Received: 23 January 2024 | Revised: 29 April 2024 | Accepted: 2 May 2024

DOI: 10.1111/aen.12692

ORIGINAL ARTICLE

Austral Entomology WILEY

Floods and fire ants, *Solenopsis invicta* (Hymenoptera: Formicidae): The Australian experience

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Funding information
Australian Commonwealth, States, and Territories

Abstract

The rafting behaviour of the red imported fire ant, *Solenopsis invicta*, in response to flooding events is well documented, although studies generally have focussed on the mechanisms of raft assembly and the behaviour of the raft's occupants. Flooding as a means of dispersal of *S. invicta* is frequently mentioned in the literature, although there are few data on the distances travelled or how effective it is compared to natural flight. In Australia, *S. invicta* is a priority invasive species with a national eradication program operating for 23 years, focussed on the population in southeast Queensland, which currently encompasses more than 700 000 ha. Flooding presents a risk to the success of the program through extending the infestation area or recolonising successfully treated areas. We used the program's extensive spatiotemporal dataset of known fire ant colony locations to assess the effects of two significant flood events on the dispersal or displacement of *S. invicta* in Queensland. Results indicated that flooding did not spread *S. invicta* beyond the known boundaries of infestation but contributed to localised spread, particularly for sites with known polygyne infestations. This situation could change if the ant spreads to new river catchments. A novel method developed to assess the risk of *S. invicta* dispersal through flooding is presented, alongside program actions that can be applied to mitigate this risk.

KEYWORDS
eradication, flooding, invasive ant management, red imported fire ant, spread risk

INTRODUCTION

The red imported fire ant, *Solenopsis invicta* Buren, evolved on the flood plain of a major river system that is under water for months at a time (the Pantanal of Brazil, Paraguay and Bolivia) and is, therefore, well adapted to flooding events. Tschinkel (2006) describes their response as follows: 'As the water rises in their nest chambers, the entire colony moves upward, finally setting sail from the top of the mound, a couple of hundred thousand ants holding hands to form a floating mat. Workers, brood, sexuals, the queen, all together pull up anchor to drift for weeks, living off food stored in worker crops and eventually cannibalizing their brood like seafarers cast adrift on the South Pacific. Finally, the flood subsides, or they drift ashore, whereupon they dig a new nest and move in. Crisis over.'

Fire ant rafting behaviour has been documented for well over a century (see Adams et al. 2011), but it is only in more recent times that the mechanisms of raft assembly and the behaviour of the raft's occupants have become better understood (Adams et al. 2011; Hooper-Bui et al. 2020; Mlot et al. 2011; Purcell et al. 2014). Flood as a means of dispersal of *S. invicta* has frequently been mentioned in the literature (e.g., see Morrill 1974), although there are few data on the distances travelled. Green (1967) observed that 'floodwater floating of colonies from inundated mounds will spread them for miles downstream', and Lennartz (1973; cited in Buren et al. 1974) suggested that, in South America, flooding could easily account for the far south and far north populations of *S. invicta* along the Paraguay and Guapore rivers, respectively. Worldwide, there have been numerous studies on the effects of flooding on ant populations (Ballinger et al. 2007; Kolay & Annagiri 2015; Mertl et al. 2009), but few involved *S. invicta*, apart from those focussed on the rafting process itself.

The implication in both literature and media reports of rafting is that flooding is a major mechanism for *S. invicta* dispersal. However, there is little evidence that this dispersal mode is as effective or more effective than natural flight to extend their distribution, except in the case of protracted, non-turbulent river floods, such as those that occur in their native Pantanal (Alho 2008). Monogyne (single queen) colonies of *S. invicta* spread predominantly by flight and can disperse up to 5 km, or more with wind assistance, to successfully found new colonies (Markin et al. 1971; Vogt et al. 2000). The polygyne social form has multiple queens (700 recorded in a single nest by Glancey et al. 1975), and natural spread is primarily by budding of a new colony overground (King et al. 2009). Rafting on floodwaters for a monogyne colony is essentially a displacement event, involving the movement of a single queen and her entourage from one place to another. In contrast, flooding may cause the 'splitting' of a polygyne colony through the physical separation of queens into different raft fragments and the establishment of multiple new colonies at disembarkation. The chance of successful dispersal and proliferation by flood is thus higher for polygynes compared to monogynes.

In Australia, a national eradication program (the program) for *S. invicta* has been in operation since 2001 when the ant was first detected in Brisbane, Queensland (Wylie et al. 2016). It is currently the world's largest eradication program for an invasive ant species, with expenditure now exceeding A$600 million. Significant flooding presents a risk to the success of the program through potential expansion of the infestation area or by recolonisation of areas successfully treated for eradication and cleared. Over the past two decades, there have been two major flood events within the known boundaries of the *S. invicta* infestation in southeast Queensland, now encompassing 700 000 ha.

The program, since its inception, has maintained a large dataset of known locations of *S. invicta* derived both from verified public reports and its own surveillance activities. We used this dataset in combination with the mapping of known flood events to examine possible flood effects on the dispersal or displacement of *S. invicta* in Queensland. Observations on the ant's behaviour during these floods informed our consideration of the key factors that influence the success of rafting and colony establishment and the subsequent development of a risk assessment method to guide the program. To our knowledge, this is the first formal analysis of its kind for *S. invicta*.

MATERIALS AND METHODS

Our study area encompassed the known extent of *S. invicta* infestation in southeast Queensland as of November 2022, centred around the cities of Brisbane, Logan, Ipswich and Gold Coast, lying within the Brisbane River, Pine River, Logan–Albert River and South Coast hydrological catchments (Figure 1). Flood maps used in this study were sourced from the State of Queensland Department of Resources (2015) and the State of Queensland Department of Mines, Resources and Energy (2017).

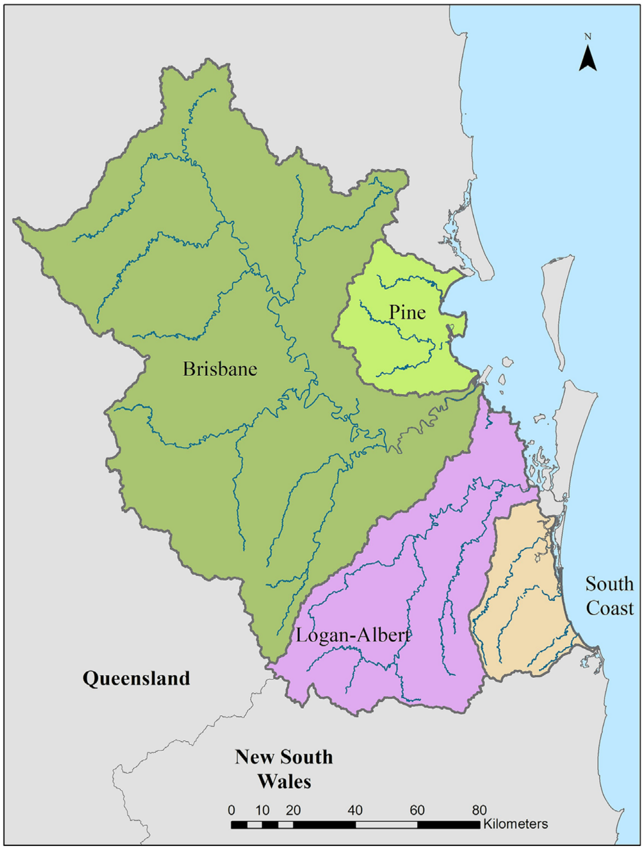

FIGURE 1 A map showing the study region in southeast Queensland and its hydrological catchments.

Several methodologies were used in our analysis: (1) a broad examination for evidence of spread by floodwaters using historical data, (2) a case study of a flooded site with a known polygyne *S. invicta* infestation, (3) a formal spatial analysis of two major flood events in the infested area in 2011 and 2017 and (4) a collation of spread risk criteria for use following flood events.

Examination of historic infestation data

For the spatial analysis of historic pre-flood and post-flood occurrences of *S. invicta* colonies, we used the comprehensive dataset contained in the program's Fire Ant Management System (FAMS). We first looked for broad patterns of spread that may have been caused by flooding in previous years by visually inspecting the annual time series of known infestation within the study area, especially near creeks and rivers. Particular attention was paid to the polygyne social form of *S. invicta*, which is thought to present a greater risk of expanding the infestation area through major flood events. It was hypothesised that if flooding was a significant factor in *S. invicta* spread, then there would be 'clustering' or a higher density of nests along waterways in comparison to the density of infestations in the broader infestation area. In support of this hypothesis, such 'clustering' of nests is very evident along major road corridors within the *S. invicta*-infested area in southeast Queensland, signalling these as important routes for dispersal of the pest with human assistance, and there are similar findings from the United States (Hung & Vinson 1978; King et al. 2009) and Taiwan (Lin et al. 2021).

Case study: Flooding of a known polygyne site

In October 2010, localised flooding occurred over a 70-ha rural grazing property at Purga in the western part of the southeast Queensland infestation. This property had a high-density polygyne *S. invicta* infestation (257 mounds/ha) and was intended for use by the program as an experimental site for bait efficacy trials. Ten 0.28-ha experimental plots were established in September 2010, and mounds were counted and marked in each plot, although the flood occurred before bait could be applied. When floodwaters receded, the trial plots and surrounding areas were assessed for fire ants.

Spatial analysis of two major flood events in southeast Queensland

A detailed analysis of changes in fire ant spatial distributions was conducted for two major flood events for which comprehensive flood maps were available: the 2011 flood of the Brisbane River and the 2017 flood of the Logan–Albert River. Our aim was to detect changes in patterns of *S. invicta* colony abundance or distribution. Our hypothesis was that floods would primarily cause mortality of *S. invicta* colonies, but a major displacement of colonies could also occur. Our first prediction was that major displacement might be evident in the year following the flood, as increased numbers of colonies within 50 m of the maximum flood height. Based on the experience of program scientists, this was expected to represent the average distance that a colony may move within a year of disembarking a raft at the high-water mark. However, we also predicted that major displacement within the flooded area would be difficult to identify because colony numbers would be expected to decrease. For each of these two flood events, we extracted four counts of *S. invicta* colonies:

1. colonies located within the flood extent, which were observed and recorded up to 1 year prior to the estimated peak flood height: The flood affected area was defined as the maximum flood extent (high-water mark) plus an additional 'buffer' of 50 m;
2. colonies located within the flood affected area, which were observed and recorded up to 1 year following the estimated peak flood height;
3. colonies located beyond the flood affected area, which were observed and recorded up to 1 year prior to the estimated peak flood heights: The area beyond the flood affected area was defined as an area that was equal in size to the flood affected area, which created a uniform buffer length of 250 m for the Brisbane River 2011 flood and a uniform buffer length of 400 m for the Logan–Albert River 2017 flood; and
4. colonies located beyond the flood affected area, which were observed and recorded up to 1 year following the estimated peak flood heights.

The colony counts beyond the flood affected area were examined as a pseudo-control comparison against counts within the flood affected area, because they were thought to be largely unaffected by the floods. The extent of these two major flood events and the sample study areas chosen for analysis are shown in Figure 2.

Development of a decision-support tool for assessing *S. invicta* spread risk following flood events

In the context of the program and its operational activities, there is a need to understand the risk of fire ants being dispersed by flood events. Based on the results of our analyses and the available literature, we identified and compiled a list of criteria relevant to assessing *S. invicta* spread risk after flooding.

RESULTS

Examination of historical infestation data

A visual examination of historical data revealed no difference in the pattern of *S. invicta* infestation along waterways, in comparison to those in the general infested area. This accords with an earlier program analysis of data for the period 2001–2007, which examined colony distance from a waterway using two categories: greater than 50 m from a waterway and less than 50 m from a waterway. This was based on earlier program observations that most disembarking rafting colonies re-establish within a short distance of the high-water mark, which, in this analysis, was taken to be within 50 m of a river, creek or stream waterline. Fire ants were first detected in Brisbane in 2001, and no major flood events occurred during this

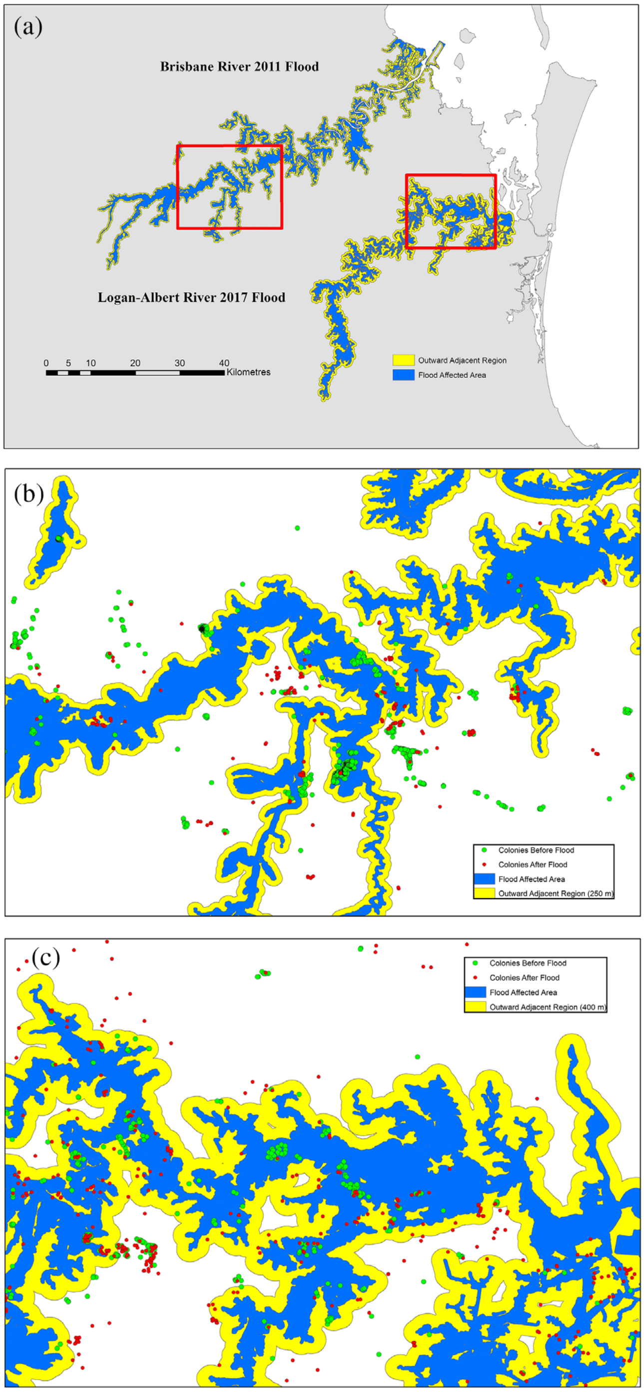

FIGURE 2 (a) Extents of the two major floods studied, as well as mapping extents (in red) of sample colony locations from the Brisbane River 2011 flood and the Logan–Albert 2017 flood. (b) A detailed map of sample colony locations and flood extents for the Brisbane River 2011 flood. (c) A detailed map of sample colony locations and flood extents for the Logan–Albert River 2017 flood.

period, which was during the 'millennium drought'; this drought lasted from 1997 to 2009 and affected large areas of eastern Australia, but minor flooding did occur in some creek systems. Analysis showed that of 3434 known colony locations, 55 or 1.6% were within 50 m of a waterway. It was concluded from these data that flooding was playing a minimal role in the long-distance dispersal of fire ants in southeast Queensland but was most likely a local dispersal agent.

Case study: Localised flooding of a known polygyne site at Purga Creek in 2010

After the floodwaters receded on the Purga Creek site, masses of the ant with brood were observed in clumps of grass and other vegetation or at the bases of trees, above the waterline (Figure 3a,b). Large numbers of ants were found in debris along the margins of the floodline, but no cohesive groups were observed at that time. However, within the flood zone, ants with brood and alates were commonly found associated with larger diameter woody debris, either scattered or piled in heaps against trees (Figure 3c). They were also common in tree stumps and logs, which may have been only partly submerged, and on small, elevated hillocks dotted through the flood zone (Figure 3d). As the water subsided, live workers and brood were found in many nests that had been submerged for at least 24 h, suggesting that they had been caught in flash flooding before they had time to evacuate. In one instance, live workers and brood were found in a nest that reportedly had been under water for 5 days.

A mound count was conducted in all 10 plots 2 months after flooding. Total mound counts before and after the flood were 792 and 1201, respectively, an increase of 51% overall, although three plots recorded increases of 70%–80%. This indicated considerable colony migration, 'splitting' and local movement in response to the flood. Significant colony mortality was observed among marked nests in one plot that had been underwater for 5 days. Nevertheless, the mound count in this plot increased by 16% after the flood, which may be due in part to its greater accumulation of woody debris, compared with other plots, which provided refuge for displaced or fractured colonies. Surveys along the path of the flood showed a high incidence of mounds just above the high-water mark, and concentrations of infestation were found in oxbows in Purga Creek over about 2 km (Figure 4).

Spatial analysis of two major flood events in southeast Queensland

Major flooding in the Brisbane River catchment in 2011

On 13 January 2011, the Brisbane River reached the peak inundation of a major flood event that began several days prior, following heavy rainfall at the start of January. An analysis conducted 12 months after the flood in the Brisbane River catchment showed no notable difference

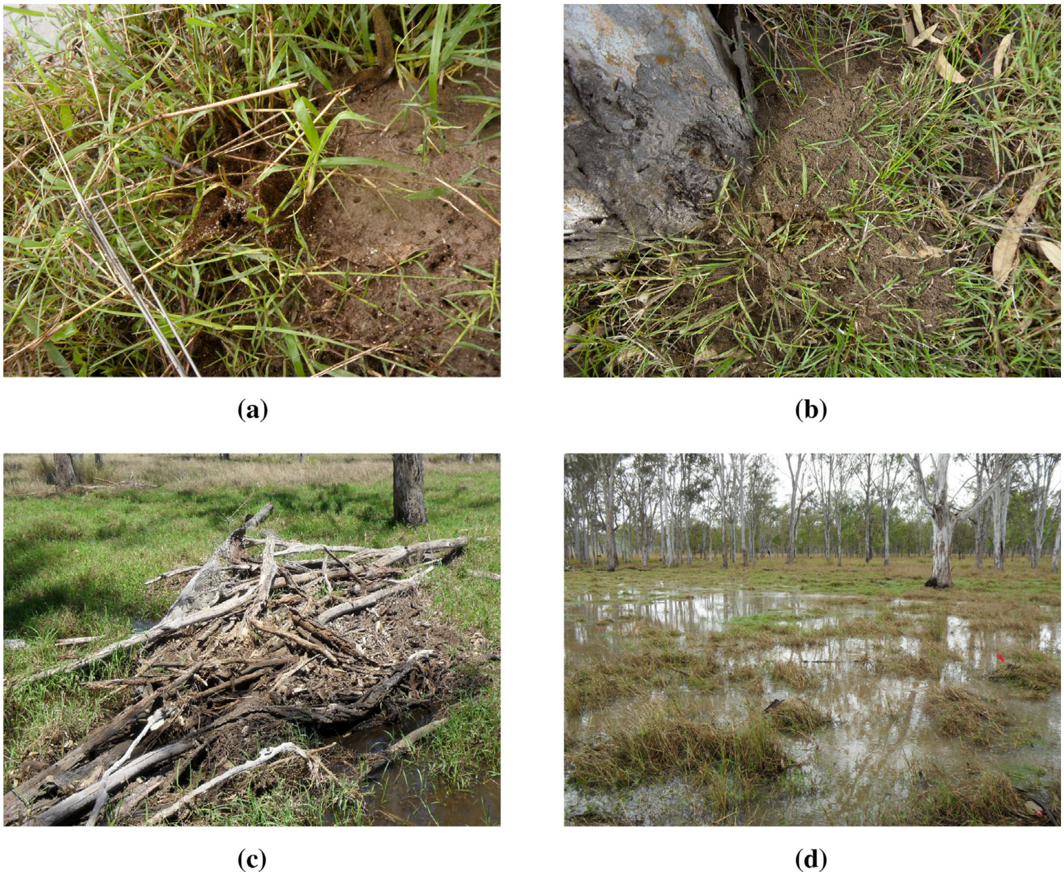
(a)
(b)
(c)
(d)

FIGURE 3 Study site at Purga, southwest of Brisbane, immediately after the flood in 2010 showing (a) masses of *Solenopsis invicta* with brood in clumps of grass just above the waterline, (b) an *S. invicta* nest at the base of a tree just above the waterline, (c) woody debris in one of the plots and (d) hillocks dotted through the area that harboured surviving *S. invicta*.

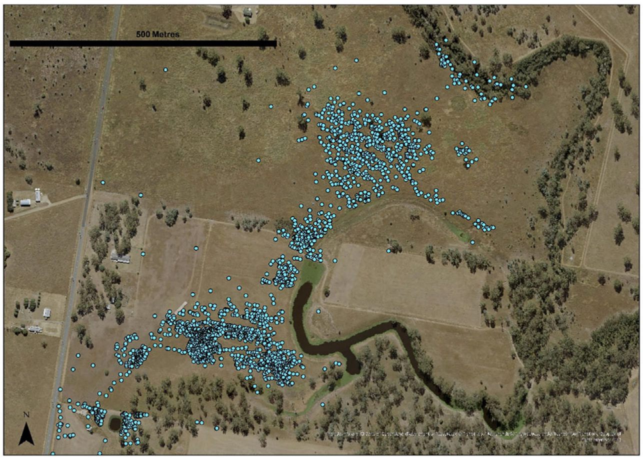

FIGURE 4 Distribution of recorded *Solenopsis invicta* mounds (blue dots) at the study site in Purga, southwest of Brisbane, in 2010 after the flood, showing aggregations at slower flowing bends in Purga Creek.

in the number of fire ant detections in flooded versus unflooded areas after taking into account the relative size difference between these two areas. Extensive post-flood surveillance of the coastline on either side of the mouth of the Brisbane River found no evidence of *S. invicta* survival or establishment in those areas. In general, counts of known colonies decreased in the year following this flood within the flood affected area, as well as beyond the flood affected area (Figure 5a).

Major flooding in the Logan–Albert River catchment in 2017

In 2017, rainfall in the wake of ex-cyclone Debbie caused major flooding in the Logan and Albert River catchments in the east of the known fire ant infestation from 30 March to 1 April. There were several public reports of *S. invicta* rafting. Flooding spread the ant through large areas of canefields along the coastal strip between Brisbane and the northern Gold Coast but still within the boundaries of the infested area. All nests that had been recorded before the flood in this area were monogyne (single queen), so the flood resulted in displacement rather than proliferation of nests. The detailed analysis showed that counts of known colonies decreased in the year following the flood within the flooded area but increased within the areas beyond the flood affected area (Figure 5b).

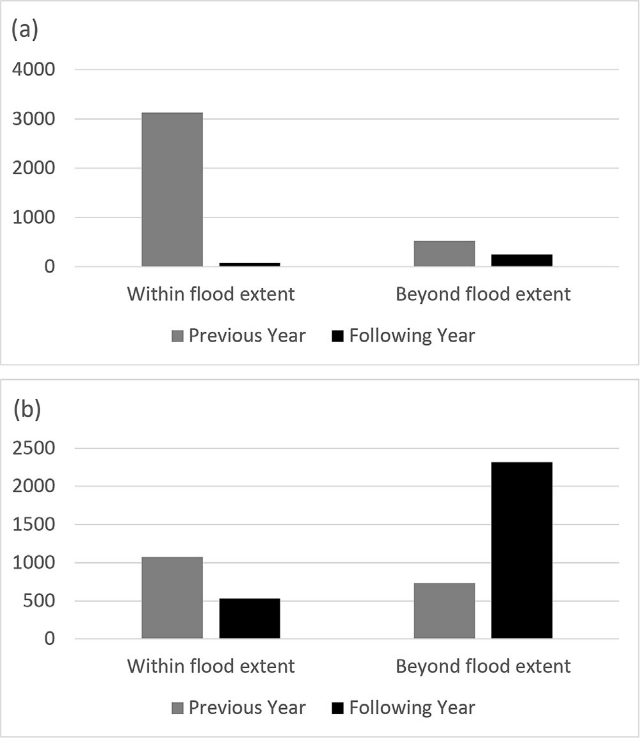

FIGURE 5 Counts of observed and recorded *Solenopsis invicta* colonies both within and beyond the flood affected areas for the single years preceding and following each event. Counts are shown for (a) the Brisbane River 2011 flood and (b) the Logan–Albert River 2017 flood.

Spread risk criteria by flooding for *S. invicta* infestation

Based on the results of our analyses and the available literature, the criteria listed below can be used to assess *S. invicta* spread risk after flooding.

Criteria 1: Were there known polygyne nests in the flooded areas?

Rationale
Polygyne colonies, with their multiple queens, are a greater risk of spread and proliferation by flooding than monogyne colonies with a single queen. If a monogyne nest is forced to relocate, there is still only a single colony at the point of disembarkation. However, flooding can cause 'splitting' of polygyne colonies, and several new viable nests may result from this (see above case study on polygyne site).

Criteria 2: How fast did the waters rise?

Rationale
If floodwaters rose slowly, then the ants would have time to evacuate the whole colony (workers, brood, queen and sexuals) and load them onto a raft formed by interlinked workers. If they rose quickly, then the ants would bunker down in their nest to wait out the flood. In this, they are aided by the waterproofing of the chambers within the mound (Green 1967). They are also likely, like other ants, to be able to cope with any build-up of carbon dioxide in the chambers (Nielsen 2011). If the inundation persists, they can enter a suspended animation and revive once the waters recede (Vinson & Sorensen 1986).

FIGURE 6 Photo of *Solenopsis invicta* rafting during floodwaters in the Logan River at Logan Reserve, south of Brisbane, in 2022 (photo by Yvette Eynon).

Criteria 3: How turbulent were the floodwaters?

Rationale
The degree of water turbulence required to break up a fire ant raft is yet to be determined, and most studies of these rafts have been conducted on static water surfaces (e.g., Mlot et al. 2011; Wagner et al. 2021). Ko et al. (2022) note that the rafting behaviour of *S. invicta* evolved in the Pantanal wetlands, which flow more slowly than rivers. Their studies on the influence of flow showed that fire ant rafts elongate under fluid flows, and turbulent flow can tear a raft apart (Ko et al. 2022). It is therefore likely that many rafts will be broken up in fast-flowing/turbulent waters and the colony will perish. Slow-rising waters favour successful rafting, and a higher incidence of newly founded colonies after the flood is more likely along bends in the rivers or creeks where flow is gentler (Figure 6).

TABLE 1 Matrix for assessing the risk of spread of fire ants by flooding based on combinations of particular risk factors and criteria.

Risk criteria	Risk factors	Polygynes present	Slow-rising water	Low turbulence	No recent treatment	Recent treatment	High turbulence	Fast-rising water	Polygynes absent
Spread potential	Polygynes present		Very high	Very high	Very high	High	Moderate	Moderate	NA
Raft formation	Slow-rising water	NA		High	High	Moderate	Low	NA	NA
Raft survival	Low turbulence	NA	NA		Moderate	Moderate	NA	NA	NA
	No recent treatment	NA	NA	NA		NA	NA	NA	NA
	Recent treatment	NA	NA	NA	NA		NA	NA	NA
	High turbulence	NA	NA	NA	Low	Very low		NA	NA
Raft formation	Fast-rising water	NA	NA	Low	Low	Low	Very low		NA
Spread potential	Polygynes absent	NA	Moderate	Moderate	Moderate	Low	Low	Low	

Note: The risk criteria considered were spread potential given the presence of polygynes, the potential for raft formation and the likelihood of raft survival. Each of these criteria was considered against several factors including the attributes of the flood event and whether or not treatment had recently occurred. The flood risk factors used are subjective and based on program experience. NA indicates where a risk factor does not apply to that particular criterion. Orange tones indicate higher risk combinations, and green tones indicate lower risk combinations.

Criteria 4: Had flooded areas previously received treatment with insect growth regulators (IGRs) or toxicant bait?

Rationale

Baiting with IGRs or toxicants reduces or eliminates the later life stages of brood necessary for raft buoyancy (Adams et al. 2011). Rafting is thus less likely to be successful in areas that have previously received IGR or toxicant treatment.

Criteria 5: In what direction do the creeks and rivers flow?

Rationale

Throughout the history of the program since 2001, the flow of all rivers and creeks has been into the program's operational area, so any dispersal by rafting would be into the infested area and then out to sea. This situation could change if the infestation spreads beyond the current known boundaries.

Criteria 6: Are fire ants likely to survive when they reach the sea?

Rationale

S. invicta die in saltwater, but recent studies have shown that they can raft for about 24 h before the raft begins to collapse (Hooper-Bui et al. 2020). In constructing a raft, the workers use the third- and fourth-instar larvae as floatation devices because the hairs on their body trap air bubbles (Purcell et al. 2014), a behaviour termed by Adams et al. (2011) as bulloferation. In saltwater, the brood begins to shrivel within 24 h and drops from the bottom of the raft, which affects its buoyancy (Hooper-Bui et al. 2020). As well, saltwater environments around river mouths are often turbulent and are likely to break rafts apart, regardless of salinity.

The above criteria have been incorporated into a decision-support tool to assess the likelihood of spread by floodwaters and the consequences of any spread (Table 1). For any flood event, quantitative data on the rate at which floodwaters rise and the degree of turbulence will be difficult to source given that these can vary between individual catchments or sub-catchments and indeed within a stream itself depending on topography. However, information can be obtained from localised reports by program staff, other government agencies, media and the public to assist in decision-making on levels of risk across the flood zone. Depending on the assessed level of risk (Table 1), potential program actions after flooding may include increased surveillance along affected creek/river catchments, as well as additional treatment as considered necessary.

DISCUSSION

Our analysis of flood events in southeast Queensland in the past two decades indicates that flooding has not spread *S. invicta* beyond the known boundaries of infestation but has contributed to localised internal spread.

Geography has played an important part insomuch as river and stream catchments flow into areas of known infestation and out to sea where surviving rafting ants are likely to die in saltwater before re-establishing a colony. No new colonies have been detected after the flood in the immediate coastline around the mouth of the Brisbane River, although wider dispersal on floating debris remains a possibility. The fast-flowing, turbulent waters experienced in most floods will break up the ant rafts, greatly reducing the likelihood of colony re-establishment. Slow-rising and slow-flowing water may allow rafts to remain intact, but the distances travelled before the rafts encounter vegetation or high ground may not be great.

Around the world, ant species nesting in environments that are regularly or irregularly inundated have evolved a variety of behaviours to cope with these events. These include the construction of earthen levees around the nest entrance after heavy rains (LeBrun et al. 2011), raft formation (Morrill 1974), nest relocation (Adis 1982), sealing of nest entrances (Nielsen 2011) and nest designs facilitating drainage of seeping water (Peeters et al. 1994). Some ant species that live in the internodes of bamboo or in other plant stems remove water from their nests by a bailing behaviour described by Maschwitz and Moog (2000) and by Klein et al. (1993). During heavy rain, workers block nest entrances with their heads to reduce water influx, but rainwater may still intrude into the nest chamber. The ants respond by drinking the water, leaving the nest and excreting or regurgitating water droplets on the outer stem surface. Another adaptation by some ant species to inundation is the ability of foragers to ‘walk’, ‘swim’ or ‘jump’ across the water surface (Nielsen 2011). Workers of several species that forage in intertidal areas, including *Solenopsis* species, are known to ‘surf’ on the foam of rolling waves onto the beach, then dry themselves and resume foraging (Jaffe 1993).

Our observations on the response of fire ants to flooding in southeast Queensland match those reported for *S. invicta* elsewhere, namely, rafting of colonies or nest relocation if the water rise allows time to evacuate or, if the water rises rapidly, bunkering down in their nest to wait out the flood. Trapping air in nest galleries is a common survival mechanism for ants whose nests are periodically flooded, such as mangrove mud-nesting ants (Nielsen 2011). For *S. invicta*, this process is assisted by ‘a bonding or waterproofing substance the ants use with the soil as the mounds are constructed. The surfaces of galleries have a waxy feeling to the touch, and the mounds will withstand complete inundation with little apparent ill effects’ (Green 1967). Rhoades (1977; cited in Yensen et al. 1980) mentions a fire ant colony found in Florida on a sandbar that was covered by the tide twice a day. In an experimental plot at Purga in southeast Queensland, one colony survived after 5 days underwater, although most other marked nests were dead by this time. Nielsen (2011) provides several examples of other ant species surviving total submergence for long periods (9 days or more), albeit at low water temperatures. Air bubbles are the most important factor in allowing the survival of submerged ants in warmer climate where ant metabolic rates are higher (Nielsen 2011).

As discussed, the polygyne form of *S. invicta* with its multiple queens poses more risk during flooding than does the monogyne form, as evidenced by the increased mound count after the flood in the predominantly polygyne site at Purga. This risk has been mitigated somewhat by the program in that a specific treatment protocol has been implemented to target and eliminate any polygyne infestations that are detected. Particular attention is paid to polygyne detections within potential areas of flooding, triggering enhanced surveillance and increased genetic testing of samples upstream and downstream of that detection and treatment in these areas. Any new polygyne infestation near a waterway may have been the source or product of the spread by floodwaters. Currently, less than 2% of all known detections in southeast Queensland are polygyne (Wylie et al. 2021). Another important mitigating factor is that many areas within the known *S. invicta* infestation have received broadscale treatment with bait containing IGRs prior to flooding. This reduces or eliminates third- and fourth-instar larvae, which are used as flotation devices by the ant in constructing rafts, thus reducing buoyancy and promoting raft breakup (Adams et al. 2011).

An observation sometimes overlooked is that flooding can also represent a threat to *S. invicta* colony survival. Morrill (1974) mentions the demise of ants in turbulent water. Wiltz et al. (2006) in the United States mapped the distribution of this ant, and other ant species, in areas of New Orleans impacted by flooding in the aftermath of Hurricane Katrina in August 2005. Many parts of the city were fire ant-free following the flood, also containing few or no native ants. Based on these results, they developed a plan to delay the re-introduction and establishment of fire ants in areas where they had been eliminated. Our studies in plots at Purga showed that many colonies were trapped by rapidly rising floodwaters, and there was considerable mortality in colonies that had been submerged for more than a few days. The apparently higher colony mortality recorded in flooded areas in the Brisbane River catchment in 2011 compared to the 2017 flood in the Logan–Albert catchment may reflect the time colonies remained inundated, although no definitive data are available. Certainly, the 2011 flood was of greater magnitude and longer duration than the 2017 flood. The large increase in colony numbers outside the flood affected area in 2017, compared to 2011, may reflect differences in program treatment regimens operating at those times.

Our analysis of both the Brisbane River and Logan–Albert River floods showed a marked decline of observed monogyne *S. invicta* within flood affected areas compared to non-flood affected areas. We suggest that this is probably the result of monogyne colony mortality as a result of the flood. Another possible explanation is that the colonies did not experience high mortality and were rather washed downstream to a different, less obvious location. Our observations of polygyne *S. invicta* colonies are that they are more robust to flood events and more likely to survive and be washed downstream, where they tend to collect en masse in river bends. We did not observe similar aggregations of monogyne colonies, which reinforces our belief that monogyne colonies were not appreciably surviving downstream transport.

There are several limitations to our data that make formal quantitative analyses and definitive conclusions about the spread of *S. invicta* with flooding difficult. The program's internal data management system—while a comprehensive spatiotemporal representation of known detections of *S. invicta* in southeast Queensland—is nevertheless only a partial data collection. Not all *S. invicta* colonies in an area are detected, or are detectable, at any time point by current surveillance methodology. Incipient colonies may show no visible indication of their presence for 3–5 months after the founding event (Tschinkel 2006). Another complication is that, in accordance with program protocols, detected colonies are generally destroyed upon discovery and the surrounding area baited using IGRs or toxicants. There is no reliable method of determining the exact age of a colony, which makes it difficult to distinguish between flooding and regular nuptial flights as a cause of spread. Determining colony mortality versus relocation in a flooded area is also problematic. However, even given these limitations, our data collection is sufficient to identify obvious cases of spread that could be caused by rafting during flooding.

This combination of factors supports our conclusion that flooding has not been a major cause of the spread of *S. invicta* in southeast Queensland to date and that, while localised dispersal has occurred, it has not significantly increased the risk to the program. This situation could change if the ant spreads beyond the current river catchments. Also, as the program progresses to the stage of declaring certain treated areas within known boundaries of infestation as free of *S. invicta*, then rafting of the insect during floods could threaten eradication success.

ACKNOWLEDGEMENTS

We acknowledge the financial support provided to the National Red Imported Fire Ant Eradication Program by the Australian Commonwealth, States, and Territories. We thank the program staff who assisted with the post-flood assessments at the Purga Creek site, Catherine Walsh and Ava Simms for assistance with the mapping of *S. invicta* infestation after the flood and Dr Tracey Churchill for comments and feedback on the manuscript. Open access publishing facilitated by Queensland Department of Agriculture and Fisheries, as part of the Wiley - Queensland Department of Agriculture and Fisheries agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors have declared that no competing interests exist.

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How to cite this article: Wylie, R., McKinney, M., McLennan, A. & McNaught, M.K. (2024) Floods and fire ants, *Solenopsis invicta* (Hymenoptera: Formicidae): The Australian experience. *Austral Entomology*, 1–10. Available from: https://doi.org/10.1111/aen.12692