

Coupling Meta-population Models with GIS to Predict Freshwater Biotic Invasions

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EXTENDED ABSTRACT

Freshwater aquatic systems in Australia are being increasingly colonised by invasive species that are having a wide range of social, economic and environmental impacts. The study of the spread of such invasive species is constrained by the inherent difficulties of obtaining relevant data in a timely manner and in conducting critical field experiments. Consequently the modelling of invasion scenarios takes on increased importance in forecasting the potential outcomes of an invasion.

This study is a first synthesis of a modelling tool for determining the spread rates of a generalised invasive species in a linear freshwater system. The model consists of a population dynamics model in S-PLUS, which is linked to geographic locations via ArcView GIS. The population dynamics model is a stage/age based, meta-population model and incorporates both environmental and demographic stochasticity. Run from within ArcView, this is a closely coupled modelling system using the S-PLUS for ArcView link software. The relevant spatial data available for river systems is limited to the section length, with the possibility of including further data relevant to establishment. Factors thought to influence recruitment and transport, such as the frequency of floods were incorporated in parameterising the population model.

A case study looking at the effect of floods on the spread rates of invasive species along a section of the Murray River was carried out using a hypothetical species, with similar life history characteristics to salvinia, cabomba, alligator weed and parrots feather. Population growth and spread was simulated over 50 years at annual time steps,

with a proportion of the population spreading into a downstream section after each time step.

The results of the case study found that the larger the initial population size and the more frequent the flood events, the higher the final population size and the faster the rate of spread. The timing of floods in relation to the initial colonisation had little effect on these outcomes.

Future model development may include habitat suitability modelling to determine the likelihood of establishment. Upstream dispersal will also be considered, along with river network geometry, as this has been found to influence invasion dynamics.

1. INTRODUCTION

Models of spatial spread have been studied for decades (Okubo, 1980; Williamson 1996; Shigesada and Kawasaki 1997). The first model was by Fisher (1937) looking at the rate of spread of genes through a population. His partial differential equation considered spread in one dimension, but can be extended to two and assumes a random diffusion process. Skellam (1951) changed the equation to have exponential growth, modelling the spread of muskrats, finding a constant rate of spread. Together, they are called the Fisher-Skellam theory and are described as reaction-diffusion equations. Both equations are deterministic and assume a homogeneous environment. However, in order to use these equations the diffusion coefficient and the intrinsic rate of increase need to be estimated. Both values will vary with climate, geography, habitat and the environment (Williamson 1996; Hastings *et al.* 2005).

The Fisher-Skellam models however, are not spatially explicit. Spatially explicit models allow for the interaction of ecological processes and space. They also allow environmental context specific aspects of species to be included. As spatially explicit models are geographically referenced, they can be linked to Geographical Information Systems (GIS) (Higgins *et al.* 1996). The need to link ecological models to GIS data has been well documented (e.g. Coleman *et al.* 1994; Steyaert and Goodchild 1994; Theobald and Gross 1994; Ming and Albrecht 2004). There have been many successful attempts to do this with spread models (Ming and Albrecht 2004; Crossman 2004), but mostly in terrestrial environments, where rich spatial data are more readily available.

Ming and Albrecht (2004) developed a model framework for simulation of biological invasions that used a GIS based percolation model, a stochastic spatial model and a dynamic diffusion model. The species potential distribution was modelled using GIS and a decision tree analysis to predict the suitability of each grid cell for propagation. Using the stratified diffusion model, the range expansion of the species was determined in a heterogeneous environment. A percolation model was then used to link the spatial database and diffusion process, performing statistical analysis to characterise the spatial structure for the potential area of range expansion. Percolation models use a grid system, with cells being classed as either 'invader' or 'defender'. The model allocates a random number to each site with the 'invader' invading defender sites with the lowest

random number. The percolation model and stratified diffusion model was linked to a shared database and a program written in ARC Macro Language. Results from this model are in the form of GIS data, with the S-PLUS model using spatial data.

Crossman (2004) developed a model of spread of the invasive European olive. The first stage of the model was to determine the areas that are suitable for range expansion. This was done using Genetic Algorithm for Rule-set Production (GARP) and using GIS data on land use and vegetation. GARP is a set of rules for determining the non-random association between species distribution and environmental data. This is done using an iterative approach where several algorithms produce rules that form part of the rule-set. The species distribution data are randomly split into two groups; one is used to develop the model, while the other set is used to test the model. The final output is in the form of GIS raster data (Stockwell and Peters 1999; Peterson *et al.* 2001; Anderson *et al.* 2002; Anderson *et al.* 2003).

The second stage of Crossman's model looked at the population dynamics using transition matrix models. This matrix was dynamic in time, as density-dependent fecundity and maximum adult carrying capacity were substituted for values within the transition matrix. Both long distance and short distance dispersal were considered. A dispersal kernel, which is a curve of probability distribution versus dispersal, was developed using a three-component model of vertebrate dispersal.

Crossman compared and contrasted three different modelling approaches to forecast spread: a diffusion model using the Fisher-Skellam equation, neighbourhood-based cellular automata (CA) model and an individual-based model (IBM). CA models consist of a lattice grid of cells, with their state defined by their neighbours and their state at the previous time step. The value of the cells are updated each time step according to a set of rules (Higgins and Richardson 1996; Cole and Albrecht 1999; Kari 2005). IBMs are defined as simulation models that model individual organisms. The dynamics of these individuals and their interactions represent the ecological system (Grimm *et al.* 1999; Bercé 2002; Busing and Maily 2004). Both CA and IBM are spatially explicit, with populations and time being discrete. They are also stochastic and include environmental heterogeneity (Higgins and Richardson 1996). Crossman concluded that the IBM was the best spread model as it includes spatial heterogeneity and long-distance dispersal. However, this type of model requires long processing times. The Fisher-

Skellam model was the least favourable model as it was spatially implicit, assuming a homogeneous environment and uniform spread. The CA was the second best model, as it included heterogeneous landscapes and limited long-distance dispersal. It also had reasonable computer processing times.

Although both of the models described above included population dynamics and were spatially explicit, they are based in terrestrial systems and are therefore subject to different modelling constraints compared to aquatic environments, including dispersal mechanisms and pathways. Here we aim to build a generic, spatially explicit, meta-population spread model in a freshwater river system. The consequences of changes in propagule pressure on the outcome of the invasion are explored by simulating different initial population sizes in the most upstream section of the system and differences in flood frequencies over the whole system.

2. METHODS

The model consists of two parts: a population dynamics model developed in S-PLUS 6.2 (Insightful Corporation 2003) and a GIS model developed in ArcView 3.2 (ESRI 1999), and is integrated through the link software S-PLUS for ArcView GIS 1.1 (Insightful Corporation 2001).

The population dynamics model includes demographic and environmental stochasticity, with survival being modelled using a binomial distribution ($Bin(M,S)$ with survival S , of M individuals) and reproduction modelled with a Poisson distribution ($Poisson(SM)$, where both the mean and variance are equal to the product of S and M) to the next time step (Todd *et al.* 2004; Todd *et al.* 2005). A lognormal distribution was used to determine stage specific fecundities, using set means and standard deviations. Survival rates were assumed to be perfectly correlated and independent of the production of reproductive individuals. An annual time step was used for the model (1).

$$N_{jk}^0(t+1) = \sum_{i=1}^j \left(Bin(N_{ik}^1(t), T_{ij}(t+1)) + Ndrift_{i(k-1)}(t+1) \right) + \sum_{i=1}^4 Poisson((1-dr)(S_{ij}(t+1)SR_i(t+1) + V_{ij}(t+1)Veg_i(t+1))N_{ik}^1(t)),$$

$$Ndrift_{jk}^1(t+1) = \sum_{i=1}^4 Poisson(dr(S_{ij}(t+1)SR_i(t+1) + V_{ij}(t+1)Veg_i(t+1))N_{ik}^1(t)),$$

for $j = 1K-4$

(1)

where:

T_{ij} represents the transition and survival probabilities from the i th stage to the j th stage

S_{ij} is the transition and survival of offspring produced by sexual reproduction from the i th stage moving to the j th stage

SR_i represents the number of individuals produced via sexual reproduction

V_{ij} is the transition and survival of offspring produced by vegetative reproduction from the i th stage to the j th stage

Veg_i represents the number of individuals produced via vegetative reproduction

dr represents the proportion of the population drifting downstream, where individuals arrive in section K from section $K-1$.

Gender differences are not considered in the equations above (in vertebrate models, individuals are modelled as females, with males not limiting the population in any way). The model must therefore be parameterised accordingly. The model also included density-dependence in a similar way to that described by Todd *et al.* (2004). This accounts for the interactions between stages (2).

$$N_{jk}^1(t+1) = \begin{cases} CC(t+1) - \sum_{i=j+1}^4 N_{ik}^0(t+1) & CC(t+1) - \sum_{i=j+1}^4 N_{ik}^0(t+1) \leq N_{jk}^0(t+1) \\ N_{jk}^0(t+1) & CC(t+1) - \sum_{i=j+1}^4 N_{ik}^0(t+1) > N_{jk}^0(t+1) \end{cases},$$

for $j = 1K-4$

(2)

The section's carrying capacity, CC , is normally distributed about a specified limit, $SectionCC$, i.e. $CC: Norm(SectionCC, (0.1 \times SectionCC)^2)$.

The spatial model is currently restricted to the determination of the adjacent river sections and their lengths. ArcView provides S-PLUS with the section lengths (calculated from the 1:25000 GIS coverage, Geoscience Australia 2005), from which the carrying capacity, i.e. the maximum number of individuals that can colonise a given section, is approximated. Population spread downstream occurs only between adjacent sections at each time step.

The level of integration of the two programs is described as closely coupled (Goodchild 2003). Close coupling is similar to loose coupling in that two separate software packages are used and data files are passed between them (Sui 1998; Brimicombe 2003; Goodchild 2003). However, these files can be directly read by both programs, avoiding the need for file format conversions (Goodchild 2003). Furthermore, unlike loosely coupled models, there is also a common user interface, ArcView, from where the S-PLUS program is run. However, the S-PLUS parameter

values are currently altered manually in the S-PLUS code prior to running the model.

Basic analysis is carried out at the end of each time step, including the mean population size and the proportion of iterations occupied. These results can be saved as tables or maps. All of the results from each of the time steps are saved to file. The whole modelling process is automated using Avenue, the programming language for ArcView 3. Further summary statistics are produced in SAS (SAS Institute Inc. 1999-2001) at the completion of a model run.

There are a number of parameters that can be set for each model run. The number of iterations, river sections, time steps, the initial population size and the flood frequency and timing can all be altered in the S-PLUS code. In a flood year the fecundity of the population is increased. Flood frequency and timing could be used to simulate the release of environmental flows in the form of water released from dams to improve river health (Howell and Benson 2000), by regulatory agencies. As Australian river systems are often highly regulated (Harman and Stewardson 2005), random flood events were not included.

3. CASE STUDY

There has been an increase in the environmental flows allocated to many rivers over recent years (Harman and Stewardson 2005). By modelling different flow regimes, together with different invasion scenarios, it will be possible to determine the effect on the movement and rate of spread of invasive species.

3.1. Methods

Given the lack of data on any one species, the model was parameterised for a hypothetical one-stage plant species that reproduced asexually by fragmentation only, and had a maximum local density of 5 individuals per m², occupying 2 meters of bank on either side of the river. The model is based on weed species that have two stages in their lifecycle, fragments and established plants, with the fragments becoming established within one year. The model parameters were $j=1$;

$$T_{11} : \text{Norm}(0.7, (0.07)^2);$$

$$V_{11} : \text{Norm}(0.1, 0.01);$$

$$\text{Veg}_1 : \text{Floodlevel} \times \text{Lognormal}(25, 5);$$

$$dr=0.2;$$

$$\text{Floodlevel} = 0.1 \text{ or } 1.$$

Parameters relating to sexual reproduction were set to zero. This parameterisation could represent significant weeds such as salvinia (*Salvinia molesta*), cabomba (*Cabomba caroliniana*), alligator weed (*Alternanthera philoxeroides*) and parrots feather (*Myriophyllum aquaticum*) which spread primarily through vegetative fragments (Parsons and Cuthbertson 2001).

A series of model simulations was run, altering the initial population size set in section 1 at time 0 (50, 500, 5000), flood frequency (no floods, 0.1 or 0.2 floods per year) and flood timing (occurrence in year 1, 5 or 10). Each simulation was run for 1000 iterations over 50 years (1 year time steps).

The model was tested using the Murray River from the Hume Reservoir to Wentworth. This river segment was split into 8 sections according to major tributaries and dispersal barriers at which management actions on flow regime may be feasible. Each section was numbered in order downstream, for directional spread (Figure 1).

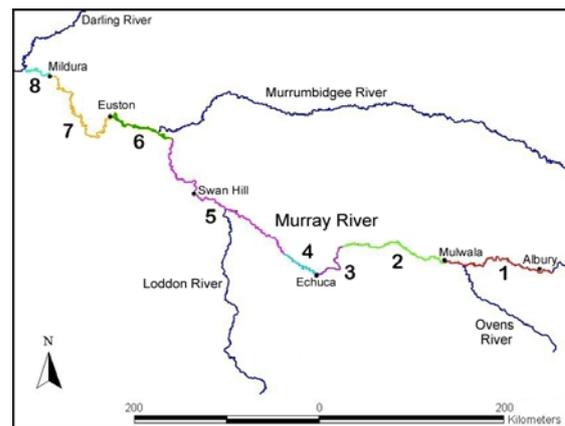


Figure 1. Map of the Murray River indicating the modelled sections on it and some major tributaries.

3.2. Results

Initial population size greatly affected the rate of spread, with the largest initial population size travelling faster compared to the smaller sizes (Table 1). Those models that had a high flood frequency also had higher spread rates than models with less frequent, or no floods. Those models that had no flood events, and low initial population size, had less than half their iterations with non-zero values and consequently had low mean population sizes (Table 1).

Models with no flood events had very low population growth, with the only increase in population size being due to the drift from upstream sections. Both the initial population size

and flood frequency caused major increases in population sizes downriver (Table 1). Floods were set to increase the reproductive rate by a factor of ten and so they had the largest effect on population growth and the number of individuals dispersing.

Table 1. The effect of initial population size and flood frequency on the mean population size at time step 50 for section 8 and on the median time taken to invade section 8.

Initial population size	Flood frequency (/year)	Mean population size	Median time (years)
50	0	<1	>50
	0.1	41	31
	0.2	31,407	21
500	0	<1	>50
	0.1	388	22
	0.2	307,166	16
5000	0	4	35
	0.1	3,941	18
	0.2	872,551	13

However, the size of the initial population, which varied by two orders of magnitude, also directly translated into larger populations and faster spread. At the higher parameter values, there was a diminishing effect as the carrying capacity of a section was approached. In section 8, the approximate carrying capacity was 1.2 million and the highest population achieved after 50 years was about 0.9 million (Table 1).

By contrast, the timing of flood events with respect to time 0 did not greatly influence the rate of spread or population size.

3.3. Discussion

Our case study shows that an increase in the frequency of floods is likely to increase the spread rate and population size of invasive species. Similar results have been found in other studies showing that environmental flows will be of benefit to invasive species, resulting in increased spread and abundance (Howell and Benson 2000; Gehrke and Harris 2001). Furthermore, regulated streams are highly disturbed environments, with flood events causing added disturbance, further favouring invasive species (Gehrke and Harris 2001). With the aim of increasing river health through environmental flows, control programs must be implemented to manage the abundance of invasive species as well as control spread rates.

4. MODEL LIMITATIONS AND IMPROVEMENTS

Environmental heterogeneity can affect all stages of the invasion process (With 2002; Hastings *et al.* 2005) and species spread rates (Hastings *et al.* 2005). The model currently assumes a homogeneous environment and that all areas are suitable for invasion. However, it is likely that some of these areas do not provide suitable habitat for establishment. Model improvements could include habitat suitability modelling through the use of climatic matching programs such as CLIMATE and CLIMEX (Kriticos and Randall 2001) or using environmental niche models such as BIOCLIM and GARP (Kriticos and Randall 2001; Peterson 2001; Peterson *et al.* 2001).

However, environmental heterogeneity can be difficult to implement (Ming and Albrecht 2004; Hastings *et al.* 2005). These habitat suitability models are designed to be used in terrestrial systems, as they use climatic data from terrestrial weather stations. Regulated rivers in general have been found to have different temperature, dissolved oxygen and salinity levels to that of unregulated streams, caused by reduced flow through parts of the year (Turner and Erskine 2005).

Information on water characteristics such as dissolved oxygen, temperature and nutrient levels are easily acquired and freely available. However, this information is only available in tabular form and not as part of a GIS database (Victorian Water Resources 2005). In this form these data are not easily accessible for inclusion in GIS models and extensive data translation would be required to make these data suitable for incorporating in the model. As well as this, the vegetation data in the riparian zone that would be important for these species have rarely been mapped at suitable scales.

Other improvements to the model would include a consideration of upstream movement as the model currently only considers downstream dispersal. Given the importance of flow on passive dispersal in plants, invertebrates and larval fish, this represents a realistic scenario, but ignores that many fish do disperse upstream and may show a bias towards upstream spread (Skalski and Gillian 2000). The model also considers the river as a linear system, rather than a branching network. River network geometry has been found to be important when considering invasion dynamics (Johnson *et al.* 1995; Cumming 2002). As the model does not include upstream spread, it is not important for branching, as we assume that the species is only located in the specified branch.

Finally, spread is modelled as downstream movement between adjacent stream sections. This may be unrealistic under natural, large flood events, when long distance dispersal across several sections may also be important.

5. CONCLUSIONS

This is the first implementation of a spatially explicit spread model in rivers and it has shown the capacity to develop and compare management scenarios, including those strategies that affect reproduction, survival and flow management. The effects that flood frequency and propagule size have on spread rates and overall abundance have been demonstrated. It is likely then that the increasing water allocations to environmental flows occurring in Australia's regulated rivers will need to be coupled with management strategies for invasive species to improve the overall health of our rivers.

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