

Influence of reproductive biology on establishment capacity in introduced Hymenoptera species

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Abstract

Introduced species face numerous biological barriers before they can establish in a new environment. Understanding how they overcome these obstacles is crucial for the development of effective risk assessment and regulation. Reproductive biology is known to influence establishment capacity in plants and is widely used for risk assessment. This biological field should receive more attention, and particularly in the case of insects, as they display a wide range of reproductive traits and have a great impact on the economy and environment. Among insects, the order Hymenoptera is of interest for its diversity, both in terms of reproductive traits and introduction history, as invasive species and biological control agents. We review the main reproductive strategies of Hymenoptera, spanning parthenogenesis, sex determination and mating strategies, and evaluate their effect on invasive potential. For instance, thelytoky could decrease the strength of Allee effects while Arrhenotoky could increase adaptive potential. A species with complementary sex determination could be more affected by inbreeding than other species, while paternal genome elimination could lead to high levels of homozygosity. Finally, some reproductive behaviours could decrease inbreeding, facilitate mate location or adaptation by encouraging admixture. The two invasive species *Apis mellifera scutellata* and *Leptocybe invasa* and the biocontrol agent *Aphidius ervi* serve as case studies to illustrate the effect of reproductive traits on species capacities to become established in a new area.

Key words: Invasive species, Insects, Reproductive traits, Introduction, Biological control

Introduction

There are now so many introductions of non-native species that nations need to prioritize the management of the species that present the highest risks (McGeoch et al. 2016). Management frameworks that can prioritize the control of certain species are already in place in some countries (Ward et al. 2008; Courtois et al. 2018). However, these frameworks still involve high

management costs and low success rates. Additionally, despite the large number of attempts to introduce biological control agents into new areas, many fail (Hajek 2018). Management strategies and biological control programs could both benefit from the consideration of the influence of reproductive biology on the establishment success of exotic species.

Reproductive traits such as sex determination, gametogenesis and mating strategies impact population dynamics (Baker 1955; Maynard Smith 1978; Courchamp et al. 1999; Wiernasz et al. 2004; Zayed and Packer 2005), adaptation (North et al. 2011; Hartfield and Keightley 2012), fitness (Tregenza and Wedell 2002; Mattila et al. 2012; Poorjavad et al. 2018) and population genetics (Gerrish and Lenski 1998; Rabeling and Kronauer 2013; Arca et al. 2015). For these reasons, some have argued that reproductive strategies are one of the factors that influence the capacity of insects to establish (Stouthamer 1993; Holway and Suarez 1999; Aron 2001; Kronauer et al. 2012). Other factors that also affect the capacity of insects to establish are propagule pressure (Lockwood et al. 2005), life history traits (Sakai et al. 2001) or ecological niches (Peterson 2003). Yet, despite this evidence, reproductive biology is rarely used as a predictive tool for risk assessment or as a building block of management programs against invasive insects.

The order Hymenoptera (e.g. bees, wasps, ants) exhibits a great diversity of reproductive traits. For this reason, this order can be used to illustrate the effect of reproductive biology on establishment capacity in insects. This order is also a highly diverse group of insects that contains numerous invasive species. Invasive hymenopteran species can have substantial negative ecological and economic impacts, and as a result, are of concern to policy makers and regulators in many countries. Hymenoptera are also commonly used for the regulation of arthropod pests (Austin and Dowton 2000). For example, 286 of the 574 biocontrol agents introduced in New Zealand since 1870 are Hymenoptera (Ferguson et al. 2007). The advantage of using Hymenoptera as biocontrol agents is that they often have a high degree of host specificity and consequently, a reduced likelihood of non-target impacts which can threaten biodiversity in the introduced range (Van Driesche and Hoddle 1997).

While some past publications have argued that reproductive biology impacts establishment success in insects, the application of this knowledge in management programs is still rare (Ward et al. 2008). The effect of reproductive biology on the invasive capacity of ants has been more widely reviewed in the literature than in any other groups of Hymenoptera. For more information on ant invasions, we invite the reader to refer to Ross and Fletcher (1986); Yamauchi and Ogata (1995); Aron (2001); Suarez and Tsutsui (2008); Kronauer et al. (2012) and Eyer et al. (2018). The aims of this review are i) to collect evidence from the literature and to build an argument towards the use of reproductive biology for the improvement of management programs against exotic insects, ii) to highlight the reproductive traits in Hymenoptera that still require investigation and iii) to offer concrete examples of how management programs should implement this knowledge.

Influence of the types of parthenogenesis on establishment capacity

Advantages of thelytoky over arrhenotoky: population dynamics

In the context of species invasion, thelytoky offers three advantages as compared to arrhenotoky. Thelytoky allows a single female to start a population while decreasing the strengths of Allee effects and might increase population growth (**Fig 1**). These advantages are reflected by the dominance of thelytokous species among invasive insect species in North America (Niemelä and Mattson 1996). Moreover, in some species that exhibit both arrhenotoky and thelytoky, thelytoky is more common among introduced populations than in populations from the native range, like in the ant *Cerapachys biroi* (Kronauer et al. 2012).

Reproductive traits		Effects of the reproductive traits on the elements of the invasion process						
Parthenogenesis	Arrhenotoky							
	Thelytoky							
	Alternation between arrhenotoky and thelytoky							
	Polyembryony							
Sex determination system	Complementary sex determination							
	Maternal imprinting							
	Paternal genome elimination							
	Segregation of the female and male genome							
Reproductive mechanism	Sib-mating							
	Premating dispersal							
	Discrimination against genetically incompatible mates							
	Monoandry							
	Polyandry							

Legend							
	Adaptation	Allee effect	Inbreeding depression	Diploid male extinction vortex	Population growth	Sex ratio	Fitness

Fig. 1. The reproductive traits of hymenoptera (i.e. parthenogenesis, sex determination mechanisms and reproductive mechanisms) can affect the invasion process, either positively or negatively, by acting on various elements of population dynamics (i.e. population growth, Allee effects, adaptation, inbreeding depression, diploid male extinction vortex, fitness and sex ratio). The green drawings represent a positive effect of a reproductive trait on the invasion process (i.e. supports invasion), while the red drawings represent a negative effect (i.e. hampers invasion). Supporting references are given in the text

A single thelytokous female can start a population in a new area. Conversely, a single non-mated arrhenotokous female cannot establish a population, except if she lives long enough to mate with her own sons. The advantage of using asexual reproduction rather than reproducing sexually is an extension of Baker's law. Baker's law states that self-compatible species of plants are more likely to establish a new population after long distance dispersal than self-incompatible species (Baker 1955; Stebbins 1957). Baker points out that a single self-compatible plant can start a new population while self-incompatible species need at least two individuals to do so. Baker was a botanist, but he realized that his law could be extended to other taxa where asexual and sexual species can be compared (Baker 1955; Cheptou 2012). An illustration of this capacity of single thelytokous females to found new populations is the commonality of invasive thelytokous populations that exhibit a single haplotype (MacQuarrie et al. 2007; Kronauer et al. 2012; Dittrich-Schröder et al. 2018; Martinez-Sañudo et al. 2019).

After establishment, when the population is growing, thelytokous species suffer from weaker Allee effects than arrhenotokous populations (**Fig 1**). Firstly, the primary cause of Allee effects is the decrease in the likelihood of locating a mate for reproduction (Courchamp et al. 1999). This constraint does not apply to thelytokous species. Another cause of Allee effects is inbreeding depression due to the low genetic diversity that is usually associated with small population size. In thelytokous species, the level of homozygosity or inbreeding depression within a population depends on the type of thelytoky (**Fig 2**), and not on genetic diversity (Rabeling and Kronauer 2013).

Thelytoky

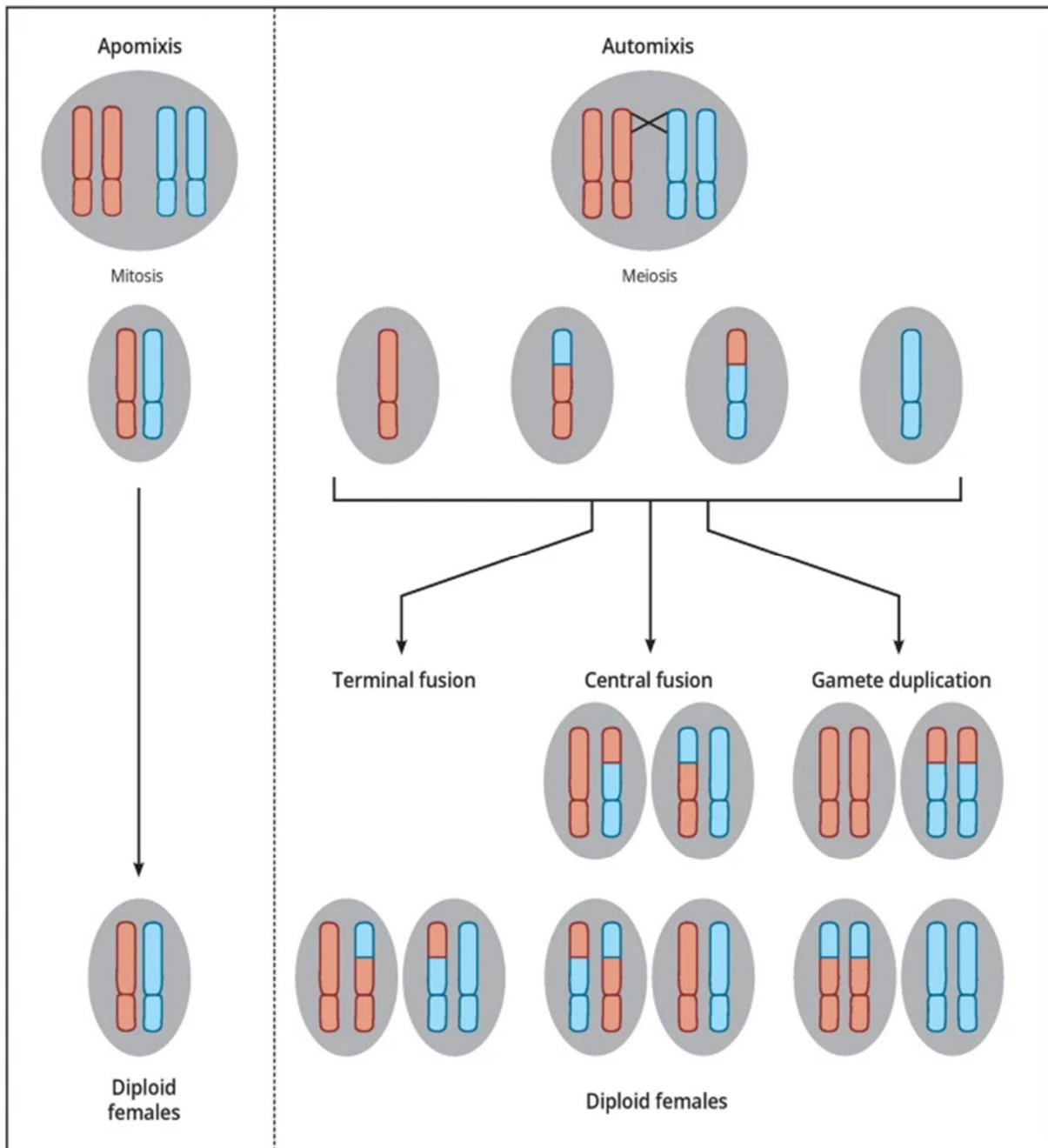


Fig 2. Effects of the types of thelytoky on the levels of heterozygosity in the progeny

(Adapted from (Rabeling and Kronauer 2013))

Therefore, the only factor that could lead to an Allee effect in both a thelytokous and an arrhenotokous population is weakened intraspecific facilitation. When population density is

low, cooperation between individuals is reduced. This can lead to an overall reduction in individual fitness and to an Allee effect (Fauvergue and Hopper 2009).

The impact of Allee effects on invasive populations and on their biocontrol agents are reviewed in Taylor and Hastings (2005). This review highlights that to eradicate an invasive species that exhibits an Allee effect, management programs can aim at reducing populations below the threshold under which the size of the population is too low to expect recovery (Liebhold and Bascombe 2003). Furthermore, depending on the cause of the Allee effect (i.e. decreased mate location, inbreeding depression, reduced intraspecific facilitation), different methods of management should be used and can be combined (Suckling et al. 2012). The authors also highlight available literature (Deredec and Courchamp 2003; Bompard et al. 2013) that suggests that the threshold of a biocontrol agent should be lower than the threshold of their host. This can prevent the extinction of the biocontrol agent while the population of the pest is collapsing.

Theoretical models have predicted that one of the main advantages of asexual over sexual reproduction is that females that reproduce asexually do not use energy in the search for a mate nor in the production of male progeny (Maynard Smith 1978; Otto and Lenormand 2002; Lehtonen et al. 2012). Hence, thelytokous females should produce more daughters than arrhenotokous females, leading to faster population growth in thelytokous populations (**Fig 1**). However, those predictions are not easy to demonstrate experimentally (Lehtonen et al. 2012). Studies that compared the life history traits of thelytokous and arrhenotokous lineages of Hymenoptera species (Stouthamer and Luck 1993; Wang and Smith 1996; Miura and Tagami 2004; Poorjavad et al. 2018) either found a lower or higher intrinsic rate of increase of thelytokous lineages. The link between asexual reproduction and a high population growth rate is not necessarily simple and often varies among species and environmental conditions (Stouthamer and Luck 1993). Furthermore, to our knowledge, no field studies have yet compared the population growth of thelytokous and arrhenotokous lineages over long time scales. This relationship must be quantified to appreciate the effect of thelytoky on

management programmes and on biological control programmes. For example, Stouthamer (1993) suggested that, depending on the population density of the pest, either an arrhenotokous or thelytokous population of the biocontrol agent could be used for mass releases. Future field studies should compare the establishment capacity (i.e. rate of success of establishment, population growth rate, parasitism rate, duration of lag time before spread) of thelytokous and arrhenotokous populations of biocontrol agents introduced in the same conditions (i.e. propagule pressure, host density and abiotic conditions).

The hypothesis of the general purpose genotype (Baker 1965) also highlights an advantage of asexual reproduction over sexual reproduction. This hypothesis suggests that asexual populations tolerate a broader range of environmental conditions compared to their sexually reproducing counterparts. By exhibiting a high phenotypic plasticity, asexual populations could compensate for their lack of genetic recombination and their reduced capacity to create new genotypes (Vrijenhoek and Parker Jr. 2009). *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae) is an example of broad environmental tolerance in an invasive clonal population (Avtzis and Matoševi 2013). The invasive populations of the gall wasp present across southern Europe were constituted of only one haplotype (Martinez-Sañudo et al. 2019). Furthermore, this haplotype is also largely distributed across the native range of the gall wasp, in China. Another example are the globally distributed invasive haplotypes of *Leptocybe invasa* (Dittrich-Schröder et al. 2018).

Advantages of arrhenotoky over thelytoky: genetic diversity and adaptation

Despite the long-standing debate over the advantages of sexual over asexual reproduction, it is largely agreed that sex facilitates adaptation (**Fig 1**) thanks to chromosome segregation and recombination (Maynard Smith 1978; Gillespie 1998; Otto and Lenormand 2002; Hartfield and Keightley 2012). During the invasion process, sexual reproduction allows admixture to occur between successively introduced populations of the same species or even hybridization between two closely related species (Boissin et al. 2012). Through this process, an introduced population can acquire new alleles or even new genes by mating with a different population or

species. For example, Harpur et al. (2012) demonstrated that, due to admixture, North American and European managed honeybees are now more genetically diverse than their progenitor populations from Eastern and Western Europe.

The subsequent recombination and shuffling of alleles to form new genotypes gives sexually reproducing species a wider range of genotypes on which natural selection can act (North et al. 2011). For example, Plantard et al. (1998) compared the genetic diversity of eight thelytokous and two arrhenotokous populations of *Diplolepis spinosissima* (Hymenoptera: Cynipidae). They found 26 and 46 different genotypes in the two arrhenotokous populations, but no more than three in the thelytokous ones. An exception is *Leptopilina clavipes* (Hymenoptera: Figitidae) where arrhenotokous and thelytokous populations exhibit the same level of genetic diversity (Pannebakker et al. 2004). However, Pannebakker et al. (2004) demonstrated that arrhenotokous individuals regularly turn thelytokous, creating new asexual lineages. Hence, the high level of diversity observed in the thelytokous populations originates from the sexually reproducing populations and not from successive mutations in thelytokous individuals. The cases of *D. spinosissima* and *L. clavipes* indicate that a thelytokous population is unlikely to create new genotypes without the intervention of sexual reproduction.

Certain types of thelytoky are disadvantageous to introduced species. Automictic parthenogenesis always results in increased homozygosity within the progeny, with automixis with central fusion leading to less homozygosity than automixis with terminal fusion and gamete duplication (Rabeling and Kronauer 2013) (**Fig 2**). For example, both the ant *Cataglyphis cursor* and the honey bee *Apis mellifera capensis* show a decrease in heterozygosity over time due to apomictic parthenogenesis with central fusion (Baudry et al. 2004; Pearcy et al. 2006). Additionally, Mateo Leach et al. (2012) studied the population genetics of *Venturia canescens* and compared arrhenotokous and thelytokous populations and observed that arrhenotokous populations had significantly higher heterozygosity than thelytokous populations. The level of heterozygosity within a population affects the chances that a population will survive a changing environment and adapt over time. Consequently, if a

species is introduced in an area with environmental conditions that differ from the native range, an arrhenotokous population would have a higher chance of establishment compared to a thelytokous one.

A thelytokous population only obtains new beneficial allelic combinations through mutation and migration. In an introduced thelytokous population, introduced genotypes would not mix but rather would compete with one another. This form of intraspecies competition is called clonal interference. Rare mutations that are beneficial could then be lost if the individuals carrying them belonged to a genotype that was outcompeted (Muller 1932; Gerrish and Lenski 1998). To our knowledge, the phenomenon of clonal interference has never been observed nor studied in the hymenoptera and thus should receive more attention. Population genetics studies that focus on introduced thelytokous species should follow changes of population structure over time in order to detect the replacement of a genotype by another during establishment and spread. The rarity of mutation events, the absence of recombination and clonal interference all work against the increase of allelic richness in a thelytokous population and would reduce the rate of adaptation.

The capacity of a biological control agent to adapt after introduction is crucial for the success of a management programme. Tomasetto et al. (2017) demonstrated that *Listronotus bonariensis* (Coleoptera: Curculionidae) evolved resistance to its biocontrol agent, the parasitoid *Microctonus hyperodae* (Hymenoptera: Braconidae). The appearance of resistance in the pest led to a 44% decrease of the size of the parasitoid population and to high pasture damage. The biological control agent is thelytokous and might have reduced adaptive capacity compared to its sexually reproducing host. For biocontrol, species using arrhenotoky and other reproductive traits facilitating adaptation, should be chosen over thelytokous species. To compensate for the stronger Allee effects faced by arrhenotokous species, biological control programmes can increase the diversity of populations by increasing propagule number and diversifying origins.

Advantages of exhibiting both arrhenotoky and thelytoky

Some species are not strictly arrhenotokous or thelytokous, but exhibit both reproductive strategies either in different populations or across different generations. In the wasp *Venturia canescens* (Hymenoptera: Ichneumonidae) some populations are thelytokous while others are arrhenotokous (Schneider et al. 2002). Species like this might have an advantage over strictly arrhenotokous or thelytokous species for introduction and invasion. In the parasitoid wasp, *V. canescens*, arrhenotokous and thelytokous populations occur sympatrically (Schneider et al. 2002) and mating is possible between an arrhenotokous male and a thelytokous female (Schneider et al. 2003). They also found that 30% of mating events led to the appearance of the male genome in the progeny. This study highlighted the possibility of gene transfer between arrhenotokous and predominantly thelytokous populations. The use of both reproductive strategies could modify the processes of invasion of a species by facilitating the adaptation of thelytokous populations to new environmental conditions. This could occur if a species is introduced from two populations that exhibit different reproductive strategies. The recombination of favourable alleles and fast adaptation that arise in the arrhenotokous population could be channelled to the thelytokous population. The thelytokous, potentially faster growing population, could then spread more easily.

Some species exhibit cyclical parthenogenesis, where the alternation between both reproductive strategies is observable within the same population (Stone et al. 2007). An example of cyclical parthenogenesis is found within the family of gall forming wasps Cynipidae that alternates each generation between arrhenotoky and thelytoky (Folliot 1964). Species that exhibit parthenogenetic cycling benefit from the advantages of both arrhenotoky and thelytoky (**Fig 1**) (Folliot 1964; Stone et al. 2002). The thelytokous generation can avoid strong Allee effects (Courchamp et al. 1999) and result in rapid population growth (Lehtonen et al. 2012). For example, in the thelytokous generation of the cynipid gall wasp, *Andricus quercuscalicis* (Hymenoptera: Cynipidae), females carry 1000 eggs on average while the sexual females carry an average of 10 eggs (Hails and Crawley 1991). This difference in fecundity influences

population dynamics in the field where the thelytokous generation causes significantly higher levels of infestation (35-60%) than the arrhenotokous generation (2-8%). For a successful invasion, an introduced species should be fast growing, first to avoid the impact of genetic drift due to a bottleneck after release (Frankham 2005) and then to disperse rapidly during the spreading phase. To establish and become invasive, introduced species must also be able to adapt to new environmental conditions. In the arrhenotokous generations of a species with parthenogenetic cycling, reshuffling of alleles can promote adaptation (Plantard et al. 1998; Pannebakker et al. 2004). Because fast population growth is generally associated with thelytoky (Poorjavad et al. 2018), and adaptation with arrhenotoky (North et al. 2011), a species alternating between thelytoky and arrhenotoky could experience the benefits of both reproductive strategies.

Effects of polyembryony on establishment capacity

When compared with non-polyembryonic species, polyembryonic species benefit from a greater fecundity, which, in the right conditions, can lead to a greater population growth (Kfir 1981) (**Fig 1**). *Copidosoma koehleri* (Hymenoptera: Encyrtidae) and *Apanteles subandinus* (Hymenoptera: Braconidae) are two biological control agents of the potato tuber moth, *Phthorimaea operculella* (Watmough et al. 1973). *Copidosoma koehleri* is polyembryonic and produces around 3000 offspring in its lifetime (Kfir 1981). On the same host species, *A. subandinus*, which is not polyembryonic, produces around 300 offspring (Cordona and Oatman 1975). Fast population growth reduces the likelihood that a population will go extinct after introduction by suppressing Allee effects that are due to inbreeding depression (Frankham 2005). Consequently, polyembryony might facilitate introduction (**Fig 1**). However, polyembryonic females produce a reduced number of genotypes equal to the number of oviposition events (Craig et al. 1997). In *C. koehleri*, females produce around 100 genotypes (Kfir 1981) against 300 in *A. subandinus* (Craig et al. 1997). It is assumed that lower variation among the progeny can reduce the capacity of polyembryonic species to adapt to new environmental conditions (**Fig 1**).

For an introduced species, polyembryony might offer an advantage for a population introduced in low densities and that does not need to adapt to its new environment. Conversely, polyembryony might reduce the chances of adaptation and survival for populations experiencing strong selective pressure in the introduced range. Polyembryonic species are frequently introduced and used as biocontrol agents against a wide variety of insect pests. Some studies have compared the efficiency of polyembryonic and non-polyembryonic species in terms of insect pest regulation after a successful establishment (Pucci et al. 2003; Unruh et al. 2003). However, the establishment capacity of exotic polyembryonic parasitoids has not been studied in terms of their proneness to suffer Allee effects, local adaptation or lag time between establishment and spread.

Influence of the sex determination mechanisms on establishment capacity

CSD and the diploid male extinction vortex

The influence of CSD on population dynamics has been studied in the context of species conservation. Zayed and Packer (2005) demonstrated that si-CSD increases the chances of extinction through the diploid male extinction vortex (**Fig 1**), a feedback loop precipitating the extinction of small populations with si-CSD. For such a process, small population size can facilitate genetic drift and the loss of allelic diversity at the sex determination locus. Consequently, there is a higher chance that females will mate with a male carrying the same allele and will produce diploid males. The resulting production of diploid males leads to a reduced number of females and a decrease in population growth. Similarly, in introduced populations, the introduction bottleneck could trigger a diploid male vortex and ultimately reduce the likelihood of establishment.

The introduction of *Vespa velutina nigrithorax* (Hymenoptera: Vespidae) in Europe demonstrates that species using CSD can successfully establish and subsequently invade with a limited amount of diversity (Arca et al. 2015). Due to the production of inviable or infertile

diploid males, the *csd* loci are under diversifying selection where rare alleles are favoured. By studying an introduced population of *Apis cerana*, Gloag et al. (2016) demonstrated that within seven years after introduction, the *csd* alleles reached an equilibrium under which they all appeared in approximately equal frequencies. This reduces diploid male production, decreasing the likelihood of extinction.

CSD and paternal genome elimination: effects on the sex ratio

A disadvantage shared by species with paternal genome elimination or CSD is the effect of these sex determination mechanisms on sex ratio (**Fig 1**). In non-social species, females change the sex ratio of their progeny based on environmental cues such as the amount of resource available (Charnov 1982; Charnov and Skinner 1984; Craig et al. 1992; Bono and Herbers 2003) or local mate competition (Hamilton 1967). Plasticity in the determination of sex ratio allows populations to respond to variability in the environment (Hardy and Cook 1995). Hence, in an introduced population, plasticity can increase the chances of survival and establishment (Wilson et al. 2009; Nyamukondiwa et al. 2010). Complementary sex determination and paternal genome elimination reduce the capacity of females to manipulate the sex ratio of their offspring to suit environmental conditions (Skinner 1982). Consequently, CSD and paternal genome elimination might decrease the fitness of introduced females.

Complementary sex determination also affects the sex ratio in social species. This was reported in the invasive hornet *Vespa velutina nigrithorax* (Hymenoptera: Vespidae) after its introduction in Europe (Darrouzet et al. 2015). Because of the low genetic diversity present in the newly introduced populations, the colonies of the hornet produced large amounts of diploid males that had been destined to develop into females. Because males do not contribute to colony maintenance and growth, diploid males slowed down the establishment of *V. velutina nigrithorax* in Europe.

Advantages of the segregation of the female and male genomes

From the perspective of facilitating establishment, and the subsequent spread from the area of introduction, the most advantageous sex determination mechanism might be the segregation of female and male genomes. Of the few species known to have this mechanism three have been introduced outside of their native range, two of which are considered invasive (Wetterer and Porter 2003; Wetterer 2008; Wetterer et al. 2015). The ant, *Paratrechina longicornis* (Hymenoptera: Formicidae) uses this sex determination mechanism, and mating between related individuals does not negatively impact the survival of the progeny (Pearcy et al. 2011). Consequently, inbreeding depression and mate location constraints are less likely, and these species are less likely to experience Allee effects (**Fig 1**). Segregation of the female and male genome also allows interspecific mating, or sperm parasitism where a female mates and uses the sperm of a different, but closely related species (Nonacs 2006). In most taxa, mating between two different species results in the production of non-viable or infertile progeny. In the case of species having segregated female and male genomes, the only individuals produced sexually are non-reproductive workers. Nonacs (2006) hypothesized that when parents belonging to two different species are closely related enough to produce viable offspring, the resulting worker progeny is likely to have a niche broader than either of the parental species. For an introduced species with segregated female and male genomes, interspecific mating with a species native to the invasive range could facilitate survival of the non-native population in the new environment (**Fig 1**).

Maternal imprinting: neutral reproductive trait

Maternal imprinting is not expected to decrease establishment capacity as much as CSD and paternal genome elimination. However, it also does not provide the advantages that the segregation of the female and male genomes gives to introduced species. This sex determination mechanism would then have an intermediate effect on introduced species (**Fig 1**).

Influence of the mating strategies on establishment capacity

Mate location in small populations: sib-mating, intranidal mating and premating dispersal

Sib-mating in gregarious and semi-gregarious species might be advantageous for introduced species immediately after arrival when the population density is still low. This trait should facilitate mate location because conspecifics are aggregated (**Fig 1**). For example, Hopper and Roush (1993) modelled population dynamics to demonstrate that low population density can prevent the establishment of introduced populations due to constrained mate location. Aron (2001) also attributed part of the success of the invasive Argentinian ant to intranidal mating for the same reasons. Consequently, for populations introduced at very low densities, sib-mating or intranidal mating might be advantageous traits while premating dispersal would be disadvantageous.

Influence of mating strategies on homozygosity

The different mating strategies of Hymenoptera can affect the genetics of populations, which affects establishment capacity (**Fig 1**). Sib-mating leads to the highest levels of homozygosity and inbreeding (Chapman and Stewart 1996), while discrimination of incompatible mates promotes high levels of heterozygosity and outbreeding (Brown 1997). Premating dispersal and polyandry can lead to intermediate levels of heterozygosity that vary depending on the amount of genetic diversity present in populations after introduction (Sundström 1993; Darvill et al. 2007). For an introduced population, mate discrimination and high levels of heterozygosity could have three advantages. First, originating from a source population with high levels of heterozygosity means that the introduced population is more likely to be diverse. This would increase the likelihood of establishment after introduction and the chances of adaptation to new environmental conditions. Then, if the introduced species uses CSD as its sex determination mechanism, premating dispersal and discrimination between genetically

compatible and incompatible mates might decrease diploid male production and promote the avoidance of the diploid male extinction vortex (avoidance of genetically incompatible mates: Thiel et al. 2013; premating dispersal: Faria et al. 2016). The last advantage of discriminating against incompatible mates is the fact that it promotes mating between genetically different individuals which could result in admixture between introduced and local populations or related species (Boissin et al. 2012). For the same reasons as arrhenotoky, this mating behaviour would facilitate rapid adaptation at every stage of the invasion process.

Effects of polyandry on establishment capacity

To date, we have an incomplete understanding of why females of most species mate with multiple males despite the costs associated with mating (Slatyer et al. 2012). During introduction, polyandry can have several advantages that vary between non-social and eusocial species. In non-social species polyandry can increase the size of the gene pool at introduction and reduce inbreeding depression (**Fig 1**). When they are released in a new area, founding polyandrous females carry with them their own alleles, as well as the alleles of the males with which they have mated. Consequently, mated females from a polyandrous source population might carry more diversity than females from a monandrous population (**Fig 1**). Arca et al. (2015) compared the diversity between the mitochondrial and nuclear DNA of *Vespa velatina* in France and hypothesized that a single polyandrous female had been introduced. The fact that the foundress had mated multiple times might have resulted in genetic diversity high enough for the maintenance of the wasp population.

With polyandry females increase their chances of mating with a genetically compatible male. By doing so variance in fitness among females is decreased and, therefore, the cost of inbreeding reduced (**Fig 1**) (Pusey and Wolf 1996; Tregenza and Wedell 2002). An extreme case of inbreeding depression is the genetic load of CSD. In this case, polyandry reduces diploid male production, hence decreasing the chances of a population to face extinction (Page 1980; Tarpy and Page 2001). The capacity of polyandry to reduce the genetic load of CSD is particularly relevant in species in which females can bias their sperm use towards a subset of

the sperm they collected through multiple mating. This behaviour has been observed in *Cotesia glomerata* (Ruf et al. 2012).

For eusocial species polyandry has additional advantages after introduction. By increasing the genetic diversity within the colony, polyandry increases the fitness, productivity (Mattila et al. 2012), growth rate (Wiernasz et al. 2004) and the capacity of a colony to respond to environmental change (Oldroyd and Fewell 2007). Wilson (1963) also demonstrated that small populations of ants could theoretically increase their effective size if the queen mated with multiple males. Social hymenoptera are extreme examples of effective population size being smaller than the number of adults within a population. This gap being more pronounced outside the reproductive season. By mating multiply, future queens preserve the genetic material of numerous males. Polyandry could then slow down the loss of genetic diversity linked to small population size by allowing populations to conserve genetic diversity that would otherwise be lost.

In some polyandrous species, mating with a single male or with males that cannot provide enough sperm can lead to sperm depletion in females (Godfray 1990; Kraus et al. 2004). In introduced populations of a polyandrous species, females could face mating constraints because finding enough males is challenging due to low population density. Depleted females would not fertilize all their eggs, leading to a skewed sex ratio. This phenomenon could cancel the benefit of polyandry for introduced populations by increasing Allee effects (**Fig 1**).

Influence of reproductive parasites on establishment capacity

Making males scarce: male killing and feminization

Male killing and feminization induced by bacterial endosymbionts have rarely been reported in the Hymenoptera (Werren et al. 1986; Giorgini et al. 2009). However, these phenomena greatly impact the population dynamics of insects (Hatcher et al. 1999; Hurst and Jiggins 2000)

and should not be ignored in the context of biological invasions. Both male killing and feminization bias the sex ratio of populations towards females (Kageyama et al. 1998; Fialho and Stevens 2000). In extreme cases, this can lead to sperm limitation in females, ultimately reducing female fecundity (Dyson and Hurst 2004) and population growth (Rankin and Kokko 2007).

Cytoplasmic incompatibility

In the Hymenoptera, cytoplasmic incompatibility can be induced by the reproductive parasites *Wolbachia* (Vavre et al. 2002) and *Cardinium* (Gebiola et al. 2016). During introduction and establishment, cytoplasmic incompatibility could have two main effects, strengthening Allee effects and preventing secondary introduction events that usually lead to an increase in genetic diversity within the invasive population (Suarez and Tsutsui 2008). In newly introduced populations, the low population density usually prevents mate location, leading to Allee effects (Courchamp et al. 1999). However, if the rare individuals that achieved to mate become sterile due to an incompatibility between their bacterial symbiont and that of their mate, population growth would be further impacted. Mochiah et al. (2002) demonstrated that cytoplasmic incompatibility negatively affected the population growth rate of the biocontrol agent *Cotesia sesamiae* if populations from different geographical origins were mixed during release.

The success of an invasion or of a biological control program often depends on secondary introduction events that increase genetic diversity and lead to admixture (Suarez and Tsutsui 2008; Garnas et al. 2016). Cytoplasmic incompatibility could prevent the establishment of newly introduced individuals carrying additional genetic diversity. It could also prevent gene flow and admixture between the already established and the newly introduced populations of the insect (Engelstädter and Telschow 2009).

Parasite induced parthenogenesis

Thelytoky can be induced in the Hymenoptera by reproductive parasites such as *Wolbachia* (Schilthuizen and Stouthamer 1997), *Cardinium* (Matalon et al. 2007) and *Rickettsia* (Giorgini

et al. 2010). Populations that became asexual following an infection by a bacterial symbiont could benefit from similar advantages compared to populations of Hymenoptera in which thelytoky is genetically induced. Some of these advantages would be the capacity of a single non-mated female to found a population (Baker 1955; Cheptou 2012), the weaker Allee effects (Courchamp et al. 1999), the potential broader environmental tolerance (Baker 1965; Vrijenhoek and Parker Jr. 2009) and the rapid population growth (Lehtonen et al. 2012).

Case studies

We review three historical introductions of Hymenoptera and consider how the reproductive biology of the introduced species may have influenced the invasion process. These include the invasive species *Apis mellifera scutellata* (Hymenoptera: Apidae) and *Leptocybe invasa* (Hymenoptera: Eulophidae), as well as the biological control agent, *Aphidius ervi* (Hymenoptera: Braconidae). In all three cases ecological and abiotic factors have played a role in the establishment of these species in new areas. However, by investigating the reproductive traits of these species, we demonstrate that reproductive biology should not be ignored as it played an important role in their establishment success. These examples were chosen because all three had a rapid spread after introduction but differ in their reproductive strategies. The aims are to use the theoretical concepts described above to reflect on the measures taken by countries to avoid introduction, slow the spread of introduced species or to facilitate introduction of biocontrol agents. ***Apis mellifera scutellata***

The invasion history of *Apis mellifera scutellata*, the African honeybee, in the Americas, is one of the best documented biological invasions (Schneider et al. 2004). Since the sixteenth century, the European honeybee has been present in the Americas. However, the European honeybee is less productive in the introduced range than in its native range because it is poorly adapted to the tropical climate of South America. Consequently, the African honeybee, which produces less honey but is better adapted to warm conditions, was imported from South Africa

to Brazil (Kerr 1957). The African honeybee was kept in quarantine with the intention of crossing the European and African subspecies to obtain a breed of honeybees more productive in the South American climate. The African honeybee escaped from quarantine and feral colonies established and spread over the continent, from northern Argentina (Sheppard et al. 1991) to southern Nevada and Utah (USDA, 2011). This expansion in introduction range was at the expense of the more productive and less aggressive European honeybee (Kent 1988).

The African honeybee has a faster growth rate than the European honeybee due to a higher investment in pollen collection and brood production (McNally and Schneider 1992, 1996). This higher growth rate allows the African honeybee to swarm more often during the year. Swarming is a reproductive process where a queen leaves the hive with some of the workers to create a new colony. Considering the high growth rate and the high frequency of swarming of the African honeybee, it is expected that the invasive bee would have the capacity to rapidly build up population levels and expand its range. In fact, to be able to reach Nevada in 1998 (CABI 2019a) after escaping from quarantine in Brazil in 1957 (Kerr 1957), the invasive range of the African honeybee must have grown by more than 200km per year. This fast range expansion may suggest that the reproductive traits of the African honeybee contribute to its capacity to spread to new areas.

Other beneficial reproductive traits of the African honeybee are arrhenotoky and the presence of nuptial flights that prevents inbreeding between individuals of the same colony (Koeniger and Koeniger 2000). These traits could have facilitated the adaptation of the African honeybee by allowing hybridization with the European honeybee. Some studies have shown that, shortly after its introduction, the African honeybee was rarely hybridizing with the European honeybee and that hybrid lineages lost European alleles over time (Smith et al. 1989; Hall 1990). However, more recent studies, using populations at the edge of the introduced range [i.e. Argentina (Sheppard et al. 1991); Texas (Pinto 2005); Puerto Rico (Galindo-Cardona et al. 2013)] have demonstrated the appearance of persistent hybrid

populations. The hybrid population, called Africanized honeybee, exhibits traits from its African parent that are undesirable for beekeepers. These traits include reduced honey production and increased aggression compared to the European honeybee. Consequently, the Africanized honeybee is considered invasive, like its African parent.

The different levels of hybridization between populations of the African honeybee on the American continent shows that the advantages of reproductive traits are context dependent. Here, the advantages that arrhenotoky provides to the African honeybee depend on the selective pressures acting on the bee populations. In South America, African honeybee populations were well adapted to the climatic conditions. The warm climate facilitated the displacement of the European honeybee by the African honeybee. As the African honeybee expanded its invasive range and reached areas with colder climates (i.e. southern Argentina, North America and Islands with an oceanic climate), hybridization with the European honeybee, well adapted to long restriction periods and cool temperatures, would have been adaptive (Clarke *et al.*, 2002). It is possible that the African honeybee did not require hybridization with the European honeybee to adapt to local temperatures. The cooccurrence of hybridization and temperature adaptation could be incidental and does not necessarily imply causation. However, the possibility that the African honeybee is now adapted to colder climates thanks to a hybridization event with the European honeybee should not be ignored as it can influence management strategies.

Invasive species risk assessment often involves modelling of the potential distribution of species based on climatic conditions (Venette *et al.* 2010). These models are a good indicator of the quality of the fit between the climatic envelop of a pest and the climatic conditions in an area at risk. Today, species distribution modelling is widely used by authorities to compile lists of potentially invasive species to guide the development of legislation and policies designed to limit the introduction of non-native species. In the case of species capable of hybridization, species distribution modelling should include information on the distribution of

closely related species and sub-species to avoid an increase of the breadth of an invader's niche (i.e. suitable climatic envelope, host).

Leptocybe invasa

Leptocybe invasa, commonly called the blue-gum chalcid, is a gall-wasp that infests numerous *Eucalyptus* spp. (Mendel et al. 2004; Quang Thu et al. 2009; Dittrich-Schröder et al. 2012). *Leptocybe invasa* is native to Australia (Dittrich-Schröder et al. 2018) where natural enemies control the populations of the wasp and prevent economic loss. Conversely, in countries where *L. invasa* has been accidentally introduced, the forest industry suffers from extensive yield losses. Eucalyptus are planted by numerous countries and, to date, has been introduced in a wider range than *L. invasa* (FAO 2012; CABI 2019b). Hence, the invasive range of the wasp may expand in the future.

Leptocybe invasa exhibits both arrhenotoky and thelytoky. For a long time, *L. invasa* was believed to be strictly thelytokous because males had not been recorded (Chen et al. 2009), and because virgin females can produce viable daughters. However, males have been observed in China (Chen et al. 2009) and Dittrich-Schröder et al. (2018) demonstrated the occurrence of hybridization between two haplotypes in South East Asia. These two observations demonstrate the capacity of *L. invasa* to also reproduce *via* arrhenotoky.

Thelytoky allows a single female to start a population (Baker 1967), decreases the strength of Allee effects (Stouthamer 1993), and might increase the rate of population growth (Stouthamer and Luck 1993). Together, these advantages should allow *L. invasa* to establish from a small introduced population and to show rapid population growth. This could cause an invasion bridgehead effect where alien populations serve as sources for subsequent introductions into new countries (Lombaert et al. 2010). This pattern is visible in the invasion history of *L. invasa*. For example, the invasive population of *L. invasa* present in southern Russia since 2014 (Orlova-Bienkowskaja et al. 2018) was probably introduced from France or Italy only 7 years after they were first reported in these areas (FAO 2012). Additionally, Israeli

populations served as a source for subsequent introductions to eastern Africa in 2002 (Maatouf and Lumaret 2012), only two years after they were first recorded in Israel (Mendel et al. 2004; Dittrich-Schröder et al. 2018).

Because *L. invasa* can spread and establish in new areas at a fast rate, it is difficult for the forestry industry and governments to record and report the spread of the wasp in real time. Official reporting of the presence of a pest is crucial for invasive insect management because countries can ban the importation of hostplants to avoid releases into new countries (FAO 2012). However, if a pest spreads rapidly, the ban can be based on a list of countries shorter than the list of countries where the pest is present (Eschen et al. 2015). In the case of species with thelytokous reproduction with a rapid spread, the ban should be put on the importation of plant hosts from all origins.

Thelytoky may have facilitated introduction of *L. invasa* into a growing number of countries, but arrhenotoky might allow the wasp to adapt to and resist control strategies in countries already invaded. In the case of *L. invasa*, the regulating tactics vary among invaded areas (Nyeko et al. 2007; Quang Thu et al. 2009; Kulkarni et al. 2010). For example, the biocontrol agents released, and the resistant tree species planted are site specific because they depend on the local conditions and on the genotype of the pest (Goud et al. 2010; Prasanth Jacob et al. 2015; Huang et al. 2018). If the genotype of the pest is unlikely to change over time, then the biocontrol programmes and the tree defences are likely to remain efficient. However, if secondary introductions occur in countries where the pest is already present, arrhenotoky can lead to admixture. The populations could become more diverse and increase their capacity to infest hosts or to resist natural enemies. Consequently, to promote the eradication and the management of invasive species, arrhenotokous pests should remain on quarantine lists after their introduction to prevent the introduction of additional genotypes and the occurrence of admixture.

Aphidius ervi

Aphidius ervi (Hymenoptera: Braconidae) is a Palearctic species (Stary 1974), common in Europe, but with a native distribution as far east as Japan (Takada 1968). The wasp has been introduced intentionally as part of biological control programmes in Chile, the USA, New Zealand, and Australia (Milne 1986; Zúñiga et al. 1986; Cameron and Walker 1989; Hufbauer et al. 2004). Due to the expansion of the introduced range or new accidental introduction events, *A. ervi* is now also found in Canada, Brazil, Argentina and South Africa. *Aphidius ervi* is commonly used as a biocontrol agent for the regulation of aphids causing damage to crops (e.g. vegetables and cereals), ornamental plants and young trees (CABI 2019c). The host range of *A. ervi* includes several aphid species (Powell and Wright 1988). Consequently, the wasp can be used as a biological agent for several aphid species simultaneously. Species from the genus *Aphidius* can locate their hosts even at low densities and can be used as preventive measures in green houses (Van Driesche et al. 2008) and in field conditions (Stary 2002).

Aphidius ervi is an arrhenotokous species likely using sl-CSD as a sex determination mechanism (Salin et al. 2004). Compared to thelytokous species, arrhenotokous species face stronger Allee effects (Stouthamer 1993). Moreover, species that use sl-CSD like *A. ervi* are more likely to experience extinction after an introduction because of the diploid male extinction vortex (Zayed and Packer 2005). *Aphidius ervi* displays male biased dispersal which reduces sib-mating (Zepeda-Paulo et al. 2015). Nonetheless, the potential for this reproductive behaviour to reduce inbreeding is limited in small incipient populations with low genetic diversity and high relatedness among individuals. Considering those reproductive traits, it could be predicted that the introduction of this parasitoid for biocontrol would regularly fail. However, the introduction of *A. ervi* is usually successful, due to the large number of individuals introduced. In the USA, more than 1000 *A. ervi* individuals were introduced from France and the Middle East (Hufbauer et al. 2004). In New Zealand, more than 54000 individuals were introduced from Japan, Belgium, Uzbekistan and Tasmania (Cameron and Walker 1989). In

the case of *A. ervi*, high propagule pressure appears to have compensated for reproductive traits that increase the likelihood of extinction after introduction.

Aphidius ervi has a short development time of 12 days (Hofsvang and Hågvar 1975) and mates only a few hours after reaching the imaginal stage (He et al. 2004). This results in a generation time approximately as short as its development time. In parts of its range, *A. ervi* has as many as 10 generations a year (Hufbauer 2001), facilitating a rapid response to natural selection. Moreover, arrhenotoky allows the recombination of the parental genomes. This reproductive trait facilitates adaptation, especially when consecutive introduction events happen and introduce a new pool of alleles on which natural selection can act. The short development time and the arrhenotokous reproduction of the wasps should facilitate adaptation.

Several studies have demonstrated that geographic isolation between populations of *A. ervi*, coupled with natural selection have resulted in local adaptation to available hosts and climate (Takada and Tada 2000; Henry et al. 2008, 2010; Tougeron et al. 2018). Takada and Tada (2000) compared the rate of parasitism of two *A. ervi* populations on various host species. They demonstrated that, while both populations were able to parasitize all aphid species, the rate of parasitism of the two populations differed among hosts. Those studies demonstrate the high capacity of the parasitoid to adapt to locally available hosts. This is expected considering the reproductive traits of the parasitoid wasp.

Conclusions

In this review, we highlight the importance of considering the reproductive traits of introduced species for the design of regulation strategies and biocontrol programmes. We focused on the insect order Hymenoptera because of its diversity of reproductive strategies and ecological functions; however, the regulation of all insect orders could benefit from the consideration of reproductive traits as indicators of invasiveness.

Some traits have been identified as strongly beneficial for introduction and establishment. Hence, while further research should be carried out, we believe that three major points should be investigated for the design of future risk assessment and management programmes. First, species using arrhenotoky and exhibiting reproductive traits that encourage admixture (e.g. segregation of the male and female genomes, pre-mating dispersal and discrimination of genetically incompatible mates) should remain on quarantine lists after an initial introduction. Furthermore, species distribution modelling and risk assessment should consider the presence of species closely related to the invasive species of interest. Secondly, the description and management of thelytokous species that demonstrate a rapid population growth after introduction should be prioritized to minimize bridgehead effects. Finally, the success of biological control programmes could also be increased by favouring arrhenotokous lineages of the biocontrol agent when possible. This would facilitate introduction while allowing the agent to remain effective over longer timescales. However, the use of a sexually reproducing agent requires large propagule pressure.

Through this work, we also highlight areas that still require investigation. Out of all the sex determination mechanisms observed in the Hymenoptera, complementary sex determination has received the most attention. How other species determine sex and the effect of these mechanisms should receive more attention as they impact population dynamics and population structure. How introduced species overcome the burden of complementary sex determination and the effects of polyembryony on population growth are still widely ignored by experimental studies. The genetic mechanisms behind thelytoky and the switch from or towards arrhenotoky is also understudied despite the growing number of invasive species using this form of reproduction. A deeper understanding of these issues will allow for the development of more efficient programmes that aim at regulating the introduction of insect pests or at controlling invasive insects after introduction.

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