Research Article

Preparing to eradicate a novel invader of unknown biology: a case study from Australia

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Abstract

Although there have been many attempts at eradicating exotic ant incursions, most efforts have been unsuccessful, and a lack of specific biological knowledge is believed to have been a major contributing factor. In early May 2013, an exotic ant species, *Lepisiota frauenfeldi*, was found for the first time in Australia. Identifying the species proved difficult, and little biological information about the species was available. In making the decision to eradicate and develop the treatment protocols, four assumptions were made about the ant's biology. Here we detail rapid and basic research that was used to assess the assumptions underpinning the decision to eradicate, contribute to determine some eradication protocols for this understudied species, as well as how our understanding increased following the discovery of two other incursions of this species in Australia. The research found that all initial assumptions of the ant's biology used in the original eradication plan were wrong. Distribution modelling found the ant could potentially inhabit a larger area than first thought, and updating the model with the subsequent incursions greatly increased the area of suitable climate in Australia. The ant's foraging and reproductive regimes were not as expected, so too its nutrition pathways to queens, which had implications for the treatments. Our work serves as a clear warning for invasive species practitioners that management decisions that are based on assumptions, "gut feelings" or knowledge based on information from elsewhere in the world, or from other species, can be expected to be flawed. Rapid, small-scale and strategic research conducted on-site can enhance management outcomes.

Key words: Ants, biosecurity, *Lepisiota frauenfeldi*, management, research

Introduction

Despite growing global efforts to prevent the accidental transport of species with trade, such dispersals and subsequent establishments of species in new locations keep increasing (Bertelsmeier et al. 2018; Seebens et al. 2018; Hulme 2021). Consequently, the number of attempts to eradicate unintentionally introduced species is also increasing (Tobin et al. 2014; Hoffmann et al. 2016; Jones et al. 2016). Yet eradication of most taxa from any location, especially mainlands, remains a very difficult outcome (Veitch et al. 2011; Holmes et al. 2015).

A lack of understanding or incorporation of the basic biology of target species has been long recognized as a major factor of eradication failure (Williams et al. 2001; Donlan et al. 2003). Such biological information is vitally important for at least two reasons. First, it is an essential component of risk analysis, assessing the risks posed by an exotic species, the risks associated with management, and the likelihood of success of management actions (Leung et al. 2012; Kumschick and Richardson 2013). Second, specific biological knowledge is often vital for the development of effective management protocols (Donlan et al. 2003; Hoffmann 2015), especially idiosyncrasies of species that make them susceptible to management actions (Simberloff 2003). It is often important that this knowledge is gained on-site because the biology and ecology of species can vary greatly between the native and exotic range, as well as among exotic ranges (Bøhn et al. 2004; Wilder et al. 2011; Kelehear et al. 2012). For example, the northern tamarisk beetle *Diorhabda carinulata*, introduced into North America as a biocontrol agent against *Tamarix* spp. was effective in some regions, on some species, but failed in others (Bean et al. 2007). Ensuing research found different *Tamarix* species and genotypes were affected unequally by different beetle ecotypes (Dudley et al. 2012), and that beetles at different latitudes were behaving differently (Bean et al. 2012). A subsequent taxonomic revision of the beetle into numerous species, as well as determination of the mismatches between host and control agent, and the agent and climatic suitability, has led to more targeted use of these beetles and to better management outcomes (Bean et al. 2013).

Many ant species that have been accidentally spread throughout the world have significant economic, environmental and social impacts in areas that they now infest (Angulo et al. 2022; Gruber et al. 2022). Although there have been many attempts at eradicating exotic ant incursions, most efforts have been unsuccessful, and a lack of specific biological knowledge is believed to have been a major contributing factor (Williams et al. 2001; Hoffmann et al. 2016). For example, baiting during periods when queen brood are in pupal stage will not achieve eradication because these pupae will not be affected by the treatments and can potentially emerge to initiate new colonies. A lack of site-specific information can also hinder effective assessment of treatment success. For example, reduced activity following treatment may simply reflect a normal activity cycle rather than a treatment effect. Clearly, if management decisions and protocols based on the target species' biology are to be effectively applied, the biological knowledge is therefore best obtained on-site.

In early May 2013, an exotic ant species in the genus *Lepisiota* was detected at Perth airport (Figure 1) by the Commonwealth Department of Agriculture. Photographs of the specimens were not perfectly matched with specimens in ant collections contacted globally, but it was decided

Figure 1. Locations of the three *Lepisiota frauenfeldi* incursions in Australia.

that the best morphological fit was the Mediterranean ant species *Lepisiota frauenfeldi*. This identification has since been confirmed genetically (Tay et al. 2022). The detection was promptly reported to the national Tramp Ant Consultative Committee (TACC), which at the time was a committee comprised of representatives of all Australian state and territory governments, as well as key federal government departments, charged with the responsibility to determine if new ant incursions in Australia should be approved for a nationally-funded eradication attempt, and if so to assess the progress of such eradication programs. A literature review was also conducted to determine as much as possible about the biology of the species, but very little information was available. By early July 2013, an eradication plan was developed based on "best guess" assumptions of the species' biology grounded on whatever could be gleaned from the literature about this and related species as well as general ant biology. Ultimately, TACC resolved that despite almost nothing being known about this species, eradication should be attempted based largely on the precautionary principle (i.e. better to eradicate now while the incursion was small and eradication was still feasible rather than waiting to document impacts that justify eradication but resultantly losing the ability to eradicate because the ant had uncontrollably spread to more locations and inhabited a greater area).

In making the decision to eradicate and develop the treatment protocols, specifically it was assumed: 1) the potential distribution of the ant within Australia would not be so great and predominantly in southern Australia given that it appears to have a relatively restricted native range within the Mediterranean region which has little climatic resemblance to Australia; 2) the ant may not be thermophilic (extremely heat-tolerant) and would forage in the evening and potentially at night at least when temperatures were suitable as at least one other invasive ant species does in parts of Australia (Hoffmann 2015); 3) reproductive brood would be produced at the onset of spring (August); and 4) queens would preferentially receive protein over carbohydrates, and therefore a protein-based bait might be best. We also hypothesized that this feeding may occur via larval hemolymph (Tschinkel 1988; Borgesen 2000), not direct from worker to queen.

Knowing that accurate biological knowledge is critical for making correct decisions and effective eradication protocols, in September 2013 (at the end of the Perth winter), prior to any management action being conducted, we embraced an active adaptive approach (Walters and Holling 1990; Hauser and Possingham 2008; Hoffmann and Abbott 2010), whereby research was conducted on-site to gain knowledge specific to the location and program to refine and improve decisions, management actions and thus management outcomes. Specifically, we identified what we considered to be key components of the ant's biology that are important to create knowledge-based protocols, and we researched them using field, laboratory and desktop investigations. Here we detail that rapid and basic research that was used to formulate the eradication protocols for this understudied species, and especially showcase how the research found that all initial assumptions of the ant used in the original eradication plan were wrong. We also present additional work that was conducted following the discovery of two other unrelated incursions (Tay et al. 2022) of this species in Australia, the first being in Darwin on 15 July 2015 which also gave rise to another population near Kakadu discovered on 29 September 2020, and the second being in Brisbane on 23 April 2019.

Materials and methods

Potential distribution

We present two models of potential distribution: The first being what we produced in 2013 with knowledge at that time, and another conducted in 2022 containing more distribution points of other locations the ant was later found inhabiting outside of its native range. Both models were conducted using the exact same technique and bioclimatic data so that the outputs are directly comparable. Species distribution models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of suitable habitat. This method assumes that the species' niche remains consistent when extrapolations are made in space (new potential habitat). Because such models should include the full set of climatic conditions under which the species can occur, we included occurrence points from both its invaded and native habitats (following Broennimann et al. 2007; Beaumont et al. 2009; Liu et al. 2011).

Data of the global distribution of *L. frauenfeldi* were extremely limited (58 points) in 2013 (Figure 2a), and was obtained from the CSIRO Darwin collection, the Natural History Museum in London, and AntWeb (www.antweb.org). In 2022 we included six more points from more populations

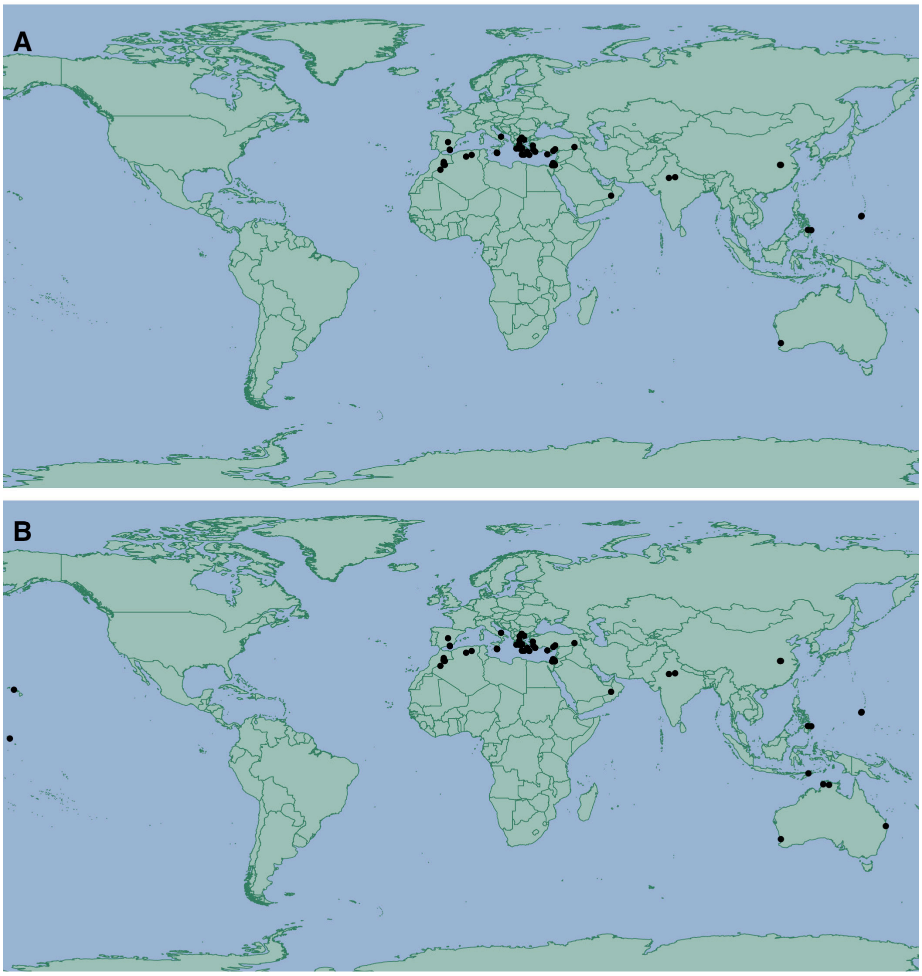

Figure 2. Distribution locations of *Lepisiota frauenfeldi* used for the climate suitability models prepared in 2013 (A) and 2022 (B).

found in Australia and overseas (Figure 2b). These points were in Brisbane, Darwin and near Kakadu National Park in Australia, a location in East Timor, Honolulu in Hawaii, and the Pacific Island nation Kiribati. For the modelling, 10,000 pseudo-absence (background) points were generated randomly from all around the world to provide background data. Presence and absence data were given equal weighting (Barbet-Massin et al. 2012).

All spatial analyses were carried out in R version 4.1.0. We obtained 19 bioclimatic variables averaged for the period 1950–2000 provided by the Worldclim database (Hijmans et al. 2005) to model the species' niche. These variables are frequently used in studies of species' climatic niches and impacts of climate change on species distributions because they are biologically meaningful (Wolmarans et al. 2010). The bioclimatic variables were derived from monthly temperature and rainfall values (Hijmans et al. 2005), and represent annual trends (e.g. mean annual temperature, annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g. temperatures of the coldest and warmest month, and precipitation of the wet and dry quarters) which are known to influence species distributions (Root et al. 2003). We used a spatial resolution of 10 arcmin (approx. 18.5 × 18.5 km pixel) which was

Table 1. Variables used in the climatic models and the Biomod2 output quantifying their relative importance, whereby the higher the number the greater the contribution to the model.

Variable	Bioclim code	Contribution to model	
		2013 model	2022 model
Min Temperature of Coldest Month	bio6	0.072	0.062
Isothermality	bio3	0.034	0.039
Annual Mean Temperature	bio1	0.865	0.793
Temperature Seasonality	bio4	0.415	0.382
Precipitation of Warmest Quarter	bio18	0.010	0.012
Precipitation of Driest Month	bio14	0.013	0.014

the best resolution/computational time combination available in 2013. Because the knowledge of the species biology was very basic, no expert knowledge could be used to preselect the environmental variables. We therefore selected six variables using the following procedure. First, we tested each variable's importance using the variable selection procedure in the Biomod2 package from the ensemble model created from the 10 modelling techniques assessed (see below) (Thuiller et al. 2009, 2016). Next, we assessed pairwise correlations among all 19 bioclimatic variables. Of the 19 variables, we used only six variables that were not collinear (pair-wise $r_{Pearson}$ <0.75), and which provided the greatest contribution averaged across all models (Table 1). The contribution of each variable was determined using the variable selection procedure in the Biomod2 package by observing the variable importance of each ensemble model.

We used ten different modelling techniques, including statistical and machine learning methods. The models were calibrated and projected using the Biomod2 package (Thuiller et al. 2009, 2016) and included (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) generalized boosted models (GBM), (4) classification tree analysis (CTA), (5) flexible discriminant analysis (FDA), (6) multivariate adaptive regression splines (MARS), (7) random forests (RF), maximum entropy (Maxent), (9) surface range envelopes (SRE) and (10) artificial neural networks (ANN).

The models were calibrated with 70% of the data selected at random and the predictive performance of each model was evaluated on the remaining 30% (Guisan and Thuiller 2005) with two evaluation metrics: the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997) and the true skill statistic (TSS) (Allouche et al. 2006). This process was repeated ten times (10-fold cross-validation).

A clear limitation of modelling is that outputs are dependent on the specifically chosen input data (Buisson et al. 2010), in this instance the algorithms. To minimise potential resultant variation we conducted consensus forecasts (Araújo and New 2007) of combined models using the ten different modelling techniques. The contribution of individual models (i.e. the spatial prediction of "suitable range") was weighted according to their TSS in order to enhance contribution of models with higher model performance values (Roura-Pascual et al. 2009). Only binary projections (presence/absence) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (Guo and Liu 2010). The combination of the individual forecasts then yields a projection (the consensus model), where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (Araújo and New 2007).

We applied a threshold rule whereby all pixels with a probability of presence exceeding 0.5 were classified as "favourable" habitat. By convention, this threshold is frequently used for binary classification for species distribution modelling. This allowed us to calculate the number of pixels of favourable habitat for each model.

Activity

Circadian activity was quantified by counting the number of ants crossing a 15 cm wide strip of concrete curbing point over 30 seconds on three foraging trails in the full sun all day at Perth. Activity data were collected hourly from 7am to 6 pm on 8 September 2013 at Perth airport. The day was mild and mostly sunny without much cloud interference. Temperature data were measured at 1 m (ambient temperature) and 1 mm (ant height) using a Fluke (Fluke Corporation USA) 50S K/J thermocouple thermometer corresponding with each ant activity count. Ant activity was expressed as the proportion of maximum activity recorded for each foraging trail. Following the discovery of *L. frauenfeldi* in Darwin we were able to repeat this same methodology in Darwin (Figure 1) on four foraging trails on 1 September 2015 at the Port of Darwin. The day was predominantly sunny and hot.

Reproductive phenology

The reproductive phenology of *L. frauenfeldi* was determined by quantifying pupae production. Samples were collected from nests in eight locations throughout the Perth airport infestation on 10 August 2013 and 6 September 2013, and six locations on both 19 November 2013 and 6 January 2014. Because individual nests could not be defined, approximately 1L of soil from the top 5 cm was gathered from each location, with the ants and brood extracted from the soil in the laboratory by hand. All pupae were determined in the laboratory as being either a worker, male or queen. Determinations were made under a dissecting microscope, with the brood being visible within the pupal case when immersed in alcohol and placed on a black background.

Resource flow

In the laboratory, twelve colonies were constructed containing four queens, and 15 workers, with six of the colonies having larvae and the other six without.

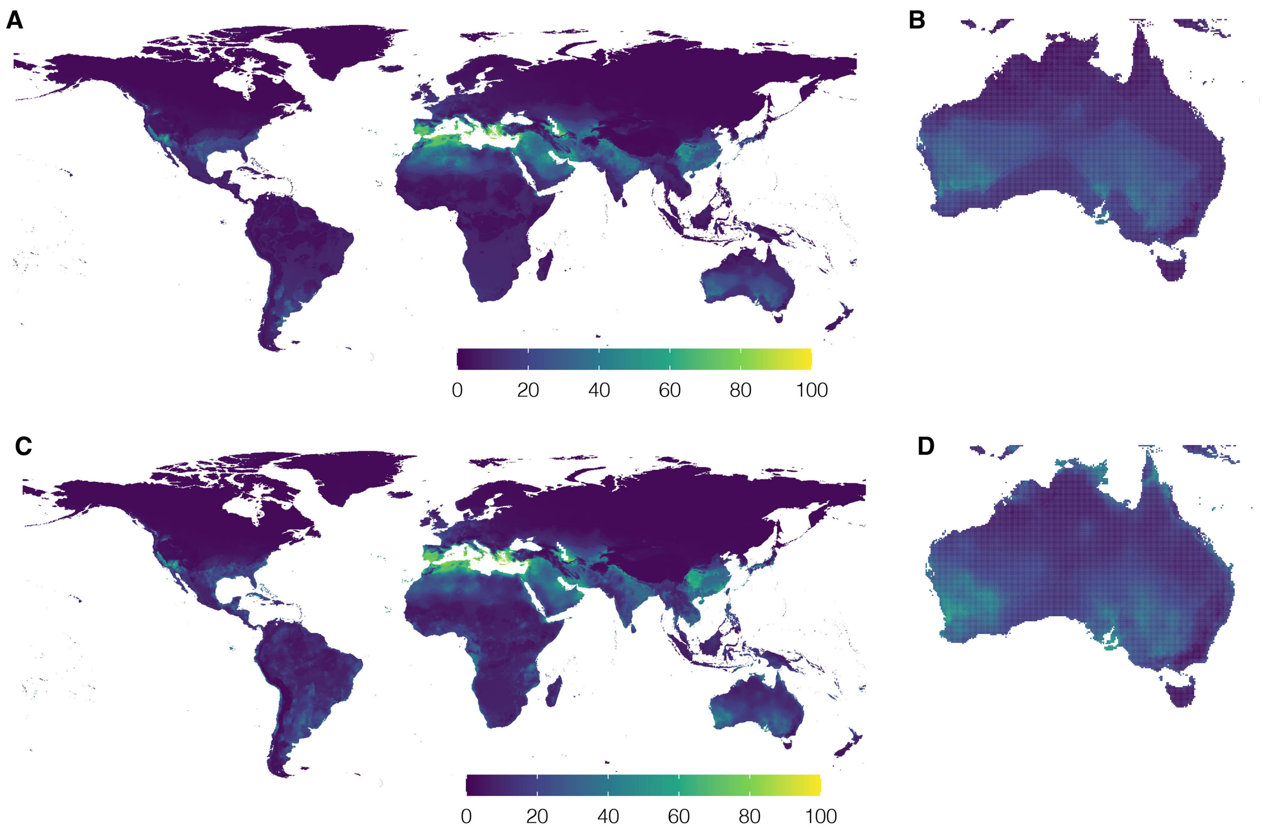

Figure 3. Global (A) and Australian (B) potential distribution of *Lepisiota frauenfeldi* based on the 2013 model and the 2022 model (C and D respectively). Yellow shading indicates high probability of suitable climate, and dark blue shading is low probability of suitable climate.

The colonies were housed in a 50 cm long, 30 cm wide, 10 cm deep container coated with fluon to prevent the ants from escaping, into which was placed an artificial nest. The artificial nest was a petri dish, with one side partly filled with moistened dental plaster, capped with a larger petri dish, and having a hole drilled into the side to allow access. The nest was covered with a black plastic container to provide a dark environment, which also had gaps at the base to allow ant entry. Additional workers in different containers were fed 0.8M sucrose solution or protein consisting of egg powder, with both the carbohydrate and protein food sources containing red Envirodye® (Active constituent Diazo Dyestuff, SST Australia), hereafter referred to as dye. Five fed workers were added to each of the twelve colonies giving a two-factorial design of protein vs carbohydrate food and larvae present vs larvae absent. After 48 hours all individuals were killed in a freezer, preserved in ethanol, and later dissected and inspected for the presence/absence of dye.

Results

Potential distribution

Distribution modelling in 2013 found that *L. frauenfeldi* has a potentially great global distribution within Mediterranean and temperate climates, including 4.8% of Australia (Figure 3a). The Australian regions of greatest

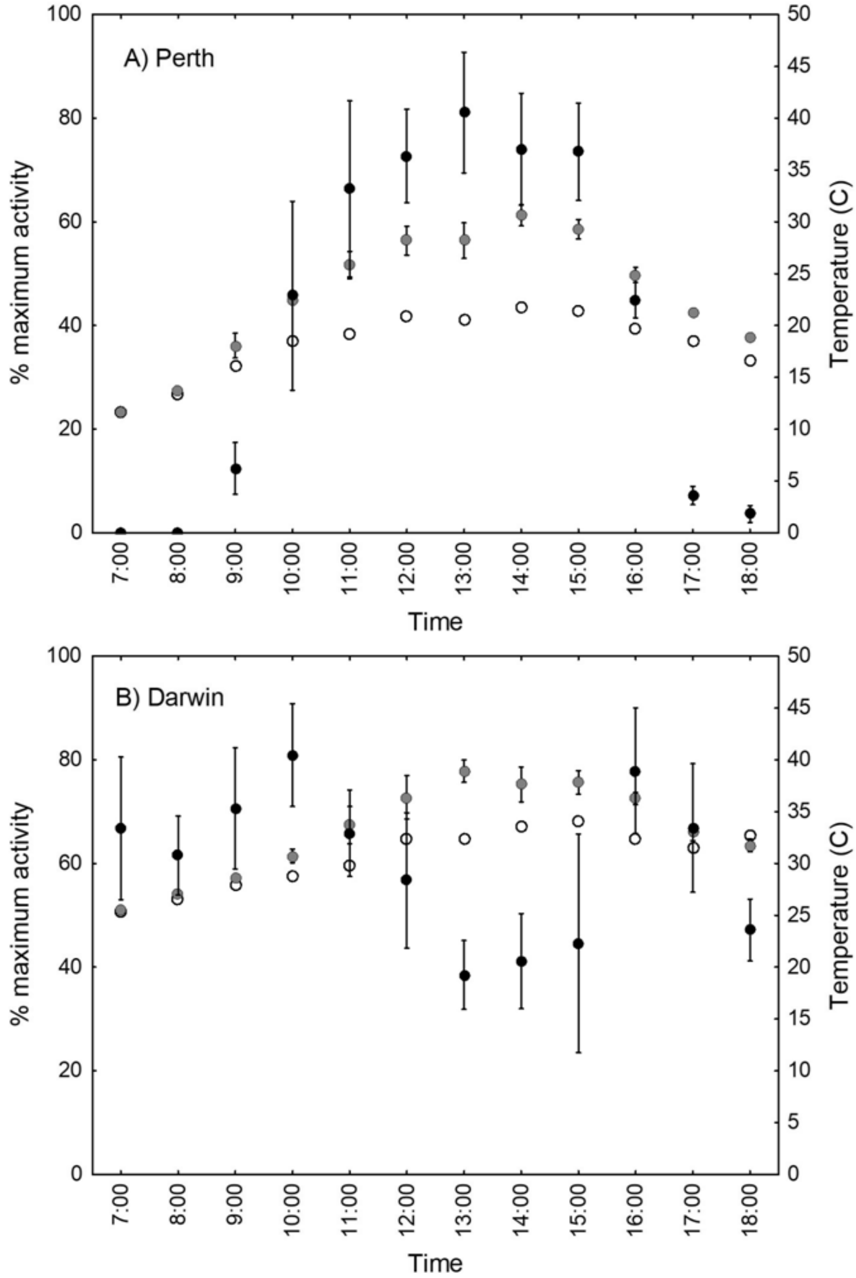

Figure 4. Mean (± SE) *Lepisiota frauenfeldi* activity rates (black circles), ambient temperature (white circles) and temperature at ant height (1 mm) (grey circles) in Perth (A) and Darwin (B).

suitability were in SW Western Australia, coastal and semi-arid South Australia, semi-arid New South Wales and the coastal regions of northern Australia and to some extent eastern Australia. The repeated model in 2022 using additional distribution points found that the potential distribution within Australia was more than double that of the 2013 model, increasing to 10.6% (Figure 3b).

Activity

In Perth, *L. frauenfeldi* activity on the mild spring day followed a unimodal pattern, commencing when temperatures exceeded 15 °C, and peaking at mid-day around the highest temperatures (Figure 4a). In the hotter environment

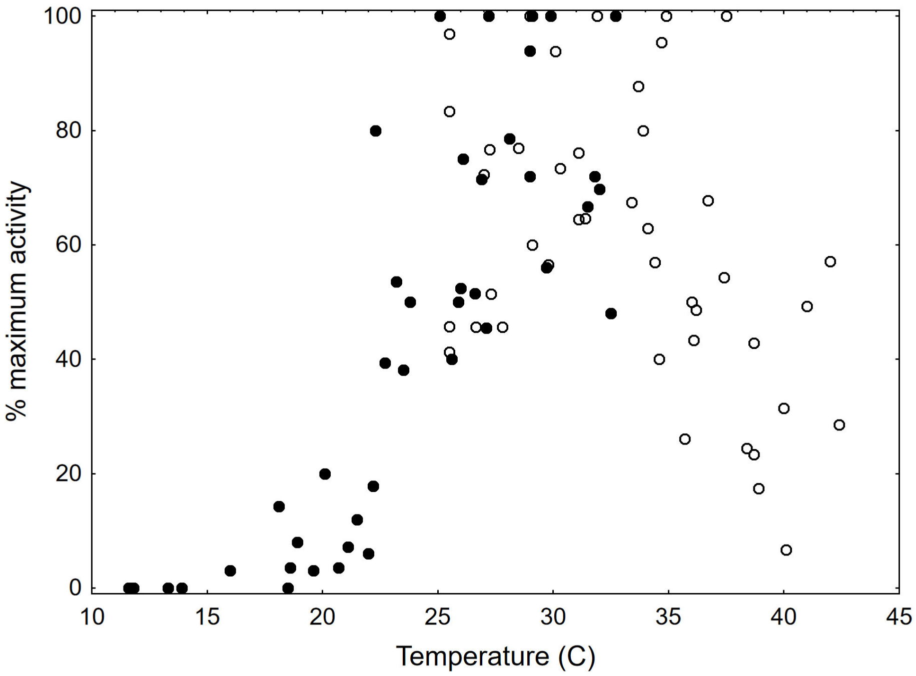

Figure 5. Relationship between *Lepisiota frauenfeldi* activity and temperature at ant height (1 mm) as found in Perth (black circles) and Darwin (white circles).

of Darwin, *L. frauenfeldi* activity followed a bimodal pattern, being active at first light, increasing in the morning, but dramatically decreasing during the middle of the day, having a resurgence of activity in the late afternoon but rapidly decreasing near sunset (Figure 4b). Multiple opportunistic observations at night in Perth and Darwin did not find workers foraging, even though temperatures were appropriate.

Lepisiota foraging overall had a clear unimodal relationship with temperature (Figure 5), with maximal activity occurring between 25 and 35 °C temperature at ant height (1 mm), which corresponded with an ambient temperature range of 20–35 °C.

Reproductive phenology

No pupae were collected in the August sample, indicating a lack of reproduction during winter. In September, 958 pupae were collected, all being workers. In November, 14 male pupae were found among almost 10,000 pupae, the remainder being workers. In January 19 males (0.28%) were found among over 4200 pupae. No queen pupae were found, but two winged queens were found with a winged male in an informal collection on 6 September 2013.

Resource flow

The two food treatments gave contrasting results. For carbohydrates, of the 24 queens, 21 contained dye indicating great flow of resources to the queens. Of the queens without larvae, only two did not contain dye (one each in two colonies), and when larvae were present no larvae were found containing

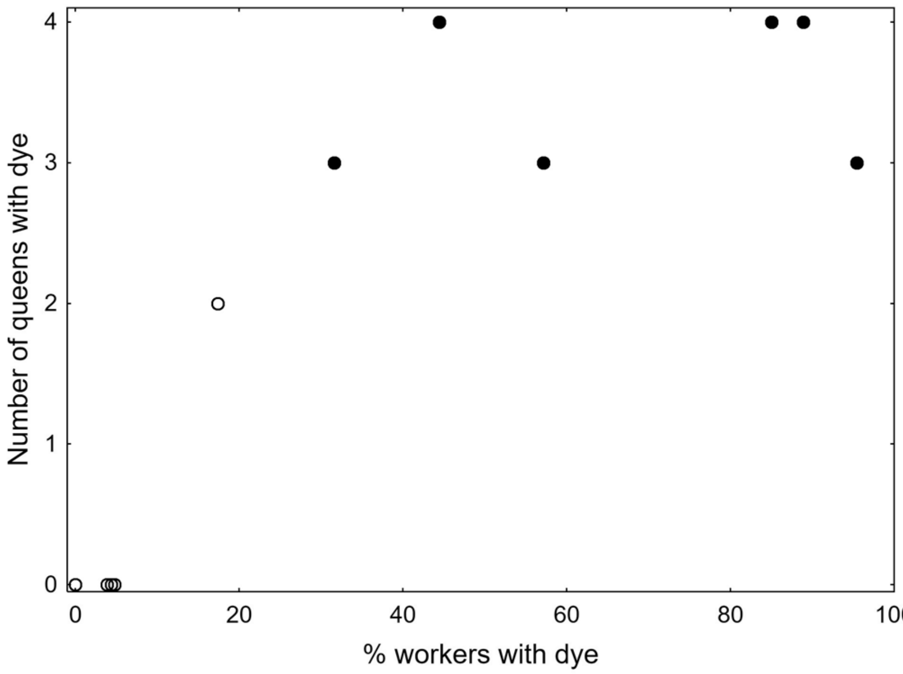

Figure 6. Relationship between the number of queens containing dye with the percentage of workers containing dye when the workers were fed with carbohydrates (black circles) or protein (white circles).

dye, indicating that larvae were not part of the feeding process for queens. On average, 67% of workers contained dye, ranging from 32–95%. For protein, only two of the 24 queens contained dye, both within a single replicate containing brood. On average, only 5% of workers contained dye, ranging from 0–17%. Overall, no clear relationship was found between the number of queens with dye and the percentage of workers containing dye (Figure 6), with most or all queens receiving carbohydrates irrespective of the percentage of workers that had obtained carbohydrates.

Discussion

Management implications of the research

The habitat suitability models found that rather than just a small portion of southern Australia containing suitable climate for this species, much of Australia contained climates that were within the thresholds of its current global distribution, and therefore theoretically suitable for habitation. This potentially great range was particularly prominent following the find of the incursion in Darwin in the monsoonal tropics, as well as in other tropical locations like Hawaii, Kiribati and East Timor. Notably, the latest model output still represents a minimal estimate of suitable area because species can often inhabit climates very different to their native or known ranges (Broennimann et al. 2007; Tingley et al. 2014), but such suitability in new environments is not known until they establish within those environments. It is highly likely that the species could inhabit a wider variety of climatic conditions, but this will remain unknown until it establishes in other locations and the model can be updated. Ultimately, because the species had a substantively larger potential distribution throughout Australia than initially thought, this supported the view that eradication should be attempted.

The vastly different activity profiles of the ant in the two locations demonstrated that knowledge from one location is not necessarily transferable to other locations and consequently different protocols are needed in different locations. Just based on time of day in "typical" weather, in Perth which has a temperate climate, treatments should not be conducted after 2pm, because ant activity rapidly declines after this time, whereas in Darwin in the tropics, treatments could be conducted in the mid to late afternoon (i.e. 3pm onwards) because ant activity increased temporarily after this time. Such behavioural variation among geographic locations is common globally, with other such examples including timing of alate production in yellow crazy ant *Anoplolepis gracilipes* (Hoffmann 2015), variation of microhabitat use by fence lizards *Sceloporus occidentalis* (Asbury and Adolph 2007) and growth form (tree vs vine vs shrub) of Brazilian pepper *Sachinus terebinthifolius* depending upon habitat (Spector and Putz 2006). Clearly, location-specific data are best for forming protocols best suited to each location and environmental scenario.

The species did not have the reproductive cycle first thought, and the exact timing of the production of new sexuals remains unclear. The casual observation of both winged male and queen castes indicates that low levels of sexual production may occur throughout the year, typical of the reproduction of many invasive ant species (Broekhuysen 1948; Passera et al. 1998; Hoffmann 2015). Importantly for management, the lack of production of sexuals at the onset of Spring in Perth reduced the need for the expediency of treatments (from the sole perspective of preventing sexual production), but treatments were still conducted as soon as possible.

We found that the flow of carbohydrates (and probably protein) within the colony is direct from worker to queen, and does not involve processing by larvae. This, coupled with the high rate of queen feeding indicated that any active constituent consumed by workers within a carbohydrate-based bait or solution would likely be rapidly fed to many (if not most) queens. Notably we could only assume that the laboratory trials would reflect what would occur in the field in the absence of such trials being repeated in the field. Standard bait palatability trials using many ant control products were conducted in the field (data not presented), but none were found to be particularly attractive to the ants until an experimental form was trialled that contained double the standard sugar and protein coatings over the corn matrix. Upon this finding, the chosen treatment method was first an application of this experimental bait (then called Distance Plus) which contained an Insect Growth Regulator as the active constituent, followed approximately one week later with a spray containing a low dose of fipronil. This treatment regime was used on the basis that most if not all ants would be killed by the spray, but any individuals capable of reproduction left alive would hopefully first be sterilised by the granular bait. The efficacy of this double treatment relative to just spraying remains unknown.

Outcomes to date

The information that was gained from the rapid research not only helped to make the decision to attempt eradication by providing certainty of some aspects of the species' biology where there otherwise was just uncertainty, but also helped determine the treatment protocols. These protocols have been very successful at eliminating populations of this species, and eradication from Australia is considered to be fully achievable. Since the first detection was made, a total of 10 spatially discrete populations were found in Western Australia around Perth from 2013 to 2021 covering a combined area of 102 ha. To date, five of these populations covering 83 ha have been declared eradicated, and in March 2023 the remaining populations have undergone their final post-treatment assessment by a detector dog, and because no ants were detected the formal process is now being taken to declare the species eradicated from Western Australia. Also, arising from a separate incursion, eight populations covering 86 ha were found in the Northern Territory, seven around Darwin and one near Kakadu National Park, and of these seven populations covering 30 ha have also been declared eradicated. Finally, a very small (< 1 ha) third incursion was found in Brisbane on 23 April 2019 and has since been declared eradicated. Details of these eradications will be the subject of other publications.

Summary

As trade increases and more species enter trade systems, it is inevitable that additional species will be targeted for eradication in novel locations, but with little to no knowledge available of the biology of those species. The rapid science conducted on the multiple incursions of *L. frauenfeldi* in Australia found that much of what was assumed about the species was not correct, which serves as a clear warning for invasive species practitioners that management decisions that are based on assumptions, "gut feelings" or knowledge based on information from elsewhere in the world or from other species, can be expected to be flawed. Management protocols based on on-site data that is not confounded by geographic variations in the species' biology will no doubt enhance management outcomes. The work presented here, coupled with the rapid management actions taken, add to a growing list of eradications that are being achieved based on solid science.

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Authors' contribution

BH designed the experiments, BH and MQ conducted the field work, OB conducted the modelling, BH did the data analysis, interpretations and led the writing, all authors provided comments and input into the draft manuscript and approved the final manuscript.

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