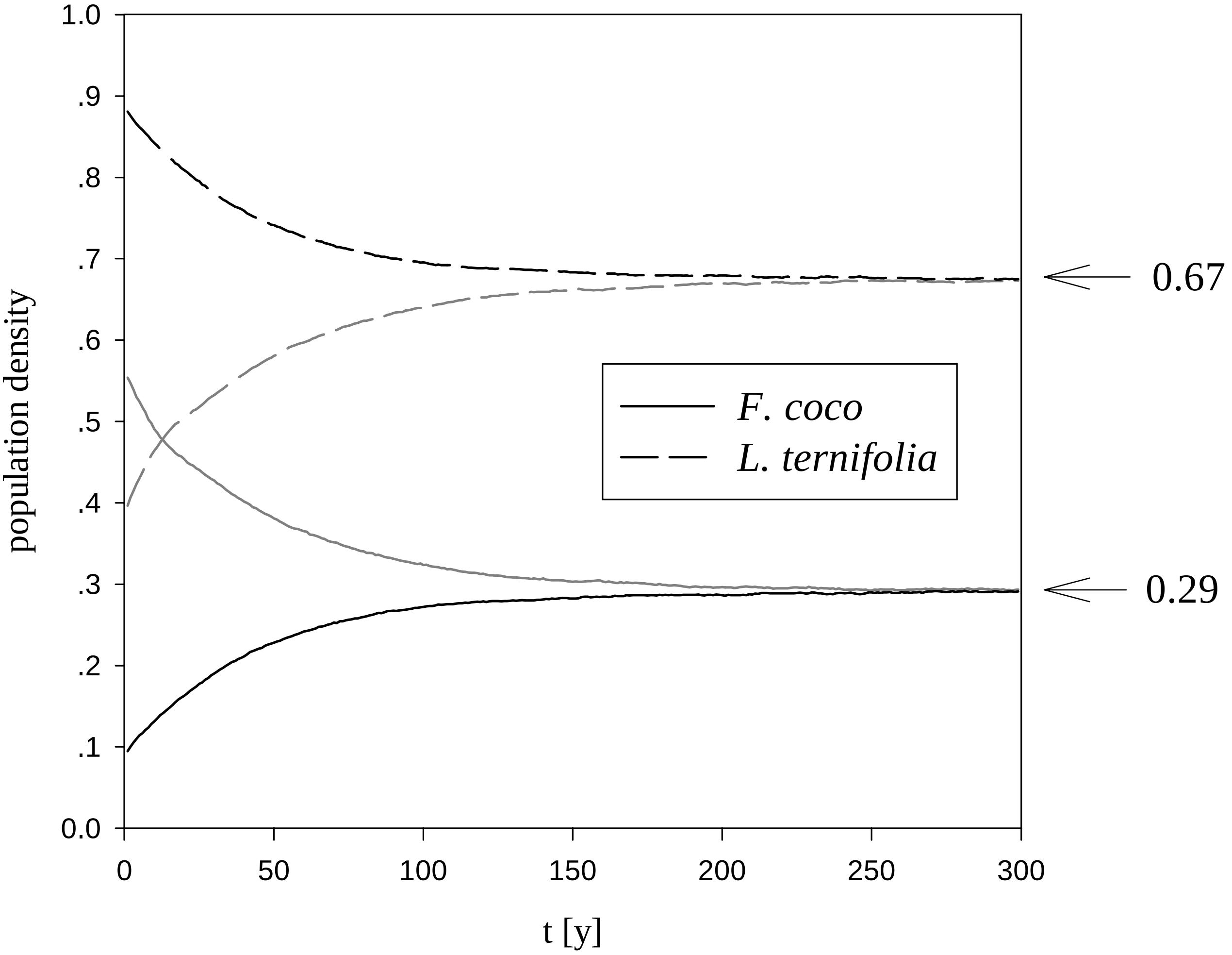
t=20 y

t=500 y

t=200 y

t=2000 y

Figure 7


1.0
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0.0
population density
0
50
100
150
200
250
300
t [y]
F. coco
L. ternifolia
0.67
0.29

Figure 8