MODELLING THE SPREAD OF INVASIVE SPECIES — PARAMETER ESTIMATION USING CELLULAR AUTOMATA IN GIS

Vivienne Cole **Jochen Albrecht**

Department of Geography
University of Auckland, New Zealand
{vcol001, ja}@geog.auckland.ac.nz

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ABSTRACT

The research presented in this paper uses a GIS-based cellular automata (CA) framework to study and create an applied and ecologically significant model of spread for invasive plant species. Cellular automata (CA) coded within a Geographic Information System (GIS) are employed to test the ability of studied parameters of vegetation dynamics to represent spatial growth patterns. This method combines the well-established spatial data management and presentation capabilities of GIS with the spatial and temporal modeling capabilities of CA theory, creating the ideal tool for applied, data rich modeling.

Instead of conventionally testing a previously created model, parameters are examined through simulation for their contribution to spread and the resulting spatial pattern. Initial simulation runs focus on the different effects of stochastic versus deterministic parameter values. Further studies examine the effect of different relationships, conditions and interactions between parameters. Upper and lower bounds to parameters, the interactions between parameters, and the relative importance of each parameter are examined in a number of combinations. Each parameter is then accepted or declined to create a conceptual model outlining the ecologically most significant features of the species. The authors show how models of invasion and vegetation dynamics can effectively be transposed into a contextually rich environment through a GIS-CA framework of model creation.

1. INTRODUCTION

Ecological models of spread and dispersal have been created for a variety of species over many decades. Technological development over the last few years has only recently allowed spatially data sets to be simulated in a temporally explicit environment, or vice versa, dynamical models to become spatially explicit. Thus, only the most recent studies of vegetation spread and the invasion of introduced species incorporate GIS as well as some form of dynamic modeling in one- or two-dimensional space. Most work, however, concentrates on presenting a predetermined model in an abstract computer simulation environment. The focus has been on the system's ability to display the model (results), as opposed to its ability to develop or compose a model, acting as a creative tool in an applied situation.

This paper is an introduction to the use of GIS and cellular automata (CA) in modelling the contextually complex real world phenomenon of species invasion. Most importantly, it advocates creative exploration and play as a means to examine a real world parameter space through simulation. Section Two introduces Cellular Automata, examining its formal definition and uses, developing the ideas of complexity that inhibit CA based modelling. Modelling theory, the use of space and time in ecological modelling, an understanding of creative exploration and play and the use of dynamic models are examined to support our discussion of applied modelling situations in sections Three to Five. Section Six introduces our case study species *Rhamnus alaternus* and examines the process of model conceptualisation and simulation strategy used to explore the species invasion. We finish with a discussion of the implications of CA use in modelling, implementation potential and ideas of moving agents.

2. CELLULAR AUTOMATA

Formally, cellular automata (CAs) are composed of the four elements *cell*, *state*, *neighborhood* and *rule*. A CA consists of a regular uniform lattice, which could be infinite in extent. The square *cells* of the lattice make up the cellular space (Wolfram 1986). The cellular space could be one-, two- or three-dimensional (Batty 1997). Every cell has a discrete variable. The values of the variables at each cell specify the *state* of the cellular automaton. The state of a cell depends on the states of other cells in the neighborhood of that specific cell. The *neighborhood* is defined by the immediately adjacent cells. The most common types of neighborhood in CAs are the von Neumann neighborhood and the Moore neighborhood. The state or value of the cell is updated according to the neighbouring pixel. Wolfram (1985) distinguishes totalistic CAs and outer totalistic CAs. Totalistic CAs update pixel values considering the value of the neighborhood, whereas outer totalistic CAs consider the neighborhood as well as the previous value of the pixel. The updating of pixels takes place in discrete time steps according to fixed *rules* (Wolfram 1986). Each time step could be called a generation, iteration or cycle. The rules of a CA are supposed to be local and uniform. Local in that context means that action takes place locally only. No action at a distance is permitted to determine the state of a cell; the cell state is updated according to the neighbors of that specific cell only (Toffoli 1987)[1]. Uniform means that the laws or rules of the CA are uniformly applied to every cell, regardless of the position of that cell within the geographic space. Although these rules can be of very simple construction, CAs produce complex behavior in most cases.

Even in the simple 'game of life' (Gardner 1970), complex patterns can evolve from a few rules and just two cell states. Starting from most initial configurations, a number of well-designed effects will occur which are evidence of the self-organizational ability of CAs (Toffoli and Margolus 1987). The 'game of life' shows that CA are able to model phenomena like reproduction, self-organization and a complex evolution, all typical of living communities (Benati 1997). Toffoli and Margolus (1987, p. 141) state that 'in spite of their wide interdisciplinary appeal, cellular automata would have remained at the level of a parlor game if they had not been shown to be capable of playing a serious role in the modeling of physics'. Stephen Wolfram (1983, 1985) was the first to systematically use the ability of CA to provide models where physical phenomena like ordering,

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[1] Note that this does not contradict Batty. If action-at-distance is required, a larger neighbourhood is defined. Therefore, the updating of the cell can still be considered as a local phenomenon.

chaos, turbulence, fractality etc. can be isolated (Toffoli and Margolus 1987).

3. MODEL (THEORY) CREATION AND VERIFICATION

Ecological processes are inherently complex. The process-orientated nature of the physical environment is complicated by biological systems, population dynamics and spatial heterogeneity. Models have been used to study many aspects of species and community ecologies. Many recent studies of vegetation spread and invasion of introduced species incorporate GIS and some form of dynamic modeling in one- or two-dimensional space. Most work, however, concentrates on presenting a predetermined model in an abstract computer simulation environment. The focus has been on the system's ability to display the model (results), as opposed to its ability to develop or compose a model, acting as a creative tool in an applied situation.

Mathematical models have traditionally been derived from multiple complex iterations of approximate data. This was mostly due to parameters being unmeasurable, and hence resulted in an overall lack of accuracy. Because equation based models involve averages and approximations, they can not provide information on individual components or properties (Wolfram 1984, Itami 1994). This is a disadvantage in study of plant dispersion, as it is often extreme events and migrations that can cause the invasion and spread of an organism. Thus, the variability of movement within a population is more representative of true invasion rates (Itami 1994, Goldwasser *et al.* 1994). In early ecological study, space was represented in mathematical models as a single explicit statement describing the area of influence (Silvertown and Lovett-Doust 1993). Ecological modeling emphasized temporal dynamics through the projection of state changes occurring at one location over time (Hunsaker *et al.* 1993).

Many ecological models have focussed dispersal based on internal, or population based conditions, such as density or extinction (Molofsky 1994, Tilman 1994). This is a justified approach, however the 'canvas' has been a one dimensional, continuous, and homogeneous cell based structure. These authors have then taken their results and claimed conclusions about the behavior of spread of a species across two dimensional, heterogeneous space, an assumption that is unrealistic in complex environments.

The complexity of calculations and variables involved in spatial reasoning (Renshaw 1991) and lack of computational power, prevented the exploration of spatial and temporal restraints on ecological populations in a large and unrestricted manner until recently (Itami 1994, Bascompte and Sole 1995).In this respect, another research characteristic of CAs becomes important, i.e., their use in building simple conceptual models of spatially distributed dynamical models. CAs are dynamic systems that exhibit the same kind of dynamics as partial differential equations. Therefore, they can be used to build simple conceptual models of spatially distributed dynamic models. As an example, CAs could be used to determine the best set of rules for an object to go from state A to state B. Furthermore, given a set of rules, a CA can tell how many iterations it takes to get from state A to B (Wagner 1997).

Through many decades of population modeling and vegetation analysis there has been debate between the use of stochastic and deterministic based parameters. Stochastic based modeling chooses a response to an input (for example) from a set of possible responses according to a fixed probability distribution. They are often used to simulate real systems under random conditions.

For creative thought to occur in scientific research there needs to be a method with which to explore with information. This can be achieved by playing with objects, variables and relationships within the known parameter space of a phenomenon. The ability to creatively explore an environment over time and space is possible non-destructively only through simulation. Simulation lends itself to detailed experimentation and creativity, pushing the boundaries of our current paradigms.

Itami (1994) argues for the use of deterministic based models in his simulation of spatial dynamics utilising Cellular Automata theory within a Geographic Information System. Itami quotes Signorini (1989), in saying that although the evolution of a simulation is often deterministic, it is not predictable, as new organisational devices present themselves during simulation experimentation. This is particularly true where locality in two dimensional space, as well as heterogeneity over time, contribute to complexity.

Cellular automata is an ideal tool for the manipulation of ecological parameters in simulation models as it utilises a "ground-up" modeling approach. CAs utilise parameters, rules and cell states to create models, instead of complex, averaged algorithms or non-spatial statistical methods. This makes CA a good tool for testing different components of complexity (as in Wolfram 1986).

4. SPACE AND TIME IN ECOLOGICAL MODELS AND CAs

Space and time have always been recognised as crucial components of ecological change (Colasanti & Grime 1993). Aggregated distributions of plant community species (at one or more scales) and juxtaposed neighbourhood competition, has led to continued study of spatial patterns of vegetation (Silvertown et al 1992, Baltzer et al 1998).

Population processes such as dioecious reproduction and interspecies competition are affected by the initial spatial arrangement of a species. The history of a species in a landscape is determined by spatial and temporal autocorrelation. The temporal range in which different species (or individuals encounter each other, and "how much space each occupies when contact is made" (Silvertown *et al.* 1992, Tilman 1994). The "null hypothesis" to this theory of spatial interrelatedness is that the future state of a landscape unit is independent of adjacent units (Hunsaker *et al.* 1993).

Spatially explicit models are "expected to increase our ability to accurately model population subject to complex processes" (Baltzer *et al.* 1998). The inclusion of space in vegetation models introduces more complex rules into a simulation than those created from simple parameters. This can lead to unpredictable chaotic simulation and non-linear dynamics (Silvertown *et al.* 1992).

Geographic space in a GIS is absolute and determined by the coordinate system used. In a CA, space is proximal, i.e., defined by the adjacency and influence of the neighborhood (Couclelis 1991). There is disagreement among authors whether space in raster GIS should be considered absolute or relative. Peuquet (1994) argues that the vector-raster dichotomy mirrors the absolute-relative space distinction. Couclelis (1997), however, believes that the essence of space in GIS is the georeferenced location, no matter if expressed in raster or vector format. However, it can be stated that raster GIS and CA share the same model of tessellation or cellular space. Even if the notion of space in a raster GIS is not originally of proximal nature, the cellular space model enables the application of certain analysis tools that simulate proximal space (Wagner, 1996). Many spatial analytical operators in a raster GIS behave like transition rules in a CA. Filter simulating the neighborhood notion could operate through adjacency or influence operations and enable the analysis of proximal space. Couclelis (1997) regards proximal space as the theoretical bridge between absolute and relative space.

Couclelis (1997) also distinguishes between two meanings of proximity or neighborhood. Basic spatial proximity can be described as simply being next to an object. Functional proximity implies influence on objects from neighbouring objects. The second meaning of proximity is well known as Tobler's First Law of Geography (Tobler 1975). The integration of CA with GIS that has been attempted in the last decade has helped to make CA more applicable as a potentially useful tool for qualitative forecasting (Couclelis 1997). The combination of the proximal space within CA and the GIS functionality as data storage, query and display tool delivers a technique to probe hypotheses about the large-scale effects of interactions that take place at micro-scale (Couclelis 1997).

5. FROM STATIC TO DYNAMIC MODELS

The modeling of plant dispersal is but one example for such complexity where some interrelations and functions contributing to the dispersal process remain unknown. Spatial interactions of environmental parameters like soil type, vicinity to the coast, slope and bird movement influence the spread of plants.

Variability over space points to variability throughout the population imposed by environmental conditions and resource division. Goldwasser *et al.* (1994) discussed possible links between life history characteristics and position at the leading edge of an invasion wave front.

Mathematical models of spread have traditionally been derived from multiple complex iterations of approximate data. This was mostly due to parameters being unmeasurable, and hence resulted in an overall lack of accuracy. Because equation based models involve averages and approximations, they can not provide information on individual components or properties (Wolfram 1984, Itami 1994). This is a disadvantage in study of plant dispersion, as it is often extreme events and migrations that can cause the invasion and spread of an organism. Thus, the variability of movement within a population is more representative of true invasion rates (Itami 1994, Goldwasser *et al.* 1994). By focussing on the behavior of the individual object, variability within a population can be examined at different scales. Thus, we can see both the wood in aggregation and the individual trees.

For many truly dynamic problems, contemporary GIS are considered poor performers. GIS have a poor ability to handle dynamic spatial models and the temporal dimension (Wagner 1996). A CA is operating in discrete time steps or iterations, which model a dynamic pattern that is changing for every iteration. Though CAs provide a very good modeling and analysis tool, a drawback is the lack of satisfying capabilities for data input, storage and display. Therefore, they cannot stand alone but should be combined with a GIS.

Unfortunately, there is not much literature on the actual implementation of a CA within a Geographical Information System. As Couclelis (1997), most authors discuss the specific properties of CA, the notion of space peculiar to CA and GIS, and the advantages and disadvantages of the use of a CA within a GIS.

Wagner (1997) examines the similarities between GIS and CA and the ability to implement each in the other and conclude that raster GIS provide all basic requirements of a cellular automaton. Multiple bit planes, neighbourhood structures, a language for specifying rules and the ability to apply rule sets synchronously are features of most raster GIS. Different data layers in the GIS simulate the bit planes, which represent past, present and future states of cells. Neighborhood structures can be constructed by using filters of different size and weighting. User-defined operations specified with a raster GIS language can be combined with predefined operations and enable a powerful tool to specify and apply rule sets. Wagner (1997) lists user-defined filters, overlay, cross-classification and reclassification as the most important of these operations.

In contrast to Wagner (1997), Wu (1998), who worked on an integrated GIS and CA approach in order to simulate land conversion, concludes that the natural affinity of GIS and CA justifies an integrated approach by using conventional GIS software. Wu acknowledges the fact that there are still many issues that need to be addressed in future research, like the analysis of sensitivity of a CA or the introduction of statistical methods for defining transition rules. Most projects on the integration of a CA within a GIS are only prototypes of simulation models (Wu 1998). The issue of sensitivity of CAs is a very difficult topic of research, as CAs often develop self-organizing patterns which cannot be predicted from initial conditions or configurations. A slight change in the initial values can lead to a very different pattern. Therefore, it is hard to predict how a CA reacts to a range of input values. In the following section, we discuss the method for transferring data from reality into simulation. In abstracting objects and relationships from a real world system, complexity of the system and the spatial and temporal context of its operation need to be considered.

The research presented in this paper uses a GIS-based cellular automata (CA) framework to study and create an applied and ecologically significant model of spread for the invasive plant species *Rhamnus alaternus*. The case study area and species are exemplary in that invasion is currently at a small scale, at an individual level and is in a contextually rich environment.

6. FROM REALITY TO SIMULATION

6.1. *RHAMNUS ALATERNUS*: A SPECIES FAR FROM HOME

Due to its effect on coastal ecosystems, the plant species *Rhamnus alaternus* (evergreen buckthorn) has been deemed an invasive species in New Zealand (ARC 1998, Harre 1998). *Rhamnus* was introduced to New Zealand in the late 19th century as an ornamental plant, its thick glossy green leaves and dark red berries making an attractive addition to garden hedges (Fromont 1996, ARC 1998). New Zealand's wild *Rhamnus* population is currently focussed in the Hauraki Gulf as it favors the warm coastal breezes of the inner islands and is predominately bird dispersed (Fromont 1996, Fromont 1997, Cameron 1999, Mitchell 1999). Species found to favor the plants fruit include blackbird (*Turdus merula*), starlings (*Sturnus vulgaris*) and song thrushes (*Turdus philomelos*) (Fromont 1996). These birds are all introduced species that have been found to be diverse feeders, moving amongst a range of environments (Day 1995, Anderson 1997). This means that disperser behavior is a prominent effect at smaller spatial and temporal scales rather than over large areas. *Rhamnus* grows in coastal environments, resulting in direct competition for space with endemic *Pohutukawa* trees, which are often roosts for the birds that disperse fruit (Harre 1999). Due to this effect on the coastal ecosystems of the Hauraki Gulf, *Rhamnus* has been declared a 'total control' plant pest by the regional authorities who are now initiating control methods (ARC 1998, Harre 1998).

6.2. RULE BASE SPECIFICATION

Fruiting plants survive in unique and specific spatial landscapes controlled by seasonal change associated with pollinator and disperser behaviour. These spatial and temporal constraints act as the conceptual building blocks in modelling dispersal and spread of a species. To focus a simulation in time and space while maintaining complexity of the system, a set of rules can be produced ranging from explicit constraints to intrinsic and extrinsic parameters.

The conceptual model of *Rhamnus* growth and spread (see appendix A1) outlines a basic lifecycle model of a dioecious plant species, with specific constraints on growth and spread as well as neighbourhood competition in space and time. The conceptual model acknowledges the cyclical nature of and within the lifetime of an individual plant. Phenological data was gathered from studies by Fromont (1996, 1997) and Herrera (1984, 1995) and from discussions with local experts (Cameron, Harre and Mitchell 1998, 1999). Field work and interviews by Cole (1999) on Waiheke Island in the Hauraki Gulf produced spatial floral information contributing to rule base specification and environmental constraints. The work of Anderson (1997), Williams & Karl (1996) and Day (1995) examining New Zealand bird species behaviour over different floral landscapes provides further data on which to base disperser assumptions and simulation strategies.

Distinct objects and relationships defined in the conceptual model are formalised as in appendix A3. Temporal and spatial extent and resolution, as well as minimum and maximum parameter values specify each object. Fixed definitions of objects and relationships are strengthened by model assumptions (see appendix A2), which make the creation of the rule base as transparent as possible. These assumptions determine implementation constraints such as sub-cellular homogeneity and absence of long term climatic change.

The initial rule base follows the temporal cycle of the conceptual model, incorporating constraints such as substrate, parental and coastal proximity. It must be acknowledged that incorrect approximation of disperser behaviour parameters can be a major factor in simulation model error (Ruckelshaus *et al.* 1997). Because of this, the rule base incorporates several indicators of disperser movement including favouring roosting perches such as the native coastal canopy species Pohutukawa (*Metrosideros excelsa*) and Karo (*Pittosporum crassifolium*) (as noted by Harre (1999) and Cole (1999)), and temporal and spatial floral competition landscapes for pollinators and dispersers (Buchmann & Nabham 1996). The rule base is a simple ASCII file that can be created by any domain scientist regardless of their GIS expertise.

6.3. SIMULATION STRATEGY

Ruckelshaus *et al.* (1997) suggested through their own simulation study that incorrect disperser parameter caused greater error in modeling than misclassification of land type. Disperser efficiency and effectiveness are key parameters to understanding plant dispersal. As defined by Reid (1989), disperser efficiency is the probability that a seed dispersed by the vector will lodge in a safe site and germinate. This is incorporated in our model two fold through landscape surfaces of germination probability and by differential success rates at different locations. This is a backward approach to disperser efficiency in that the focus is on space rather than following the disperser. Disperser effectiveness is the proportion of seedlings in a population that a particular seed disperser is responsible for disseminating. This is illustrated in our model through allocation of fractions of fruit volumes between gravity and bird dispersal. This division needs to be explored to determine effect.

The simulation needs to test for the following:

1. Scale of effect of disperser behaviour: efficiency and effectiveness.
2. Perpetual success of pollination
3. The effect of neighbouring species (as attractors and detractors)

The first test constricts the disperser range – in long range and short range distribution, from total movement, to smaller steps. This reduces the bird dispersers effect on spread and tests the dependency of *Rhamnus* on bird dispersal. The second test alters the volume of successful fruiting and hence population numbers that can be dispersed. The third strategy examines the effect that neighbouring (native and introduced) species have on *Rhamnus*. This will be primarily examined by phenology of common species, to create an appropriate level of competition against *Rhamnus* in particular areas dependent on assumed pollinators and temporal competition.

7. DISCUSSION

Species invasion is a prime example of a complex and not well understood problem in the realm of dynamic spatial modelling. We can distinguish between well-understood phenomena where this complexity is addressed by stochastic modelling and less informed conceptual models that require an exploratory approach. In instances where there is a lot of data, neural networks have been successfully employed to develop a plausible model. The disadvantage of neural networks, however, is their lack of explanatory capacity. True cellular automata are ideal tools to deal with the complexity of the problem at hand but are restricted by their notion of neighbourhood and the idea of homogeneous space. In many respects, this study exhibits characteristics of agent based systems. Software agents, and especially their spatial variants (Kohler *et al.* 1996, Booth 1997, Manrubia *et al.* 1999), however, are complex constructs in themselves. The evolutionary character of agent based systems can be examined and interpreted (e.g. with respect to the similarity of modelling results with observed real world phenomena) but they do not lend themselves to the kind of automatic self documentation that is inherent to the GIS implementation presented here. The CA theory informed parameter estimation in GIS (that is) presented in this paper, strikes a fine balance between the simple elegance of CAs and the complexity of agent-based systems in a technical environment that has by now almost ubiquitous character.

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10. APPENDICES

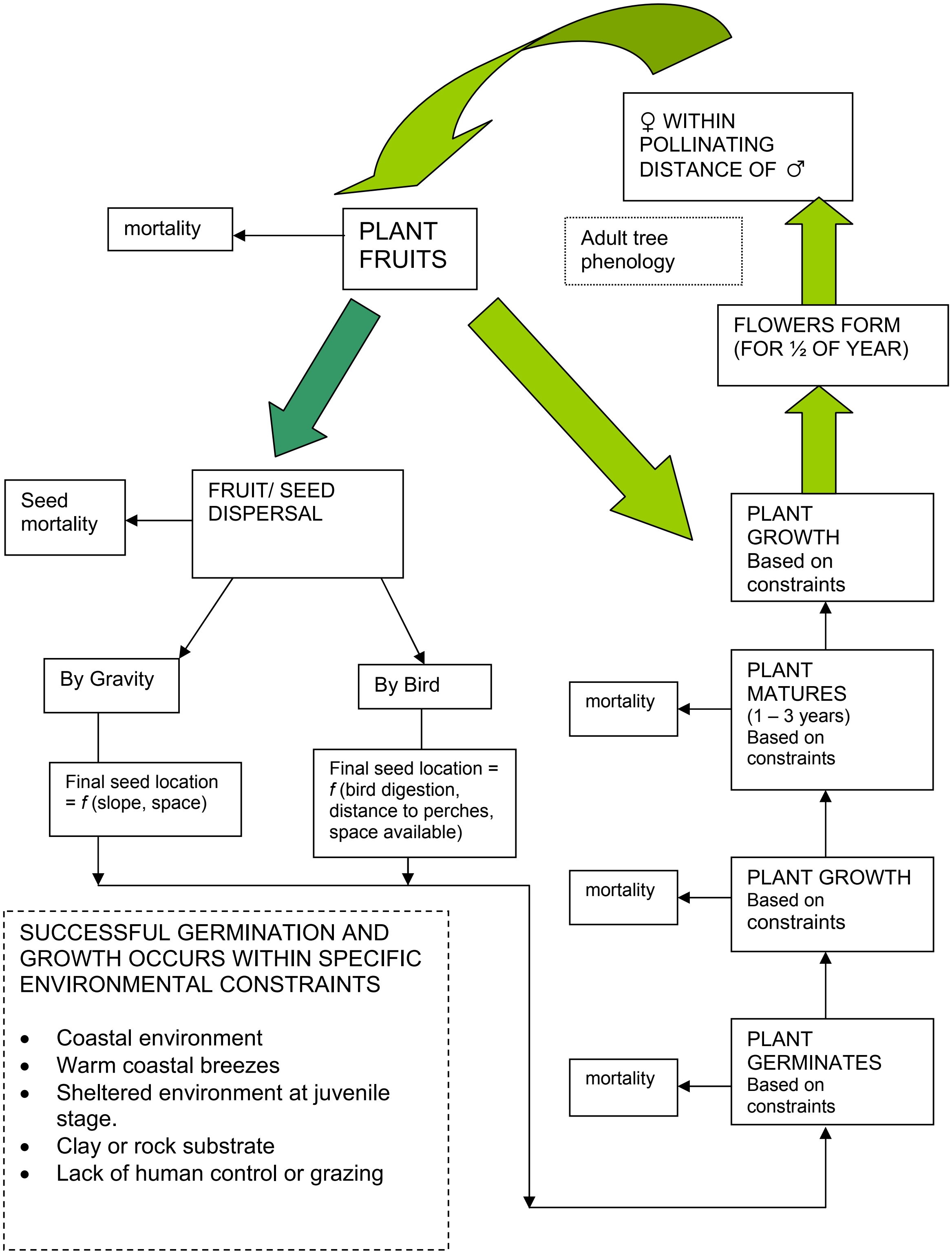
A1 Conceptual Model of *Rhamnus alaternus* dispersal

A2 Assumptions for Implementation

A3 Parameter Boundaries for the Conceptual Model

A4 Rule Base

A1. CONCEPTUAL MODEL OF *RHAMNUS ALATERNUS* DISPERSAL



A2. ASSUMPTIONS FOR IMPLEMENTATION

1. Success of life stages is dependent on environmental (external) and inter and intraspecies population constraints.
2. All flowers are successfully pollinated and fruit will be produced on any female within a certain distance of male plants.
3. Location of long distance dispersal is random after volume of species reaches a set space or volume
4. Closely grouped individuals will compete for space to exclusion of successive individuals over time until one plant occupies each space. There is no 3D modelling of stratification of the canopy.
5. Other sub-cellular processes will be parameterised to the 2x2m cell and 100x100m coarse grid cell size within a hierarchical data structure.
6. There is no human control, or change in current landuse patterns over the duration of the simulation.
7. Climate remains constant and appropriate to growth, reproduction and germination over the temporal extent of the model.
8. Food required by dispersers < food available to dispersers.
9. The disperser population spends most time in the area with the highest fruiting density.
10. Assume homogeneity of environment within grid cells (2m x 2m).

A3. PARAMETER BOUNDARIES FOR CONCEPTUAL MODEL

- *Parameter*: Germination

Definition: Seed germinates dependent on space availability and environmental constraints.
Units: Number of individuals / grid cell.
Minimum value: 0
Maximum value: 10
Spatial resolution: Individual plant (within 2 x 2 m grid cell)
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Growth

Definition: Plant grows, increasing spatial occupation and vegetative volume (and hence fruiting potential if female) dependent on space and environmental constraints.
Units: Metres / year
Minimum value: 0
Maximum value: f(age, substrate, location).
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Maturity

Definition: Time from germination to adult able to reproduce dependent on environmental constraints.
Units: Years to mature plant
Minimum value: 1
Maximum value: 5
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Flower

Definition: Male and female plants flower, ready for pollination.
Units: Number/m²
Minimum value: 0
Maximum value: average = 10000/5 m²
Spatial resolution: individual – within 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Gender

Definition: Dioecious species.
Units: Individual – male or female
Minimum value: 35% female
Maximum value: 50% female
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly association at germination

- *Parameter*: Fruiting

Definition: Female individuals fruit for 2 months per year.
Units: Fruit(seed)/m²/female tree
Minimum value: 0
Maximum value: average = 10,000(30,000)/5m²/vegetative volume of female tree.
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Pollination

Definition: Dioecious species. Distance between female and closest male *Rhamnus* individuals for pollination.
Units: Metres (grid cells) – between closest edges of grid cells.
Minimum value: 0 (0)
Maximum value: 16 (8)
Spatial resolution: 2 x 2m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

Parameter: Gravity aided dispersal
Definition: Dispersal of seed through fruit fall from tree. Distribution local to parent tree. Dependent on slope
Units: Metres (grid cells) from parent tree - between closest edges of grid cells
Minimum value: 0
Maximum value: f(slope)
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Bird aided dispersal

Definition: Fruit ingested by birds distributes seed across frugivores home range. Initiates long range dispersal of plant species. Dependent on pattern of bird visits, slope and bird digestion.
Units: Metres (grid cells) from parent tree
Minimum value: 0
Maximum value: full extent of study area
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Space

Definition: Area available for germination and growth of plant.
Units: Metres²
Minimum value: 1/15 of grid cell space for seedlings
Maximum value: 8 x 8m² for large mature tree
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

- *Parameter*: Slope

Definition: Slope of topography
Units: Degrees
Minimum value: 0
Maximum value: 90
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Constant

- *Parameter*: Perches

Definition: There is a positive correlation between proximity to bird perch trees and clusters of *Rhamnus alalternus*, i.e. – a distance decay function from large trees in constrained area.
Units: Metres
Minimum value: 0
Maximum value: Extent of grid – with decreased probability.
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly.

- *Parameter*: Continentality

Definition: Species prefers coastal habitat.
Units: Metres from coastline
Minimum value: 0
Maximum value: To centre of island – distance decay probability
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Constant

- *Parameter*: Warm coastal breezes

Definition: Species grows best in warm aspect conditions. Better growth and reproduction
Units: Aspect in degrees
Minimum value: 0
Maximum value: 360
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Constant

- *Parameter*: Shelter

Definition: Germination and juvenile stages require some shelter for success.
Units: Metres from shelter
Minimum value: 0
Maximum value: Distance decay from sheltered aspects and vegetation
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly.

- *Parameter*: Substrate

Definition: Species prefers clay or rock substrate for growth.
Units: Nominal class [clay, rock, sand, humus]
Minimum value: -
Maximum value: -
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Constant.

- *Parameter*: Seed crop

Definition: Spatial and temporal differentiation of volume of seed produced.
Units: Proportion of potential
Minimum value: 0
Maximum value:1
Spatial resolution: 2 x 2 m grid cell
Spatial extent: Waiheke Island / Hauraki Gulf
Temporal Resolution: Yearly

A4. RULE BASE (All input grids that are necessary to run the model are displayed in *italics*.)

1. Cell states = {germinating(g), juvenile(j), adult male(m), adult female(f), fruiting female(F), empty(e)}
2. Grids of constraints
   COASTAL = { Distance decay inland from coastline }
   PERCHES = { Distance decay from bird perches }
   SUBSTRATE = { clay, rock, sand, humus }
   SHELTER = {sheltered, not sheltered } = f(aspect)
   RHAMNUS = { initial distribution of *Rhamnus alaternus* plants}
3. Successful FRUITING (F) = MATURITY + POLLINATION + [FLOWER*GROWTH] .
4. Dispersal = if F > 5 in NEIGHBOURHOOD
   then 2/3 * FRUITING = BIRD_DISPERSAL
   and 1/3 * FRUITING = GRAVITY_DISPERSAL
   else ½ * FRUITING = BIRD_DISPERSAL
   and ½ * FRUITING = GRAVITY_DISPERSAL
5. BIRD_DISPERSAL = distance_decayPARENT(F) + PERCHES + SPACE
6. GRAVITY_DISPERSAL = distance_decayPARENT(F) + distanceSLOPE + SPACE
7. GERMINATION(g) = [BIRD_DISPERSAL or GRAVITY_DISPERSAL] + anySUBSTRATE + lowprobCOASTAL + SHELTER
8. GROWTH(j) = at one iteration from (g) → [anySUBSTRATE + highprobCOASTAL] * $1/8m^2$ + (GROWTH(j)n – 1) if at iteration: x(i) = $(g)^n > 1$ individuals then $(j)^n = n - 1$ at x(i + 1) until n = 1
9. MATURITY[(m), (f)] = [claySUBSTRATE or rockSUBSTRATE] + highprobCOASTAL + [[1 iteration < GROWTH > 5 iterations] since GERMINATION]
10. GROWTH [(m) , (f)] = MATURITY + [GROWTH(j) + (GROWTH ~ [(m),(f)]n – 1) + $1/4m^2$]
11. MATURITY[f → F] = (f)FLOWER + POLLINATION
12. directionGROWTH = SPACE + clay/rockSUBSTRATE + highprobCOASTAL
13. long_rangeDISPERSAL = randomDISPERSAL → coarse grid.
14. mortality (j) = if x(6), (j) ≠ (m), (f) or (F)
    then n = 0 and cell = e
15. mortality (g) = if x(2), (g) ≠ (j)
    then n = 0 and cell = e