

Biological control of the invasive wasp *Vespula germanica* in Australia: Assessing socio-economic feasibility

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ABSTRACT

Invasive species cause significant damage to economies, human health, biodiversity and society in general. Social insects are among the most successful invaders, often becoming major pests when they establish outside their native range. Once established they can be difficult to eradicate or contain, and classical biological control is usually the only feasible management option.

Successful classical biological control programs must be both technically and economically feasible. A technically feasible program — where a biological control agent establishes, spreads and suppresses the growth and spread of the pest — is a necessary pre-requisite for economic feasibility, where benefits and costs of a biological control program are subsequently assessed. We investigate whether the highly invasive eusocial wasp *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae) could be a candidate for a renewed biological control management program in Australia, where it established almost 60 years ago.

The potential impacts of *V. germanica* on horticulture, apiculture, tourism, outdoor social activities, and biodiversity are estimated to be AUD 2.6 billion over 50 years, should *V. germanica* continue to spread unhindered. We found median benefits of AUD145 million to AUD385 million, depending on effectiveness and growth rates of the biocontrol, with non-market benefits exceeding market benefits by 50%.

1. Introduction

Invasive species cause significant damage to economies, human health, and society in general (Marbuah et al., 2014; Pyšek et al., 2020; Diagne et al., 2021), and they also are a leading cause of biodiversity loss globally (Bellard et al., 2016; Mollot et al., 2017; IPBES, 2023). Social insects – wasps, termites, bees and ants – are among the most successful invaders (Lowe et al., 2004), becoming major pests when they establish outside their native ranges (Moller, 1996; Eyer and Vargo, 2021). Among this group, *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae), also known as the European wasp, is a particularly damaging insect pest. *V. germanica* is native to Europe, Northern Africa, and temperate Asia, and introduced in North America, Chile, Argentina, Iceland, Ascension Island, South Africa, Australia and New Zealand

(Lester and Beggs, 2019). It can tolerate or adapt 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.

Vespula germanica established almost 60 years ago in Australia. Local extirpation programs were typically initiated upon first discovery of the pest in a region, but were subsequently abandoned as the pest became widespread (Crosland, 1991). Presently, in the eastern states of Australia, control of *V. germanica* is a private pest management issue.

The damage caused by *V. germanica* in the south-eastern part of Australia has not been calculated, although is likely to be substantial given the lack of any sustained and widespread control strategies during this time. An ongoing eradication program in Western Australia costs \$250,000 per year and is estimated to be preventing annual damages to

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pollination, apiculture, viticulture and households of at least \$3.9 million for the period 2010–2040 (Cook, 2019). In Victoria, by 1997, the annual economic and health impacts of *V. germanica* were conservatively estimated at more than AUD\$2million at that time (Honan 1997 cited in Canyon et al., 2011). In New Zealand, the total quantifiable annual impact of *Vespa* wasps on primary industries, human health, traffic accidents, and local governments was estimated at NZD133 million, including an option value for apiculture development of NZD58 million (MacIntyre and Hellstrom, 2015).

Established pests such as *V. germanica* are often overlooked as candidates for coordinated management programs (eradication and/or containment) because the use of traditional control techniques over very large areas becomes uneconomic. Classical biological control (Hajek, 2004; Van Driesche et al., 2008; Stenberg et al., 2021), where the goal is permanent establishment of one or more introduced specialised natural enemies (biological control agents) to control the pest rather than eradicate it, is usually the only economically feasible option for managing established, widespread exotic pests.

In New Zealand, biological control of *V. germanica* was attempted in 1980 when a biological control natural enemy, the parasitoid *Spheco-phaga vesparum vesparum* (Curtis) (Hymenoptera: Ichneumonidae) was collected from Europe and imported for host range testing and subsequent mass rearing (Donovan and Read, 1987). Field releases of *S. v. vesparum* began in 1987 (via parasitoid cocoons placed next to known wasp nests) and continued for at least four years (Read et al., 1990; Moller et al., 1991). Adults emerge from the cocoons, enter the wasp nest, and parasitise the developing larvae. Monitoring at release sites, however, indicated there were difficulties establishing the agent (Moller et al., 1991). In conjunction with the New Zealand biological control program, *S. v. vesparum* was imported into Australia, approved for release following mandatory host-specificity testing (Field and Darby, 1991), mass reared and subsequently released (Darby and McLaren, 1993; Lefoe et al., 2001). However, post release monitoring was not well-funded, and as a result no evidence of *S. v. vesparum* establishment has been documented (Ede et al., 2014).

The poor performance of the biological control agent *S. v. vesparum* in controlling *V. germanica* in New Zealand is thought to be possibly due to a genetic bottleneck because all releases were derived from a single parthenogenic female parasitoid (Beggs et al., 2008; Ward, 2014). It is possible that sourcing different genetic strains of parasitoids would see an improvement in agent performance, but the potential range for improvement is unknown. The availability of a biological control agent that has already undergone risk assessment and been approved for introduction (Field and Darby, 1991), means that new introductions could be conducted at relatively low cost, assuming the agent has been screened appropriately to avoid negative impacts of agent introduction (Barratt et al., 2010). However, as Australia has no native Vespinae, the likelihood of *S. v. vesparum* posing a threat to native wasp species is considered low (Field and Darby, 1991). The question then is whether the potential improvement in the performance of the biological control agent in reducing in *V. germanica* abundance is likely to be large enough to produce positive net benefits to industry, community and the environment.

We turn the question on its head and explore the conditions that would make this biological control program successful. We use a simulation model based on the population dynamics of the wasp and the biological control agent (Cacho and Hester, 2022, 2023), combined with spatial data on industry, environment, human populations and pest detections. The combined model provides flexibility in the analysis of management scenarios under uncertainty, allowing us to determine the conditions under which biological control is technically and economically feasible with high probability. The benefits of biological control are the reduced nuisance value to households and recreation, and reduced impacts of *V. germanica* on pollination services, apiculture, viticulture (Cook, 2019), and threats to native biodiversity in natural environments (Potter-Craven et al., 2018) that occur when *V. germanica* populations

are suppressed.

The approach and findings of this study are applicable beyond the specific case study presented. In fact, determining the conditions that make a biological control agent successful, is a useful first step in planning any biological control program.

2. Material and methods

The conceptual diagram in Fig. 1 represents the decision analysis model designed to analyse the costs and benefits of *V. germanica* control in south-eastern Australia. Central to the model is the population dynamics of the pest and the biological control agent. The population dynamics model accounts for growth and spread of the insect pest and the biological control agent as well as their interaction. This interaction will ultimately determine the likelihood that management of the pest through biological control will succeed (see Cacho and Hester, 2022 and 2023, for details). For generality, we abstract away from details of the particular biological control species and focus on the modes of action, through which the biological control agent suppresses reproduction and spread of European wasp nests (see below).

On the output side of the model (top of Fig. 1) are the damages, divided into impacts that are readily monetised (market damages) and those that are not (non-market damages). Market damages of *V. germanica* include impacts on pollination, honey production and horticulture, whereas non-market damages include impacts on nature conservation, use of public places for recreation and sporting activities, and damages to households that go beyond market costs. To estimate these damages, and to calibrate the population dynamics model, spatial information was required on the value of agricultural production; land use patterns; *V. germanica* habitat suitability; *V. germanica* detections over time; and human population density (left section of Fig. 1). The required data were obtained from different sources and they were aggregated and converted as needed to obtain a spatial grid covering the area of interest in south-east Australia. Damages were converted to dollar values through market and non-market valuation. Benefit-transfer was used to calculate non-market impacts. No benefits of *V. germanica* for Australia have been reported in the literature.

The situation where no management occurs is the worst-case-scenario for *V. germanica* impacts over time. This is the baseline scenario and shows the dollar value of damages against which all other management outcomes are compared. The benefits of biological control are the damages that are avoided when *V. germanica* abundance is reduced. Agent selection, testing, importation, rearing and releasing are the main component of program costs (bottom right, Fig. 1).

The marginal benefits of introducing the biological control agent (in present value terms) are estimated as the difference between the baseline ‘no control’ simulation and various technically feasible ‘control’ scenarios (right section of Fig. 1). The scenarios selected reflect different sets of biological control parameter values and biological control release strategy options. All biological control parameter sets tested were technically feasible in the sense that they would become established and reduce *V. germanica* populations through nest mortality and reduced *V. germanica* reproductive output.

2.1. Lifecycles of pest and biological control

Vespa germanica colonies are highly eusocial, consisting of reproductive females (gynes and queens), reproductive males (drones) and sterile females (workers). The normal colony lifecycle is annual, proceeding as follows: (1) new queens and males are produced within nests each autumn; (2) the new queens disperse to mate and subsequently hibernate in sheltered areas during winter; (3) reproductive queens emerge in spring to found new colonies; (4) colonies (or nests) grow rapidly over summer, often consisting of several thousand workers at their peak (Ward et al., 2002; Kasper et al., 2008; Lester and Beggs, 2019). As new queens disperse in early autumn, the old queen and

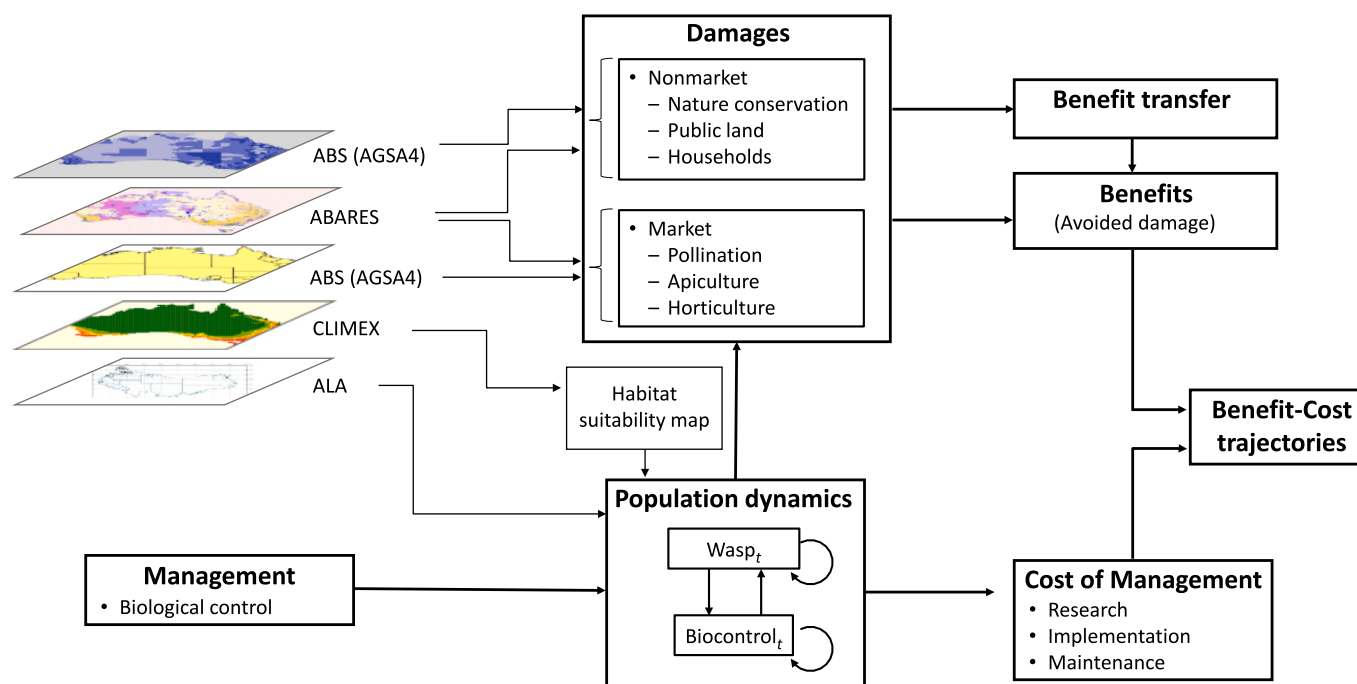


Fig. 1. Conceptual diagram of the decision analysis approach showing the data sources and the main components of the model.

colony typically die off, but nest construction can continue throughout the year in locations experiencing mild winters (Spradbery and Maywald, 1992; Widmer et al., 1995; Kasper, 2004).

As mentioned earlier, we try to abstract away from any given biological control species details, and focus on modes of action. However, the case of the parasitoid *S. v. vesparum* provides a good base from which to start the search for feasible sets of parameters for growth and spread of the putative biological control agent. Adults of the parasitoid lay eggs in *V. germanica* nests and emerging larvae feed on wasp pupae, this reduces *V. germanica* population growth, sometimes killing the full nest depending on biological control effectiveness parameters. Chemical deception, repellency, partial chemical mimicry, and behavioural adaptations have been proposed as strategies used by *Sphecophaga* spp. to evade detection within nests (Donovan, 1991; Dubiner et al., 2020; Oi et al., 2020). The biological control agent can also reduce reproductive output of *V. germanica* by parasitising and killing immature queens before they disperse to establish new colonies in spring (Donovan and Read, 1987).

2.2. Estimating impacts

In regions where it has invaded, *V. germanica* can have significant negative impacts on human activity, the environment and the economy. This analysis considers the damage caused by *V. germanica* via six specific types of damage: to public areas; households; nature conservation; honey production; pollination; and fruit (Table 1).

Impacts of *V. germanica* on human activity occur in public areas where they disrupt outdoor activities, as well as in individual households where they attack humans and pets, sometimes threatening life. Environmental impacts occur through competition with native species for space and food sources, as well as through direct attack and predation. Impacts on primary industries include losses to beekeeping, and to horticultural industries through their impact on pollination, honey production and damage to ripened soft fruits, all of which were considered in this study. Other impacts on workers and livestock through stinging were not considered due to difficulty obtaining data.

2.2.1. Spatial datasets used

Five spatial datasets were used to calibrate the model and run simulations:

1. Map of *V. germanica* habitat suitability (HS) in Australia based on CLIMEX (Sutherst and Maywald, 1985; Kriticos et al., 2015) simulations from de Villiers et al. (2017) at a resolution of 0.5 degrees. The Habitat Suitability map (HS) consists of 522 cells where the modelled Ecoclimatic Index (EI) contained a positive value ≥ 1 (all cells with EI = 0 were excluded).
2. National map of land uses and agricultural commodities from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES).¹ The number of agricultural commodities in this dataset is 27.
3. Maps of agricultural commodities (2017–18) at SA4 level from the Australian Bureau of Statistics (ABS) for value of production, area planted and yields.^{2,3}
4. Number of households and income at SA1 level from the ABS 2016 Census Community Package.⁴
5. Atlas of Living Australia (ALA) occurrence download at <https://biocache.ala.org.au/occurrences/search?q=qid:1590909475236> accessed on Sun May 31 17:18:47 AEST 2020.

The unit of analysis is determined by the CLIMEX HS map and a series of matrix manipulations were used to convert the original source

¹ ABARES (2016). Land use of Australia 2010–11, Available from <https://www.agriculture.gov.au/abares/aclump/land-use/land-use-of-australia-2010-11>

² ABS (2019). 7503.0 - Value of Agricultural Commodities Produced, Australia, 2017–18. Available from <https://www.abs.gov.au/AUSSTATS/abs@.nsf/DetailsPage/7503.02017-18?OpenDocument>

³ ABS (2019). 7121.0 - Agricultural Commodities, Australia, 2017–18; Available from <https://www.abs.gov.au/AUSSTATS/abs@.nsf/DetailsPage/7121.02017-18?OpenDocument>

⁴ ABS (2017) 2016 Census Community Profiles. Available from https://quicksats.censusdata.abs.gov.au/census_services/getproduct/census/2016/communityprofile/036?opendocument

Table 1
Impacts of *V. germanica* considered in this study.

Impact	Description
Impacts on primary industries	
Honey production	European wasps cause significant losses to apiculture by attacking bees and bee hives – the wasps kill honey bees and their larvae for protein, rob hives of honey and spread bee diseases (Clapperton et al., 1989; Widmer et al., 1995). While strong bee colonies are able to repel attacks, significant losses may still occur from sustained attack (Goodman, 2014). Defending hives against wasps reduces bee foraging time.
Pollination damage	European wasps affect pollinators through competition for resources and predation. In depleting honey-bee colonies, wasps impact on pollinator-reliant crops. Crops experiencing reduced yield because of reduced pollination, and their level of pollinator reliance are given in Table 2 (Supplementary Material).
Fruit damage	Social wasps opportunistically exploit any available source of concentrated sugar, including the sweet liquids from fruits, and use these as an energy source for adult wasps and developing young (Evans and Eberhard, 1970 cited in Richter, 2000). European wasps are known to cause yield losses by hollowing out fruit (Goodall & Smith as cited in Cook, 2019) and damage wine grapes by introducing diseases (Lester and Beggs, 2019). In Australia, wine grapes and strawberries have reportedly been damaged by European wasps, with yield losses of 10–25% being reported.
Impacts on human activity	
Public area damage	European wasps are a major nuisance because of their synanthropic behaviour – they aggressively forage for human food (sugar and protein), disrupting outdoor dining and recreational activities, sporting activities and use of public places in general.
Household damage	European wasps are more aggressive than bees and will attack when their nests are disturbed and they are capable of inflicting multiple painful stings on humans and pets. Unlike bees, European wasps do not die after stinging. Wasp stings may cause allergic reactions, and a sustained attack from a large swarm can result in life-threatening envenomation (McGain et al., 2000). While relatively rare, deaths have occurred as a result of European wasp stings, and there are many records of stings requiring medical attention and even hospitalisation (Widmer et al., 1995; Levick et al., 1997). People have to avoid outdoor areas where wasps might live.
Environmental Impacts	
Nature conservation damage	European wasps have a broad, omnivorous and opportunistic diet that includes honeydew, nectar, insect prey, vertebrates and carrion (Lester and Beggs, 2019; Spencer et al., 2020). As a result, they may have disruptive impacts on a range of ecosystem process, including reducing the numbers of some arthropods (Sackmann et al., 2000; Kasper, 2004). In New Zealand the pest is known to reduce faunal diversity as a result of direct competition for food, particularly honeydew (Elliott et al., 2010), predation on other insects (Harris, 1991) and even nestling birds (Moller, 1990). There may also be adverse impacts on local flora due to wasp predation on insects responsible for pollination and other forms of nutrient transfer (Fordham, 1991). There is little information about environmental impacts of European wasps in Australia, although local reductions in arthropods have been reported in Tasmania (Bashford, 2001; Potter-Craven et al., 2018).

data to a final dataset where each row represents a cell on the map and columns represent the different variables listed above (see Supplementary Material).

2.2.2. Damages

The impacts of *V. germanica* considered in this study are detailed in Table 1. The market damages considered—to pollination, apiculture and horticulture—are all related to agriculture. Market damages were estimated spatially based on data from ABARES and ABS (maps 2 and 3 in Section 2.2.1). More details are available in the Supplementary Material.

Non-market damages—to nature conservation, public land and households—were estimated using benefit transfer (BT), based on a study by Rolfe and Windle (2014). Benefit transfer incorporates a set of methods for applying previously estimated values from a ‘study site’ to a ‘policy site’ of interest. The ‘policy site’ refers to the area and environment affected by the incursion where no values are currently available (Tait and Rutherford, 2018). Values from the study site are adjusted for differences in income, prices, demographic variables, and scale. The data used in the benefit transfer come from ABS Census maps as illustrated in Fig. 1. The application of economic non-market valuation methods to value public preferences for infestation control benefits, such as environmental outcomes, is likely to be incomplete because these methods do not typically capture the full range of ecological, social, and cultural impacts. Moreover, valuation exercises can overlook non-quantifiable benefits and intrinsic values that people place on the environment, leading to an underestimation of value generated by infestation control efforts. While the Benefit Transfer valuation exercise here does not attempt to be exhaustive, our intent is to identify whether the extent of impacts that we do value exceeds the cost of control efforts, which results indicate is the case.

Rolfe and Windle (2014) conducted a choice experiment (CE) survey estimating willingness to pay (WTP) for reductions in impacts of *Solenopsis invicta* Buren (Hymenoptera: Formicidae; red imported fire ant). This is an ideal study site, because both *V. germanica* and *S. invicta* are social insects that build nests and disperse through queens. In addition, both species are highly aggressive and from an anthropocentric perspective, we argue that similar values are associated with broad

categories of environmental and social impact. For example, the first type of non-market value to be estimated concerns preferences for avoided sting threat and/or nuisance impact in homes, recreation areas, gardens and picnic areas, where due to their scavenging habits and choice of nesting sites *V. germanica* may pose a threat (McGain et al., 2000; Pérez-Pimiento et al., 2007; Welton et al., 2017). The second value to be estimated concerns preferences for avoided biodiversity impacts of wasps. In common with other social wasps, the *V. germanica* workers catch various insects and spiders which are malaxated and fed to the larvae, including Diptera, Araneae and Lepidoptera (Madden, 1981; Kasper, 2004; Potter-Craven et al., 2018). There is also the possibility of ecological and further biodiversity impacts on species that compete with wasps for these insect food sources. This impact has been ecologically established in the New Zealand beech forest context (Beggs and Wilson, 1991; Beggs, 2001), but not in the Australian context.

In the current context, the selected study site (Rolfe and Windle, 2014) is consistent with the policy-site context—a similar focus on public values for increased infestation control in Australia, where the control reduces the threat of sting and nuisance in houses, parks and recreation areas; and where impacts are reduced on biodiversity in native land including on insects, spiders and birds. Overall, we consider that the degree of similarity between study and policy site attributes is acceptable to support a valid Benefit Transfer exercise.

Rolfe and Windle (2014) conducted their study in the city of Brisbane, Australia, whereas the policy site is a large area in south-eastern Australia, so their values need to be adjusted to the full area of interest. The benefits of controlling fire ants included avoiding health impacts, maintaining lifestyle and amenity values, and avoiding environmental damage. The benefits they estimated (Table 2) were reductions in:

- the number of homes affected by stinging events;
- recreation, sporting and school areas affected; and
- protected natural bushland areas affected.

The description of the valuation context presented to survey respondents reveals a high level of commodity consistency with the benefits of *V. germanica* control considered for the benefit transfer in the

Table 2

WTP estimates from Rolfe and Windle (2014) in 2009 and adjusted for inflation. Values are in AUD.

Attribute	WTP/household	
	2009	2020
Reduce number of homes affected	\$0.13/1000 homes	\$0.16
Reduce recreational, sporting and school areas affected	\$172/100 ha	\$215
Reduce protected areas affected	\$0.08/100 ha	\$0.10

current project. In fact, Rolfe and Windle (2014) explicitly consider how their WTP estimates could be used in BT applications for similar incursion contexts. Respondents to the survey were willing to pay AUD 0.13 to reduce the impact of *S. invicta* per 1000 homes, AUD172 per 100 ha to protect public areas such as recreational, sporting and school areas, and AUD0.08 per 100 ha to protect natural bushland. These amounts represent annual WTP for a ten-year period to 2020. Apart from adjusting the original (2009) values in Table 2 for the effects of inflation, values needed to be scaled to suit the current context. The full process of benefit transfer is summarised in the Supplementary Material.

The economic impact model generates an estimate of wasp nest density at a spatial scale of a habitat suitability (HS) cell as explained above, and for each year over a planning horizon. *Vespa germanica* density increases are linked to negative outcomes on health, amenity and biodiversity. Control options modelled cause reductions in *V. germanica* nest density. It is the impact of this change in nest density that is valued in the benefit transfer exercise.

Damages were estimated for a planning horizon of 50 years and measured in present-value terms. Multiple simulations were conducted and results for each run were saved as matrices for each variable, where rows represent cells on the map and columns are time periods.

2.3. Biological control assumptions

Biological control programs typically involve significant periods of time and resources to select, test, import, rear and release biological control agents. Many of these costs are context-specific (Nordblom, 2003; Paine et al., 2015; Naranjo et al., 2019). In this case we assume a once-off release of agents that extends over a period of four years, which would then become a self-sustaining population under the right conditions. We tested only technically feasible combinations of parameter values, consisting of growth and mortality rates which result in a self-sustaining population of the biocontrol.

The population dynamics of the wasp and the parasitoid are modelled using Ricker equations, which consider density dependence as the population grows. The model is described in Cacho and Hester (2022, 2023) and the equations are not replicated here. The variables and parameters of the model are listed in Table 3.

2.3.1. Biological control scenarios

Four technically feasible biological control scenarios were tested based on parameter values for growth, mortality and effectiveness of the agent, as detailed in Table 3:

1. LL: Low growth and mortality with low effectiveness ($\alpha_B = 2$; $\mu_B = 0.4$; $\rho_B = \varphi_B = 0.02$)
2. LH: Low growth and mortality with high effectiveness ($\alpha_B = 2$; $\mu_B = 0.4$; $\rho_B = \varphi_B = 0.04$)
3. HL: High growth and mortality with low effectiveness ($\alpha_B = 3$; $\mu_B = 0.5$; $\rho_B = \varphi_B = 0.02$)
4. HH: High growth and mortality with high effectiveness ($\alpha_B = 3$; $\mu_B = 0.5$; $\rho_B = \varphi_B = 0.04$)

In these scenarios, the biological control agents are initially released

Table 3

Variables and parameters of the population growth model.

Name	Value	Description (source)
Variables		
$W_{s,t}$	*	Number of wasp nests per ha in spring of year t
$W_{a,t}$	*	Number of wasp nests per ha in autumn of year t
$B_{s,t}$	*	Number of adult biological control agents per ha in spring of year t
$B_{a,t}$	*	Number of adult biological control agents per ha in autumn of year t
Parameters for <i>V. germanica</i>		
α_W	3.237	Wasp growth parameter in Ricker equation (a)
β_W	$\frac{\ln \alpha_W}{\kappa_W \theta_W}$	Wasp growth exponent in Ricker equation (c)
κ_W	0.912	Carrying capacity of wasps (nests/ha) when $\theta = 1$ (a)
θ_W	(0,1)	Wasp habitat suitability of site (d)
γ_W	4.925	Dispersal parameter for wasps (a)
δ_W	0.341	Wasp detection probability parameter (a)
Parameters for the biological control agent		
α_B	0.2, 0.3	Agent growth parameter in Ricker equation (e)
β_B	$\frac{\ln \alpha_B}{\kappa_B W_{s,t}}$	Agent growth exponent in Ricker equation
κ_B	235	Carrying capacity of agent (cocoon per wasp nest) (b)
μ_B	0.4, 0.5	Agent winter mortality (e)
ρ_B	0.02, 0.04	Reduction in wasp growth rate per adult biological control agent (e)
φ_B	0.02, 0.04	Winter mortality of wasp nests per adult biological control agent (e)
γ_B	2, 3	Dispersal parameter for agent (e)

Notes: (a) Estimated through simulation based on ALA data; (b) Barlow et al. (1996); (c) algebraic estimation; (d) based on CLIMEX map ($\theta = 1$ when Ecoclimatic Index = 100); (e) used in sensitivity analysis; * state variable time trajectories are solved within the model for a given initial condition in each cell of the map.

as cocoons, close to existing wasp nests. The adults that emerge enter the wasp nest and lay their eggs on the developing larvae. For each of the above scenarios, the base assumption was that over the 4-year release period, ~330,000 cocoons of the biological control agent were introduced to infested sites. The final year of the release was year 1 of the simulation. All costs of the biological control program (Table 4) were scaled to year 1 in the simulation (i.e. the cost assigned to the program in year 1 is the compounded total cost of 4 years of rearing and releasing cocoons).

In further analysis beyond the base case, we consider combinations

Table 4

Costs and length of time associated with the biological control program.

	Host Specificity Testing		No Testing	
	Cost (\$'000)	Time (Y)	Cost (\$'000)	Time (Y)
Research costs (fixed)				
Submission seeking decision on requirement for host testing	50	0.5	50	0.5
Import agent; establish rearing colony	646	1	646	1
Host specificity testing	646	1	0	0
Total	1342	2.5	696	1.5
Implementation costs per 250,000 cocoons				
Mass rearing, release	2619	4	2619	4
Long-term monitoring and impact assessment	1220	>3 y after release; x 5 y	1220	>3 y after release; x 5 y
Total	3839		3839	
Total costs per cocoon (\$)	20.72		18.10	

Values are in AUD.

of two decision variables for release of the biological control agent:

- x_p : the proportion of *V. germanica* nests that are inoculated with biological control agent cocoons on a given site.
- x_c : the spatial coverage of the biological control release, expressed as the top percentile value of infested sites selected for inoculation. For example, a percentile of 10 indicates that only the top 10% of sites in terms of *V. germanica*-nest density are selected for release of the biological control.

The analysis was limited to cells in the map that were modelled as being climatically suitable for *V. germanica* establishment in the Eastern states of Australia. A probability of presence map was generated for the relevant region based on ALA reports of *V. germanica* presence (Fig. 2). The starting point for all simulations reflects 60 years of past *V. germanica* spread throughout south-eastern Australia, with only ad hoc control undertaken by households and local councils as nests are detected. Each scenario is run for 1000 iterations over a planning horizon of 50 years.

2.3.2. Costs of biological control

In the current context, where we focus on releasing a new accession of a biological control agent previously used to control *V. germanica*, costs required for agent selection do not apply. We present the costs of biological control in an Australian context, for ‘with’ and ‘without’ host specificity testing under the broad categories of research and implementation (Table 4).

The research stage incorporates fixed costs associated with clarifying the need for importing the agent, and host-specificity testing if required. Testing adds an additional year to the research stage and an additional ~AUD650,000. The implementation stage involves mass rearing and release of agents via the production of cocoons (one agent per cocoon), and long-term monitoring. We calculated the unit cost of cocoons based on the costs incurred during a previous program involving mass rearing and release over 4 years of the biological control agent to control *V. germanica*. In that program, 250,000 cocoons were produced (R. Kwong, personal communication, July 14, 2020). This included costs of distribution and program evaluation. With an additional five years for monitoring, the total costs of the biological program amount to approximately AUD20.70 per cocoon with testing, or AUD18.10 without

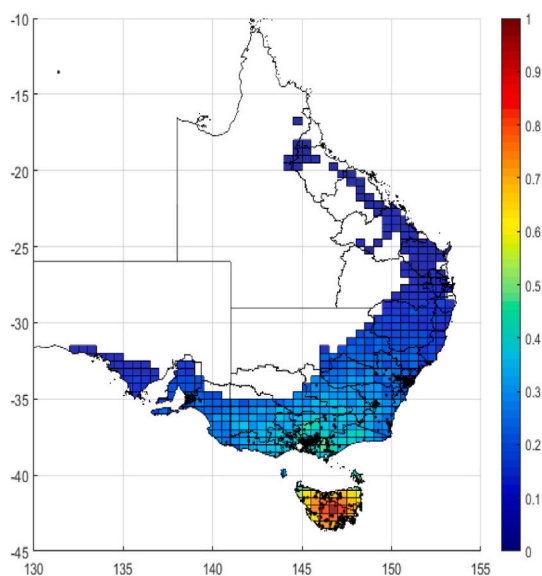


Fig. 2. Probability map of *V. germanica* presence generated by the model (coloured cells) and Atlas of Living Australia reports of *V. germanica* presence (black dots) overlaid on the relevant SA4 regions from ABS.

testing. The cost of scaling up the biocontrol release in the simulations was calculated as the number of additional cocoons released times the AUD20.70 cost per cocoon. We abstracted away from details of how this would be achieved (eg. additional number of years in the release program vs more cocoons produced per year).

3. Results

Testing for technical feasibility is the first step in selecting scenarios for analysis. Any combination of parameter values that did not result in establishment of the biological control agent and reduction in the abundance of wasp nests were discarded, as there is no point testing them for economic feasibility. The process of testing for technical feasibility of the biological control agent using the population dynamics model is illustrated in Cacho and Hester (2022).

3.1. The impact of biological control

Due to model uncertainty, results are presented as pseudo-probability distributions (the uncertainty is not calibrated with observation data). When biological control is effective, damage caused by *V. germanica* is reduced. The level of reduction depends on the values of parameters in the model and the model structure. Fig. 3 illustrates the typical pattern of the modelled reduction in damages that takes place for one set of biological control parameter values (blue line), compared to a ‘no control’ scenario (red line). Damages in Fig. 3 are shown as cumulative distribution functions (CDFs), indicating the range of values for damage (x axis) and the cumulative probability that each value will occur (y axis). When biological control is applied, CDFs shift to the left, showing that damages will be lower for any given probability band.

The reduction in damages under the four selected biological control scenarios are shown in Table 5. The mean value of damages from 50 years of *V. germanica* spread without control is AUD2,659 million. Almost half this value is attributed to the damage caused by *V. germanica* to outdoor and sporting activities (use of public areas), followed by damage to pollination and ripened soft fruit.

Of the four biological control scenarios, the largest reduction in damages (AUD95 million) is from scenario HH – high growth and mortality rates of the biological control with high effectiveness. The lowest reduction in damages (AUD 14.1 million) is from scenario LL – low growth and mortality with low effectiveness. Biological control also reduces the number of nests that private citizens and public agencies will need to destroy, at an assumed cost of AUD250 per nest.⁵ The value of this reduction (killing costs) is given at the bottom of Table 5.

3.2. Decision analysis for biological control management

In the analysis above, the benefit of biological control for each scenario was estimated by comparing damages relative to the do-nothing case — four scenarios were selected for comparison based on the assumed population parameters of the biological control agent. The decision variables were fixed at $x_p = 20$ and $x_c = 5$, indicating that 20% of wasp nests were targeted for biological control release in the top 5 percentile of sites based on wasp abundance. Spatially, this is only 5 percent coverage of cells on the map and the program relies on natural dispersal of biological control agents to increase coverage over time.

In this section we work with Scenario LH (low growth and mortality and high effectiveness) and vary the decision variables to study their effects on the benefits and costs of the program.

Fig. 4 shows the results of a 5×5 factorial experiment to test the effects of the decision variables within the ranges $x_p = (10, \dots, 30)$ and $x_c = (1, \dots, 5)$. Based on benefits, the best outcome is achieved with $x_p = 30$ and $x_c = 4$, indicated as point A (Fig. 5 (a)). This solution requires an

⁵ Jim Bariesheff, personal communication, June 29, 2020.

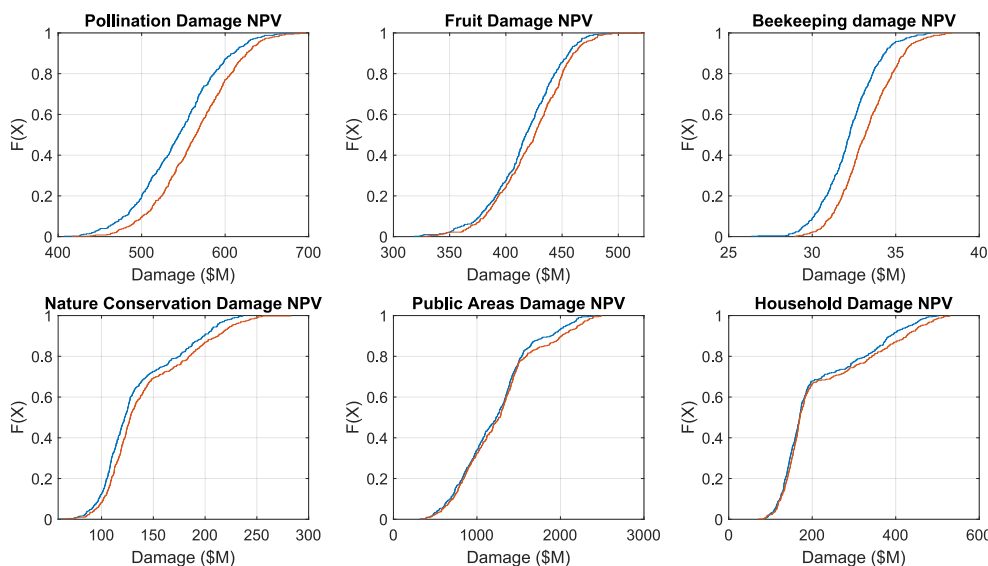


Fig. 3. Cumulative distribution functions for damages under the ‘no control’ (red) scenario and for the ‘control’ (blue) scenario which achieves the greatest reduction in damage within the set tested in the base case. The control results are based on the HH scenario.

Table 5
Reduction in damages (as present value) from the no-control and various biological control scenarios with a discount rate of 5% over a period of 50 years. Values are in AUD.

	Mean damages (\$m)	Reduction in damage* (\$m)				
		No control	LL	LH	HH	
Market damages						
Pollination	564		2.0 (±3.7)	5.1 (±3.7)	14.0 (±3.3)	20.4 (±3.5)
Fruit	423		0.1 (±2.2)	1.2 (±2.2)	4.9 (±2.1)	5.9 (±2.2)
Honey	33		0.2 (±0.1)	0.4 (±0.1)	0.8 (±0.1)	1.0 (±0.1)
Subtotal	1020.1		2.4	6.7	19.6	27.3
Non-market damages						
Nature conservation	143		1.6 (±1.7)	3.1 (±1.7)	6.8 (±1.8)	8.1 (±2.0)
Public areas	1272		7.3 (±30.5)	16.3 (±30.8)	40.3 (±32.8)	49.0 (±30.3)
Households**	225		2.8 (±4.1)	4.6 (±4.2)	10.7 (±4.6)	10.6 (±5.2)
Subtotal	1639		11.7	23.9	57.8	67.7
TOTAL (\$m)	2659		14.1	30.6	77.4	95.0
Killing costs	1061		20.4 (±10.1)	30.1 (±10.3)	61.1 (±11.2)	70.0 (±11.2)

* Numbers in brackets are the 95% confidence intervals.
** Households refers to changes in the number of homes affected by wasps.

initial release of ~423,000 cocoons (Fig. 5 (b)). The option to reduce x_p from 30 to 10 is indicated by point B. This solution requires an initial release of only ~141,000 cocoons. Moving from A to B would reduce the number of cocoons required (and hence the cost of the biological control program) but would also reduce benefit from AUD110 million (B_A) to AUD 84 million (B_B) in present value terms for the 50-year evaluation horizon.

Fig. 5 presents the full distributions associated with points A and B. The uncertainty associated with the project is evident by the wide range of values in the horizontal axis.

3.3. Sensitivity analysis

So far, we have identified ranges of parameter values that would

make the biological control program feasible and estimated the potential benefits of the biological control program under selected strategies regarding breeding and release of the biological control agent. Given the uncertainty in the ‘true’ values of some of the parameters and the model structure, in this section we carry out additional tests using an expanded range of strategies for biological control release.

For this analysis we focused on the two extreme biological control scenarios (LL and HH) and ran an 11 × 11 factorial experiment with x_p in the range (5, 50) and x_c in the range (1,10). Fig. 6 presents the results based on the number of cocoons released under each of the release strategies tested. The high variability of results reflects the uncertainty involved in the analysis, however, there are many cases where benefits are >0 with high probability.

To determine whether supporting the program is justified based on benefit-cost ratios we need to compare these results with the cost of the biological control program. Based on Fig. 6, the highest median benefits are AUD143 million and AUD385 million for the LL and HH scenarios respectively, whereas the 5th percentiles are AUD89 million and AUD282 million. The number of biological control agent cocoons required to achieve these results is 1.6 million. Assuming a cost per cocoon of AUD 20.70 (Table 4) this program would have an estimated cost of AUD33 million, which is well below the 5th percentile of AUD89 million under the LL scenario. This suggests that there is a high probability that the benefits will exceed the costs of the program, with benefit-cost ratios of 4.3 and 12.5 at the median, and 2.7 and 9.1 at the 5th percentile, for LL and HH scenarios respectively. It is important to note that these results do not consider the fixed costs associated with selecting potential agents, including undertaking risk assessments. The cost of these activities is typically significant.

4. Discussion

4.1. Technical feasibility of the biological control program

Assuming that a healthy colony of *S. v. vesparum* has been successfully imported, the success of the biological control program hinges on two factors: (1) the feasibility that the biological control agent will establish and spread following an effective mass rearing and release effort; and (2) the effectiveness of the agent in suppressing growth and spread of *V. germanica* nests. If technical feasibility for the biological control is unlikely, there is no need to undertake further evaluation of its potential benefits, as the organism will be unable to establish a viable

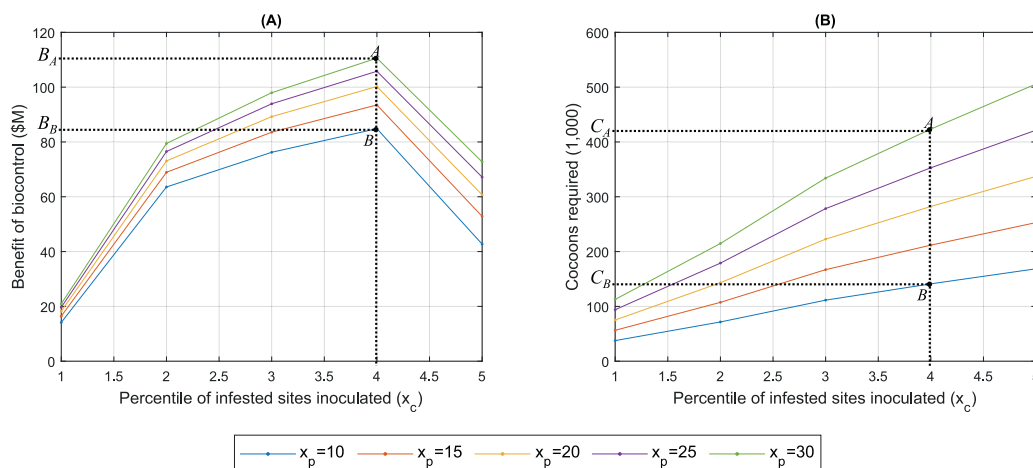


Fig. 4. Effects of biological control decision variables on the benefits of the biological control program (a) estimated benefits (b) number of biological control cocoons required. Coloured lines represent different proportions of wasp nests that are inoculated in the biocontrol release (x_p) with values tested ranging from 10 to 30%. Simulation results based on Scenario LH.

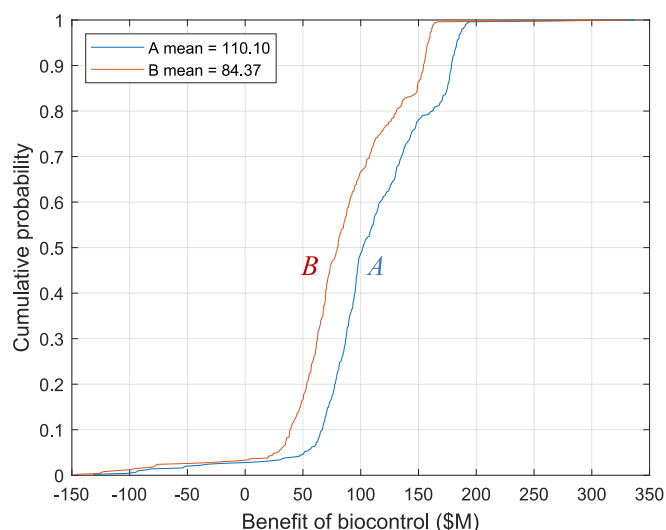


Fig. 5. Cumulative probability functions of the benefit of biological control for two decision alternatives for (x_p, x_c): A = (30, 4), B = (10, 4). Simulation results based on Scenario LH.

population. In that case the main question is whether there are mechanisms for increasing the likelihood of establishment and/or the effectiveness of the biological control and at what cost. This could involve assessing the success of the agent if it has already been released for the biological control of *V. germanica* elsewhere, conducting a smaller trial release program to improve establishment success, or investigating alternative biological control agents or groups of agents.

Once the biological control agent becomes established, its effectiveness hinges on its ability to suppress growth and spread of *V. germanica* infestations. The interaction between the biological control agent and the target pest may converge to an equilibrium depending on parameter values in the model (Cacho and Hester, 2022).

4.2. Estimated impacts

The non-market impacts of *V. germanica* were estimated to be >1.5 times the market impacts. For the baseline scenario analysed, non-market impacts would amount to AUD1.6 billion dollars over 50 years if *V. germanica* continues to spread across the landscape without any formal management program. This can be compared to market impacts

of around AUD1 billion over 50 years. Under the biological control programs assessed here, the benefit-cost ratios are therefore significantly higher with the inclusion of non-market impacts.

Our analysis of environmental impacts is based on benefit transfer, which was derived from a choice modelling experiment. This type of analysis is based on willingness to pay by people to reduce the damage and nuisance of the pest, and is, by nature an anthropocentric approach. We acknowledge that the specific effects on the environment were not estimated, but we argue our estimates are useful from a policy standpoint, as taxpayers' willingness to pay influences the likelihood that a control program will be funded.

Results in Table 5 showed a large mean reduction in damage related to use of public areas, but there was also a large margin of error. In the case of LL and LH scenarios, the range in possible values would result in some scenarios where damage increases as a result of the biological control program. This would suggest there are simulated cases where the low growth and mortality of the biological control agent results in spread of *V. germanica* across the landscape that is largely or completely unhindered.

In the scenarios considered, not only does the biological control program lead to a reduction in market and non-market damages, it also reduces the number of nests that private citizens and public agencies will need to destroy, at an assumed cost of AUD250 per nest.⁶ The value of this reduction (killing costs) is given at the bottom of Table 5. As would be expected, the scenario with the largest reduction in damage (HH) is the scenario with the largest avoided costs for nest control (AUD 70 million) as the biological control agent has a larger impact on nest density over the 50-year period. These savings to consumers and public agencies represent a loss to pest controllers, which are often small businesses. There could also be environmental benefits due to reduced use of chemicals, which in turn would result in reduced revenues to chemical companies. Given these additional complications we report the avoided control costs separately to distinguish them from unambiguous avoided damages.

Damages to the honey industry (Table 5) tend to be relatively small as a proportion of total market damages, but they represent a significant cost for beekeepers. Where *V. germanica* are present, beekeepers must devote resources to manage hives in order to prevent destruction and raiding by wasps. It has been estimated that in 2019, beekeepers in New Zealand lost between 0.6% and 1.6% of their bee colonies to *V. germanica* (Stahlmann-Brown et al., 2020) and in a bad wasp year

⁶ Jim Bariesheff, personal communication, June 29, 2020.

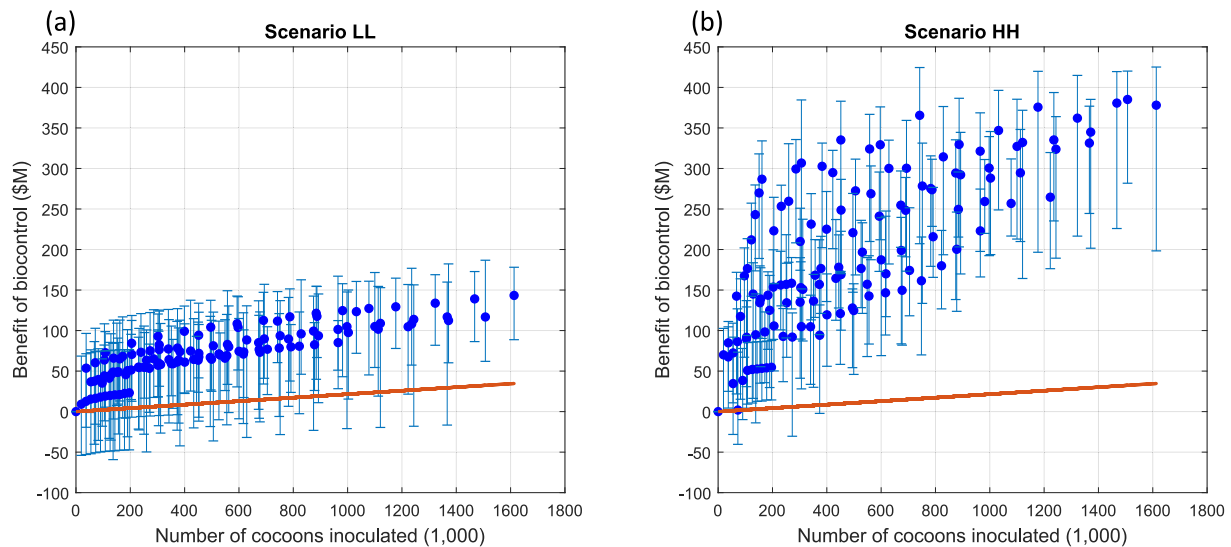


Fig. 6. Benefits of biological control against the number of cocoons inoculated for different cocoon release strategies, ranging from (x_p, x_c) : (5, 1) to (50, 10) in a full factorial design. Circles are medians and error bars are the 5th and 95th percentiles of the distribution of simulation results based on Scenarios LL and HH. The red line indicates the cost of the cocoons released based on Table 4.

they could expect to lose up to 5% of their hives (Spradbery 1986 cited in Widmer et al., 1995). It is thought similar damage could be expected in Australia (Crosland, 1991).

Losses to beekeeping in NZ from the direct effect of *V. germanica* on hives was estimated at NZD8.8 million per annum (MacIntyre and Hellstrom, 2015). This value captures wasp control management costs; the cost of hives lost to wasps; and production losses from bees focusing on defence rather than food collection. Cook (2019) estimated the damage to apiculture in Western Australia, where *V. germanica* is the subject of an eradication program, would reach more than AUD1.1 million per year if wasps were left unmanaged. Managed hives in Western Australia typically produce at least 1600 t of honey per year worth around AUD5 million.

The cost of the biological control program for the base case is assumed to be fixed at AUD6.75 million given the number of cocoons released and the fixed cost of the program. Clearly, based on these results of the biological control scenarios investigated, the benefits of control outweigh the cost of the biological control program. However, those scenarios assume the biological control has already been identified and screened. The additional costs of those two activities will result in reduced benefit-cost ratios, although, given the size of the additional costs relative to the benefits, these are likely to remain positive for all scenarios reported here.

4.3. Decision analysis and economic feasibility

To determine the best biological control release strategy from the options in Fig. 6, we need to know the expected cost of the biological control program and the likelihood of success. Using a simple scenario, assume that each ‘established’ cocoon costs AUD20.70, then the biological control cost of option A would be AUD8.8 million and for option B it would be AUD2.9 million. If plotted in Fig. 6, these costs would be close to the zero-mark given the scale of the x-axis. This means that in about 98% of the simulations, the benefits would have exceeded the costs for each of these options. Of course, this would be the case only if the biological control parameters were those assumed in the LH scenario, and this example does not account for the probability that the biological control could fail to become established. This suggests that further analysis should tackle two key issues: (1) the likelihood that the biological control will be able to achieve the parameters assumed in these scenarios; and (2) the likelihood that the biological control agent

will become established where inoculated, and will be able to spread in the landscape to other areas where wasp nests are present.

Our results suggest that, provided the assumed conditions for technical feasibility can be met, economic feasibility is high, with benefits likely to exceed costs by a substantial amount in present value terms. Benefit-cost ratios were between 2.7 and 12.5 for the scenarios analysed; and the size of the budget to implement a biological control program could range from as low as AUD3 million to as high as AUD33 million depending on the cocoon-release strategy and the desired benefits. It is important to note that, although the parasitoid *S. v. vesparum* is used as a model for the life cycle of the biological control agent, the mortality parameter value reported for this species in New Zealand (0.85; Barlow et al., 1996) is considerably higher than the threshold value found to meet technical feasibility requirements in this study (0.5). The main question then is whether the mortality of the agent can be decreased to feasible levels in Australia, and at what cost.

Notably, the costs of inaction or delay with respect to biological control of invasive species can be nontrivial (Hajek et al., 2016). The economic model used for the ‘slow the spread’ campaign against *Lymantria dispar* in the USA provides a useful framework for understanding the positive benefits of a biological control program against an invasive pest species (Sharov and Liebhold, 1998). By both slowing the spread of the organism and reducing its impacts in areas in which it has spread, early implementation of a biological control program magnifies the net benefits. Given that programs typically involve significant periods of time and resources to select, test, import and rear agents, there is a strong case for pre-emptive or pre-release efficacy assessments (McClay and Balciunas, 2005; Avila et al., 2023) to save time in the event that a biological control is required to reduce the impact of a pest that has become established in the landscape. Efficacy assessments can also rule out ineffective agents from those that pass screening and host-specificity testing.

4.4. Biocontrol release strategies

We defined the biocontrol release strategy in terms of two variables, representing the spatial coverage of the release (x_c) and the intensity of release in a given area (x_p). Together these two variables determine the number of cocoons required, which creates the link to program costs. There are other aspects of the release that we did not explore, and which may influence effectiveness and cost of the release. For example,

releases could be prioritised based on the type of environments infested, remoteness, human population density, or other factors that vary spatially.

Regarding the biocontrol release costs, the base case assumes a 4-year breeding and release program producing 250,000 cocoons, which was used to estimate the cost per cocoon at AUD20.70. In subsequent tests, we increased the number of cocoons released, but abstracted away from details of how this would be achieved, effectively assuming that the cost per cocoon would not change as the size of the release increases. Release of cocoons could be increased by extending the years in the release program, or by breeding more parasitoids per year. There may be differences in fixed costs associated with upscaling cocoon release in different ways, and the resources and skills available in agencies would place constraints on what can be achieved. Furthermore, costs of coordination among Federal and State agencies to fund and implement a program that spans different jurisdictions could be substantial.

The question of biocontrol release strategies in general has very little coverage in the literature. Our approach combining spatial data with population dynamics modelling can contribute to this neglected research area.

5. Concluding comments

Implementing classical biological control programs involves significant periods of time and requires resources to select, test, import, rear and release biological control agents. We have demonstrated a method that can be used pre-emptively when experts foresee the need for biological control. In this study on the economic feasibility of *V. germanica* biological control in Australia, we found median benefits of AUD145 million to AUD385 million, depending on effectiveness and growth rates of the biocontrol, with non-market benefits exceeding market benefits by 50%. These results present a clear case for public funding to control the wasp, provided the conditions for technical feasibility are met. In such case, it is advisable to start with a small trial release program to ensure the biocontrol becomes established and spreads under field conditions.

The benefits of biocontrol were calculated as avoided damages relative to a baseline where no coordinated control occurs. Our calculation of non-market values was based on people's willingness to pay to avoid damages to the environment and public spaces. This anthropocentric approach does not value specific damages to biodiversity or intrinsic values of the environment. Despite the lack of a full valuation of benefits, the approach is useful from a policy perspective to justify use of public funds. Our intent was to identify whether the extent of impacts that we did value exceeds the cost of a biocontrol program, which our results indicate is the case with high likelihood.

The modelling approach demonstrated here can be transferred to other situations by adjusting values for population-dynamics parameters that represent the particular species involved. Habitat suitability was estimated using the CLIMEX model, which can be applied to other species and geographies to identify suitable areas for pest establishment. The calculation of damages requires spatial (gridded) data on agricultural production and profits, presence of nature reserves and recreational areas, human population densities and household income. The required datasets were derived from publicly available data from Australian Government and scientific databases. Similar datasets would be available in other countries, making it possible to apply the model to other geographical areas.

Our results show a broad range of potential beneficial outcomes depending on the intensity and spatial coverage of the biocontrol release. There are spatial aspects of biocontrol release strategies that were not considered in the analysis, but which could influence the cost and effectiveness of the program. Our approach combining spatial data with population dynamics modelling can contribute to this largely neglected research area.

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CRediT authorship contribution statement

Susan M. Hester: Writing – review & editing, Writing – original draft, Validation, Project administration, Data curation, Conceptualization. **Peter Tait:** Writing – review & editing, Writing – original draft, Validation, Formal analysis, Data curation. **Raelene Kwong:** Writing – review & editing, Writing – original draft, Validation, Conceptualization. **Greg Lefoe:** Writing – review & editing, Writing – original draft, Validation, Conceptualization. **Darren Kriticos:** Writing – review & editing, Data curation, Conceptualization. **Oscar J. Cacho:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolecon.2024.108315>.

References

- Avila, G.A., Seehausen, M.L., Lesieur, V., Chhagan, A., Caron, V., Down, R.E., et al., 2023. Guidelines and framework to assess the feasibility of starting pre-emptive risk assessment of classical biological control agents. *Biol. Control* 187, 105387. <https://doi.org/10.1016/j.biocontrol.2023.105387>.
- Barlow, N.D., Moller, H., Beggs, J.R., 1996. A model for the effect of *Sphécophaga vesparum vesparum* as a biological control agent of the common wasp in New Zealand. *J. Appl. Ecol.* 33 (1), 31–44. <https://doi.org/10.2307/2405013>.
- Barratt, B.I.P., Howarth, F.G., Withers, T.M., Kean, J.M., Ridley, G.S., 2010. Progress in risk assessment for classical biological control. *Biol. Control* 52 (3), 245–254. <https://doi.org/10.1016/j.biocontrol.2009.02.012>.
- Bashford, R., 2001. The spread and impact of the introduced vespine wasps '*Vespula germanica*' (F.) and '*Vespula vulgaris*' (L.) (Hymenoptera: Vespidae: Vespinae) in Tasmania. *Aust. Entomol.* 28 (1), 1–12. <https://doi.org/10.3316/informit.074834142988662>.
- Beggs, J., 2001. The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biol. Conserv.* 99 (1), 17–28. [https://doi.org/10.1016/S0006-3207\(00\)00185-3](https://doi.org/10.1016/S0006-3207(00)00185-3).
- Beggs, J.R., Wilson, P.R., 1991. The kaka *Nestor meridionalis*, a New Zealand parrot endangered by introduced wasps and mammals. *Biol. Conserv.* 56 (1), 23–38. [https://doi.org/10.1016/0006-3207\(91\)90086-0](https://doi.org/10.1016/0006-3207(91)90086-0).
- Beggs, J.R., Rees, J.S., Toft, R.J., Dennis, T.E., Barlow, N.D., 2008. Evaluating the impact of a biological control parasitoid on invasive *Vespula* wasps in a natural forest

- ecosystem. *Biol. Control* 44 (3), 399–407. <https://doi.org/10.1016/j.biocontrol.2007.10.016>.
- Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* 12 (2), 20150623. <https://doi.org/10.1098/rsbl.2015.0623>.
- Cacho, O.J., Hester, S.M., 2022. Modelling biocontrol of invasive insects: an application to European Wasp (*Vespula germanica*) in Australia. *Ecol. Model.* 467, 109939 <https://doi.org/10.1016/j.ecolmodel.2022.109939>.
- Cacho, O.J., Hester, S.M., 2023. Modelling biocontrol of invasive insects using WaspSim: a MATLAB simulation model. *SoftwareX* 21 (101321), 8. <https://doi.org/10.1016/j.softx.2023.101321>.
- Canyon, D., Naumann, I., Speare, R. and Winkel, K. 2011. Environmental and economic costs of invertebrate invasions in Australia. In: Pimentel, D. (Ed), Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, pp 25: 50.
- Clapperton, B.K., Alspach, P.A., Moller, H., Matheson, A.G., 1989. The impact of common and German wasps (Hymenoptera: Vespidae) on the New Zealand beekeeping industry. *NZ J. Zool.* 16 (3), 325–332. <https://doi.org/10.1080/03014223.1989.10422897>.
- Cook, D.C., 2019. Quantifying the potential impact of the European wasp (*Vespula germanica*) on ecosystem services in Western Australia. *NeoBiota* 50, 55–74. <https://doi.org/10.3897/neoBiota.50.37573>.
- Crosland, M.W.J., 1991. The spread of the social wasp, *Vespula germanica*, in Australia. *NZ J. Zool.* 18 (4), 375–387. <https://doi.org/10.1080/03014223.1991.10422843>.
- Darby, S., McLaren, D.A., 1993. The role of the community in the implementation of biological control. *Plant Protect. Quarter.* 8, 155–158.
- de Villiers, M., Kriticos, D.J., Veldtman, R., 2017. Including irrigation in niche modelling of the invasive wasp *Vespula germanica* (Fabricius) improves model fit to predict potential for further spread. *PLoS One* 12 (7), e0181397. <https://doi.org/10.1371/journal.pone.0181397>.
- Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R.E., Roiz, D., Jarić, I., et al., 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592 (7855), 571–576. <https://doi.org/10.1038/s41586-021-03405-6>.
- Donovan, B.J., 1991. Life cycle of *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae), a parasitoid of some vespid wasps. *NZ J. Zool.* 18 (2), 181–192. <https://doi.org/10.1080/03014223.1991.10757965>.
- Donovan, B.J., Read, P.E.C., 1987. Attempted biological control of social wasps, *Vespula* spp., (Hymenoptera: Vespidae) with *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae) in New Zealand. *NZ J. Zool.* 14 (3), 329–335. <https://doi.org/10.1080/03014223.1987.10423002>.
- Dubiner, S., Cohen, N., Volov, M., Hefetz, A., Seltzer, R., Levin, E., 2020. The exocrine chemistry of the parasitic wasp *Sphecophaga orientalis* and its host *Vespa orientalis*: a case of chemical deception? *Insects* 12 (1). <https://doi.org/10.3390/insects12010002>.
- Ede, F., Kwong, R., Lefoe, G., Steel, J., Weiss, J., 2014. The Keith Turnbull research institute: 50 years of pest plant and animal research. *Plant Protect. Quarter.* 29, 3.
- Elliott, G.P., Wilson, P.R., Taylor, R.H., Beggs, J.R., 2010. Declines in common, widespread native birds in a mature temperate forest. *Biol. Conserv.* 143 (9), 2119–2126. <https://doi.org/10.1016/j.biocon.2010.05.022>.
- Evans, H.E., Eberhard, M.J., 1970. *The Wasps*. University of Michigan Press, Ann Arbor.
- Eyer, P.-A., Vargo, E.L., 2021. Breeding structure and invasiveness in social insects. *Curr. Opin. Insect Sci.* 46, 24–30. <https://doi.org/10.1016/j.cois.2021.01.004>.
- Field, R.P., Darby, S.M., 1991. Host specificity of the parasitoid, *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae), a potential biological control agent of the social wasps, *Vespula germanica* (Fabricius) and *V. vulgaris* (Linnaeus) (Hymenoptera: Vespidae) in Australia. *NZ J. Zool.* 18 (2), 193–197. <https://doi.org/10.1080/03014223.1991.10757966>.
- Fordham, R.A., 1991. Vespulid wasps at the upper forest margin in Tongariro National Park—a threat to the native biota? *NZ J. Zool.* 18 (2), 151–153. <https://doi.org/10.1080/03014223.1991.10757961>.
- Goodman, R., 2014. *Australian Beekeeping Guide*. Rural Industries Research and Development Corporation, p. 144.
- Hajek, A.E., 2004. *Natural Enemies: An Introduction to Biological Control*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511811838>.
- Hajek, A.E., Hurley, B.P., Kenis, M., Garnas, J.R., Bush, S.J., Wingfield, M.J., et al., 2016. Exotic biological control agents: a solution or contribution to arthropod invasions? *Biol. Invasions* 18 (4), 953–969. <https://doi.org/10.1007/s10530-016-1075-8>.
- Harris, R.J., 1991. Diet of the wasps *Vespula vulgaris* and *V. Germanica* in honeydew beech forest of the South Island, New Zealand. *NZ J. Zool.* 18 (2), 159–169. <https://doi.org/10.1080/03014223.1991.10757963>.
- IPBES, 2023. In: Roy, H.E., Pauchard, A., Stoett, P., et al. (Eds.), Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany. <https://doi.org/10.5281/zenodo.7430692> <https://zenodo.org/records/11254974>.
- Kasper, M., 2004. *The Population Ecology of an Invasive Social Insect, Vespula Germanica* (Hymenoptera: Vespidae) in South Australia. Environmental Biology, School of Earth and Environmental Sciences. University of Adelaide, Adelaide, South Australia (Doctor of Philosophy: 171).
- Kasper, M.L., Reeson, A.F., Austin, A.D., 2008. Colony characteristics of *Vespula germanica* (F.) (Hymenoptera, Vespidae) in a Mediterranean climate (southern Australia). *Australian J. Entomol.* 47 (4), 265–274. <https://doi.org/10.1111/j.1440-6055.2008.00658.x>.
- Kriticos, D.J., Maywald, G.F., Yonow, T., Zurcher, E.J., Herrmann, N.I., Sutherst, R.W., 2015. CLIMEX Version 4: Exploring the Effects of Climate on Plants, Animals And Diseases. CSIRO, Canberra, p. 156.
- Lefoe, G., Ward, D., Honan, P., Darby, S., 2001. *Minimising the Impact of European Wasps on the Grape and Wine Industry*. Final Report to Grape and Wine Research & Development Corporation. Department of Natural Resources and Environment, Frankston, Victoria.
- Lester, P.J., Beggs, J.R., 2019. Invasion success and management strategies for social *Vespula* wasps. *Annu. Rev. Entomol.* 64, 51–71. <https://doi.org/10.1146/annurev-ento-011118-111812>.
- Levick, N.R., Winkel, K.D., Smith, G., 1997. European wasps: an emerging hazard in Australia. *Med. J. Aust.* 167 (11–12), 650–651.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2004. 100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database., The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), p. 12.
- MacIntyre, P., Hellstrom, J., 2015. An evaluation of the costs of pest wasps (*Vespula* species) in New Zealand. Department of Conservation and Ministry for Primary Industries, Wellington, 44pp.
- Madden, J.L., 1981. Factors influencing the abundance of the European wasp (*Para Vespula Germanica* [F.]). *Aust. J. Entomol.* 20 (1), 59–65. <https://doi.org/10.1111/j.1440-6055.1981.tb01000.x>.
- Marbuah, G., Gren, I.-M., McKie, B., 2014. Economics of harmful invasive species: a review. *Diversity* 6 (3), 500–523.
- McClay, A.S., Balciunas, J.K., 2005. The role of pre-release efficacy assessment in selecting classical biological control agents for weeds—applying the Anna Karenina principle. *Biol. Control* 35 (3), 197–207. <https://doi.org/10.1016/j.biocontrol.2005.05.018>.
- McGain, F., Winkel, K.D., Harrison, J., 2000. Wasp sting mortality in Australia. *Med. J. Aust.* 173 (4), 198–200. <https://doi.org/10.5694/j.1326-5377.2000.tb125600.x>.
- Moller, H., 1990. Wasps killing nesting birds. *Notornis* 37, 76–77.
- Moller, H., 1996. Lessons for invasion theory from social insects. *Biol. Conserv.* 78 (1), 125–142. [https://doi.org/10.1016/0006-3207\(96\)00022-5](https://doi.org/10.1016/0006-3207(96)00022-5).
- Moller, H., Plunkett, G.M., Tilley, J.A.V., Toft, R.J., Beggs, J.R., 1991. Establishment of the wasp parasitoid, *Sphecophaga vesparum* (Hymenoptera: Ichneumonidae), in New Zealand. *NZ J. Zool.* 18 (2), 199–208. <https://doi.org/10.1080/03014223.1991.10757967>.
- Mollot, G., Pantel, J.H., Romanuk, T.N., 2017. Chapter two - The effects of invasive species on the decline in species richness: A global meta-analysis. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), *Advances in Ecological Research*, 56. Academic Press, pp. 61–83. <https://doi.org/10.1016/bs.aecr.2016.10.002>.
- Naranjo, S.E., Frisvold, G., Ellsworth, P.C., 2019. Economic value of arthropod biological control. In: Onstad, D.W., Crain, P.R. (Eds.), *The economics of integrated pest management of insects*. CAB International, pp. 49–85.
- Nordblom, T.L., 2003. Putting biological reality into economic assessments of biocontrol. Improving the selection, testing and evaluation of weed biological control agents. In: Jacob, H., Spafford, Briebe, D.T. (Eds.), *Improving the Selection, Testing and Evaluation of Weed Biological Control Agents*. CRC Technical Series No. 7. CRC for Australian Weed Management, Adelaide, Australia, pp. 75–85.
- Oi, C.A., Brown, R.L., Stevens, I., Wenseleers, T., 2020. Hydrocarbon signatures of the ectoparasitoid *Sphecophaga vesparum* shows wasp host dependency. *Insects* 11 (5), 268.
- Paine, T.D., Millar, J.G., Hanks, L.M., Gould, J., Wang, Q., Daane, K., et al., 2015. Cost-benefit analysis for biological control programs that targeted insect pests of eucalypts in urban landscapes of California. *J. Econ. Entomol.* 108 (6), 2497–2504. <https://doi.org/10.1093/jeet/tov224>.
- Pérez-Pimiento, A., Prieto-Lastra, L., Rodríguez-Cabreros, M., Reaño-Martos, M., García-Cubero, A., García-Loria, J., 2007. Work-related anaphylaxis to wasp sting. *Occup. Med.* 57 (8), 602–604. <https://doi.org/10.1093/occmed/kqm054>.
- Potter-Craven, J., Kirkpatrick, J.B., McQuillan, P.B., Bell, P., 2018. The effects of introduced vespid wasps (*Vespula germanica* and *V. vulgaris*) on threatened native butterfly (*Oreixena ptnarra*) populations in Tasmania. *J. Insect Conserv.* 22 (3), 521–532. <https://doi.org/10.1007/s10841-018-0081-9>.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., et al., 2020. Scientists' warning on invasive alien species. *Biol. Rev.* <https://doi.org/10.1111/brv.12627> n/a(n/a).
- Read, P.E.C., Donovan, B.J., Schroeder, N.C., 1990. Rearing and Distribution of the Introduced Wasp Parasitoid *Sphecophaga Vesparum* throughout New Zealand 43rd New Zealand Weed and Pest Control Conference. New Zealand Plant Protection Society, Palmerston North.
- Richter, M.R., 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu. Rev. Entomol.* 45 (1), 121–150. <https://doi.org/10.1146/annurev.ento.45.1.121>.
- Rolfe, J., Windle, J., 2014. Public preferences for controlling an invasive species in public and private spaces. *Land Use Policy* 41 (Supplement C), 1–10. <https://doi.org/10.1016/j.landusepol.2014.04.013>.
- Sackmann, P., D'Adamo, P., Rabinovich, M., Corley, J.C., 2000. Arthropod prey foraged by the German wasp (*Vespula germanica*) in NW Patagonia, Argentina. *New Zealand Entomol.* 23 (1), 55–59. <https://doi.org/10.1080/00779962.2000.9722067>.
- Sharov, A.A., Liebhold, A.M., 1998. Model of slowing the spread of gypsy moth (*Lepidoptera: Lymantriidae*) with a barrier zone. *Ecol. Appl.* 8 (4), 1170–1179.
- Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. *Food Webs* 24, e00144. <https://doi.org/10.1016/j.fooweb.2020.e00144>.
- Spradbery, J., Maywald, G., 1992. The distribution of the European or German wasp, *Vespula-Germanica* (F) (Hymenoptera, Vespidae), in Australia - past, present and future. *Aust. J. Zool.* 40 (5), 495–510. <https://doi.org/10.1071/ZO9920495>.
- Stahlmann-Brown, P., Robertson, T., Borowik, O., 2020. Report on the 2019 New Zealand Colony Loss Survey, p. 74.

- Stenberg, J.A., Sundh, I., Becher, P.G., Björkman, C., Dubey, M., Egan, P.A., et al., 2021. When is it biological control? A framework of definitions, mechanisms, and classifications. *J. Pest. Sci.* 94 (3), 665–676. <https://doi.org/10.1007/s10340-021-01354-7>.
- Sutherst, R.W., Maywald, G.F., 1985. A computerised system for matching climates in ecology. *Agric. Ecosyst. Environ.* 13 (3), 281–299. [https://doi.org/10.1016/0167-8809\(85\)90016-7](https://doi.org/10.1016/0167-8809(85)90016-7).
- Tait, P., Rutherford, P., 2018. Non-market Valuation of Environmental Impacts for Biosecurity Incursion Cost Benefit Analysis: A Guidance Manual for Public Policy. The Agribusiness and Economics Research Unit (AERU), Lincoln, NZ, p. 35.
- Van Driesche, R., Hoddle, M., Center, T., 2008. Control of Pests and Weeds by Natural Enemies: An Introduction to Biological Control. MA, Blackwell Publishing Ltd, Malden.
- Ward, D., 2014. Status of Control Options for *Vespula* Wasps in New Zealand. Richmond, New Zealand, Landcare Research New Zealand Ltd.
- Ward, D., Honan, P., Lefoe, G., 2002. Colony structure and nest characteristics of European wasps, *Vespula germanica* (F.) (Hymenoptera: Vespidae), in Victoria, Australia. *Aust. J. Entomol.* 41 (4), 306–309. <https://doi.org/10.1046/j.1440-6055.2002.00308.x>.
- Welton, R.E., Williams, D.J., Liew, D., 2017. Injury trends from envenoming in Australia, 2000–2013. *Intern. Med. J.* 47 (2), 170–176. <https://doi.org/10.1111/imj.13297>.
- Widmer, M., Davis, P.R., van Schagen, J.J., Craven, T., 1995. Report on the Occurrence of European Wasps in Western Australia for the Period 1991–1995. Agriculture Protection Board of WA, 26 pp.