Modelling biocontrol of invasive insects: An application to European Wasp (*Vespula germanica*) in Australia

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ARTICLE INFO	ABSTRACT
	Established pests are often overlooked as candidates for eradication or containment programmes because the use of traditional control techniques over very large areas usually becomes uneconomic. In such cases, classical biological control can be an attractive option. If biocontrol agents become established in equilibrium with the invasive species, there are no ongoing costs of control. Arriving at the point of biocontrol release, however, requires significant time and investment in research and testing, and success of biocontrol agents is not guaranteed. It is therefore advisable to undertake preliminary analysis of the likelihood of success. Simulation modelling using population dynamics models can be very useful in this regard. Here we develop a model for biocontrol of an invasive social insect, the European wasp (*Vespula germanica*) and derive the conditions for success of a biocontrol program.

1. Introduction

Insects are the planet's most species rich group, playing important roles in food web interactions and ecosystem processes, while also featuring prominently as invasive species in terms of their number and impact (Brockerhoff and Liebhold, 2017). The impacts of invasive insects are well known — they threaten human health via stinging and as vectors of disease, consume crops putting food supplies at risk, disrupt ecosystem function, endanger valued species and damage infrastructure. As a result, governments across the globe routinely spend significant amounts of money protecting their economies, environment and communities from the negative impacts of invasive insects. Bradshaw et al. (2016) estimate invasive insects cost a minimum of US$70.0 billion per year globally, while associated health costs exceed US$6.9 billion per year.

Depending on the stage of invasion, strategies available to biosecurity agencies to avoid or minimise impacts of invasive insects typically consist of prevention via pre-border and border quarantine activities, surveillance for early detection, rapid response with a view to eradication, or containment to slow-the-spread (Sharov and Liebhold, 1998 Cacho et al., 2008; Epanchin-Niell 2017 Hester et al., 2017). As the size of an invasion grows, so too do the costs of traditional control techniques that typically form part of eradication or containment

programmes; eventually their use over very large areas becomes uneconomic given budget constraints, and such programmes may be abandoned (Cacho et al., 2007, Epanchin-Niell and Hastings, 2010). If mitigation of impacts is still desired, biological control, where the goal is permanent establishment of an agent and control of the pest, is usually the only economically feasible option.

Classical biological control (CBC) — the introduction of populations of an exotic natural enemy into a new environment to control a pest, where the aim is permanent control of the pest without further intervention (Hajek, 2004, Van Driesche et al., 2008) — has been used in pest management for more than a century, although success has been mixed (Cock et al., 2016, Naranjo 2018). It is difficult to predict the likely success of an agent and a substantial proportion of biocontrol agents fail to control their target (Beggs et al., 2008). A recent analysis of CBC programmes for the control of insect pests found that since the 1970s 33% of the introductions led to establishment, and 10% resulted in satisfactory control (Cock et al., 2016). Where programmes do succeed, economic analyses suggest very large benefit-to-cost ratios (Naranjo et al., 2015). Despite this, the number of classical biological control programmes and releases have decreased in recent decades, due in part to the increased regulatory oversight imposed in many countries out of concerns about non-target and indirect effects that may be caused by agent introduction (Hajek et al., 2016). As the cost in time and resources

required for host-specificity testing has increased, the number of natural enemies proposed for release has slowed (Hajek et al., 2016). Furthermore, biological control programmes are typically constrained by small budgets and short timetables (Godfray and Waage, 1991).

Given the long-time frames involved in testing agents, the uncertainty surrounding successful control and limited budgets for CBC programmes, mathematical models of biological control can provide useful prospective information about the conditions required for success prior to significant investment occurring. Models of biological control exist in the literature. They range from the simple analytical models of theoretical population biology, which allow very general predictions about equilibrium population levels (e.g Beddington et al., 1978., Davis et al., 2006, Kaser and Heimpel, 2015), to detailed simulation models (e.g Gutierrez et al., 1988., Gutierrez et al., 2008, Portela et al., 2020, Poggi et al., 2021) which contain a large number of parameters to be estimated in order to apply the model, and which may not be useful in information-poor and time-limited contexts (Godfray and Waage, 1991). In this paper we develop a simulation model of 'intermediate complexity' for an invasive insect in an attempt to strike a balance between model applicability and data needs. We apply the model to the case of the European wasp, *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae) in Australia, where the pest has significant potential to spread further (de Villiers et al., 2017, Cook 2019), and we determine the conditions that would make the biocontrol successful based on combinations of parameter values in the model.

The European wasp is native to Europe, Northern Africa, and temperate Asia, and introduced into North America, Chile, Argentina, Australia, New Zealand (Spradbery and Maywald, 1992). It is adaptable to a wide range of habitats and climates (de Villiers et al., 2017) and has significant negative impacts on communities, industry and the environment in regions where it has been introduced (MacIntyre and Hellstrom, 2015, Cook, 2019, Lester and Beggs, 2019).

The European wasp is widespread in New Zealand and south-eastern Australia, and was the subject of a past biological control program in both countries, with mixed success (Field and Darby, 1991, Moller et al., 1991, Lefoe et al., 2001, Beggs et al., 2008). The poor performance of the chosen agent, *Sphecophaga vesparum vesparum* (Curtis) (Hymenoptera: Ichneumonidae) is thought to have been caused by a 'genetic bottleneck' because all releases were essentially derived from a single female parasitoid (Beggs et al., 2008; Ward, 2014). Unfortunately, no other information that could assist in understanding agent performance in Australia was recorded during the release program. The possibility of improved control from using different genetic strains of the agent, and the likelihood of reduced screening and testing requirements has spurred renewed interest in using *S. v. vesparum* to control wasps. However, there are other candidates that could be considered and tested with the model developed here. These include two agents recently approved for import and release in New Zealand: the wasp-nest beetle (*Metoecus paradoxus* (Linnaeus) (Coleoptera: Ripiphoridae)) and a hoverfly (*Volucella inanis* (Linnaeus) (Diptera: Syrphidae)) (Landcare Research, n.d.). *M. paradoxus* has a complex lifecycle — adults lay eggs in wood and bark outside wasp nests and once hatched, larvae are transported into nests inadvertently by foraging wasps, attacking wasp larva once inside (Ward ,2014). In contrast, adult females of *V. pellucens* enter wasp nests, laying eggs which hatch, with larvae dropping to the bottom of nests and feeding on wasp young and dead adults (Ward ,2014).

The goal of this work is to develop a general model that allows an improved understanding of biocontrol programmes for invasive insects. To demonstrate the model we use *S. v. vesparum* as the biological control agent for *V. germanica*, although the model could be easily adapted to understand other pest-biological control interactions.

1.1. Life cycles of V. germanica and S. vesparum

The European wasp is a social insect, and possesses characteristics of eusociality that allow it to succeed as an invasive species (Moller, 1996,

Kasper, 2004, Beggs et al., 2011): there is an overlap of generations; reproduction is restricted to a few individuals; and there is cooperative brood care (Wilson and Hölldobler, 2005).

The normal colony life cycle is annual, with nests being founded by a single reproductive queen in the spring. The reproductive cycle progresses as follows: the queen emerges in spring to forage and prepare new nests of about 20 cells in size; workers emerge 4–6 weeks after egg-lay and assume foraging, nest protection and nest building duties, thus freeing up the queen for egg laying; the nest grows over summer and new queens are produced in autumn; these queens mate with drones in autumn then fly off to hibernate in sheltered areas during winter (Widmer et al., 1995).

In their native range, European wasp colonies naturally die off in winter. This is not the case in locations experiencing mild winters, including parts of Australia, where nest construction can continue throughout the year, and over-wintered nests are common (Spradbery and Maywald, 1992, Widmer et al., 1995, Kasper, 2004). Overwintering is a modification of the usual annual life cycle, where polygyny (multi-queening) occurs – more than one, and often many hundreds, of productive queens share the same nest. As a result, overwintered nests can reach very large sizes in summer, producing thousands of individuals.

While the process of predation by *S. v. vesparum* on European wasp is relatively straightforward – it attacks European wasp nests and feeds on the developing larvae and pupae – its life cycle is complex (Beggs et al., 1996, Harris and Rose, 1999). During spring, winged male and female *S. v. vesparum* emerge from cocoons in the remains of old wasp nests, one to four springs after their cocoons were formed. Females enter new wasp nests and lay eggs onto larvae or pupae, with the parasitoid larvae feeding on the host and subsequently forming one of three types of cocoons: yellow, weak-walled yellow and white. Yellow cocoons are thick-walled that will remain dormant in the nest, producing winged adults up to four years later. Weak-walled yellow cocoons produce winged adults capable of flight within two weeks. Weak-walled white cocoons produce short-winged females within two weeks and these continue to lay eggs within the parental nest so that multiple generations follow during the same season (Harris and Rose, 1999).

2. Method

The model is centred on the population dynamics of the invasive wasp and a biocontrol agent that affects the viability of wasp nests as well as the ability of colonies to reproduce.

2.1. Model

Studies from Australia (Kasper, 2004) and New Zealand (Barlow et al., 2002) have modelled the population dynamics of European wasp using a Ricker equation (Ricker, 1975), incorporating weather effects and density dependence. We modify the model of Barlow et al. (1996) to represent the growth of wasp and parasitoid populations and their interaction, and introduce dispersal equations for spatial spread of both the wasp (W) and the biocontrol agent (B). We also introduce the option for detected nests to be destroyed based on the probability of encounter between wasps and humans, which in turn depends on the density of households and wasp nests in the given location. The model is presented below and a summary of model parameters and descriptions is given in Table 1.

2.1.1. Population dynamics

Based on the life cycles discussed earlier, the wasp population is expressed as number of nests per km^2 in spring (W_s) and autumn (W_a), whereas the biocontrol population is expressed as number of adults per km^2 in spring (B_s) and autumn (B_a). The value of B_a is a proxy for the number of cocoons (of all types) that overwinter in wasp nests. Growth of the two populations is given by:

Table 1

Model parameter definitions.

Symbol	Description	Equation
European wasp		
α_W	Ricker growth parameter for wasp	(1)
β_W	Ricker growth exponent for wasp	(1)
κ_W	Wasp maximum carrying capacity (wasp nests km^{-2})	(7)
θ_W	Habitat suitability of site	(7)
γ_W	Median dispersal distance for wasp (km)	(9)
δ_W	Wasp detectability parameter	(12)
Biocontrol agent		
α_B	Ricker growth parameter for biocontrol	(3)
B_B	Ricker growth exponent for biocontrol	(3)
K_B	Biocontrol carrying capacity (adults per wasp nest)	(8)
μ_B	Mortality of biocontrol	(4)
γ_B	Median dispersal distance for biocontrol (km)	(9)
Biocontrol effect on wasp population		
ρ_B	Reduction in growth rate of wasp nests	(5)
φ_B	Winter mortality of wasp nests	(6)

$$W_{a,t} = \alpha_W \left(1 - E_{\alpha,t}\right) \, W_{s,t} \, e^{-\beta_W \, W_{s,t}} \tag{1}$$

$$W_{s,t+1} = W_{a,t} \, \left(1 - E_{\mu,t}\right) \tag{2}$$

$$B_{a,t} = \alpha_B \, B_{s,t} \, e^{-\beta_{B,t} \, B_{s,t}} \tag{3}$$

$$B_{s,t+1} = B_{a,t} \, \left(1 - \mu_B\right) \tag{4}$$

Where α and β are growth parameters in the Ricker equations, and μ are mortality parameters, with the subscripts representing wasps (*W*) or biocontrol (*B*). $E_{\alpha,t}$ and $E_{\mu,t}$ are proportional effects of the biocontrol on growth and winter mortality of wasp nests respectively, defined as linear functions of biocontrol agent density:

$$E_{\alpha,t} = min\left(\rho_B \, B_{s,t}, 1\right) \tag{5}$$

$$E_{\mu t} = \min\left(\varphi_B \, B_{s,t}, 1\right) \tag{6}$$

The shape of these functions is open to debate, but a linear relationship is a good start in the absence of other evidence. The biocontrol efficiency parameters are the reduction in the wasp growth rate (ρ_B) and the winter mortality of wasp nests (ϕ_B) caused by the agent in spring. The exponents of the Ricker equations (β) in (1) and (3) are functions of the carrying capacity (κ) of the site, defined as the maximum number of nests per km^2 in the case of wasps and the maximum number of cocoons per wasp nest in the case of the biocontrol:

$$\beta_W = \frac{\ln\alpha_W}{\kappa_W \, \theta_W} \tag{7}$$

$$\beta_{B,t} = \frac{\ln\alpha_B}{\kappa_B W_{s,t}} \tag{8}$$

In the model, the growth exponents in (7) and (8) are intermediate parameters that depend on carrying capacity (κ) for a given α. In the case of the wasp, κ_W in (7) is adjusted based on habitat suitability of the site (θ_W). In the case of the biocontrol, κ_B in (8) is adjusted based on the number of wasp nests on the site in spring ($W_{s,t}$), which essentially measures habitat available to colonise. The time step (*t*) is one year, with each year starting in spring when wasp queens emerge to start building up new nests.

2.1.2. Dispersal

Each spring, queens emerge from hibernation and start building nests and multiplying their colonies. Dispersal to new sites can occur early in the season as queens find nesting sites, and later in the season as new queens establish new nests. For simplicity we assume that dispersal occurs in spring. The probability that a queen emerging in site *i* will move to site *j* and establish a nest there is given by:

$$p_{i,j} = \frac{1}{\pi \, \gamma \, \left(1 + \left(\frac{d_{i,j}}{\gamma}\right)^2\right)} \tag{9}$$

Where γ is a median dispersal distance and *d* is the distance between points *i* and *j*. The area under this curve in the interval -∞ to +∞ equals 1, whereas the area in the interval -γ to +γ is 0.5 (see *SM* section A). The same dispersal kernel is applied for both species, but with γ replaced by the corresponding parameter γ_W or γ_B. In the numerical model the landscape is represented as a grid with *n* square cells of equal size (or sites) and distance is expressed as a matrix **D** of dimensions $n \times n$, representing the distance between each cell and every other cell on the map (composed of elements $d_{i,j}$). This allows dispersal probability to be estimated for all sites at once using Eq. (9), yielding the matrices $\mathbf{P}_W$ and $\mathbf{P}_B$ of the same dimensions as **D**. The expected numbers of wasp nests and biocontrol agents after dispersal are:

$$W_d = P_W \, W_t \tag{10}$$

$$B_d = P_B \, B_t \tag{11}$$

Where *W* and *B* are column vectors of *n* elements containing the density of wasps and biocontrol agents in every site on the map. Leung et al. (2010) present an application of this dispersal kernel in 2-dimensional discrete space. The approach we followed, using matrices representing discrete sites in space, is similar to theirs.

In stochastic simulations, the actual dispersal for each run of the model is selected randomly by sampling from a uniform distribution against matrix **P**. The numerical process is explained in SM Section A.

2.1.3. Detection

We assume that all nests detected by humans are destroyed when the wasps are active during spring and summer. The probability that a nest will be detected is given by:

$$p_d = 1 - e^{-\delta_W \, W_{a,t} \, H} \tag{12}$$

where *H* is the number of households per km^2 in the given site and δ_W is a detectability parameter related to the probability of encounter between humans and wasps given their respective local density. The number of nests destroyed is:

$$K_t = p_d \, W_{a,t} \tag{13}$$

and after destruction, the number of nests is updated to:

$$W_{a,t} = W_{a,t}(1 - p_d) \tag{14}$$

2.2. Running simulations

All the variables above are expressed as column vectors of dimension *n*, where each row represents a site on the map. The results of solving the model (1)-(8) for a planning horizon of *T* years are presented as matrices of dimensions $n \times T$, where columns are time periods. There is one such result matrix for each vector. Such that:

W = $W_{s,t}$ solved for *t*= 1,…,*T*
B = $B_{s,t}$ solved for *t*= 1,…,*T*
K = K_t solved for *t*= 1,…,*T*

This matrix representation of results is useful for analysis of patterns in space as well as in time. The model is implemented in Matlab language (Mathworks, 2020a). Each scenario was run for 1000 stochastic iterations over a planning horizon of 60 years.

To initialise the simulation, we need initial values $W_{S,0}$ and $B_{S,0}$ for the wasp and biocontrol populations (see Eqs. (1) and (3)) for each site. Expressed as vectors for the area of interest, the initial states are $\mathbf{w}_0$ and $\mathbf{b}_0$, of dimensions $n \times 1$ for each stochastic iteration. The values of $\mathbf{w}_0$ were generated randomly based on Atlas of Living Australia data (ALA) (see 2.3) and the wasp parameters for the area of interest. For

convenience, a matrix $\mathbf{W_0}$ of dimensions $n \times 1000$ was created and used to initialise all the simulation runs, with each column providing the $\mathbf{w_0}$ value for the corresponding random iteration.

The initial vector $\mathbf{b_0}$ depends on the biocontrol release strategy for the given $\mathbf{w_0}$. We consider two decision variables for the biocontrol program:

- x_p: the percentage of wasp nests that are initially infested with the biocontrol agent on a given site.
- x_c: the spatial coverage of the biocontrol release, expressed as the top percentile of wasp infested sites selected for inoculation. For example, $x_c = 10$ indicates that only the top 10 percent of sites in terms of wasp-nest density are selected for release of the biocontrol.

Several combinations of these decision variables were selected for exploratory runs, within the ranges $x_p = 10$ to 50 and $x_c = 1$ to 20. These experiments represent strategies with different combinations of spatial coverage and intensity of control per site.

2.3. Data and model calibration

Model calibration was carried out based on data from the literature combined with four spatial datasets (maps A to D in Table 2) and overlaid onto map E (Table 2) to create the final dataset for analysis and modelling. The following variables were created as column vectors of 2462 elements representing the cells (sites) on the grid map (E):

- ALA reports of European wasp presence per site: estimated by overlaying the point data in map A with the grid (map E) and summing the number of points that fall into each site.
- Area: The area of the site in km^2 — not all sites are the same area because of truncation along the coastline.
- Household density: households per km^2 estimated by intersecting SA1 (map C) with the grid (map E), estimating the weighed sum of households for each site, and dividing by its area.
- Land use proportion: estimated by overlaying the raster in map B onto the grid (map E) and calculating the proportion of the area of each site that is covered by each of seven categories of land use. The seven categories were aggregated from the Australian Land Use and Management (ALUM) classification (see SM for an explanation of this process).

Table 2
Spatial datasets used to calibrate and implement the model.

Map ID	Description	Details
A	Atlas of living Australia (ALA) reports of European Wasp (*V. germanica*) presence*.	Point data in decimal degrees with details of report including date.
B	ABARES (2021): Catchment Scale Land Use of Australia – Commodities – Update December 2020.	Raster data (50 m), projection GDA_1994_Albers, converted to point data in decimal degrees.
C	ABS Census 2016, number of households per Statistical Area 1 (SA1).	Vector data at the smallest level of resolution provided by ABS.
D	ABS Statistical Area 4 (SA4) map for SE Australia.	Vector data used to select the relevant area for analysis in SE Australia and delimit map E.
E	Grid map of 0.2° cells for Australia intersected with map D to select the area of interest.	Grid created by overlaying a fishnet of 0.2° resolution on map D to create the final dataset for analysis and modelling. The full space comprised 2462 cells.

* Atlas of Living Australia occurrence download at https://biocache.ala.org.au/occurrences/search?q=lsid%3Aurn%3Alsid%3Abiodiversity.org.au%3Aafd.taxon%3A182e9eae-5358–4261–8a17-b123c1200c8d accessed on 25 January 2021.

2.3.1. Vespula germanica parameters

Parameters for the population dynamics of European wasps are available for New Zealand (Plunkett et al., 1989, Barlow et al., 1996, Beggs et al., 2008) and England (Archer, 1985) but not for Australia. Some parameters reported in the literature provide a starting point for calibrating our model, but differences between countries need to be considered. Notably, the maximum number of wasp nests per ha (κ_W) reported for beech forests in NZ (~12 nests per ha) is too high for Australian conditions (Crosland, 1991, Kasper, 2004, Tennant et al., 2011). There is also uncertainty regarding the number of years it takes for the population to reach saturation in the absence of control, which is determined by α_W for a given κ_W. Other important sources of uncertainty are the dispersal parameter (γ_W) and the detection probability parameter (δ_W). These four parameters were estimated through simulation using a genetic algorithm (GA) combined with the occurrence data from ALA. Wasp detection records in ALA start as early as 1960, with increasing reports since 2010 (Fig. 1).

To estimate likely values of uncertain parameters a likelihood function was created based on data from ALA, and the simulation model. The likelihood function minimised by the GA is:

$$f(u) = \omega_N \left(N_{obs} - \overline{N}_{pred}(u_i) \right)^2 + \omega_A \left(A_{obs} - \overline{A}_{pred}(u_i) \right)^2 \quad (15)$$

with $\omega_N + \omega_A = 1$, $0 \leq \omega_N \leq 1$, $0 \leq \omega_A \leq 1$

Where $u_i = [\alpha_i\ \kappa_i\ \gamma_i\ \delta_i]$ is the vector of parameter values representing chromosome i in the population of possible solutions, N_{obs} is the total number of cells in the cluster for which wasp presence has been reported in ALA, and A_{obs} is the area of the minimum convex hull enclosing all those infestations (the area invaded). The predicted variables $\overline{N}_{pred}$ and $\overline{A}_{pred}$ are the means of predicted number of cells and area invaded over the n_r stochastic runs of the model. The number of infestations and area invaded are weighed by ω_N and ω_A in the minimization. The weights were set at (0.5, 0.5) for this analysis.

The problem was solved using the Matlab *ga* function (Mathworks, 2020b), with a population of 50 individuals — 50 sets of parameter values (chromosomes) that evolve over time in a stochastic environment according to a given fitness function (15) . This process is analogous to that used by (Hester and Cacho, 2012) (See SM Section C for further details).

2.3.2. Biocontrol parameters

Parameters for the biocontrol agent would vary depending on the organism selected. Some parameter values for New Zealand exist for *S. v. vesparum* in the literature — for example, Barlow et al. (1996) estimated the winter mortality parameter (μ_B) at 0.85 and the carrying capacity parameter (κ_B) at 235 parasitoid cocoons per wasp nest.

Given the uncertainty in the values of biocontrol parameters, and lack of data for Australia, simulations were conducted using a factorial experiment with 4 factors × 3 levels, resulting in 81 parameter sets consisting of all combinations of $\alpha_B = (2, 3, 4)$; $\mu_B = (0.1, 0.3, 0.5)$; $\gamma_B = (1, 3, 5)$; $\rho_B = \varphi_B = (0.05, 0.1, 0.2)$. Each of these 81 parameters sets was used to run a 60-year simulation with 1000 stochastic iterations.

3. Results and discussion

3.1. Occurrence data and wasp population parameters

European Wasp occurrence reports in ALA remained relatively low from 1960 until the mid-1990s (Fig. 1A), with an average of 2 reports per year. From 1997 the number of reports started to increase at an increasing rate, to reach 191 reports in 2020. This has been accompanied by a growing spatial extent starting in Tasmania (1960) and spreading to Victoria (1982), New South Wales and Western Australia (2010), and South Australia (2011). We know that European wasps have been present in mainland Australia before their first reports in ALA (Spradbery and Maywald, 1992, Crosland 1991), but that is not relevant
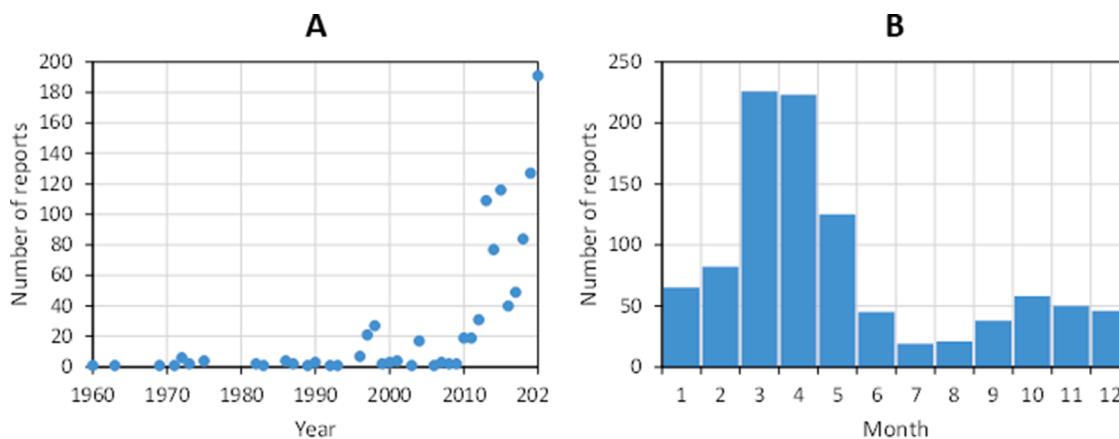
Fig. 1. European wasp occurrence reports in Atlas of Living Australia, 1960–2020, by year (A) and month (B).

for our purpose of estimating population parameters given the data available and the scale of the analysis. Increasing numbers of reports in ALA over time indicate growing wasp population densities, which increase the probability of contact with humans and therefore the probability that the encounter will be reported to ALA.

In terms of seasonality (Fig. 1B), reports tend to increase in late summer and early autumn (March and April), when the wasps are most active and populations are growing. The lowest number of reports occur in winter (June to August), when wasps are less active and outdoor human activity is reduced. These patterns are consistent with other studies. (Crosland 1991, Kasper et al., 2008).

The majority of reports (305) have occurred in urban residential areas (Table 3), followed by conservation areas (246), agriculture and forestry (142), and recreation areas (132). These are all areas where humans are likely to come into contact with wasps, and where wasps are likely to disrupt recreational and work activities.

We selected only observations from Eastern Australia for further analysis (Fig. 2). Visual inspection suggested that there are 4 different clusters, and this was confirmed by applying cluster analysis to the point data based on distance. These clusters were used to estimate parameter values for the wasp population using a GA as explained in the Methods section.

The parameter values estimated independently for each of the clusters were generally consistent (Table 4). Average values of α_W (growth rate) and κ_W (carrying capacity) were 3.69 (ranging from 3.48 to 3.88) and 1.28 (1.26–1.30) respectively. The dispersal parameter (γ_W) had an average value of 3.24 but with lower values for TAS and VIC (1.50 and 1.89) compared to NSW and SA (4.75 and 4.81). These differences reflect the temporal patterns of spread, which were slower in the former

Table 3
European wasp occurrence reports in Atlas of Living Australia*, 1960–2020, by land use estimated by overlaying maps A and B from Table 2. See SM Section B for details on the aggregation of ALUM codes into these seven categories.

Land use	Reports
Urban residential	305
Conservation and Natural Environments	246
Agriculture and Forestry	142
Recreation and culture + public services	132
Transport and communication	56
Rural residential	55
Other	47
Total	983

* Atlas of Living Australia occurrence download at https://biocache.ala.org.au/occurrences/search?q=lsid%3Aurn%3Alsid%3Abiodiversity.org.au%3Aafd.taxon%3A182e9eae-5358–4261–8a17-b123c1200c8d accessed on 25 January 2021.

clusters than in the latter ones. The detection parameter (δ_W) had an average value of 0.59, with a range of 0.52 in NSW to 0.63 in TAS. Now that plausible parameter values for the invasive wasp have been obtained, the focus can shift to feasibility of the biocontrol.

3.2. Biocontrol feasibility

The success of the biocontrol program hinges on two factors: (1) the feasibility that the agent will establish and spread; and (2) the effectiveness of the agent in suppressing growth and spread of wasp nests. Factor (1) is related to three biocontrol parameters: growth rate (α_B), winter mortality (μ_B) and spread rate (γ_B). Factor (2) is related to two biocontrol parameters: the reduction in wasp growth rate (ρ_B) and the winter mortality of wasp nests (ϕ_B) that are infested by the agent.

The relative rate of increase for a population, $R = B_{s,t+1}/B_{s,t}$, must be > 1 in order for the population to grow. Fig. 3A shows that, for this example, when $\alpha_B = 2$, winter mortality must be < 0.5 in order for the biocontrol population to establish and grow, given the presence of wasp nests. This is lower than the mortality of 0.85 estimated by Barlow et al. (1996) and so an important question is whether this rate may be lower in Australia given the dryer conditions compared to New Zealand. The curves in Fig. 3A and 3B will shift as the value of the fixed parameter (α or μ in panels A and B respectively) changes, but the bottom line is that if $R < 1$ for the biocontrol, there is no need to undertake further evaluation, as the organism will be unable to establish a viable population. In this case the main question is whether there are other suitable species for biocontrol with high values of R.

Regarding the dispersal parameter, Barlow et al. (1998) estimated a velocity of spread of 1.15 to 1.6 km per year in New Zealand, which is equivalent to γ_B values of ~0.4–0.6 (see SM Section A). These may be too low to keep up with the spread of the wasp, given the average γ_W value of 3.24 in Table 4, and this has implications for the spatial pattern of biocontrol release.

The effectiveness of the biocontrol in the model occurs through ρ_B and φ_B. These are uncertain parameters that have not been measured for Australian conditions – while some Australian release sites of *S. v. vesparum* were monitored (G. Lefoe, pers. comm) there was no evidence in subsequent years that the parasitoid established at any of those sites (Lefoe et al., 2001). However, using the model we can explore combinations of parameter values that would make the program feasible in the sense of *classical* biological control, where the biocontrol agent becomes established and maintains the population of the pest at a low level (Hajek et al., 2016).

The model is a simplified version of the life cycle and does not represent different types of cocoons explicitly. The density of biocontrol adults in spring is represented by B_s; this variable influences (negatively) the growth rate of the European wasp population in spring and summer.
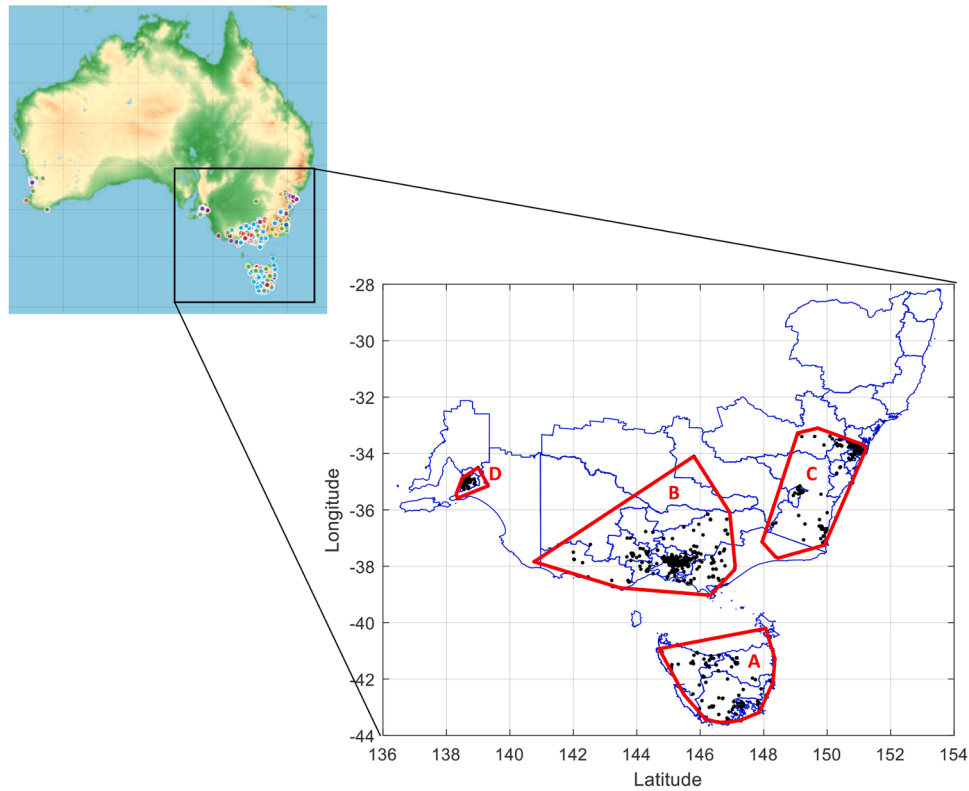
Fig. 2. European wasp reports downloaded from Atlas of Living Australia (black points) overlaid on the ABS SA4 map for the area of interest (blue lines).and the four clusters identified (A) Tasmania, (B) Victoria, (C) New South Wales, (D) South Australia.

Table 4

Parameter estimates for European wasp growth (α_W), carrying capacity (κ_W), spread rate (γ_W) and detection probability (δ_W), obtained by running the population model within a genetic algorithm, for clusters identified in Fig. 1, standard errors are shown in brackets under each mean. There were no differences in the estimated means of parameters α_W, κ_W and δ_W ($p > 0.1$), whereas the estimated means of γ_W were significantly different for all pair-wise comparisons between clusters ($p < 0.01$).

Cluster	State	Mean parameter estimate			
		α_W	κ_W	γ_W	δ_W
A	TAS	3.61	1.27	1.50	0.63
		(0.20)	(0.10)	(0.00)	(0.05)
B	VIC	3.79	1.30	1.89	0.61
		(0.18)	(0.12)	(0.00)	(0.07)
C	NSW	3.48	1.26	4.75	0.52
		(0.22)	(0.09)	(0.01)	(0.05)
D	SA	3.88	1.29	4.81	0.60
		(0.22)	(0.10)	(0.01)	(0.06)
Mean		3.69	1.28	3.24	0.59

The density of biocontrol cocoons in *V. germanica* nests at the end of autumn is B_a; this variable influences the mortality of wasp nests during winter. In this way we can represent two different mechanisms for the effect of the biocontrol on the pest: one on the mortality of wasp nests (given by φ_B in Eqs. (2) and (6)), and the other on the rate at which new queens establish new nests during spring and summer (given by ρ_B in Eqs. (1) and (5)). We tested different options and identified sets of parameter values that would make the biocontrol program feasible (Fig. 4). In all phase diagrams the system starts on the top left (high wasp density - low biocontrol density) and moves down and to the right towards some sort of dynamic equilibrium. All four cases in Fig. 4 are feasible in the classical biological control sense.

The effectiveness parameters interact with growth and mortality parameters of the pest to result in different population patterns through time (Fig. 4). In all cases there is a cyclical behaviour in the population densities of both species as expected, but in some cases the system settles into an equilibrium point over time. At high growth and mortality rates, both the frequency and amplitude of the cycle are higher (curves a and b) than at the corresponding low growth and mortality rates (curves c and d). It is interesting that relative high effectiveness ($\rho_B=\varphi_B= 0.03$) increases the fluctuations in both wasp and biocontrol populations (curves b and d) compared to the case of low effectiveness (curves a and c). In case b, the biocontrol grows fast and is highly effective, causing the wasp population to collapse, leading to a collapse of the biocontrol as less wasp nests become available, which in turn allows the wasp population to increase, and so on in a cyclical equilibrium where wasp populations can become as high as 0.7 nests per km^2 in some years.

The cases we are interested in are those that tend towards some sort of equilibrium between the two species, with wasp density maintained at a relatively low level. These are the cases for which classical biological control can succeed in the long term. Our modelling approach allows us to screen alternatives before considering the costs and benefits of the program. At this stage, scientists may be able to assess whether it is likely that the biocontrol agent will reach the required levels of growth, mortality and pest suppression to make the program feasible, perhaps through additional research targeted at measuring the most uncertain parameters.

3.3. Simulation results and decision analysis

Above we have seen conditions for feasibility of the biocontrol program for a given site, without considering the spatial distribution of the invasion as it progresses through time. Once we introduce dispersal in the simulations, we need to track the wasp and biocontrol populations in space as well as in time. This is done through matrices **W** and **B** of dimensions $n \times T$, (see section 2.2), where each of the n rows represents a
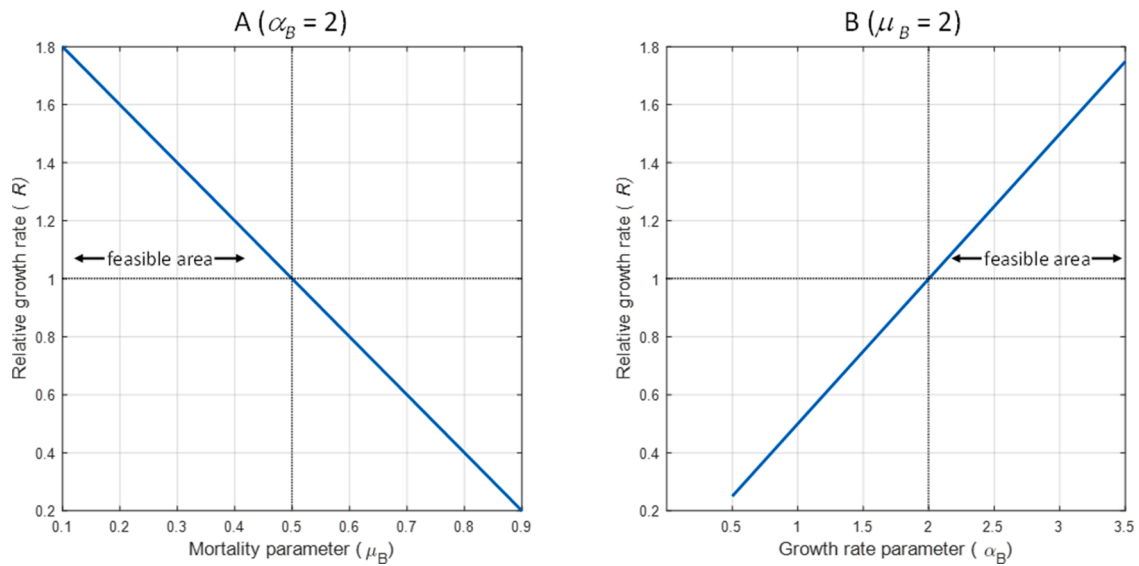
Fig. 3. Conditions for feasibility of the biocontrol program based on growth and mortality parameters. These curves were derived numerically as explained in SM Section D.
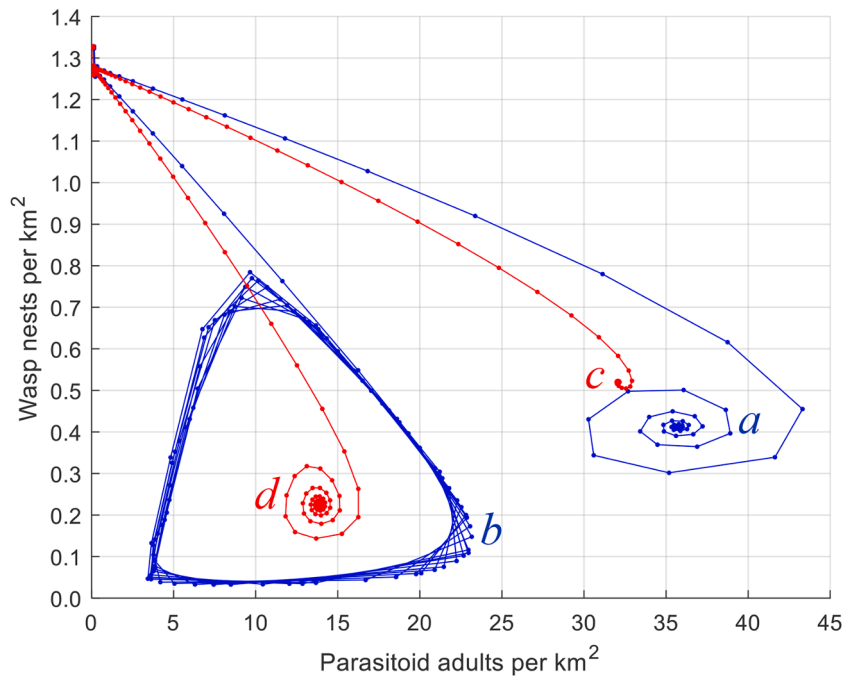

Fig. 4. Phase diagrams for selected combinations of biocontrol parameters; curve *a*: $\alpha_B = 3$, $\mu_B = 0.5$, $\rho_B = \varphi_B = 0.01$; curve *b*: $\alpha_B = 3$, $\mu_B = 0.5$, $\rho_B = \varphi_B = 0.03$; curve *c*: $\alpha_B = 2$, $\mu_B = 0.4$, $\rho_B = \varphi_B = 0.01$; curve *d*: $\alpha_B = 2$, $\mu_B = 0.4$, $\rho_B = \varphi_B = 0.03$. The wasp parameters were set at the mean values from Table 4.

site on the map and the columns represent time periods (1,…,*T*).

We selected clusters, B (VIC) and C (NSW) from Table 4, for further analysis. This provides an interesting comparison between two sites that have similar growth parameters ($\alpha_W = 3.79$ and 3.48, $\kappa_W = 1.30$ and 1.26) but differ in terms of dispersal parameters ($\gamma_W = 1.89$ and 4.75).

The areas of interest were selected by finding the minimum convex hull of clusters B and C in Fig. 2 and adding a buffer of 0.5°. The ALA reports were overlaid on the grid map (map E in Table 2) to calculate the number of reports per cell (Fig. 5). Each cell (site) on the map for the given cluster is represented by one row of the state matrices **W** and **B**.

The number of sites (*n*) using this selection method were 658 for VIC (244,681 km²) and 389 sites for NSW (144,493 km²). Not all sites have the same area because of truncation of cells along the coastline. The

spread simulations were conducted on this discrete representation of space (Fig. 5), using the centroids of cells to calculate the distance matrix **D** of dimensions $n \times n$ with elements d_{ij} as in Eq. (9).

Several combinations of the two decision variables associated with the biocontrol release x_p (intensity of inoculation per site) and x_c (spatial coverage of the release) were simulated. Fig. 6. shows phase diagrams for a selection of those simulations. Amongst the 81 parameter sets tested, 15% of simulations resulted in failure of the biocontrol with (x_p, x_c) = (10, 20), and 35% failed with (x_p, x_c) = (50,1). This suggests that the low biocontrol release coverage in the second case increases the probability of failure for any set of biocontrol parameter values. For cases that led to establishment of the biocontrol, the final density of biocontrol agents tended to be higher in NSW than in VIC (notice the
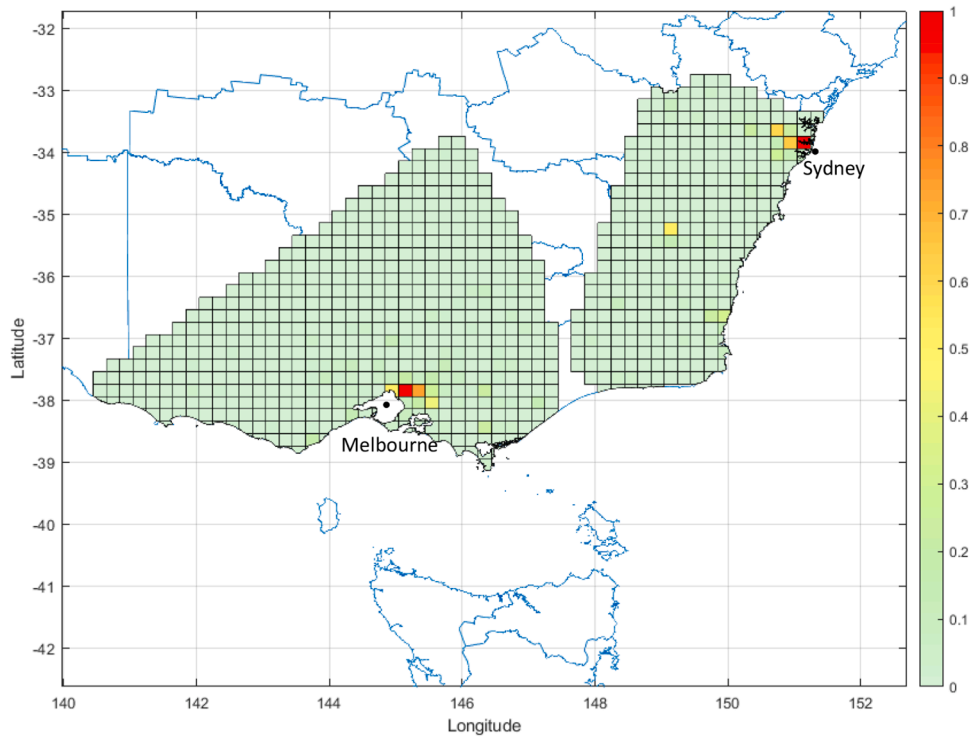
Fig. 5. The two clusters selected for further analysis mapped as grids of shaded cells (0.2° per side), VIC on the left and NSW on the right, colours represent the number of European wasps reports in the ALA database (1960–2020) expressed as a proportion of the maximum in the corresponding cluster.
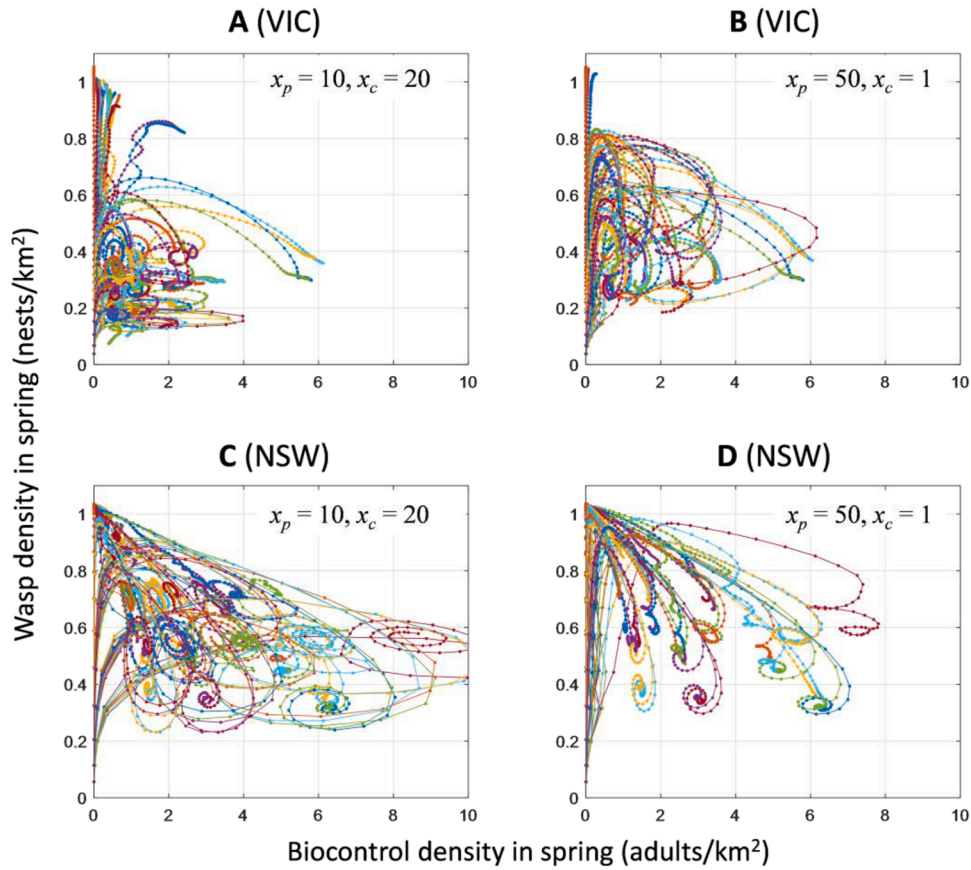

Fig. 6. Phase diagrams for two clusters (VIC and NSW) using 81 biocontrol parameter sets (coloured curves) and two different biocontrol release strategies: low x_p, high x_c (A and C) and high x_p, low x_c (B and D).

higher density of points towards the right of the plots in Figs. 6C and D compared to A and B). The 95th percentiles of final biocontrol density were 4.5 adults km^{-2} in VIC and 6.2 adults km^{-2} in NSW (see SM, Section D for details).

There are interesting differences between cases in the phase diagrams (Fig. 6). Comparing the top panel (VIC cluster) against the bottom panel (NSW cluster) and focusing on the best parameter combinations (those with final values towards the bottom of each plot), the mean state trajectories tend to a long-term equilibrium of ~0.24 wasp nests per km^2 in VIC and ~0.34 wasp nests per km^2 in NSW. The equilibrium density of the biocontrol also tends to be higher in NSW as seen above. Both clusters have similar wasp growth parameters (see Table 4) but very different dispersal parameters, γ_W in NSW is more than double the value in VIC (4.75 vs 1.89). This is reflected in wider cycles in the approach to equilibrium for NSW (Figs. 6C and 6D) compared to VIC (Figs. 6A and 6B), as wasp invasions can move longer distances to new sites.

Comparing the left panel to the right panel of Fig. 6, we have two extreme cases. With $x_p = 10$ and $x_c = 20$ (Figs. 6A and 6C), the biocontrol release covers a larger area (the top 20 percent of invaded sites) but at low intensity per site (only 10 percent of wasp nests are targeted in each site). With $x_p = 50$ and $x_c = 1$ (Figs. 6B and 6D), we have the opposite situation, where the biocontrol release has lower coverage (only the top 1 percent of invaded sites) but at high intensity per site (with 50 percent of wasp nests targeted in each site). These differences in release strategy affect the actual pattern of approach to equilibrium, but have a minor effect on the final densities of wasps and biocontrol for the best parameter sets.

Results presented so far are average values for a whole cluster of n sites, and the overall patterns shown above are the results of aggregate trajectories, ignoring spatial variation. One of the important aspects of the model is the assumption that nests that are detected are destroyed (see Eqs. (12) to (14)). The probability of detection depends on the density of wasp nests and the density of humans in a given site, and this leads to spatial variation in wasp density as the biocontrol becomes established towards an equilibrium. The ultimate effect is that there is a strong negative relationship between the density of households and final density of wasp nests in a simulation (Fig. 7).

In the absence of biocontrol (the counterfactual simulation), there is a pronounced decrease in the final density of wasp nests as household density on a site increases, starting from a density of ~0.15 households per km^2 (equivalent to a log value of −1.9 on the x axes of Fig. 7). To the

left of this point the effect of household density is minor. Once we introduce biocontrol, the pattern still exists but the final wasp densities are much lower: ~0.20 and ~0.35 wasp nests per km^2 for VIC (Fig. 7A) and NSW (Fig. 7B) respectively at low household densities, compared to ~1.2 wasps nests per km^2 in the counterfactual. This illustrates the effectiveness of the biocontrol, maintaining wasp density at between 20 and 35 percent of the no-biocontrol option. The question of whether this is a worthwhile investment depends on the cost of the biocontrol program compared with the avoided damages to households, businesses, government and environment. There may also be alternative biocontrol release allocations in space that account for household density, that will result in lower wasp densities in equilibrium.

The assumption that all wasp nests detected are destroyed is applied to the whole cluster, but perhaps there are spatial variations. Considering that a single European wasp nest can have tens of thousands of workers (Kasper et al., 2008) foraging for sugar and protein in late summer and early autumn, combined with their aggressive behaviour and tendency to swarm around food sources, means that this assumption is realistic at least in urban areas, where families and pets may be threatened by wasps. This assumption is also realistic for other sites where European wasps have been reported (Table 3) such as agriculture and forestry, recreation and culture + public services, transport and communication. In these cases local governments or businesses may be called to destroy wasp nests due to threats to workers and visitors. However, this assumption may be less realistic for conservation and natural environments, except for the case of visitor centres and camping areas that are maintained by rangers, as casual visitors to national parks would not attempt to destroy wasp nests. This is something to consider when planning the spatial distribution of biocontrol releases and monitoring.

The best results for each release strategy (as plotted in Fig. 7) are obtained when the dispersal parameter for the biocontrol (γ_B) is high . This highlights the importance of broad spatial coverage of the biocontrol for a successful program. In terms of biocontrol effectiveness parameters (ρ_B and φ_B), the best performers were 0.1 to 0.2 in VIC and 0.05 in NSW. An important question is whether these levels of effectiveness are realistic and, if not, whether other features of the biocontrol and/or the release strategy may make up for lower effectiveness. Alternatively, a combination of biocontrol agents attacking the wasp on several fronts may be a better option.
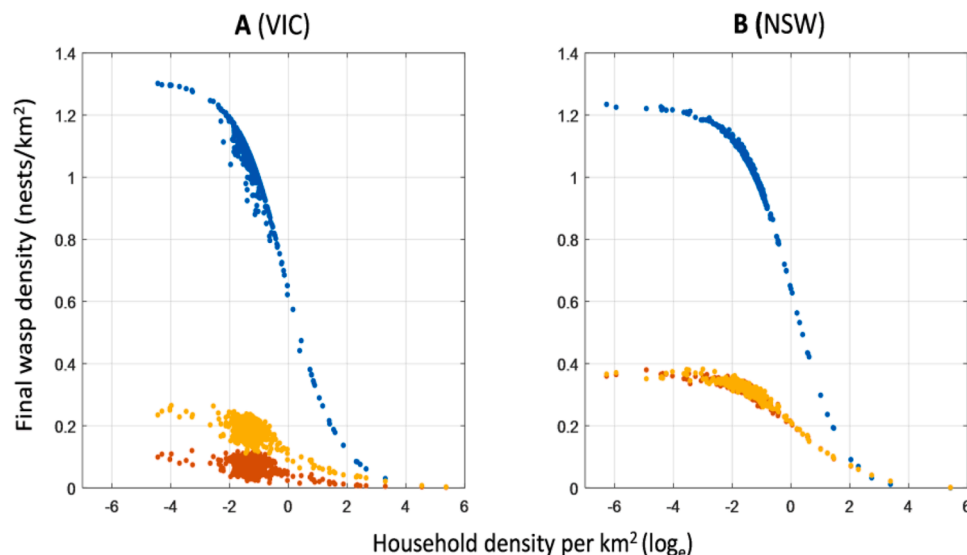

Fig. 7. Relationship between household density and mean final number of wasp nests (mean wasp nest density for the last five years of the simulation) under the no-biocontrol counterfactual (blue dots), compared to best performing parameter sets for selected simulation runs: $x_p = 0.1$, $x_c = 80$ (red dots); $x_p = 0.5$, $x_c = 99$ (yellow dots), each dot represents a site on the map for the respective cluster.

3.4. Limitations and implications of findings

We have combined a number of data sources to develop and calibrate a model for an invasive wasp and a biocontrol agent. Despite the lack of data for the specific species involved, our spatio-temporal model is based on conventional equations of population dynamics and spread, so it is on solid ground in that regard. We used a parasitoid that invades wasp nests as the agent for this example, but abstracted away from the specific species by solving the model for 81 parameter sets using a factorial experiment. We were able to show the conditions that would make biological control technically feasible — this is the necessary condition for economic feasibility. If the biocontrol is not technically feasible, then an economic evaluation is not needed. In this way, the model could help agencies avoid the time and expense of full economic evaluations for projects that are technically doomed.

In the model, the biocontrol agent supresses the wasp population in two ways: by reducing wasp growth rate, and by increasing the winter mortality of wasp nests. As such the model is flexible and can be applied to different case studies — the two parameters involved can be varied to represent any number of biocontrol species, as well as combinations of species that may act at different stages in the life cycle of the wasp. The main challenge in applying the model to other cases is the effort required for calibration. Public databases such as the ABS Census and the Atlas of Living Australia provide information at a broad scale, which helps ground the model in reality, but they are no substitute for field and laboratory trials to estimate biological parameters, which would reduce the uncertainty attached to parameter values.

The model is discrete in time and space. The annual time increments fit well with the life cycles of the species involved, but the spatial scale is arbitrary. We used a grid of $0.2°$ as a compromise between spatial resolution and computational feasibility. While increasing the spatial resolution could improve spread simulation, it is demanding in terms of memory and processing power required — the size of the distance matrix used to simulate spread increases quadratically with the number of cells (n) on the grid. This, combined with multiple runs required for stochastic simulations, limits either the scale or the resolution of the model, depending on availability of memory and processing power. This is a limitation especially when using a GA to estimate parameter values from spatio-temporal data. A GA is computationally expensive because of the large number of function evaluations required, but is also well suited for parallel processing when available.

The spatial scales we used are fairly broad ($\sim$244,000 km^2 for VIC and $\sim$144,000 km^2 for NSW), but in some cases finer scales would be preferable, such as for local government areas that may have more detailed data on wasp nests detected and destroyed. In such cases the size of the cells in the model would be reduced so that spread can be followed at the suburb scale, for example.

Spatial variation in human population was an important driver in the model (see Fig. 7), through the probability that a nest will be detected and destroyed. Spatial variation can also occur in habitat suitability — the likelihood that a queen arriving at a site will become established is based on food availability and other factors. In this case study we implicitly assumed uniform habitat suitability, with value of 1 for all cells on the map, but this can be changed spatially in the model when data are available.

Finally, our simulations for decision analysis started with cocoons of the biocontrol agent released across space depending on two decision variables: the intensity of inoculation per site (x_p) and the spatial coverage of the release (x_c). All the cocoons released are implicitly assumed to become established, but in reality there would be a proportion of failures in the release. This does not affect the application of the model, but it does affect the cost of the biocontrol program simulated. Any economic evaluation would need to account for the probability that agents fail to establish as well as for the possibility that it may take several years and repeat releases to reach the biocontrol density simulated in year 1. Related to this, the release strategy is based on

knowledge of the location and density of wasp nests. Uncertainty in these variables will also affect the cost of the release, as a poor match between wasp presence and biocontrol release will increase the failure rate.

4. Conclusion

We have addressed the question of technical feasibility of a biocontrol program based on growth, mortality and dispersal parameters of the target species and the biocontrol agent. The spatio-temporal model developed for this purpose is on solid ground in its representation of population dynamics and the interaction between an invasive insect and a biocontrol agent. The Ricker equations used are standard, and realistic ranges of model parameters are known from the literature.

Using the model and data available from public sources, we identified parameter sets that are feasible in the classical biocontrol sense, where the biocontrol agent becomes established and maintains the pest population at a low-level equilibrium. Phase diagrams of the two populations over time were found to be useful visual tools to identify feasible parameter sets.

Application of the model to the European wasp in Australia, a damaging invasive insect in that country, produced some useful insights for the specific case study and revealed the need for research to identify biocontrol species with the 'right' combination of parameters. Technical feasibility is a necessary condition for economic feasibility, and pre-screening candidates through modelling can save funds by excluding species with low feasibility from further evaluation.

CRediT authorship contribution statement

Oscar J. Cacho: Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing. **Susan M. Hester:** Data curation, Writing – original draft, Writing – review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.109939.

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