Yellow crazy ant spread model assumptions and parameterisation

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1 Overview

The yellow crazy ant (YCA) spread model is a geographic automata (Torrens and Benenson, 2005; Laffan et al., 2007). The model grid is defined by a bounding box with latitudes -16.450 to -17.941 and longitudes 145.090 to 146.149, and 0.003 x 0.003 decimal degree cells (Appendix A). This results in 175441 cells, each (approximately) 10 hectares in area. The initial YCA population spans 154 cells or approximately 1540 hectares (Figure 1).

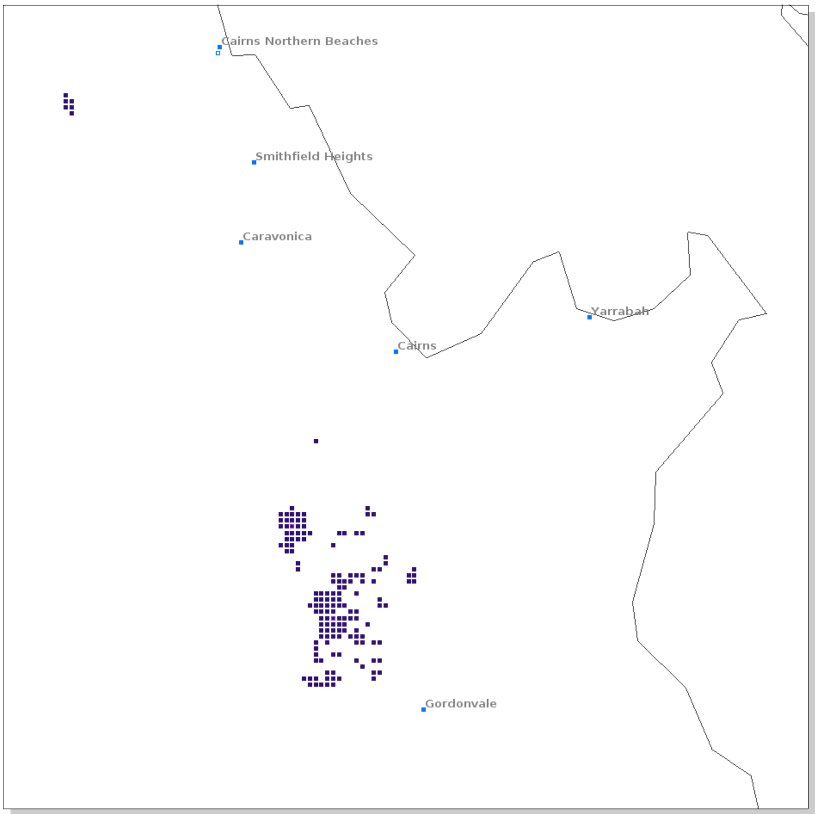

Figure **1.** Initial yellow crazy ant population

Modelling in terms of 10 hectare cells reflects the observation that a YCA supercolony spanning an area less than 10 hectares tends to be a single contiguous population, whereas a supercolony spanning an area greater than 10 ha tends to be comprised of fragmented populations (Hoffmann and Hagedom, 2014).

Crazy ant densities have previously been estimated at between 0.2M and 3.5M per hectare (Haines and Haines, 1978a), and up to 20M per hectare (Abbott, 2006). As the habitat suitability data layer for this study was very simple (land=suitable, sea/lakes=unsuitable), a conservative grid-wide carrying capacity of 2M ants per hectare was chosen. This means that every land cell is deemed equally suitable for YCA with a nominal carrying capacity of 20M. This simplistic assumption may be improved in future versions of the model by incorporating variables such as rugosity and food sources in the determination of cell suitability, which in turn would provide heterogeneity in cell carrying capacity.

The initial population sizes of the 154 seed cells were synthesized, graduating from a population of 20M in cells at the centre of large clusters, down to 2000 in cells at the edge of clusters. This resulted in an overall initial YCA population of approximately 300M spread across approximately 1540 hectares. A YCA propagule is arbitrarily defined as comprising 1 queen and 24 workers.

The <u>within-cell</u> abundance of a YCA population over time is modelled with a deterministic logistic growth function (Section 2).

The spread of YCA <u>between cells</u> is modelled through four concurrent stochastic spread pathways:

1) the steady diffusive spread of YCA over time to adjoining cells. This is mainly due to natural budding, however, in some cells the process is accelerated, for example, in cells that contain cane farms the spread is augmented by short-range hitchhiking jumps from localised cane farming activities (Section 3)

2) the sporadic spread of YCA over time to non-adjoining cells due to medium-range hitchhiking related to cane farming activities (Section 4).

Spread between cane farms is defined separately than spread from cane farms to cane railway corridors.

3) the sporadic spread of YCA over time to other_cells due to human-mediated hitchhiking that is unrelated to cane farming (Section 5)

4) the sporadic spread of YCA over time to other cells due to rafting (Section 6).

Population spread via nuptial flight of queens (fission) was not explicitly modelled as it is unclear whether this is an important means of dispersal for YCA (Rao et al., 1991; Haines et al., 1994; O'Dowd et al., 1999; Abbott et al., 2014; Hoffmann and Hagedom, 2014).

The model is an agent-based discrete-event simulation with a daily time-step. The stochastic spread pathways employ Markov chain Monte Carlo (MCMC) methods that are driven by daily probabilities of various events occurring. As the model is stochastic any given simulation scenario must be run multiple times to allow distributions of outcomes (YCA spread patterns and rates) to emerge. The summary outputs of a single example run is provided in Section 8.

2 Within-cell abundance of YCA

The abundance of the YCA population within an infested cell over time is represented by a deterministic logistic growth function (Equation 1).

$$d(t) = \frac{K}{1 + \left(\frac{K}{D_0} - 1\right) e^{-Rt}} \tag{1}$$

where

d(t) = population density (0..1) on day t

D_0 = initial population density (on day t=0)

K = carrying capacity of the cell (normalised cell suitability (0..1))

R = population growth rate

The population growth rate R is given by Equation 2.

$$R = \frac{\log_e\left(\frac{D_0}{D_x}\right) + \log_e\left(K - D_x\right) - \log_e\left(K - D_0\right)}{-x} \quad (2)$$

where

R = population growth rate

D_0 = initial population density (0..1) (on day t=0)

D_x = population density (0..1) on day t=x

K = carrying capacity of the cell (normalised cell suitability (0..1))

A logistic growth rate of R = 0.025 was estimated using Equation 2 based on the assumption that for a 10 ha cell, a YCA population will take approximately 2 years to grow from a single propagule (n=25) to 99% of the cell carrying capacity (n=19.8M) (Figure 2). This implies that 50% of the carrying capacity is reached after 454 days.

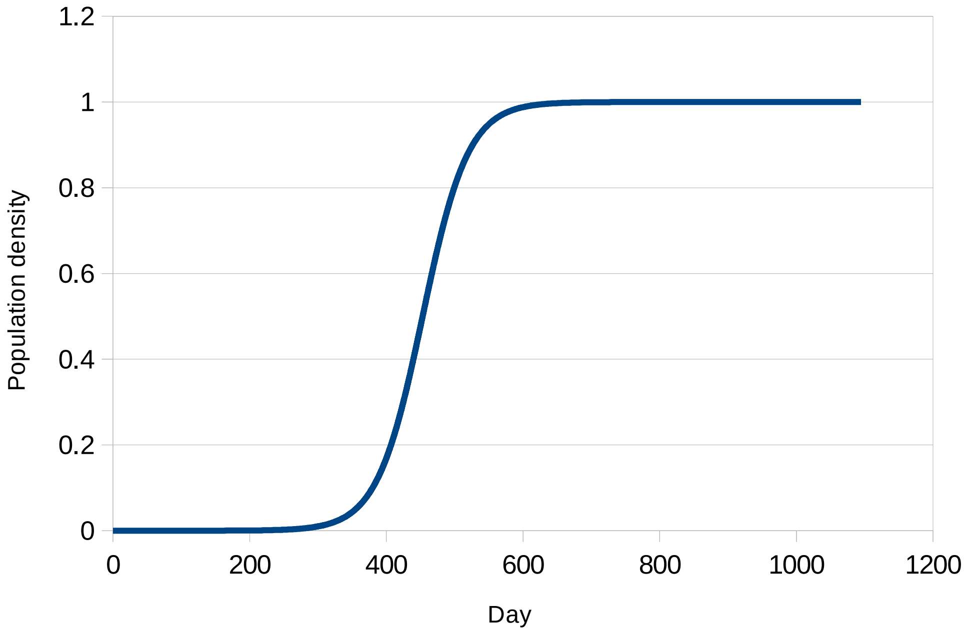

Figure 2. Yellow crazy ant within-cell population density curve

Natural contractions of YCA populations (Abbott 2006) are not modelled.

3 Diffusive spread of YCA between contiguous cells

The diffusive spread of YCA from an infested cell into an adjoining naive cell is modelled with a stochastic diffusion process based on a Markov chain. The following factors influence whether or not diffusion occurs:

- the source cell's population density
- the environmental suitability of the adjoining cell

The probability of a diffusion event occurring on any given day is given by Equation 3.

$$p_d(t) = 1 - (1 - P_d S_d w_d)^{d(t)} \tag{3}$$

where

$p_d(t)$ = probability of diffusion occurring on day t

P_d = baseline daily probability of diffusion occurring

S_d = normalised suitability of the destination cell

w_d = distance weight between the source and destination cells

d(t) = population density of the source cell on day t

The baseline daily probability of diffusion P_d is derived with Equation 4.

$$P_d = 1 - (1 - p)^{1/d} \tag{4}$$

where

P_d = daily probability of a diffusion event occurring

p = overall probability of a diffusion event occuring at least once in a specified period of interest d

d = the period of interest (days)

The overall probability of diffusion p depends on the land use category of the infested cells (Appendix B). This allows heterogeneity in the diffusion behaviour. For example, diffusion on a cane farm (where natural budding is perhaps augmented by short-range movements arising from within-farm activities such as harvesting), can be defined differently to diffusion in a national park (that is primarily due to natural budding). The baseline daily probabilities of diffusion out of a 10 hectare cell are derived using Equation 4 with the assumptions in Table 1.

Table 1. Daily probabilities of YCA diffusive spread

Land use category of source cell	**Period**	**Overall probability p**	**Daily baseline probability P_d**
Cane farm	3 years	40%	0.000466
Cane railway corridor	3 years	8%	0.000076
Managed/used land	3 years	8%	0.000076
Natural area	3 years	3%	0.000028

The distance weight w_d is derived from the distance between the centroids of the source infested cell and a candidate adjoining cell. The distance weight simply represents the decreased probability of diffusion into the north-west, south-west, north-east and south-east neighbours (w_d = 0.7071), as opposed to the north, south, west and east neighbours (w_d = 1.0).

The initial YCA population of a newly infested cell is deemed to be 1 propagule (n=25).

4 Spread of YCA between non-contiguous cells due to sugar cane farming activities

The spread of YCA from an infested cell into a non-adjoining naive cell via sugar cane farming activities is modelled with a stochastic jump process based on a Markov chain. The following factors influence whether or not a jump occurs:

- the source cell's YCA population density,
- the environmental suitability of the destination cell,
- the land use of the source cell
- the land use of the destination cell

The probability of a cane-related jump event occurring on any given day t is given by Equation 5.

$$p_j(t) = 1 - (1 - P_j S_d)^{d(t)} \tag{5}$$

where

$p_j(t)$ = probability of a cane-related jump occurring on day t

P_j = baseline daily probability of a cane-related jump occurring

S_d = normalised suitability of the destination cell

$d(t)$ = YCA population density of the source cell on day t

The baseline daily probability P_j is defined per Equation 6.

$$P_j = 1 - (1 - p)^{1/p} \tag{6}$$

where

P_j = daily probability of diffusion occurring

p = probability of a jump occuring at least once in a specified period d

d = period of interest (days)

The baseline daily probability of a jump P_j depends on the land use category of the *destination* cell (Appendix B). This allows heterogeneity in the jumping behaviour. For example, jumps between cane farms (brought about, for example, by harvesting activities spanning multiple farms), can be defined differently to jumps from cane farms to cane railway corridors (brought about by cane rail transportation). The baseline daily probabilities of diffusion out of a 10 hectare cell are derived using Equation 6 with the assumptions in Table 2.

Table 2. Daily probabilities of YCA jumps related to cane farming

Land use category of source cell	**Land use category of destination cell**	**Period**	**Overall probability**	**Daily probability P_j**
Cane farm	Cane farm	1 year	10%	0.000289
Cane farm	Cane railway corridor	1 year	10%	0.000289

Cane farming related hitchhiking jumps are independent of the human population density in the source and destination cells.

The distance of jumps due to cane farming activities are sampled from a BetaPERT distribution (minimum 0.5 km, most likely 2 km, maximum 20 km).

The initial YCA population of a newly infested cell is deemed to be 1 propagule (n=25).

Seasonal variations in cane farming activities are not modelled, i.e., the pathway represents average cane jumps over time.

5 Spread of YCA between cells due to human-mediated hitchhiking

The spread of YCA from an infested cell into another naive cell via human-mediated hitchhiking (unrelated to cane farming activities), is modelled with a stochastic jump process based on a Markov chain. The following factors influence whether or not a jump occurs:

- the infested cell's YCA population density,
- the environmental suitability of the destination cell,
- the human population of the infested cell,
- the land use of the infested cell
- the land use of the destination cell

The probability of a human-mediated hitchhiking jump event occurring on any given day t is given by Equation 7.

$$\boxed{p_j(t) \ = \ 1-(1-P_j H_s S_d)^{d(t)}} \qquad (7)$$

where

$p_j(t)$ = probability of a hitchhiking jump occurring on day t

P_j = baseline daily probability of a hitchhiking jump occurring

H_s = normalised human population density of the infested cell

S_d = normalised suitability of the destination cell

$d(t)$ = YCA population density of the source cell on day t

The baseline daily probability P_j is defined per Equation 8.

$$\boxed{P_j \ = \ 1-(1-p)^{1/p}} \qquad (8)$$

where

P_j = daily probability of a jump occurring

p = probability of a jump occuring at least once in a fixed period d

d = period of interest (days)

The baseline daily probability P_j of a jump arises from the assumption that if a cell has a maximal YCA population (i.e., is at carrying capacity), and has a maximal human population (i.e., normalised human population density of 1.0), there is (arbitrarily) a 30% chance of a human-mediated hitchhiking jump into a another cell within a year:

$$Pj = 1 - (1 - 0.3)^{(1/365)}$$

$$Pj = 0.000977$$

Human-mediated hitchhiking jumps may occur between cells with land use classifications (Appendix B) as follows:

- from managed/used land to other managed/used land
- from managed/used land to cane railway corridors
- from managed/used to land to natural areas
- from cane railway corridors to managed/used land
- from cane railway corridors to other cane railway corridors
- from cane railway corridors to natural areas
- from natural areas to other natural areas
- from natural areas to managed/used land
- from natural areas to cane railway corridors

A source cell must have a human population density greater than zero for a hitchhiking jump to occur. A destination cell generally must have a human population density greater than zero for a hitchhiking jump to occur, however, the model allows for random infrequent hitchhiking events to occasionally occur from a populated area into a non-populated area (e.g.,wilderness).

The human population density of the source cell influences the probability of a jump occurring.

Human-mediated jump distances are sampled from a BetaPERT distribution (minimum 0.5 km, most likely 10 km, maximum 75 km).

The initial YCA population of a newly infested cell is deemed to be 1 propagule (n=25).

6 Spread of YCA between cells due to rafting

The spread of YCA from an infested cell into a naive cell via rafting is modelled with a stochastic jump process based on a Markov chain. The following factors influence whether or not a jump occurs:

- the source cell's YCA population density,
- the environmental suitability of the destination cell,
- the presence of waterways in the source cell
- the presence of waterways in the destination cell
- the gradient between the source cell and the destination cell

The probability of a rafting jump event occurring on any given day t is given by Equation 9.

$$\boxed{p_j(t) \;=\; 1 - (1 - P_j S_d)^{d(t)}} \tag{9}$$

where

$p_j(t)$ = probability of a rafting jump occurring on day t

P_j = baseline daily probability of a rafting jump occurring

S_d = normalised suitability of the destination cell

$d(t)$ = YCA population density of the source cell on day t

The baseline daily probability P_j is defined per Equation 10.

$$\boxed{P_j \;=\; 1 - (1 - p)^{1/p}} \tag{10}$$

where

P_j = daily probability of a jump occurring

p = probability of a jump occuring at least once in a specified period d

d = the period of interest (days)

The baseline daily probability P_j of a jump arises from the assumption that if a 10 hectare cell with waterways has a maximal YCA population (i.e., is at carrying capacity), there is a 5% chance of a rafting jump into another cell within a year:

$$Pj = 1 - (1 - 0.05)^{(1/365)}$$

$$Pj = 0.000141$$

Rafting jumps are independent of the land use category and human population density of the source and destination cells.

The distance of a rafting jump is sampled from a BetaPERT distribution (minimum 0.5 km, most likely 0.5 km, maximum 5 km).

The initial YCA population of a newly infested cell is deemed to be 1 propagule (n=25).

Seasonal variations in rafting likelihood are not modelled, i.e., the pathway represents average rafting jumps over time.

7 Spread pathway summary

Table 3. Summary of YCA spread pathways

Spread pathway	Source cell type	Destination cell type	Baseline probability	Dependent on human population density	Distance	Initial population in a newly infested cell
Diffusion	cane railway managed natural	any any any any	0.000466 0.000076 0.000076 0.000028	no	Adjoining cells only	25
Cane farm jumps	cane cane	cane railway	0.000289 0.000289	no	BetaPERT (0.5, 2, 20) km	25
Hitchhiking (human-mediated) jumps	railway, managed, natural	railway, managed, natural	0.000977 (dampened by the source cell human population density)	yes	BetaPERT (0.5, 10, 75) km	25
Rafting jumps	water	water	0.000141	no	BetaPERT (0.5, 0.5, 5) km	25

Table 3 provides a summary of the various spread pathways where

cane = cells that contain one or more cane farms

railway = cells that contain a cane railway corridor

managed = cells that contain managed/used land

natural = cells that contain natural areas

water = cells that contain one or more watercourses

Table 4 uses Equations 5 and 7 to illustrate the daily probabilities of a jump for minimal and maximal YCA and human population densities. It illustrates how the probabilities of cane-related and rafting jumps jump are independent of the human population density of the source cell.

Table 4. Examples of daily probabilities of YCA jumps

Cell YCA population	Cell normalised YCA population density	Cell human population	Cell normalised human population density	Daily probability of cane jump	Daily probability of hitchhiking jump	Daily probability of rafting jump
min (25)	1.25×10^{-6}	min (1)	0.002	3.61×10^{-10}	2.30×10^{-12}	1.76×10^{-10}
min (25)	1.25×10^{-6}	max (531)	1.0	3.61×10^{-10}	1.22×10^{-9}	1.76×10^{-10}
max (20M)	1.0	min (1)	0.002	2.89×10^{-4}	1.84×10^{-6}	1.41×10^{-4}
max (20M)	1.0	max (531)	1.0	2.89×10^{-4}	9.77×10^{-4}	1.41×10^{-4}

8 Sample simulation results

Table 4 provides a summary of a <u>single</u> test run of 30 years of <u>uncontrolled</u> spread starting from the initial population specified in Figure 1. The resultant YCA population and infestation network are provided in Figures 3 and 4. Note that as the model is stochastic, multiple runs must be conducted before sensible analysis can occur.

Cells may have multiple land uses (e.g. cane + managed, railway + managed). Each cell diffuses based on its highest risk land use and this can artificially boost the diffusion rate for the lower risk land use of the cell (e.g. a managed cell with cane contributes correctly to the overall cane diffusion rate but over-contributes to the overall managed land diffusion rate). The resulting diffusion rates of 75 to 131 metres per year are broadly in line with published budding distances of up to 182 metres per year (Abbott, 2006), and 37 to 402 (average 125) metres per year (Haines and Haines, 1978).

Table 5. Sample simulation result of 30 years of uncontrolled YCA spread

Output parameter	**Value**
Length of simulation	10950 days (30 years)
Initial number of infested cells	154 (approx 1540 ha)
Final number of infested cells	6110 (approx 61,100 ha)
Population growth	300M -> 121B (approx)
Number of diffusions out of cane farm cells	2009
Cane farm cell median diffusion rate	131 (metres/year)
Number of diffusions out of railway cells	183
Railway cell median diffusion rate	94 (metres/year)
Number of diffusions out of managed land cells	2359
Managed land cell median diffusion rate	119 (metres/year)
Number of diffusions out of natural area cells	411
Natural area cell median diffusion rate	75 (metres/year)
Total number of diffusion events	3200
Overall median diffusion rate	112 (metres/year)
Number of cane-related jumps	2011
Cane-related jumps average frequency	67 (jumps per year)
Number of human-mediated jumps	707
Human-mediated jumps average frequency	24 (jumps per year)

Number of rafting jumps	630
Rafting jumps average frequency	21 (jumps per year)
Total number of jump events	3348
Overall jump average frequency	112 (jumps per year)

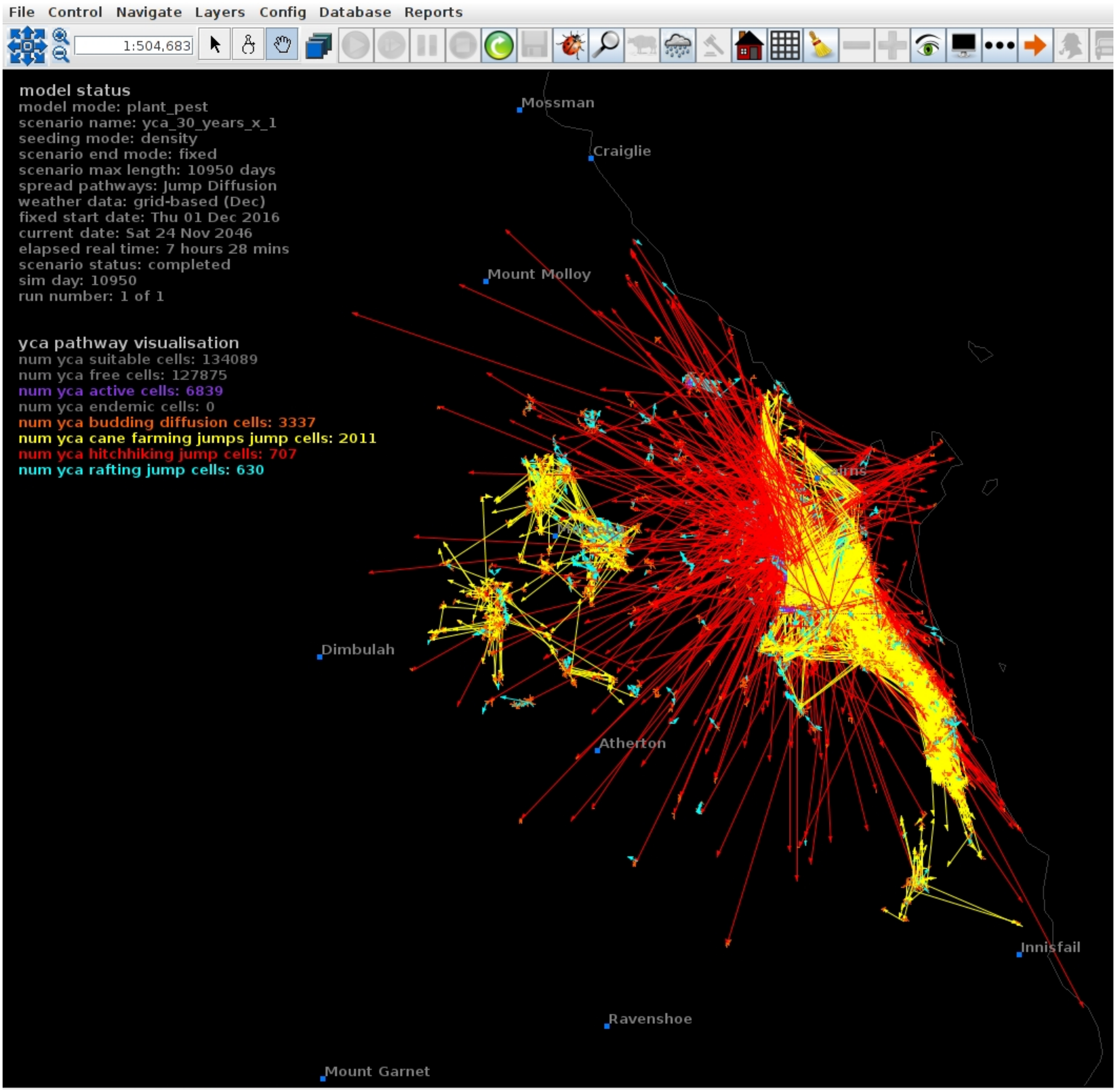

Figure 3. Sample yellow crazy ant infestation network after 30 years

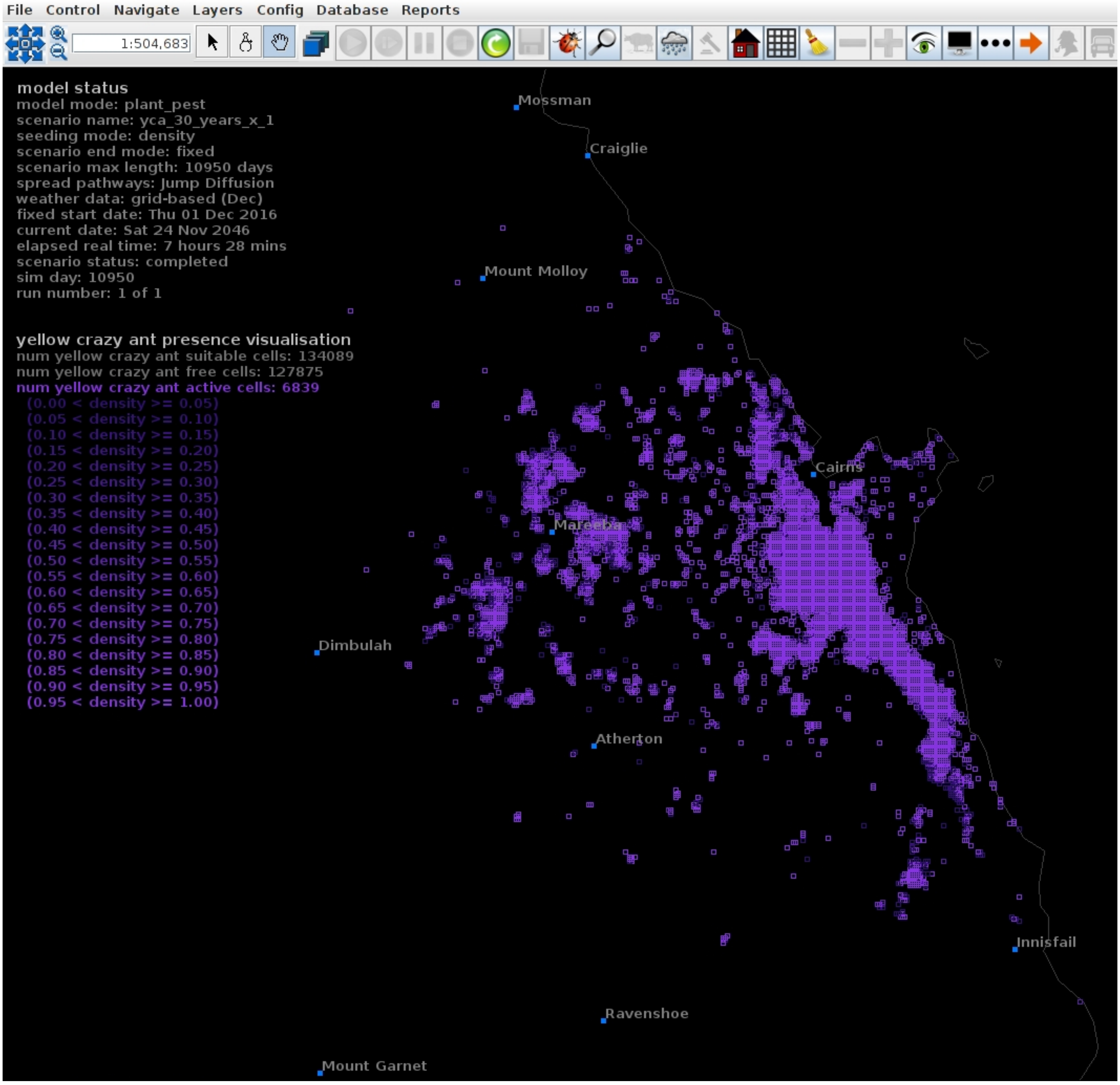

Figure 4. Sample yellow crazy ant population distribution after 30 years

9 References

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Appendix A: Model grid

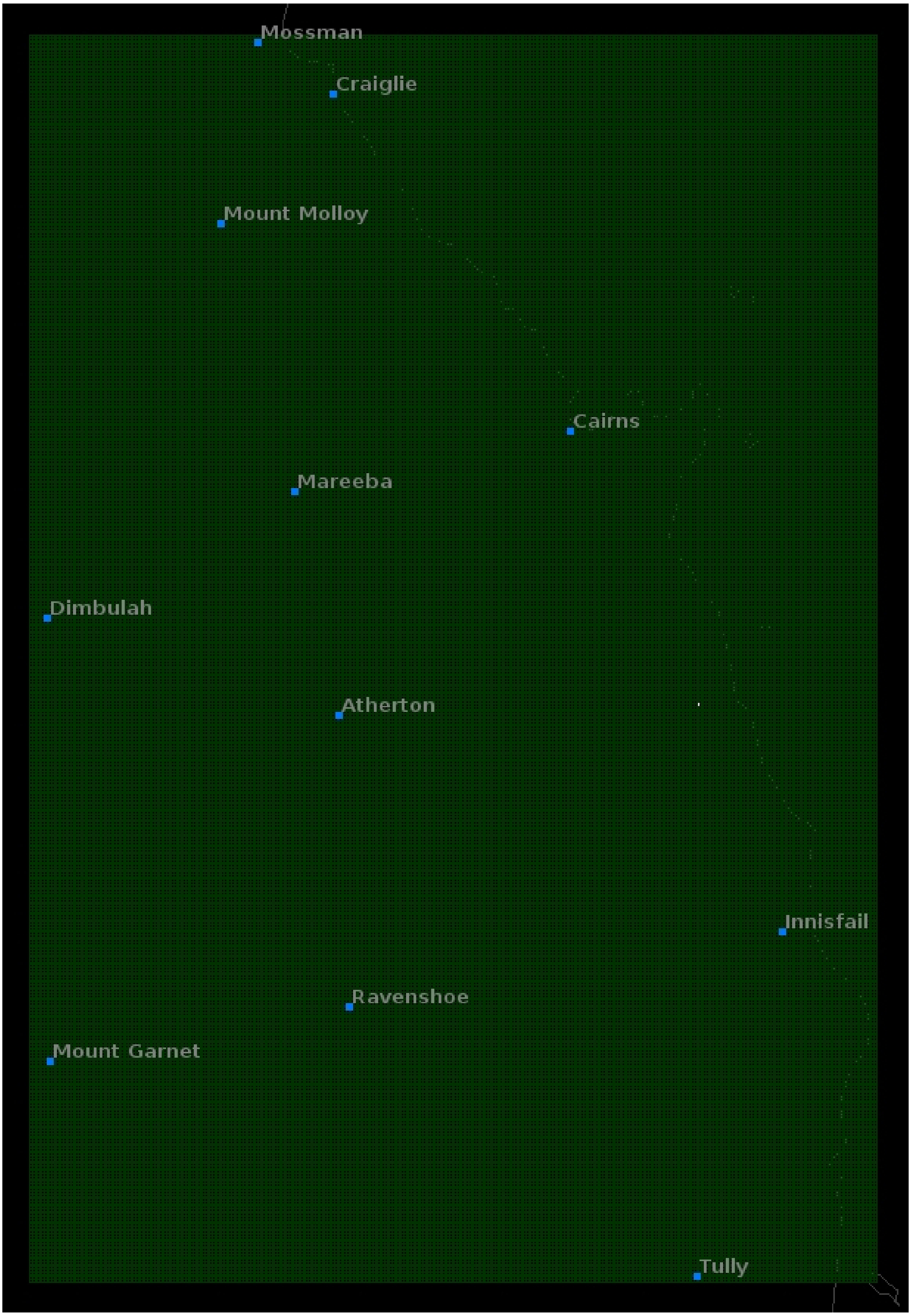

***Figure* 5.** Model grid

Appendix B: Cell static attributes

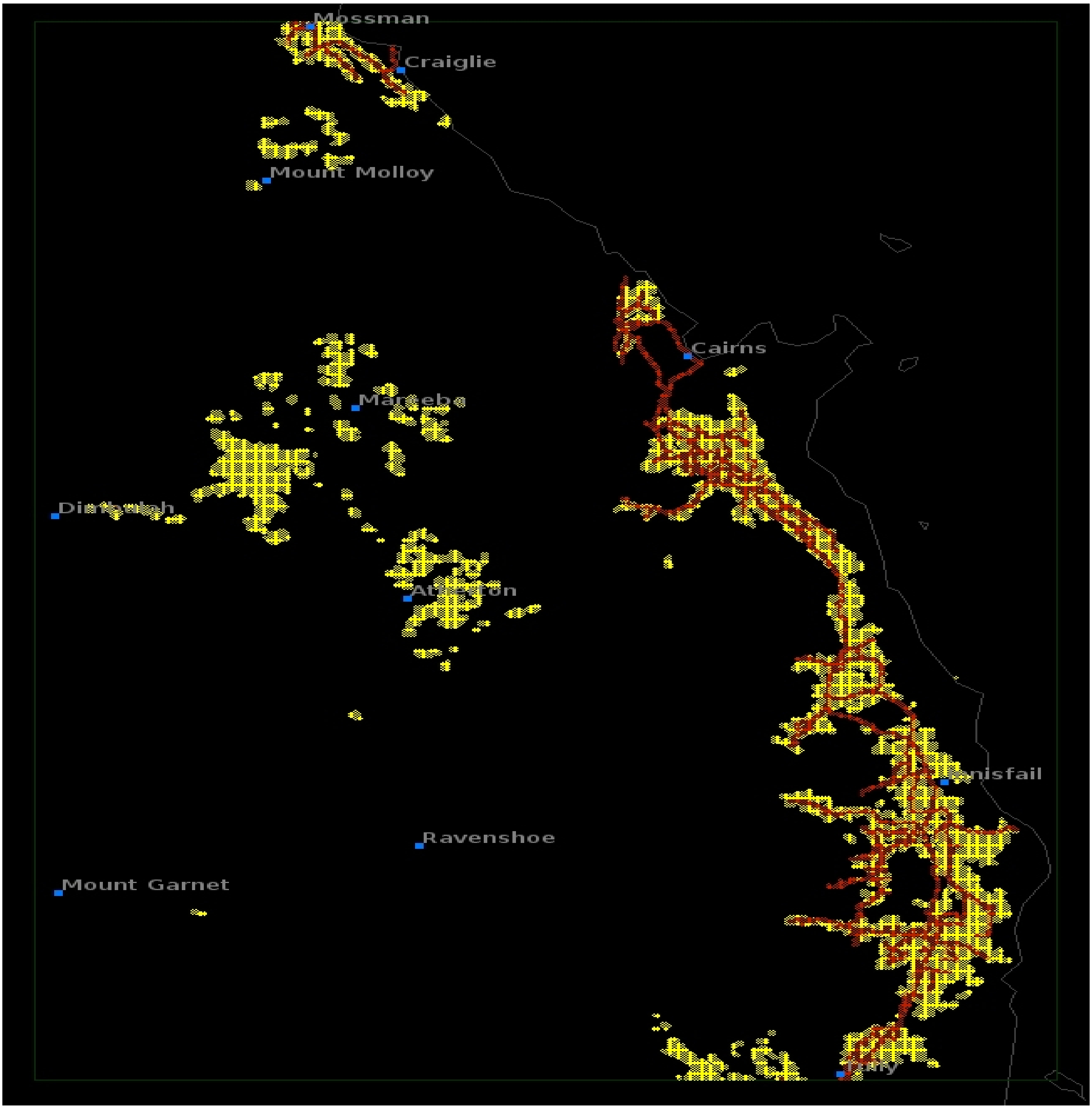

***Figure* 6.** Sugar cane farms and railway corridors

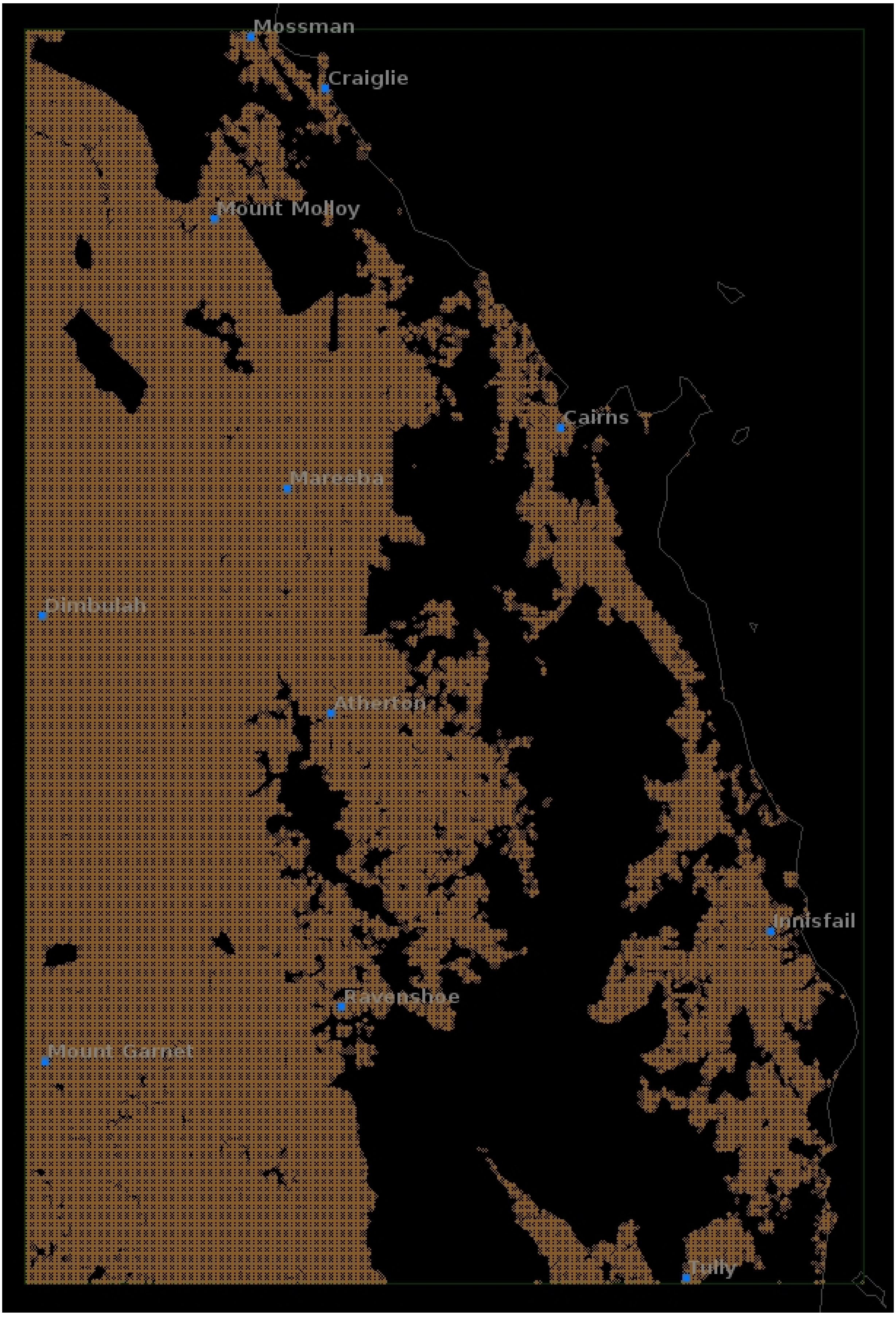

Figure 7. Managed/used land

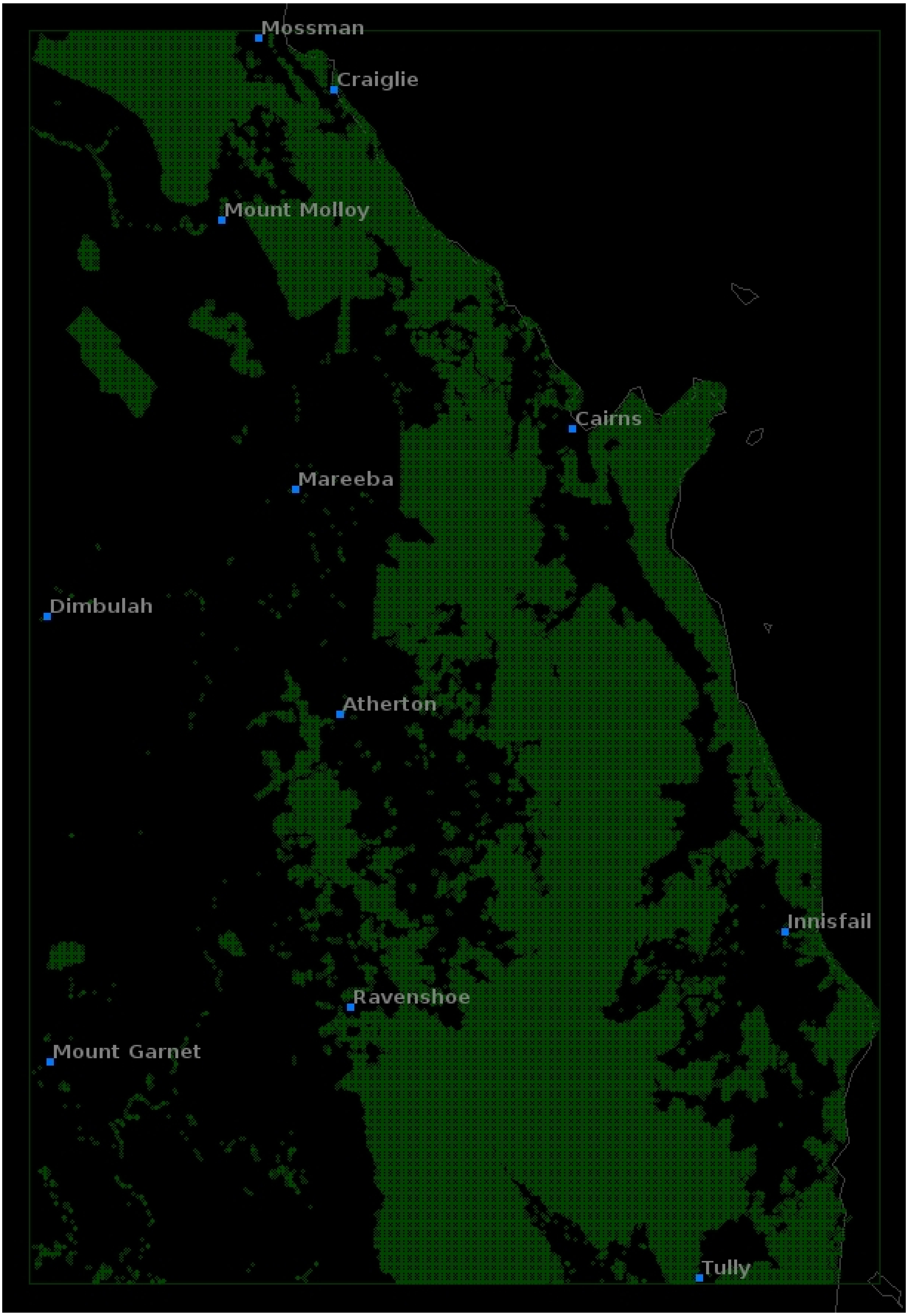

Figure 8. Natural areas

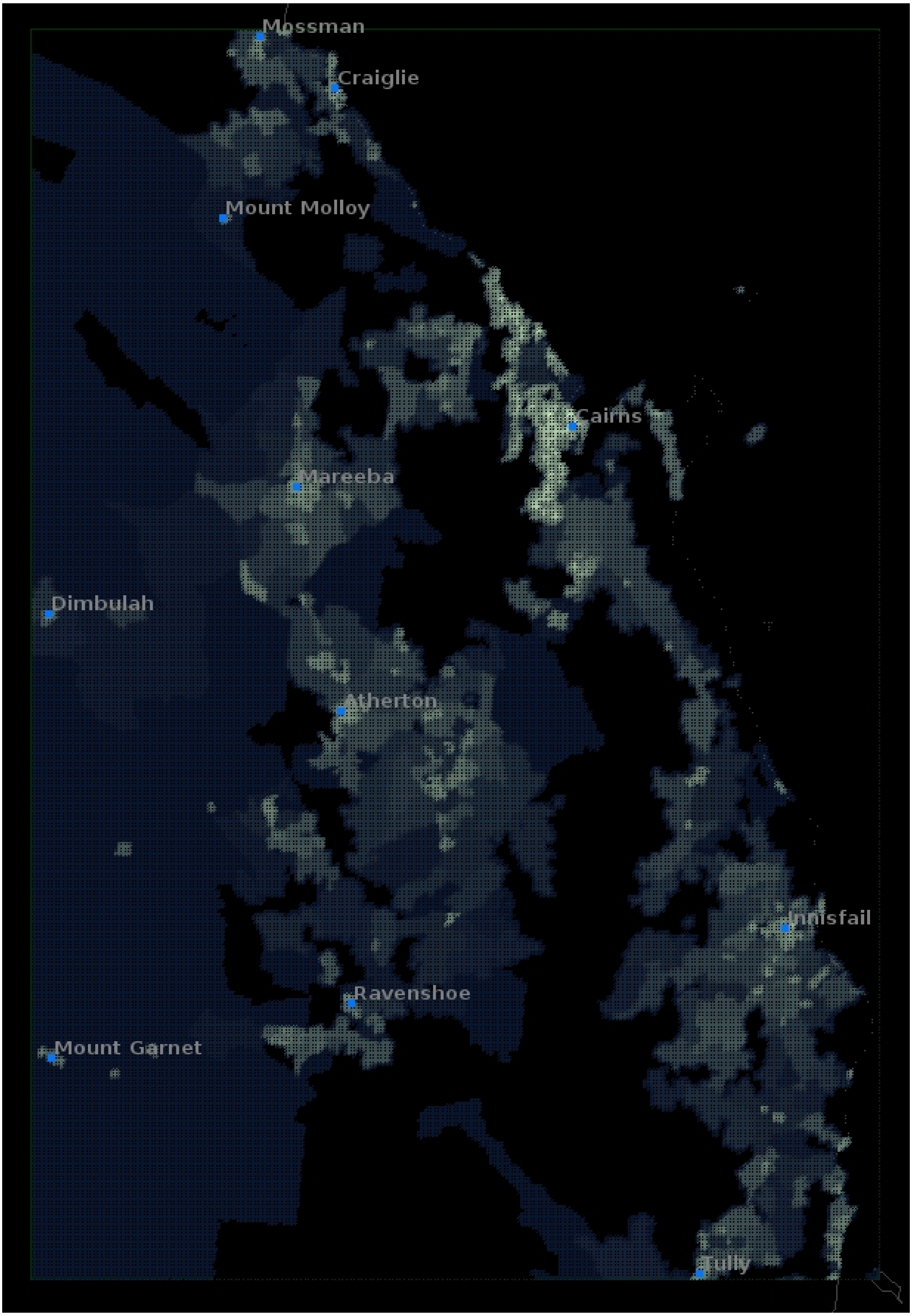

Figure 9. Human population density

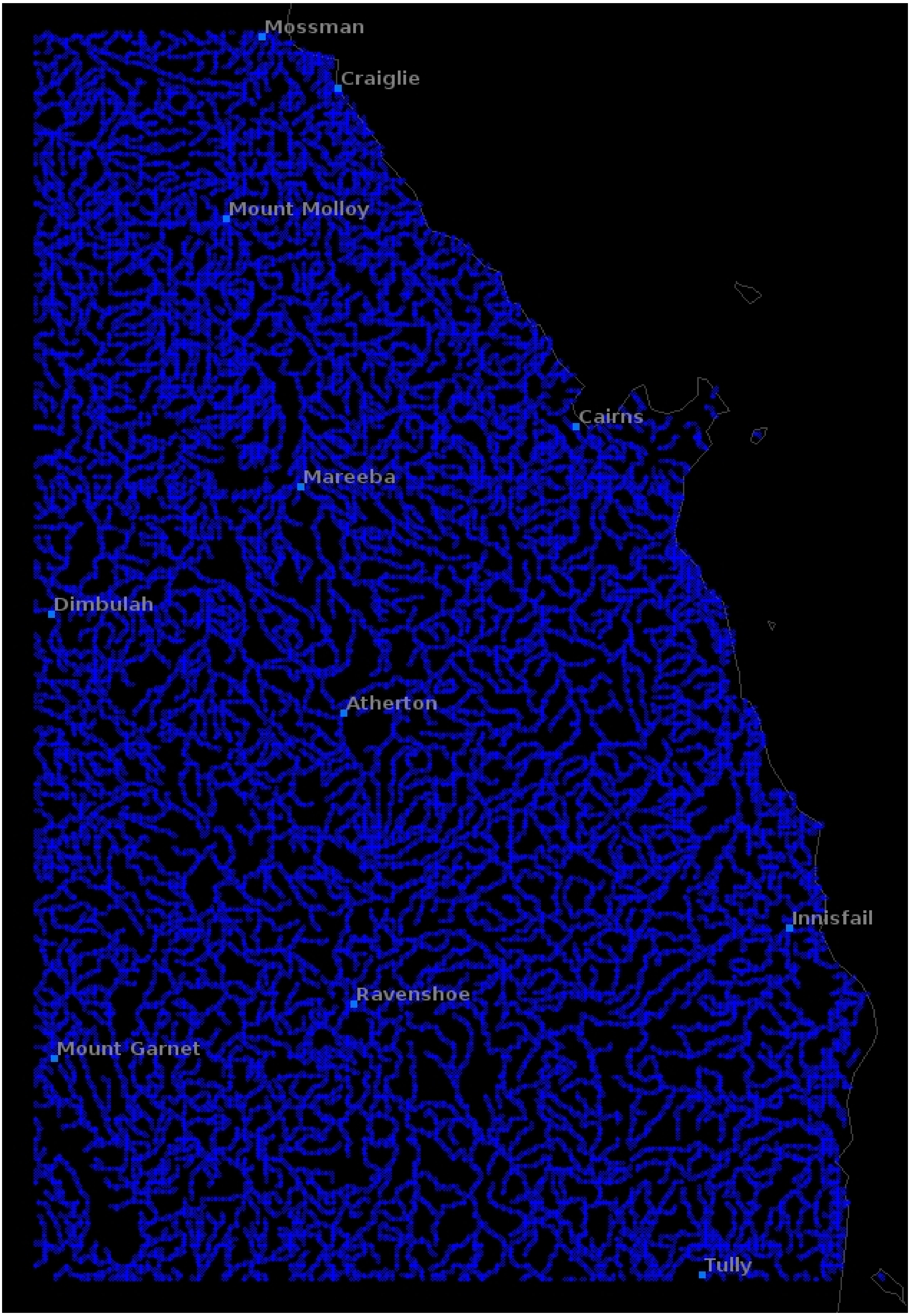

***Figure* 10.** Watercourses

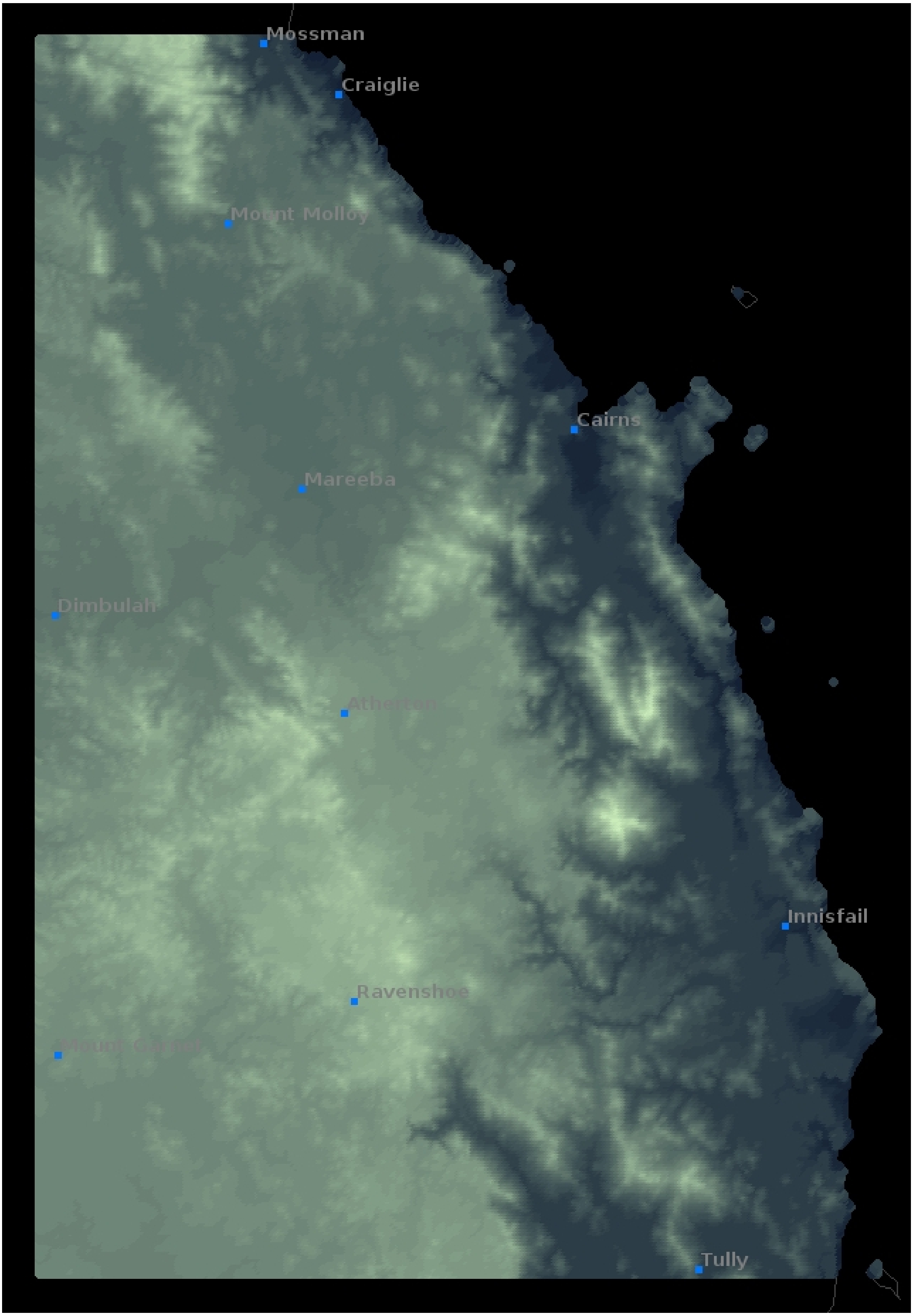

***Figure* 11.** Elevation