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# Classical biological control of an invasive forest pest: a world perspective of the management of *Sirex noctilio* using the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibaliidae)

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## Abstract

Classical biological control is a key method for managing populations of pests in long-lived crops such as plantation forestry. The execution of biological control programmes in general, as the evaluation of potential natural enemies remains, to a large extent, an empirical endeavour. Thus, characterizing specific cases to determine patterns that may lead to more accurate predictions of success is an important goal of the much applied ecological research. We review the history of introduction, ecology and behaviour of the parasitoid *Ibalia leucospoides*. The species is a natural enemy of *Sirex noctilio*, one of the most important pests of pine afforestation worldwide. We use an invasion ecology perspective given the analogy between the main stages involved in classical biological control and the biological invasion processes. We conclude that success in the establishment, a common reason of failure in biocontrol, is not a limiting factor of success by *I. leucospoides*. A mismatch between the spread capacity of the parasitoid and that of its host could nevertheless affect control at a regional scale. In addition, we suggest that given its known life history traits, this natural enemy may be a better regulator than suppressor of the host population. Moreover, spatial and temporal refuges of the host population that may favour the local persistence of the interaction probably reduce the degree to which *S. noctilio* population is suppressed by the parasitoid. We emphasize the fact that some of the biological attributes that promote establishment may negatively affect suppression levels achieved. Studies on established non-native pest–parasitoid interactions may contribute to defining selection criteria for classical biological control which may prove especially useful in integrated pest management IPM programmes of invasive forest insects.

**Keywords:** classical biological control, invasion biology, selection criteria, life history traits, host-searching and exploitation abilities, dispersal capacity

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Classical biological control, the deliberate introduction of exotic natural enemies into new habitats in which an exotic pest also causes damage, aims for a long-term reduction of the pest population (van den Bosch, 1971). Despite the fact that it is widely considered in pest management, classical biocontrol shows a great frequency of failures (Greathead & Greathead, 1992). In many failed cases, populations of the natural enemies

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could not establish in the new habitats and in others, successful establishment did not lead to persistent low-density populations of the pest (Mills, 1994). Thus, predicting and generalizing the outcome of classical biocontrol remains an elusive goal. While case-by-case detailed ecological studies of pest, crop and natural enemies are, if time-consuming, warranted, the search of broad patterns is still central to much applied ecological research. Classical biological control is considered fundamental to controlling damaging insects in many long-lived crops such as plantation forestry.

*Sirex noctilio* Fabricius (Hymenoptera: Siricidae) is a major pest of exotic tree plantations worldwide as it is responsible for severe losses to pine tree afforestation. This wood-boring wasp endemic to Eurasia and Northern Africa was accidentally introduced, mainly during the last century, into several countries. The invasion history of *S. noctilio* suggests two source populations and several pathways of introduction for globally invasive populations. Apparently, multiple independent introductions from Europe and other native areas (Asia and Northern Africa) into the Southern and Northern Hemispheres occurred followed by subsequent spread among the invaded areas (Boissin *et al.*, 2012). It has also been suggested that the spread rates of this species can be quite extraordinary, ranging from 11 to 78 km/year, depending on the geographical region (Lantschner *et al.*, 2014). Although *S. noctilio* has a wide host range, the *Pinus* species are strongly preferred (Spradbery & Kirk, 1978; Madden, 1988). Given that pines are commercially important and so planted extensively worldwide, *S. noctilio* has become a global problem (see Carnegie *et al.*, 2005 for New Zealand and Australia; Villacide & Corley, 2012 for South America; Tribe & Cillié, 2004 for South Africa and, Hoebeke *et al.*, 2005; and de Groot *et al.*, 2007 for North America and Canada).

The life cycle of this invasive wasp is well known. Female wasps lay eggs into trees together with a phytotoxic compound and spores of the symbiotic fungus *Amylostereum areolatum*, which is essential for larval nutrition and development (Madden & Coutts, 1979; Madden, 1981). The larvae excavate galleries and the combination of the fungus and the toxic mucus results in physiological stress to trees that leads to their death (Coutts, 1969; Ryan & Hurley, 2012). *Sirex noctilio* when in low populations attacks suppressed and stressed trees (Madden, 1968*a*; Villacide & Corley, 2012). Tree susceptibility to attacks can arise from different reasons such as competition in overstocked stands, physical damage because of pruning, unfavourable environmental conditions, or even other insect and disease attacks (Madden, 1988).

*Sirex noctilio* population dynamics in its non-native range is critical to damage in pine plantations. The wasp has pulse-like outbreak population behaviour (Madden, 1988; Villacide & Corley, 2012). Pulse-like outbreaks are described by a rapid, unpredictable increase in densities and are usually terminated by natural enemies, resource defences or host depletion (Berryman, 1987). During outbreaks, *S. noctilio* is capable of attacking healthy trees in addition to the stressed ones; thus resulting in high tree mortality (Corley & Villacide, 2012).

The need for damage mitigation strategies during *S. noctilio* outbreaks has led to integrated pest management measures in the invaded regions. Silvicultural practices together with the introduction of biocontrol agents are the procedures of choice. The innundative release of the entomopathogenic nematode *Deladenus* (*Beddingia*) *siricidicola* Bedding is widely used to control woodwasp populations and, is regarded as the primary biological control agent for this pest (Slippers *et al.*, 2012). In addition, several species of parasitoids have been deliberately introduced from Europe and North America as control agents in most invaded regions (Cameron, 2012). Among these species, *Ibalia leucospoides* (Hochenwarth), *Megarhyssa nortoni* (Cresson) and *Rhyssa persuasoria* (Linneaus) have become established in most regions (see for Australia: Taylor, 1967; Carnegie *et al.*, 2005; for New Zealand: Zondag, 1959; Nuttall, 1972; for South America: Klasmer *et al.*, 1998; Villacide & Corley, 2003; Eskiviski *et al.*, 2004; Iede *et al.*, 2010; and for South Africa: Tribe & Cillié, 2004). *Ibalia leucospoides* has attracted the most research on biology and behaviour, probably, because of its widespread establishment and distribution.

*Ibalia leucospoides* is considered as an effective control agent of *S. noctilio* in a number of regions (e.g., Haugen, 1990; Carnegie *et al.*, 2005; Collett & Elms, 2009); however, only a few studies suggest that under some conditions its role in regulating the pest population may be secondary to that of other parasitoids (Taylor, 1978; Corley & Bruzzone, 2009). Moreover, variability has been reported in per cent parasitism achieved by this parasitoid, among pine stands, and even within the same region. Most studies that focused on this parasitoid have looked into its host-foraging behaviour and life-history traits (Madden, 1968*b*; Spradbery, 1974; Fernández-Arhex & Corley, 2005; Martínez *et al.*, 2006; Corley *et al.*, 2010; Fischbein *et al.*, 2011, 2012, 2013). Yet none has integrated these traits with the introduction process of the natural enemy in order to understand the variable success of this species as a control agent.

Characterizing established pest–natural enemy interactions may be useful to uncover patterns and consequently improve the accuracy of our predictions of success in classical biocontrol. We review here the history of introduction, ecology and behaviour of the parasitoid *I. leucospoides* (Hymenoptera: Ibaliidae), used to manage *S. noctilio* populations worldwide. We analyse information retrospectively, choosing an invasion ecology perspective. This is because, the three steps followed in the invasion process by non-native species are, arrival, establishment and spread (Lockwood *et al.*, 2007) which are analogous to those expected through classical biological control (release, establishment and pest suppression at the regional scale). We also expect, more broadly, to contribute knowledge to the fundamental basis behind classical biological control of *S. noctilio* and of invasive forest insects in general.

## Arrival and establishment of *Ibalia leucospoides* into new areas

The first step involved in all biological invasions consists of the arrival of individuals of a species to new areas, outside of their native range. Unlike *S. noctilio* that globally has arrived into non-native regions through accidental introductions (Villacide & Corley, 2012) the main pathway by which *I. leucospoides* has arrived into new regions has been the deliberate release of individuals as biological control agents of woodwasp populations (table 1). Still, different levels of human intervention have occurred among different areas of New Zealand, Australia and South Africa. Conversely, the arrival of *I. leucospoides* to South America (Uruguay, Argentina, Brazil and Chile) was initially accidental and probably resulted from its transportation as a by-product within wood commodities attacked by *S. noctilio*. Then, natural dispersal (both active and passive movements) may have facilitated local redistribution. To date the parasitoid has

Table 1. *Ibalia leucospoides* introduction and parasitism rates in different regions in the world.

| Region | Agent[1] | Arrival mode | Origin | Reared | Established | Impact (% parasitism) | Reference |
|---|---|---|---|---|---|---|---|
| New Zealand | *I. leucospoides leucospoides* | Deliberate releases | Europe (England) | Yes | Yes | 28% (ranged: 5–54%) | Rawlings (1951, 1952), Zondag (1959), Nuttall (1970, 1972), Bain *et al*. (2012) |
|  | *I. leucospoides ensiger* |  | USA (through Australia) | Yes | Yes |  |  |
| Australia – Tasmania | *I. leucospoides leucospoides* | Deliberate releases | New Zealand and Europe | Yes | Yes | <10% | Taylor (1967, 1976, 1978) |
|  | *I. leucospoides ensiger* |  | USA (California) | Yes | Yes |  |  |
| Australia – Victoria | *I. leucospoides leucospoides* | Deliberate releases | Europe (England) | Yes | Yes | 55% (ranged: 42–73%) | Collett & Elms (2009) |
| Australia – New South Wales | *I. leucospoides leucospoides* | Deliberate releases | Victoria (original source: Europe) | Yes | Yes | 62% (ranged: 4–96%) | Carnegie *et al*. (2005) |
| *South Africa* |  |  |  |  |  |  |  |
| Western Cape | *I. leucospoides* | Deliberate releases | Uruguay (original source: unknown) | No (but field collecting and releasing) | Yes | – | Tribe & Cillié (2004) |
| KwaZulu-Natal and Eastern Cape | *I. leucospoides* | Deliberate releases | Western Cape (original source: Uruguay and before unknown) | No (but field collecting and releasing) | Yes | – | Hurley *et al*. (2007, 2012) |
| *South America* |  |  |  |  |  |  |  |
| Uruguay | *I. leucospoides* | Accidentally introduced together with *Sirex noctilio* | Unknown | No | Yes | 24% | Iede *et al*. (2010) |
| Brazil | *I. leucospoides* | Accidentally introduced together with *S. noctilio* | Unknown | No (but field collecting and releasing) | Yes | Up to 29% | Iede *et al*. (2010, 2012) |
| Argentina, South region – Andean Patagonian | *I. leucospoides* | Accidentally introduced together with *S. noctilio* | Unknown | No | Yes | 25% | Joffré & Fischbein (unpublished data) |
| North region – Mesopotamia | *I. leucospoides* | Accidentally introduced together with *S. noctilio* | Unknown | No | Yes | Up to 35% | Eskiviski *et al*. (2004) |
| Chile | *I. leucospoides* | Accidentally introduced together with *S. noctilio* | Unknown | Yes | Yes | 25–30% | Beèche *et al*. (2012) |

[1] Crossbreeding between *I. leucospoides leucospoides* and *I. leucospoides ensiger* in different introduced areas prevent the differentiation between these two subspecies (Hurley *et al*., 2007).

been introduced into the most pine-growing areas of the world, although deliberate releases of these insects as a control agent are currently known to occur in Chile, Brazil and South Africa (table 1).

The establishment of non-native populations depends mainly on propagule pressure, environmental characteristics of the invaded habitat and several life history traits of the invasive species (Engelkes & Mills, 2011).

Propagule pressure is defined as the combination of the propagule number (the frequency of introduction events) and propagule size (the number of individuals per introduction event). In the context of classical biological control, propagule pressure is akin to the deliberate releases of the natural enemies (Grevstad, 1999*a*). Hence, propagule pressure and the temporal and spatial patterns of the introductions are important to the initial establishment of the natural enemies in new environment (Lockwood *et al*., 2005; Simberloff, 2009). Increasing propagule pressure may increase the chances of establishment, this is mainly because: (1) large propagule pressure increases the probability to overcome environmental stochasticity, demographic stochasticity and Allee effects (theoretical models: Grevstad, 1999*a*; Hopper & Roush, 1993; empirical evidences: Grevstad, 1999*b*); and (2) large and continuous propagule pressure, mostly arriving from different sources, will serve to increase genetic diversity of the introduced populations which likely enhance the adaptability to new habitats and probably reduce the expected genetic bottleneck effects for small founder populations (Lockwood *et al*., 2005; Fauvergue *et al*., 2012).

The reports on the introductions of *I. leucospoides* worldwide suggest that establishment success has occurred in many, although not in all regions or areas. In New Zealand, *I. leucospoides ensiger* and *I. leucospoides leucospoides* were imported, reared and released during several years. Despite successful population establishment, the available data suggest a 'haphazard approach' to natural enemies releases (Zondag, 1959; Nuttall, 1970, 1972). In Australia, releases also occurred through successive years and the establishment of populations was successfully achieved (Taylor, 1967, 1976; Neumann & Minko, 1981; Haugen, 1990; Carnegie *et al*., 2005; Collett & Elms, 2009), but again no quantitative recommendations may be drawn from insect releases. In South Africa, establishment has succeeded too. In South America in turn, the scenario is different because *I. leucospoides* arrived accidentally together with *S. noctilio*. Despite this, it has established populations. With the exception of Chile, no other country is rearing this species for planned releases (table 1).

It is difficult from the reported experiences to determine an appropriate release strategy that not only takes into account the relative role of the number of individuals released versus number of releases, but also the configuration of releases over time and across the space. The relationship between propagule pressure and the probability of establishment might take on a variety of forms depending on the levels of environmental variability and Allee effects. While the propagule size serves to overcome demographic stochasticity and negative effects of inverse density-dependent forces (Grevstad, 1999*b*; Fauvergue & Hopper, 2009); propagule number serves to reduce the influence of environmental stochasticity (Grevstad, 1999*a*). The limited information and the lack of systematic, comparable experiences of deliberate releases, of *I. leucospoides* in this case, obscure the definition of more effective release strategies of this or other parasitoids.

Several environmental characteristics can influence the chance that forest pests and their natural enemies establish successfully in new areas. Site conditions, resource availability, climate, host tree species planted, presence of other tree-killing insects, stand management, age, tree growth rates and the size and configuration of stands in the landscape, among others. For natural enemies, climate and resource availability may be relevant not only to the establishment, but also to the level of suppression they may achieve.

Climatic matching between the native area and the new habitat is, for natural enemies of exotic pests, a search criteria used in classical biological control (Kidd & Jervis, 2005). The conventional wisdom is that a good climatic match, favours not only natural enemy adaptation to the new habitat (and its establishment), but also contributes to developmental synchrony of the natural enemy with its host. Temperature can directly affect insect development and, lack of synchronicity between pest and parasitoid can affect the stability and persistence of coupled interaction, and of course, suppression levels (theoretical model: Corley *et al*., 2004; Corley & Bruzzone, 2009). For many forest insects such as *S. noctilio*, development can be delayed and emergence spread out for several years. Prolonged diapause in insects may prove adaptive in unpredictable environments (Menu *et al*., 2000) but is affected by climate and this, in practice, might have an effect on the suppression levels achieved by parasitoids. Corley & Bruzzone (2009) have shown through modelling, how the proportion of the host population that displays extended diapause, coupled with the host rate of increase (e.g., from endemic to outbreak levels) and the kind of physiological interaction between pest and natural enemies (i.e., koinobiont *vs*. idiobiont host–parasitoid relationships), can have important consequences on host suppression levels. Specifically, the model predicts that idiobiont parasitoids are more capable of increased host population suppression at a higher proportion of the host population in prolonged diapause than koinobiont ones.

The distribution of *S. noctilio* in the Southern Hemisphere includes regions with different climatic conditions: temperate Mediterranean climates (e.g., mainland Australia and Southern South Africa) similar to the southern parts of the species native range, colder climates (e.g., Southern Argentina, Chile and Tasmania), and warm semi-tropical areas (e.g., Brazil and some parts of South Africa) (Lantschner *et al*., 2014). These climate regimes imply that different fractions of the population will develop at different rates. As such, the koinobiont parasitoid *I. leucospoides* seems to perform better in warmer and drier regimes where the incidence of prolonged diapause is lower (Taylor, 1978; Corley & Bruzzone, 2009). It is worth mentioning that in their native range *I. leucospoides* shows a greater percentage of emergence in temperate to warmer climates, whereas *R. persuasoria*, another idiobiont biocontrol agent used, does so in temperate to cold climates (Spradbery & Kirk, 1978). Thus, the local climatic conditions and how parasitoids deal with their host emergence patterns should be also taken into account when selecting natural enemies for several forest pests.

Considering that females of the vast majority of parasitoid wasps consume some kinds of food during their adult lifetime and the potentially positive effects of the dietary nutrients have on life-history traits such as longevity, fecundity or flight activity (Bernstein & Jervis, 2008), it is expected that success in establishment of natural enemies will be influenced by the availability of suitable food sources. In this context, recent studies have explored the role of food consumption on different aspects of *I. leucospoides* behaviour and biological functions, either in laboratory or in natural scale representative experiments (table 2). The results obtained show that providing adults with food in captivity does not affect their dispersal capacity (Fischbein *et al*., 2011), neither does host patch exploitation rules (Corley *et al*., 2010) nor the total egg production (Fischbein *et al*., 2013), while it has a small influence on female olfactory response to cues associated with food and host foraging (Pietrantuono *et al*., 2012). Sugar-rich foods can have a positive effect on female parasitoid longevity but only when it is provided *ad libitum*, an unrealistic case (Fischbein *et al*., 2013). It is important to note here that the beneficial effects of feeding in many species have been generally shown through laboratory experiments, and that knowledge of food foraging and its consequences on reproductive success and parasitoid performance in the field is still limited (Lee & Heimpel, 2008*a*). For *I. leucospoides*, the influence of food consumption on the metabolism of laboratory females whose feeding regime was known, together with food acquisition by free-foraging wasps in the wild was studied and compared (Fischbein *et al*., 2013). This work showed quantitative changes in carbohydrate levels for females fed in captivity, despite the lack of food effects on traits (see below for a more detailed discussion on this); and although information obtained on the feeding behaviour of free-foraging wasps is partial, it has been suggested that food intake in natural conditions, while possible, may not be frequent in tree pine plantations (Fischbein *et al*., 2013). In summary, none of the fitness-related traits studied demanded to be fuelled after emergence. This knowledge is useful to establish insect holding conditions in the context of mass-rearing and to consider that the lack of food intake may not be a handicap for this parasitoids performance in pine plantations.

Some species have traits that enable them to establish successfully even if they are released in small quantities, whereas others require significant propagule pressure to achieve the same result. Understanding the way that life-history traits and individual behaviours contribute to the establishment and growth of populations, although regarded as a prerequisite for the improvement of biological control, is neither a simple nor a straightforward issue.

The potential reproductive output and the probability of surviving long enough to realize this potential are considered the main components of parasitoids fitness, and hence, have an important role in the establishment of new populations. Females of *I. leucospoides* emerge with more than 75% of their total egg complement mature and the remaining eggs are matured throughout their adult life (Fischbein *et al*., 2013) (table 2). This high proportion of mature eggs early in life together with the total egg load ($\approx$ 600 eggs) suggests both that *I. leucospoides* is not egg-limited and that this may positively influence the success of population establishment. In addition, the significant initial investment in reproduction may represent a reproductive advantage for this parasitoid species that attacks a host with an unpredictable pulse-like outbreak dynamics and an aggregated spatial distribution. That is, female wasps could be able to use all egg-lying opportunities when hosts are available, even early in life. Parasitoid females live an average of 24 days in laboratory conditions without food (Fischbein *et al*., 2013). When food supply is provided *ad libitum* longevity increases by 42% (Fischbein *et al*., 2013). This augmentation is not negligible but modest compared with that of other parasitoids (e.g., Siekmann *et al*., 2001; Desouhant *et al*., 2005; Lee & Heimpel, 2008*b*). Females of this species may emerge with robust energy reserves to support maintenance requirements without adult feeding, besides survival seems not be a constraint to population establishment.

Dispersal capability and host-searching abilities are also important attributes to the lifetime reproductive success of parasitoid and probably contribute to the success of establishment and population growth. In turn, in harsh environmental conditions – where the host density can be very low and host distribution highly heterogeneous, as during *S. noctilio* endemic population phases – they could act as significant fitness constraints for parasitoids.

Potential dispersal capacity of *I. leucospoides* does not match that of its host. *Sirex noctilio* can fly nearly 50 km in a day in flight mills (Bruzzone *et al*., 2009) while *I. leucospoides* cannot exceed 28 km/day in identical conditions (Fischbein *et al*., 2011). Although *I. leucospoides* may be unable to track its host at a regional scale by individual flight, its flight capacity may not be a barrier to local redistribution (i.e., within a release area). The potential dispersal distance displayed by this hymenopteran species is such that it may prevent the negative impacts of very low or very high dispersal capability on establishment (table 2). Namely, a high probability of inbreeding at release sites associated with low dispersal or the high risk of Allee effects at the leading edge of the introduction front due to too much dispersal (Heimpel & Asplen, 2011).

There is evidence showing that this parasitoid is able to deal with several potential problems involved in host foraging (Corley *et al*., 2010; Fischbein *et al*., 2012) (table 2). Female wasps are able to accurately assess differences in host patch quality from a distance without the need of following a sampling process (i.e., to make direct contact with host patch). Also, females can adjust patch exploitation times to the richness of the current patch visited and probably to the profitability of the surrounding context. Finally, wasps appear not to be affected by other females foraging in the same patch. Hence, females of *I. leucospoides* seem to have evolved both a high sensitive ability to detect chemical cues specific to *S. noctilio* but moderate responsiveness to host availability while a patch is being exploited by others. It is known that *I. leucospoides* uses volatile chemical cues derived from the host fungal symbiont during the host-searching process, which provides information on the host presence (Madden, 1968*b*; Spradbery, 1974) and on the relative densities of hosts on the patches (Martínez *et al*., 2006; Fischbein *et al*., 2012). Efficiently finding the host can be translated into fitness gains especially considering *S. noctilio* ecological traits. Whereas pine plantations are generally characterized by a regular spatial arrangement, trees attacked by *S. noctilio* are typically aggregated, especially during the long lasting, endemic population phases (Corley *et al*., 2007). The distribution of attacks by *S. noctilio* within these clumps shows different degrees of heterogeneity (i.e., low or high degrees of variance in the number of woodwasp larvae per stem). On the contrary, during outbreak periods, overall infestation levels can be high, affecting many trees (i.e., 80% of a given stand) and rendering spatial distribution less heterogeneous. Accordingly, the abundance and spatial distribution of *S. noctilio* can vary not only among plantations but also within stands, and in the course of a single flight season as well as in subsequent generations, resulting in varying levels of heterogeneity. In this context, females of

Table 2. Life history traits and behaviours of *Ibalia leucospoides* female parasitoids.

| Egg load | | | | Longevity (days) | | | Potential flight capacity (km)[1] | |
|---|---|---|---|---|---|---|---|---|
| Initial egg load (21) | Lifetime potential fecundity (11) | Realized fecundity (9) | OI | Starved wasps (22) | *ad libitum* fed wasps (22) | Maximum distance flown recorded (1) | Mean distance flown (65) | Effect of housing with con-specifics on distance flown |
| 466.76 (k) | 607.91 (k) | 276.19 (k) | 0.77 (k) | 24 (k) | 35 (k) | 28.23 (h) | 10.65 (h) | No (h) |

| Host foraging behaviour | | | | Access to sugar-rich food | |
|---|---|---|---|---|---|
| Patch choice decisions and host location | Hosts patch use | Interference competition | Functional response | Affects | Not affect |
| Probably follows α and β-terpenes emitted by stressed trees to find potentially host-rich pine trees (b, c) | Patch residence time (PRT) increases with host numbers in the patch when female forages alone or with others individuals in single or mutiple-patch experiments (f, g, i) | Some interference can occur when two females forage for a host in a same patch in a single patch environment (g) | Type III (d) | | |
| Detect differences in concentration of volatile chemical cues derived from the host fungal symbiont free of tree or host chemicals (a, e) | Use the information available from the local environment to adjust patch exploitation times (i) | No interference occurs when several females simultaneously forage for host in a multiple-patch environment (f) | | | |
| Accurately assess differences in host patch quality (host numbers per patch) from a distance (i) | Activity increases with fungal volatile grown on an artificial medium (e) | | | | PRT (f)<br>Flight (h)<br>Food and host searching decisions (j) |
| Select the patch bearing the highest number of hosts (i) | | | | Longevity (k) | Egg maturation (k) |

OI, ovigeny index, estimated as the ratio between the initial egg load and lifetime potential fecundity.

[1] flight capacity measured in flight mills under laboratory conditions.

PRT, patch residence time.

Numbers between brackets are the replicates.

(a) Madden (1968b), (b) Spradbery (1974), (c) Madden (1988), (d) Fernández-Arhex & Corley (2005), (e) Martínez *et al.* (2006), (f) Corley *et al.* (2010), (g) Fernández-Arhex & Corley (2010), (h) Fischbein *et al.* (2011), (i) Fischbein *et al.* (2012), (j) Pietrantuono *et al.* (2012), (k) Fischbein *et al.* (2013).

*I. leucospoides* demonstrate abilities to manage changes in habitat profitability.

Aggregated spatial distribution of hosts may induce parasitoid aggregation which may lead to an increase in individual encounters. These congregations on a patch may promote con-specific interference resulting in a reduction of parasitism rates and maybe in a decrease of establishment probability of an initial population. However, recent works on *I. leucospoides* in which several or a pair of females were watched while foraging on logs of varying host densities suggest that interference competition is minimal and that the time allocated to the patch is more affected by host density than by the presence of other individuals on it (Corley *et al.*, 2010; Fernández-Arhex & Corley, 2010). Probably in their natural environment, wasps may not be host limited at the scale of an infested tree.

## Geographical spread of *Ibalia leucospoides*: region-wide pest control

The spread of natural enemies can be seen as the expected outcome of deliberate releases aimed at a region-wide pest control. Spread occurs when species expand their geographic range and, population growth (reproduction) and dispersal (involving short- and long-range movements) are the two key components underlying this process. Environmental factors can also be relevant, because of their direct or indirect effects on reproduction and/or dispersal behaviour. As for invasive species, human aided-transport beyond their natural dispersal range also largely contributes to geographical spread (Liebhold & Tobin, 2008).

There is limited information from which to estimate *I. leucospoides*' spread rate. There are only a few historical records of the presence of this species in areas where no deliberate releases were made for Tasmania and New Zealand (Taylor, 1967; Nuttall, 1972). From this scant information we obtained a very rough estimate of both spread rates and natural dispersal distances (as in Masciocchi & Corley, 2012). The mean spread distance for *I. leucospoides* in Tasmania was 48.74 ± 7.79 km (mean ± SE, $n = 7$), with a minimum and maximum distance covered from the point of introduction of 28.96 and 80.46 km, respectively (Taylor, 1967). The rate of spread for that region was approximately 8 km/year. In New Zealand, the mean distance was 20.19 ± 3.55 km (mean ± SE, $n = 15$), while the minimum and maximum distances covered from the nearest point of introduction was 2.81 and 51.49 km, respectively (Nuttall, 1972). The estimated rate of spread for New Zealand was of approximately 2 km/year.

For the sake of managing invasive woodwasp populations, *I. leucospoides* is unlikely to track (naturally) the leading edge of the pest populations. *Sirex noctilio* spread rates, ranged from 11 to 78 km/year depending on the geographical region (Lantschner *et al.*, 2014). As mentioned before, several factors affect the spread process; climate for instance, influences *S. noctilio* development, which can affect *I. leucospoides* population growth rate and thereby its spread. In addition, habitat characteristics such as stand connectivity at the landscape level, coupled with host resource depletion because of a possible exponential growth of the parasitoid population during a post-outbreak period could be factors that may influence spread. Further field studies are needed to actually learn whether dispersal capacity and spread act as constraints to colonize new pest-attacked habitats. Still, if the goal of the parasitoid releases is to achieve a regional control, this limitation can be overcome by human-aided redistribution of the natural enemies, following local establishment rules.

## A note on selection criteria in classical biological control

Selection criteria in biological control are, from an empirical standpoint, a controversial issue. The general idea is to favour success in natural enemy introductions prior to their importation, quarantine, mass rearing and release protocols are issued by looking for, in their native habitat, those species that are most important in terms of their potential impact on pest population. Decisions on which biological control agents are potentially better are frequently based on reductionist criteria or else by using a holistic approach. The problem with the former approach is by knowing which attributes make for better natural enemies. The holistic perspective, in turn, implies in-depth understanding of underlying mechanisms of the host–parasitoid interaction (Kidd & Jervis, 2005). In table 3, we list several attributes that could be considered in the selection process of natural enemies (based on Kidd & Jervis, 2005).

For *I. leucospoides*, none of these approaches has been clearly described. Original introductions into New Zealand consisted, as probably determined by the significance of the pest problem, in massive releases of a variety of parasitoids and empirically assaying species establishment. Despite the fact that at first sight *I. leucospoides* meets in general, sought out attributes of parasitoids for classical biocontrol, several ecological characteristics may, through an *a posteriori* approach, explain current variability in suppression success.

Significant spatial heterogeneity in parasitism in pine plantations may lead to local persistence of parasitoid–host populations but at the expense of lower suppression. This could be a possible scenario for *I. leucospoides* in all areas where it is present. Alternative explanations for the low levels of suppression achieved in some sites and regions could be linked to generation time ratio (close to 1, while this parasitoid species may be trapped in host diapause). In addition, long generation times can also decrease the capacity of *I. leucospoides* to follow variations in host density leading to a slower numerical response. *Ibalia leucospoides* has a type III functional response as described by Fernández-Arhex & Corley (2005); this implies acceleration in attacks as the parasitoid becomes increasingly efficient at finding hosts. Still in the wild, attacks probably level off rapidly because of the influence of handling time in host exploitation by this parasitoid (each oviposition takes 5–20 min; D. Fischbein, personal observation).

## Discussion and conclusions

Classical biological control likened to what is known for biological invasions, may be described as a process with at least three distinct successive stages; arrival or introduction, establishment and, spread or pest suppression at regional scale, with transitions or barriers in between that must be overcome by the control agents. Each of these stages is governed by different ecological processes, life-history traits and behaviours of the species involved in, either the invaders or natural enemies (Lockwood *et al.*, 2007; Engelkes & Mills, 2011). From this species-specific review, we may draw several conclusions for this and other host–parasitoid systems involving pests of long-lived crops where classical biocontrol is implemented.

Table 3. Biological attributes (i.e., selection criteria) of natural enemies in general (and *Ibalia leucospoides* in particular) considered as the most desirable for classical biological control (Kidd & Jervis, 2005).

| Biological attributes | Expected | Suggested qualitative value for *I. leucospoides* | Interpretation |
|---|---|---|---|
| Attack rate ($r_a$) | High | Intermediate | It is set by handling time and/or egg-limitation. *Ibalia leucospoides* displays lengthy handling times per host-decreasing attack rate |
| Spatial heterogeneity in parasitism | Intermediate | High | Spatial heterogeneity in parasitoid attacks, through host refuges, leads to a strong *trade off* between the stability of parasitoid–host populations and the degree of host suppression. *Ibalia leucospoides* aggregation may lead to local persistence but at the expense of lower suppression |
| Development time | Short | Long (and also depends on host diapause) | Longer development time leads to exponential increases in the pest equilibrium and reduce stability |
| Maximum level of parasitism in the pest's region of origin | High | Intermediate | Control outcome occurs at maximum parasitism rates in host native range of about 35%, as minimal threshold; below this level biological control rarely achieves economic success. Parasitism by *I. leucospoides* is about 21.8% (Spradbery & Kirk, 1978) |
| Fecundity | High | High | It is a key determinant of attack capacity or potential fecundity (the maximum number of hosts that a parasitoid can attack in its lifetime) |
| Gregariousness | High | Solitary | The number of female parasitoids produced per clutch has been identified as a major factor in pest suppression |
| Phenological synchrony | High | High | Phenological matching reduces the temporal refuge effect of host, reduce the host equilibrium level and stabilize the parasitoid–host population interaction |
| Intrinsic rate of population increase ($r_m$) | High | $r_m$ unknown and $r_a$ highly variable according the site | $r_m$ may enhance by a greater searching efficiency, a greater attack capacity and a greater degree of gregariousness. A natural enemy having a lower $r_m$ than that of its host would not be necessarily a poor biological control agent. The parasitoid should only have an $r_m$ high enough to offset that part of the host's $r_m$ that is not annulled by parasitism or host-feeding. |
| Numerical response | Fast | Slow/delayed | Not always a rapid numerical response is desirable. The potential value of a numerical response should be assessed in relation to the population growth rate of target pest. This can avoid delayed density dependence or overcompensation fluctuations that can limit cycles or decrease stability |
| Generation time ratio | <1 (small) | 1 | It is the ratio of the natural enemy's generation time to that of its host or prey. This relationship could be used to predict the effectiveness in controlling short-lived or long-lived pests |
| Mode of reproduction | Haplodiploidy | Haplodiploidy | Haplodiploid populations could overcome reproductive Allee effects |
| Destructive host feeding (different host individuals are used for feeding and oviposition) | Questionable | Absent | While theoretical approaches suggest this attribute as non-desirable because destructive host-feeders parasitoids are predicted to be inferior, compared to other parasitoids, with regard to establishment and success rate; database analyses shows that destructive host-feeders are as good as other parasitoids |
| Dispersal capability | Intermediate to high | Intermediate | Seeking for high dispersal capability depends on whether the aim is set at local or regional control of pest. High dispersal would allow both natural enemy to spread rapidly from the release site reducing the efforts (time and money) invested in large number of release sites to distribute populations over a wider area, and it also promotes re-invasion of areas where the natural enemy may have become extinct. However, too much dispersal may increase the risk of mate-finding failure at the leading edges of the introduced range, favouring Allee effects |

| | | | |
|---|---|---|---|
| Degree of host specificity | High | High | Specialist natural enemies have more chances of maintaining pest population at low equilibrium than generalist species that will concentrate on the more abundant alternative host. In addition, generalist organisms pose risks to non-target species |
| Degree of climatic adaptation | High | Relative to the introduced region, however, presents a wide-range successful establishment | High degree of climatic match between original and target localities increases the chance of successful establishment and effectiveness of natural enemy population |
| Handling and culturing | Easy | Difficult | This issue is considered one of the most important factors in choice of natural enemies in classical biological control programmes. The most recurrent problems in *I. leucospoides* rearing are: (1) the maintenance of the moisture content of the breeding logs over time which affects the number and larval size of *Sirex noctilio* and thus of *I. leucospoides* and, (2) the increasingly difficult to obtain nematode-free *S. noctilio* as a consequence of the policy of artificially spreading of nematode worldwide |

Firstly, we note that it is likely that the success in establishment of parasitoid populations may not always be a limiting factor. Planned releases that take into account propagule pressure over time and across the space may reduce the chances for demographic extinction and Allee effects (Grevstad, 1999*a*, *b*). For *I. leucospoides*, propagule pressure remains unknown, but successful establishment may be explained by good climatic adaptation, high reproductive potential early in life, the lack of a need for feeding in the field, great abilities to find host and a flight capacity that allows local redistribution. An important point here refers to the need for detailed quantitative descriptions of natural enemy releases in classical biological control. Such information may help in improving our understanding of those processes that may have influence on the most important causes of failure reported for biological control.

Secondly, in managing highly invasive pests, the spread capacity displayed by parasitoids is important to achieve long term, widespread suppression of the pest populations. The range potentially occupied by *I. leucospoides* is smaller than that of *S. noctilio*. But, given that natural dispersal while improving geographic spread may compromise establishment, moderate natural dispersal may be a positive trait whenever releases can be planned at the regional scale. How much parasitoid natural dispersal is optimal remains an open question of great importance, likely to be solved through modelling, given the increasing pest problems caused to forest ecosystems arising from non-native insects.

Another long-standing issue, particularly so for pests that attack long-lived crops such as forests, is how the adequate levels of pest population suppression may be possible with persistence of the interactions (Beddington *et al*., 1978; Murdoch *et al*., 1985; Kidd & Jervis, 2005). The ability and the degree by which a parasitoid can stably suppress the host population depend on several factors (Mills, 2001). The size of the host refuge from parasitism (the larger the refuge, the more hosts escape from parasitism, regardless of what attributes the biological agent may possess), the host net rate of increase and whether the parasitoid is egg or time limited are some of these factors. *Ibalia leucospoides*' attributes and the interaction with its host both suggest that the parasitoid may be a better regulator than suppressor. The spatial and temporal refuges of the host population (i.e., through host aggregated distribution and diapause, respectively) may favour local persistence, but probably reduce the degree to which *S. noctilio* population is suppressed. In addition, *I. leucospoides* has a relatively high potential fecundity and reported abilities in finding concealed hosts, although they may be restricted in total attacks probably because of long host-handling times. Finally, this parasitoid species is unable by itself, to stop a pest outbreak. In other words, persistent parasitoid populations may establish at the cost of region-wide suppression levels.

There may be variations in some life history traits among different populations of *I. leucospoides* as a consequence of environmental effects on phenotype (Ellers & van Alphen, 1997). *Ibalia leucospoides* inhabits most pine-cultivated areas throughout the southern and northern hemispheres, where it likely experiences very different environmental conditions, in terms of climate, host abundance and distribution, and potential interspecific competition. Naturally, life-history variation among populations may also be genetically based. All these elements may limit some of the conclusions we draw here. Additional studies on this and other long-standing and widespread host–parasitoid interactions that consider the genetic and phenotypic variations between populations in a biocontrol context will improve our understanding on the effects of the environment on establishment and suppression.

Throughout this review we have analysed the success of the parasitoid *I. leucospoides* as a model of classical biological control of forests pests in the light of invasion ecology (Fauvergue *et al*., 2012). Classical biocontrol is a key component of modern pest management practices and is particularly important to manage non-native pests. We suggest that through a retrospective analysis of well-studied cases, conclusions on those factors critical to success may be brought to light. Critically, further studies providing quantitative predictions of propagule pressure and natural enemy dispersal behaviour are warranted to contribute to overcome establishment failures. In turn, climatic matching, not only as a factor determining species survival (and establishment) but also through its effects on voltinism and interaction synchronicity, needs careful attention because of its consequences on pest suppression and interaction persistence. This may be especially relevant to pest management in crops such as tree plantations that are relatively long lived and occupy vast surface areas in contrasting environmental scenarios that are currently subjected to changing conditions (Corley & Jervis, 2012; Liebhold, 2012).

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