

Modelling the potential spread of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (red imported fire ant) in Australia

Joe C Scanlan^{1*} and Cas Vanderwoude^{2†}

¹Department of Natural Resources and Mines, PO Box 318, Toowoomba, Qld 4350, Australia.

²Department of Primary Industries and Fisheries, Oxley, Qld 4075, Australia.

Abstract

Quantifying the potential spread and density of an invading organism enables decision-makers to determine the most appropriate response to incursions. We present two linked models that estimate the spread of *Solenopsis invicta* Buren (red imported fire ant) in Australia based on limited data gathered after its discovery in Brisbane in 2001. A stochastic cellular automaton determines spread within a location (100 km by 100 km) and this is coupled with a model that simulates human-mediated movement of *S. invicta* to new locations. In the absence of any control measures, the models predict that *S. invicta* could cover 763 000–4 066 000 km² by the year 2035 and be found at 200 separate locations around Australia by 2017–2027, depending on the rate of spread. These estimated rates of expansion (assuming no control efforts were in place) are higher than those experienced in the USA in the 1940s during the early invasion phases in that country. Active control efforts and quarantine controls in the USA (including a concerted eradication attempt in the 1960s) may have slowed spread. Further, milder winters, the presence of the polygynous social form, increased trade and human mobility in Australia in 2000s compared with the USA in 1940s could contribute to faster range expansion.

Key words cellular automaton, *Solenopsis invicta*, transition probability.

INTRODUCTION

Solenopsis invicta (red imported fire ant) is an aggressive social species endemic to Brazil, Uruguay, Paraguay and northern Argentina (Lofgren *et al.* 1975; Vinson & Sorensen 1986; Taber 2000), where it is not particularly abundant (Porter *et al.* 1997). Much of tropical and subtropical regions of the world appear suitable for this ant (Morrison *et al.* 2004). Where it has established, it quickly expands its range (Lofgren *et al.* 1975; Callcott & Collins 1996) and dominates the biota in the landscape (Porter *et al.* 1997) to the detriment of other fauna and humans. One of its greatest adaptive strengths is its ability to survive in ruderal and disturbed habitats (Tschinkel 1987). Characteristics of *S. invicta* that enable it to survive in such environments include: aggressive colony defence; a painful sting (Rhoades *et al.* 1977; Stablein & Lockey 1981; Starr 1985; Stafford 1996; Levy *et al.* 1998; Solley *et al.* 2002); the relocation of the colony should conditions become unfavourable (or should better habitat be found elsewhere); dispersal by flight and budding (radial expansion of colonies); the presence of monogyne and polygyne colonies; and dominance of food resources (Tschinkel 1998). *Solenopsis invicta* can be regarded as a perfect 'weed species' (Tschinkel 1987).

In the 1930s, *S. invicta* was discovered in southern USA near Mobile, Alabama where it probably arrived with soil ballast from ships trading with South America (Vinson & Sorensen 1986; Taber 2000). Once established, colonies spread rapidly via flights of newly mated queens and by human-mediated translocation through the sale of nursery plants, soil and turf. Newly mated queens can disperse up to 5 km from the parent nest through flight (Vogt *et al.* 2000), although most queens settle within 1 km (Markin *et al.* 1971). Human-mediated dispersal can result in far greater distances between source and new infestations (Vinson 1997). It was not until 20 years after its initial introduction that *Solenopsis invicta* was recognised as a serious pest and the US Congress funded a large-scale attempt at eradication in 1957 (Vinson & Sorensen 1986). This eradication program featured widespread aerial baiting with heptachlor and then mirex (both organochlorine pesticides) as the active ingredients (Vinson & Sorensen 1986), and ceased late in the 1960s when the registration for mirex was withdrawn. *Solenopsis invicta* now occupies much of southern USA (Callcott & Collins 1996) and has established in California (e.g. Mescher *et al.* 2003), throughout the West Indies (Davis *et al.* 2001) and in south-east Asia (see newspaper report from 2005 – http://news.xinhuanet.com/english/2005-03/13/content_2690287.htm accessed on 15 August 2005).

Substantial economic, environmental and health impacts have been recorded in the southern states of the USA where *S. invicta* has been present for about 70 years and this led to

*joe.scanlan@nrm.qld.gov.au

†Present address: Flybusters/AntiAnts, Barry's Point Road, Takapuna, New Zealand.

concerns about its potential impacts in Australia. In the state of Texas (population ~24 million), the total economic impacts of *S. invicta* are estimated at US\$1.2 billion annually (Lard *et al.* 2002). The majority of these costs are borne by residential households. In the USA, over 80 deaths have been attributed to anaphylactic reactions to stings (Taber 2000). Environmental impacts in the USA, while harder to quantify, are substantial (Allen *et al.* 1994; Wojcik *et al.* 2001).

Solenopsis invicta was detected in the south-western suburbs (centred on Wacol) and at the air and sea ports of Brisbane, Australia in February 2001. Subsequent delimiting surveillance identified an infestation of more than 300 km² (Vanderwoude *et al.* 2004). Moloney and Vanderwoude (2002) examined the likely environmental impacts of *S. invicta* on eastern Australia's fauna, should *S. invicta* continue to spread. Early work on climatic suitability suggested that *S. invicta* could occur over much of Australia, although more recent studies suggest a more restricted suitability (Sutherst & Maywald 2005) due to aridity. Even in these environments, areas along watercourses and any areas with added water (e.g. irrigation or gardens) would be at risk (Morrison *et al.* 2004). However, the rate at which *S. invicta* might spread in the absence of control is unknown. Irrespective of the area suitable for *S. invicta*, an estimate of the likely rate of spread was required to assess the potential economic impact of *S. invicta* in Australia.

This paper describes the use of a cellular automaton model to predict the potential rate of spread of the more dispersed population of *S. invicta* in Brisbane's south-western suburbs (henceforth referred to as Wacol). This model is combined with an estimate of the number of new locations that may occur within the rest of Australia to provide an overall rate of unconstrained spread.

Model description

Within the first 6 months after discovery, it was not possible to develop a biologically based model of potential spread of *S. invicta* within Australia as there was little information available about the species in this environment. More detailed models of the number of colonies (as has been done in the

USA – Korzukhin & Porter 1994; Stoker *et al.* 1994; Killion & Grant 1995; Adams 1998) were not suited to the analysis of large-scale spread as these were of a finer resolution than suitable to estimate large-scale spread at one location or the spread across Australia. An alternative approach was required.

Cellular automaton models have been used extensively to model spatial dynamic phenomena, including forest dynamics (Lett *et al.* 1999); epidemic propagation (Sirakoulis *et al.* 2000); fire spreading (Hargrove *et al.* 2000); urban growth (White *et al.* 2000b); and land use and land cover change (White *et al.* 2000a; Soares-Filho *et al.* 2002). This type of model was considered most appropriate for projecting spread in a short period with limited data.

Two models were developed to examine two scales of interest. First, an estimate was made of the *number of locations* (defined as an area of 100 km by 100 km) within which some *S. invicta* might be found (presuming no control of spread). Moody and Mack (1988) have shown that as the number of new infestations increases, the overall rate of spread of invasive organisms accelerates. This was based on a logistic growth model. Second, the increase in area (number of 1 km by 1 km grid cells) and density (number of colonies of *S. invicta* per grid cell) *within a location* was modelled using a cellular automaton model. These combined to provide an estimate of the total extent of *S. invicta*.

Number of locations

The number of locations where *S. invicta* would be found was estimated using a simple growth model that included density-dependent (dd) and density-independent (di) components of increase (see Fig. 1a).

$$\text{Locations}(\text{total}) = \text{Locations}(\text{dd}) + \text{Locations}(\text{di})$$

where:

$$\text{Location}(\text{dd}) = \text{Random}(0,1) \times \left(\frac{1 - \text{Locations}}{\text{Max_Locations}} \right) \times \left(\frac{\text{Locations}}{\text{Doubling_time}} \right)$$

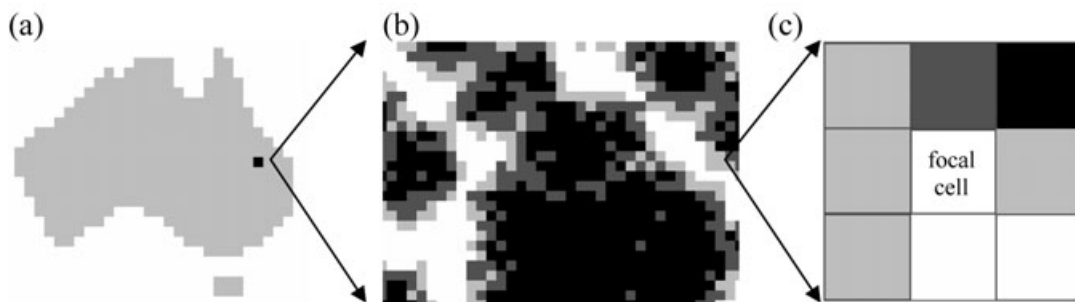


Fig. 1. Simulations were made of (a) the number of locations within Australia which may have *Solenopsis invicta* after certain time steps (years). (b) At each location, the number of cells with *S. invicta* was calculated based on (c) the state of the focal cell and the number of surrounding cells with *S. invicta*. (a) The number of locations (each 100 km by 100 km) where *S. invicta* could be found is calculated from logistic equation. Three rates of increase were simulated. (b) Within a location, the number of cells (1 km by 1 km) of different densities of *S. invicta* is calculated from cellular automaton. White is free of ants; black is dense category. Three rates of increased were simulated. (c) After each time step (1 year) in each simulation, the density of *S. invicta* in each cell at the location is determined by the current condition of the cell and the number of neighbouring cells with *S. invicta* (six in example above).

and

$$\text{Locations}(di) = \text{Random}(0,1) \times 2$$

where:

Random(0,1) is a uniform random variable between zero and one;

Locations are the number of locations (100 km by 100 km) at which *S. invicta* is found [both *Locations*(dd) and *Locations*(di) were rounded to the nearest whole number];

Max_Locations is the number of possible locations (areas of 100 km by 100 km) within Australia;

Doubling_time is number of years for a doubling in the number of locations (values used: 2, 3 and 4).

This model was stochastic in that it specified a probability for both components leading to establishment of new locations. It was not spatially explicit; the simplifying assumptions were that all suitable locations within Australia were equally likely to be invaded by *S. invicta* and that most of the continent was suitable. The increase in the number of locations was represented by the two components of spread – one that was density-independent representing new locations resulting from long-distance, anthropogenic-mediated dispersal, and one that was density-dependent representing new locations that were associated with existing locations of *S. invicta*.

The lowest, highest and median of 30 simulations were chosen to represent low, high and moderate rates of expansion of locations in Australia.

Spread within locations

This model represented the spread of *S. invicta* at one location as a stochastic, cellular automaton (see Fig. 1b). The key features of the system were:

- 1 The location was represented by a two-dimensional array (100 by 100) of identical grid cells (each 1 km by 1 km).
- 2 The state of each cell consisted of one of four 'density classes' of *S. invicta* (absent; present; common; and dense).
- 3 A neighbourhood of eight cells around the cell of interest influenced the probability that the focal cell (Fig. 1c) would change state (i.e. a Moore neighbourhood; Hogeweg 1988). The number of neighbouring cells that contained *S. invicta* was tallied; this influenced the likelihood that the density class of *S. invicta* in the focal cell would change.
- 4 The probabilities of change were represented in nine transition matrices, with one matrix for each neighbourhood category (zero neighbourhood cells with *S. invicta*; one neighbourhood cell with *S. invicta*; ...; all eight neighbourhood cells with *S. invicta*). These transition matrices were the 'rules' that determined the future state of the cell, given the current state of the cell and the condition of the neighbourhood.
- 5 All cells were simultaneously updated at each time step (1 year) (time type 2 *sensu* Ruxton & Saravia 1998).

To initialise the model we needed to know the density of *S. invicta* within each of these cells. In June 2001, *S. invicta* was positively reported in 45 grid cells in the Wacol area. These were allocated to states (density classes) as follows:

- 1 Present – only one or two properties identified as having *S. invicta*. This was equivalent to 1–10 colonies per grid cell (29 cells).
- 2 Common – several properties per grid cell with confirmed *S. invicta*. This represented 10–1000 colonies per grid cell (11 cells).
- 3 Dense – >10 properties with confirmed *S. invicta*. There would be >>1000 colonies per grid cell (5 cells).
- 4 Absent – All remaining cells at the location (9955) were free of *S. invicta*.

In this cellular automaton, the state of a system (also called the state vector) was the proportion of the system in each of four specified density classes. The state of each cell in the modelled system depended on the state of the cell at the previous time-step and a set of probabilities of change from one class to another, as influenced by the presence of *S. invicta* in the neighbourhood (see Fig. 1c). Those probabilities were assumed to be constant over time. This can be represented mathematically as:

$$S_{(t)} = \{P\}_{(i)} \times S_{(t-1)}$$

where:

$S_{(t)}$ is the state vector at the current time (t);

$S_{(t-1)}$ is the state vector at the previous time ($t - 1$);

$\{P\}_{(i)}$ is the appropriate probability matrix. This is a square matrix that contained the probability of change from every class to every other class for neighbourhood (i).

Two sets of nine matrices were developed – one representing a low rate of growth within the location and the other a high rate of growth. As well, the model was constructed so that at each time step (1 year), a low or a high rate of growth could be selected with a known probability. Thus, a mid-rate was computed by selecting a low rate for 50% of the time and a high rate for the other 50%. All other probability combinations were possible. Multiple simulations were run to obtain mean changes over time – 30 simulations were used.

The key transition probabilities were the probability of staying in the same state (Fig. 2) and of changing to the state with a greater density of *S. invicta* (Fig. 3). The probabilities that a cell may change by more than one class (e.g. changing from Present to Dense; or from Common to Absent) were very low; these are not shown in Figures 2 and 3. Another key probability was that of a cell free of *S. invicta*, and surrounded by other cells that were empty, becoming occupied (i.e. Absent to Present category). This probability was very low (0.0001); small increases in this probability caused large increases in the rate of spread, due to the invasion of a cell from which further expansion can take place. This is a common feature of systems being invaded (e.g. Moody & Mack 1988).

We derived the transition matrices (i.e. all the probabilities of change from one density category to another) after examining the number and condition of cells that existed in Wacol and from information on the biology and spread of *S. invicta*

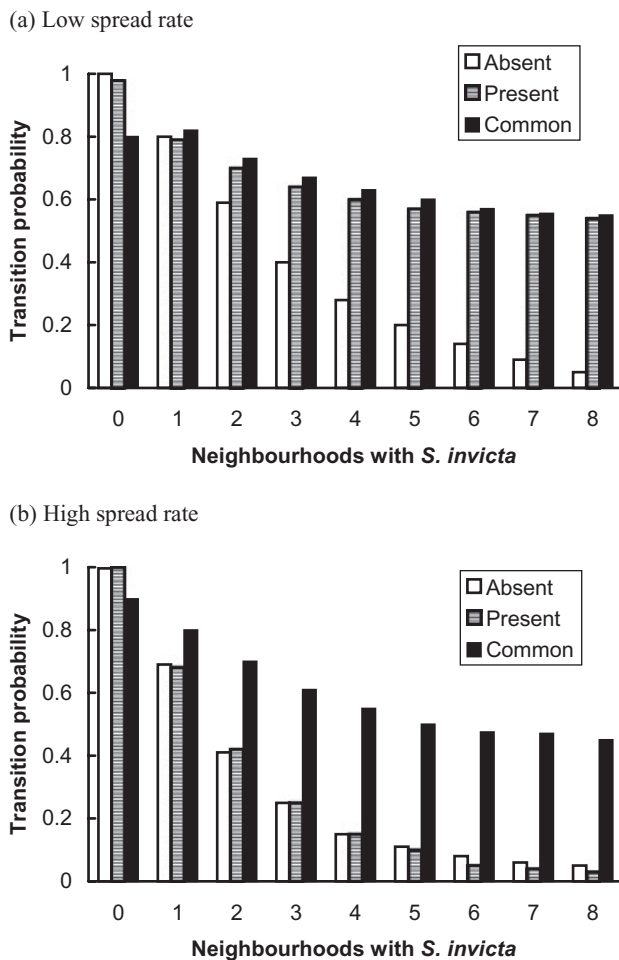


Fig. 2. The probabilities of each density class remaining the same in each time step for all neighbourhoods for (a) low rate of spread and (b) high rate of spread. (The Dense class not shown as probability for both low and high spread rates exceeded 0.998).

in the USA. It was not possible to derive these probabilities mathematically, given that only one set of observations was available in May 2001. Some refinements to the original set of matrices were required to obtain a good fit between expected and observed number and distribution of density classes reported up to the time that the modelling was performed (see Fig. 4 for a comparison of observed and predicted distributions).

For each cell at each time step, the appropriate transition matrix was selected (dependent on the number of neighbouring cells which contained *S. invicta*). A uniform random number on the interval of zero to one was generated and this was compared with the values in the selected transition matrix for that density class to determine the new density class of the cell.

One of the model assumptions was that *S. invicta* was well established at Wacol in 1996. Similarly, a commencement time for *S. invicta* in the USA had to be chosen to compare the rates of spread on the two continents. *Solenopsis invicta* was reported in the USA in about 1930, and *Solenopsis richteri*, a closely related species, was also present (Taber 2000). Prior to Buren's revision (1972, 1974 quoted in Hung *et al.* 1977)

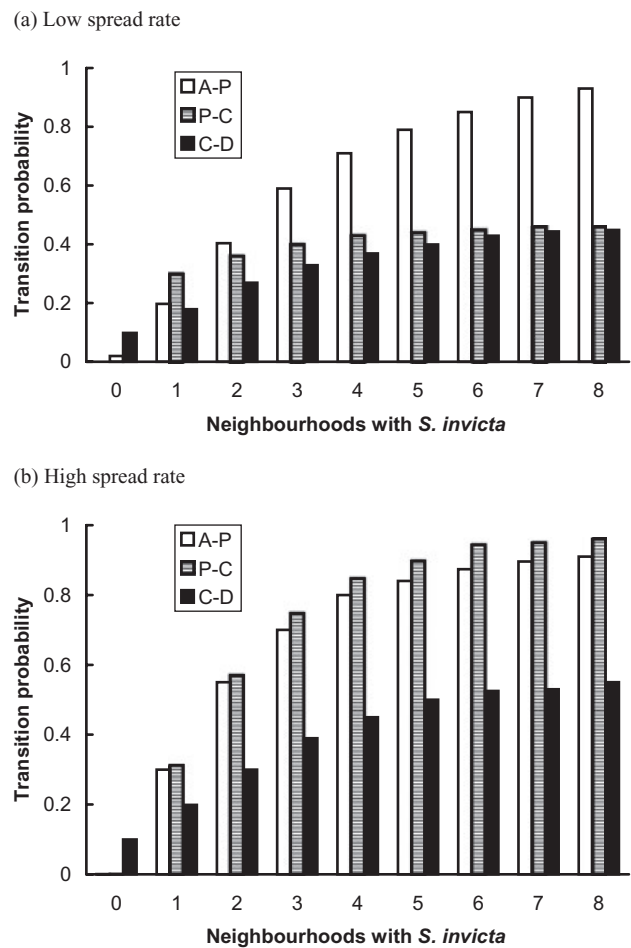


Fig. 3. The probabilities of each density class increasing to the next level of occupancy by *Solenopsis invicta* in each time step for all neighbourhoods for (a) low rate of spread and (b) high rate of spread. A, Absent; C, Common; D, Dense; P, Present. (The Dense class not shown as this class cannot increase in density).

these two species were considered to be light and dark forms of *Solenopsis saevissima*; this presents some difficulties. For the purposes of comparing the actual rate of expansion in the USA and the potential rate of expansion in Australia, we assumed that *S. invicta* was well established in the USA in 1940 and used this as the starting point for model comparisons.

In the USA, the area infested with *S. invicta* continues to increase (Levia & Frost 2004; Morrison *et al.* 2005), despite a program of eradication in the 1960s and subsequent ongoing control measures (Lofgren *et al.* 1975; Vinson & Sorensen 1986).

Total area

The total area within which *S. invicta* could be found, given uncontrolled spread, was calculated from the number of locations and the number of cells within each of these locations that contained ants. This is not a simple multiplication of two curves, as there is a different starting time for each location and the area of *S. invicta* at that location depended on how long the location had been infected.

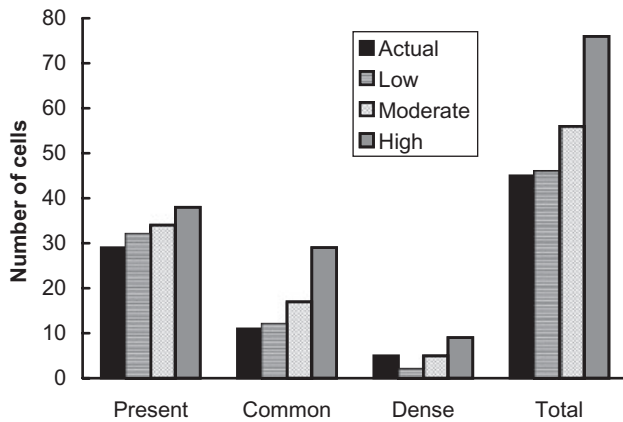


Fig. 4. Actual and simulated number of cells (1 km by 1 km) with *Solenopsis invicta* of different density classes in Wacol, using three different growth rates (100% low; moderate (50% low–50% high); and 100% high).

Three rates of increase of number of locations and three growth rates within a location were combined to produce nine possible scenarios for the area of *S. invicta* in Australia. This provided an envelope of possibilities for the actual areas of *S. invicta* that could be expected if no control were exercised in Australia.

RESULTS

Number of locations

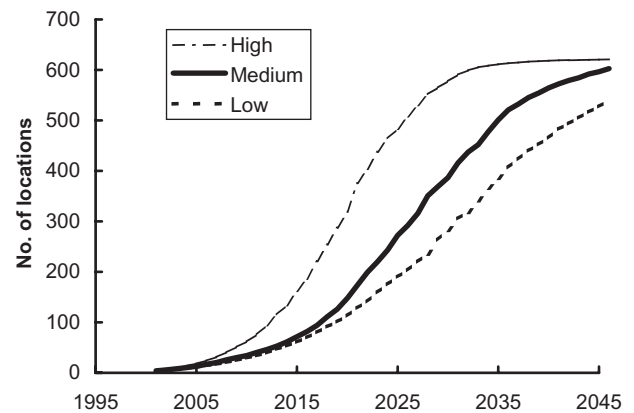
Simulations indicated that *S. invicta* would have spread to 200 locations (where a location is 100 km by 100 km) by 2017 for the high growth rate scenario, by 2023 for the moderate growth rate and by 2027 for the low growth rate (Fig. 5a). (By way of comparison, the whole of Queensland contains 173 locations.) It was predicted that, with a moderate growth rate, the most rapid period of increase in the number of locations would occur between 2020 and 2035. These general patterns of growth seemed reasonable to us (the authors) and to others who were dealing with such pest incursions (T. Kompas, Australian Bureau of Agricultural and Resource Economics, pers. comm. 2001).

Within locations

To assess the applicability of the model of growth rate at a single location, the cellular automaton was run for 5 years from end of 1996 to the present with a starting condition of one grid cell of 100 ha in the ‘present’ category at Wacol. These simulations were then compared with the surveillance data at Wacol, as of the 30 June 2001. There was good general agreement between the known density classes of *S. invicta* and the simulated results from the low and moderate cases (Fig. 4). The modelled and observed distributions for June 2001 were not significantly different ($\chi^2 = 0.26$; $P = 0.878$).

A typical simulation result was compared with the actual distribution in June 2001 in Figure 6, with the simulated

(a) Change in number of locations



(b) Change in area at one location

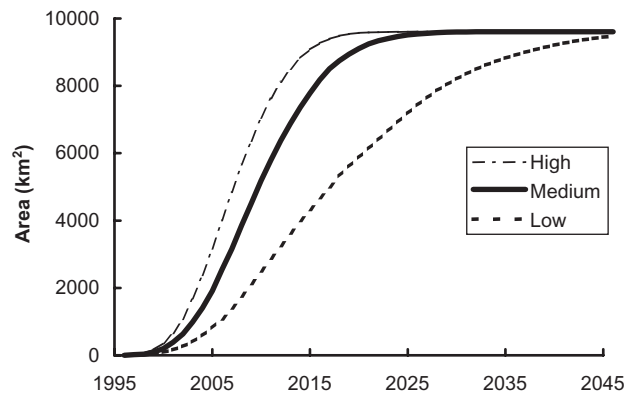


Fig. 5. (a) Simulated number of locations (100 km by 100 km) with *Solenopsis invicta* in Australia, showing the difference between three rates of increase. (b) Area of *S. invicta* within one location.

results being similar in pattern to the observations. The actual number of grid cells with *S. invicta* at Wacol was unknown at the time the model was constructed. The number of known infested cells increased slightly after model development. Thus, the ‘actual’ situation was a slight underestimate of the real number in 2001. The moderate case was the ‘most likely’ case.

The model was run forward using May 2001 as the starting point for the simulations of future spread within the location (Fig. 7a). This indicated that by 2012, over two-thirds of the Brisbane location would have *S. invicta* if there were no control undertaken (Fig. 7b).

Within Australia

The simulations indicated that *S. invicta* could cover 2 million km² within Australia by 2028, 2037 and 2048 for the high–high, medium–medium and low–low scenarios, respectively (Fig. 8a). This was quite different from Figure 5a, which

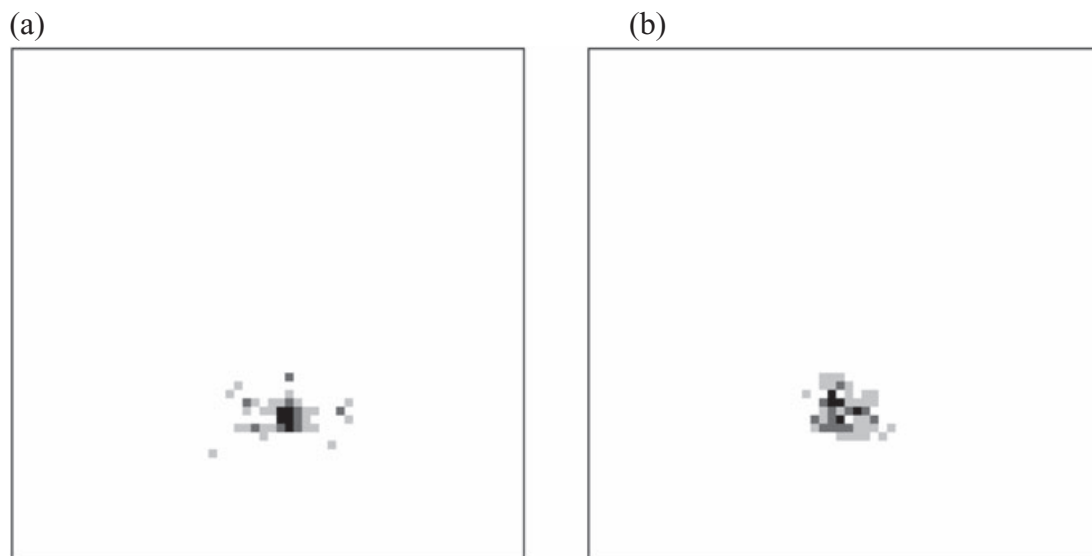


Fig. 6. Simulation of *Solenopsis invicta* spread in Wacol. (a) The distribution of cells in May 2001; (b) simulated distribution of cells in 2001 (white – Absent; light grey – Present; dark grey – Common; black – Dense).

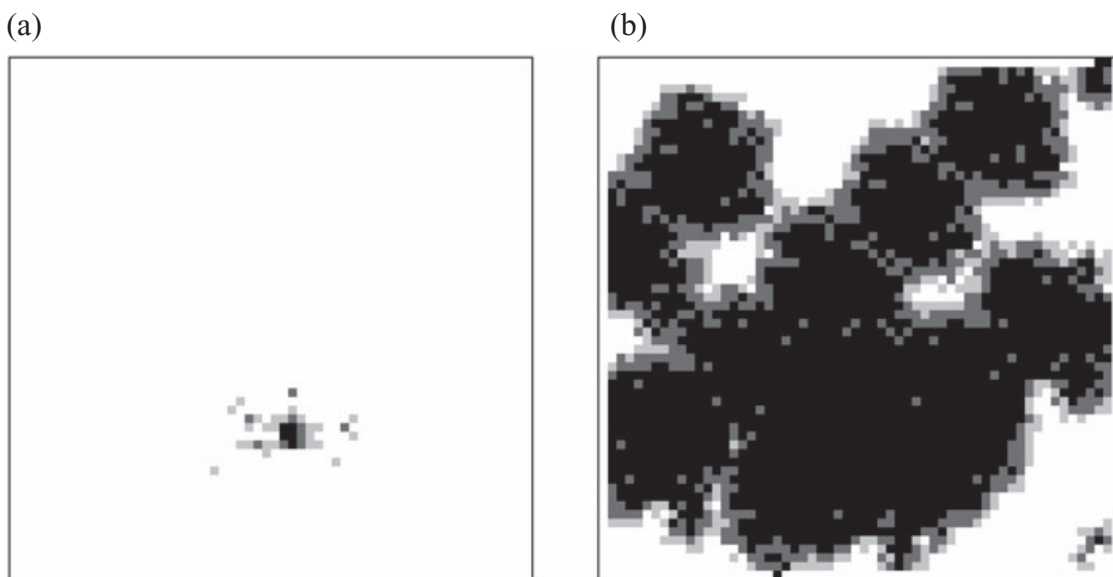


Fig. 7. Growth of *Solenopsis invicta* in Wacol starting in 2001. (a) Distribution in 2001; (b) simulated distribution in 2012 if no control undertaken (white – Absent; light grey – Present; dark grey – Common; black – Dense).

shows that 200 locations (each 10 000 km²) could contain some *S. invicta* before 2026 in all growth rate scenarios. This is because Figures 5a, and 8a represent quite different scales and densities. A location was regarded as having *S. invicta* if one or more of the 10 000 grid cells had ants present; the actual area represented only those grid cells (1 km by 1 km) in which *S. invicta* was present.

Data for the USA (Callcott & Collins 1996) were compared with the results from our simulation modelling (Fig. 8a). The data from the USA were superimposed onto the simulated data for Australia by having the same 'starting year'. The results from the USA were similar to a moderate-moderate simulation (moderate rate of increase in number of locations com-

bined with moderate rate of growth within one location), although spread in the USA was initially higher than is simulated here (Fig. 8b). However, the area of *S. invicta* in the USA approaches an asymptote of 1.1 million km² whereas in Australia, this figure was exceeded within 20–40 years, depending on which scenario was examined.

DISCUSSION

This modelling suggests that, if uncontrolled, *S. invicta* could invade over half of Australia within 35 years, using the moderate growth estimates and assuming no control measures were

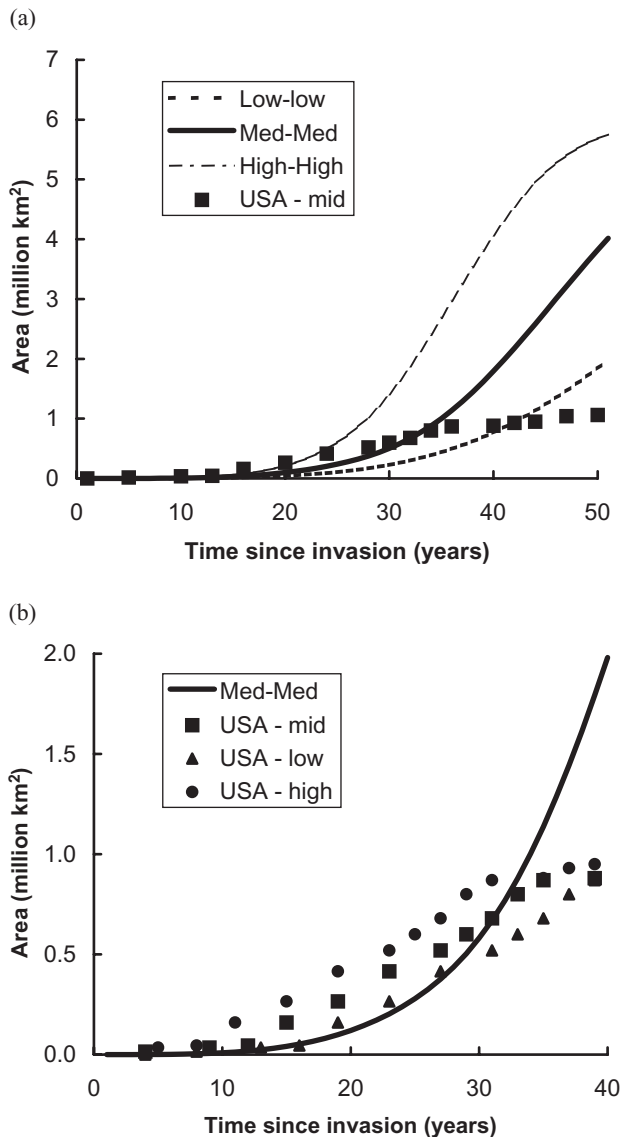


Fig. 8. (a) Total area of *Solenopsis invicta* under three different scenarios over a 50-year period. This is compared with data from the USA (Callcott & Collins 1996) where the initial introduction of *S. invicta* was assumed to be in 1940. (b) Simulated data for Australia compared with data from the USA when the initial date of establishment in the USA varied from 1935, 1940 and 1945.

taken. The area of 100 km by 100 km centred on Wacol would have about 80% occupancy of *S. invicta* by 2016, 15 years after the initial discovery.

Knowledge of the potential spread of an invasive species, based on best available data, is vital for making sound decisions regarding pest management. For example, the decision to eradicate, suppress or maintain a pest population at a stable level needs to be considered in light of the likely costs of the various management options and an estimate of the economic impact the invasive organism might have. In the case of *S. invicta*, analyses of the economic impacts in the USA, where *S. invicta* is well established, were used in conjunction with our estimates of population growth to

estimate likely future economic impacts of this species during its population growth phase (T. Kompas pers. comm. 2001). Without an accurate estimate of the rate of range expansion, such economic impacts are difficult to predict and the decision to eradicate or manage a pest on an economic basis becomes problematical.

In 2001, our estimates of rates of spread were used to develop a cost:benefit analysis of a control program for *S. invicta* (T. Kompas pers. comm. 2001) and provided the economic basis for the Australian response to the discovery of *S. invicta*. A large eradication campaign jointly funded by the Commonwealth government and Australian States was initiated in 2001 (Vanderwoude & McCubbin 2002; Vanderwoude *et al.* 2004).

In addition to providing a means of estimating the spread of *S. invicta*, the modelling approach developed here could be used to predict rates of population decline based on results of a management program. The transition matrices could be modified to reflect the control rates being achieved by the program and these used to estimate the likely number of infested properties remaining at the end of each treatment cycle. Such a modified model could predict the time frames required for eradication, given the details of how alternative control campaigns alter the transition probabilities.

The projections reported here are based on much of the Australian continent being suitable for *S. invicta*. Recent studies suggest that aridity could limit the distribution to wetter environments within inland Australia (Morrison *et al.* 2004; Sutherst & Maywald 2005). The inclusion of these issues within our model would lead to slower predicted rates of expansion.

Solenopsis invicta has several dispersal mechanisms. Short-range dispersal of the polygyne form is predominantly by budding. This form of dispersal is generally over short distances of several metres and promotes rapidly increasing density and future reproductive capacity. This spread mechanism was represented in the model by the change in density class of cells adjacent to existing cells with *S. invicta*. Medium-range dispersal results from flights of newly mated queens and is more common to the monogyne form, with new independent nests established at distances of up to 5 km (or possibly greater when assisted by wind) from the natal nest. This means of spread was represented by the possibility that, within a location, any cell without *S. invicta* and not adjacent to a cell with *S. invicta* had a (low) probability of having *S. invicta* in the next time step. Long-range dispersal depends on the human-mediated transport of goods harbouring viable fire ant colonies, for example, the original incursions of *S. invicta* to Brisbane and the USA. The rapid spread of *S. invicta* throughout the southern USA, even across hostile habitat to California, is ample evidence of the capacity of this species to travel as a result of human commerce. The recent discoveries of *S. invicta* in Malaysia (Na & Lee 2001) and Taiwan are other examples. This was represented in the model by an increase in the number of locations with *S. invicta*. The inclusion of all major forms of dispersal is necessary in any model of invasive organisms.

Large-scale experimentation to validate the results of this model is not possible due to the management decisions taken to control *S. invicta* in Australia. However, the results can be compared with historical records of spread in southern USA. The predictions for Australia suggest that *S. invicta* (uncontrolled) would spread more quickly than in the USA (see Fig. 8b), although the impact of control activities in that country is not known. This may be possible for a number of reasons. First, in the USA *S. invicta* has been subject to continual active control and quarantine efforts. During the 1960s, this comprised a concerted eradication program with stringent movement controls. Second, the climate in Australia, and especially Queensland, does not have the same extremes of cold experienced by many areas in southern USA. Therefore, it is possible that population growth will be more rapid as winters may have a smaller negative impact on individual colonies (Sutherst & Maywald 2005). Third, the number and speed of long-distance road movements are greater in Australia in the 2000s than would have been the case in the 1940s in the USA, leading to a higher potential rate of spread. Finally, both the monogyne and polygyne social forms of *S. invicta* were found in Brisbane. The polygyne form is more invasive and easier to spread via human commerce (Vinson 1997; Kintz-Early *et al.* 2003), as the probability of transporting a colony fragment containing a viable queen is proportional to the number of queens in a colony. Polygyne colonies were first reported in the USA in 1973 (Glancey *et al.* 1973) and considered unusual at that time. The polygyne form in the USA spread rapidly after it was first reported in the mid-1970s (Fritz & Vander Meer 2003).

When *S. invicta* was first found in Australia, it was not possible to develop a mechanistic model of the spread of *S. invicta* and validate model predictions against observations. However, the method we employed (even though based on imperfect data and understanding) allowed for estimates of all three dispersal mechanisms to be modelled. It 'captured' expert knowledge from a variety of sources including quarantine officers as well as biologists and provided the best available estimate of the rate of spread at the time.

This study provides a method for estimating the potential spread for a recently discovered organism for which there is little biological information. The sensitivity of the rate of spread to various assumptions can be tested. This enables an objective analysis of the costs and benefits of control to be performed.

Our modelling approach provided a useful step in the process of making decisions in the face of considerable uncertainty about the management of *S. invicta* in Australia. When invasive species are located in a new country or far from existing infestations, decisions have to be made about appropriate control measures to take. The general approach taken here was to combine estimates of the number of new locations with the rate of spread within those locations. Such an approach could be applied to any invasive organism and provides a framework within which to reduce uncertainty as further information comes to light for the invasive species.

ACKNOWLEDGEMENTS

We acknowledge the assistance of Fire Ant Control Centre Information Services staff for providing maps and infestation data. The Scientific Advisory Panel on Red Imported Fire Ants provided useful suggestions.

REFERENCES

- Adams ES. 1998. Territory size and shape in fire ants: a model based on neighborhood interactions. *Ecology* **79**, 1125–1134.
- Allen CR, Demarais S & Lutz RS. 1994. Red imported fire ant impact on wildlife: an overview. *Texas Journal of Science* **46**, 51–59.
- Callcott AMA & Collins HL. 1996. Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918–1995. *Florida Entomologist* **79**, 240–251.
- Davis LR, Vander Meer RK & Porter SD. 2001. Red imported fire ants expand their range across the West Indies. *Florida Entomologist* **84**, 735–736.
- Fritz GN & Vander Meer RK. 2003. Sympatry of polygyne and monogyne colonies of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Arthropod Biology* **96**, 86–92.
- Glancey BM, Craig CH, Stringer CE & Bishop PM. 1973. Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. *Journal of the Georgia Entomological Society* **8**, 237–238.
- Hargrove WW, Gardner RH, Turner MG, Romme WH & Despain DG. 2000. Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* **135**, 243–263.
- Hogeweg P. 1988. Cellular automata as a paradigm for ecological modelling. *Applied Mathematics and Computation* **27**, 81–100.
- Hung ACF, Barlin MR & Vinson SB. 1977. Identification, distribution, and biology of fire ants in Texas. *Texas Agricultural Experiment Station. Bulletin* **1185**, 1–24.
- Killion MJ & Grant WE. 1995. A colony-growth model for the imported fire ant: potential geographic range of an invading species. *Ecological Modelling* **77**, 73–84.
- Kintz-Early J, Parris L, Zettler J & Bast J. 2003. Evidence of polygyne red imported fire ants (Hymenoptera: Formicidae) in South Carolina. *Florida Entomologist* **86**, 381–382.
- Korzukhin MD & Porter SD. 1994. Spatial model of territorial competition and population dynamics in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Environmental Entomology* **23**, 912–922.
- Lard C, Willis DB, Salin V & Robison S. 2002. Economic assessments of red imported fire ant on Texas' urban and agricultural sectors. *Southwestern Entomologist* **41**, 123–137.
- Lett C, Silber C & Barrett N. 1999. Comparison of a cellular automata network and an individual-based model for the simulation of forest dynamics. *Ecological Modelling* **121**, 277–293.
- Levia DF & Frost EE. 2004. Assessment of climatic suitability for the expansion of *Solenopsis invicta* Buren in Oklahoma using three general circulation models. *Theoretical and Applied Climatology* **79**, 23–30.
- Levy AL, Wagner JM & Schuman SH. 1998. Fire ant anaphylaxis: two critical cases in South Carolina. *Journal of Agromedicine* **5**, 49–54.
- Lofgren CS, Banks WA & Glancey BM. 1975. Biology and control of imported fire ants. *Annual Review of Entomology* **20**, 1–30.
- Markin GP, Dillier JH, Hill SO, Blum MS & Hermann HR. 1971. Nuptial flight and flight ranges of the imported fire ant, *Solenopsis saevissima richteri* (Hymenoptera: Formicidae). *Journal of the Georgia Entomological Society* **6**, 145–156.
- Mescher MC, Ross KG, Shoemaker DD, Keller L & Krieger MJB. 2003. Distribution of the two social forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the native South American range. *Ecology and Population Biology* **96**, 810–817.
- Moloney S & Vanderwoude C. 2002. Red imported fire ants: a threat to eastern Australia's threatened wildlife? *Ecological Management and Restoration* **3**, 167–175.

- Moody ME & Mack RN. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**, 1009–1021.
- Morrison LW, Korzukhin MD & Porter SD. 2005. Predicted range expansion of the invasive fire ant, *Solenopsis invicta*, in the eastern United States based on the VEMAP global warming scenario. *Diversity and Distributions* **11**, 199–204.
- Morrison LW, Porter SD, Daniels E & Korzukhin MD. 2004. Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biological Invasions* **6**, 183–191.
- Na JPS & Lee CY. 2001. Identification key to common urban pest ants in Malaysia. *Tropical Biomedicine* **18**, 1–17.
- Porter SD, Williams DF, Patterson RS & Fowler HG. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies? *Environmental Entomology* **26**, 373–384.
- Rhoades RB, Schafer WL, Newman M *et al.* 1977. Hypersensitivity to the imported fire ant in Florida: report of 104 cases. *Journal of the Florida Medical Association* **64**, 247–254.
- Ruxton GD & Saravia LA. 1998. The need for biological realism in the updating of cellular automata models. *Ecological Modelling* **107**, 105–112.
- Sirakoulis GC, Karafyllidis I & Thanailakis A. 2000. A cellular automaton model for the effects of population movement and vaccination on epidemic propagation. *Ecological Modelling* **133**, 209–223.
- Soares-Filho BS, Coutinho Cerqueira G & Lopes Pennachin C. 2002. DINAMICA – a stochastic cellular automata model designed to simulate the landscape dynamics in an Amazonian colonization frontier. *Ecological Modelling* **154**, 217–235.
- Solley GO, Vanderwoude C & Knight GK. 2002. Anaphylaxis due to red imported fire ant sting. *Medical Journal of Australia* **176**, 521–523.
- Stablein JJ & Lockey RF. 1981. Ants and human anaphylaxis. In: *Monograph on Insect Allergy* (eds MI Levine & RF Lockey), pp. 61–67. American Academy of Allergy, New York, USA.
- Stafford CT. 1996. Hypersensitivity to fire ant venom. *Annals of Allergy, Asthma and Immunology* **77**, 87–95.
- Starr CK. 1985. A simple pain scale for field comparison of Hymenopteran stings. *Journal of Entomological Science* **20**, 225–232.
- Stoker RL, Ferris DK, Grant WE & Folse LJ. 1994. Simulating colonization by exotic species: a model of the red imported fire ant (*Solenopsis invicta*) in North America. *Ecological Modelling* **73**, 281–292.
- Sutherst RW & Maywald G. 2005. A climate model of red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications for invasion of new regions, particularly Oceania. *Environmental Entomology* **34**, 317–335.
- Taber SW. 2000. *Fire Ants*. Texas A&M University Press, College Station, USA.
- Tschinkel WR. 1987. The fire ant, *Solenopsis invicta*, as a successful 'weed'. In: *Chemistry and Biology of Social Insects* (eds J Eder & H Rembold), pp. 585–588. Verlag, München, Germany.
- Tschinkel WR. 1998. The reproductive biology of fire ant societies. *BioScience* **48**, 593–605.
- Vanderwoude C, Elson-Harris M, Hargreaves JR, Harris E & Plowman KP. 2004. An overview of the red imported fire ant (*Solenopsis invicta* Buren) eradication plan for Australia. *Records of the South Australian Museum Monograph Series* **7**, 11–16.
- Vanderwoude C & McCubbin K. 2002. *Fire Ants Down-Under: Progress to Date on the Australian National Eradication Plan for Solenopsis invicta*. Queensland Department of Primary Industries, Fire Ant Control Centre, Oxley, Brisbane, Queensland, Australia.
- Vinson SB. 1997. Invasion of the red imported fire ant (Hymenoptera: Formicidae), spread, biology and impact. *American Entomologist* **43**, 23–39.
- Vinson SB & Sorensen AA. 1986. *Imported Fire Ants: Life History and Impact*. Texas Department of Agriculture, Texas, USA.
- Vogt JT, Appel AG & West MS. 2000. Flight energetics and dispersal capability of the fire ant, *Solenopsis invicta* Buren. *Journal of Insect Physiology* **46**, 697–707.
- White R, Engelen G & Uljee I. 2000a. Modelling land use change with linked cellular automata and socio-economic models: a tool for exploring the impact of climate change on the island of St. Lucia. In: *Spatial Information for Land Use Management* (eds M Hill & R Aspinall), pp. 189–204. Gordon and Breach, London, UK.
- White R, Engelen G, Uljee I, Lavallo C & Ehrlich D. 2000b. Developing an urban land use simulator for European cities. In: *Proceedings of the Fifth EC GIS Workshop: GIS of Tomorrow* (ed. K Fullerton), pp. 179–190. European Commission Joint Research Centre, Ispra, Italy.
- Wojcik DP, Allen CR, Brenner RJ, Forsys EA, Jouvenaz DP & Lutz RS. 2001. Red imported fire ants: impact on biodiversity. *American Entomologist* **47**, 16–23.

Accepted for publication 19 August 2005.