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Integrated management of insect pests

Current and future developments

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E-CHAPTER FROM THIS BOOK



Advances in classical biological control to support IPM of perennial agricultural crops

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1 Introduction

Insect herbivores that are considered invasive pests pose significant threats to the integrity of urban, agricultural and native habitats. Some invasive species are notorious pests in their home ranges, and there are predictable negative consequences associated with their global movement that can affect the economic and ecological stability of invaded regions (e.g. Asian citrus psyllid, *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae), or palm weevils, *Rhynchophorus* Herbst, 1795 (Coleoptera: Curculionidae)). Others, however, are unrecognized as threats by the scientific community until they first become established outside their home range and cause unprecedented problems (e.g. avocado thrips, *Scirtothrips perseae* Nakahara, 1997 (Thysanoptera: Thripidae), or the polyphagous and Kuriohiro shot hole borers, *Euwallacea* Hopkins, 1915 (Coleoptera: Curculionidae)). In the invaded range, densities of non-native organisms may increase markedly and become problematic, in part, because they are largely unregulated by natural enemies that suppress population growth. This is the key concept underlying 'the enemy release hypothesis (ERH)' as lack of top down population regulation results in high pest densities (Keane and Crawley, 2002; Hoddle, 2004, 2006; Goldson et al., 2005; Messing and

Wright, 2006; Cock et al., 2012; Hoddle and Parra, 2013; Naranjo et al., 2015; Dowell et al., 2016; Hoddle et al., 2016a; Milosavljević et al., 2017a, 2018a,b).

With respect to agriculture, unchecked proliferation and spread of an invasive pest species can cause significant disruption to existing integrated pest management (IPM) programmes (Pimentel et al., 2005; Cock et al., 2012). The use of natural enemies to regulate pest population densities (i.e. biological control) has been a critical tactic in IPM programmes for a variety of different crops (i.e. perennial, annual (outdoor/indoor) agricultural crops, and in horticultural and floricultural systems). Biological control efforts that support IPM programmes in agriculture (*sensu lato*) use importation (i.e. classical biological control), augmentation, inundation and conservation of natural enemies, each of which have been used to varying degrees in IPM programmes (DeBach and Schlinger, 1964; Bellows and Fisher, 1999; see also other chapters in this book).

One powerful tool for invasive pest management, especially in the development of IPM programmes in agriculture, is classical biological control. This is the intentional introduction and establishment in invaded regions of exotic natural enemies (i.e. predators, parasitoids or pathogens) that have co-evolved with the target pest in the native range. The goal of releasing carefully selected host-specific (i.e. biocontrol agents that have a narrow host range) natural enemies is to suppress invasive pest populations in the introduced range to less harmful densities (Bellows and Hassell, 1999; Hoddle et al., 2015; Milosavljević et al., 2017a). The ultimate outcome of classical biocontrol programmes is to permanently suppress pest populations over large areas with little or no additional resource commitments after programme completion (Hoddle, 2003, 2004). As such, natural enemies are often seen as important contributors to IPM programmes developed for managing invasive pests in agroecosystems. When successful, substantial reductions in pesticide use may result (Cock et al., 2012; Morin et al., 2009) with significant economic and environmental benefits accruing over time (Hill and Greathead, 2000; Naranjo et al., 2015).

The development of a comprehensive and safe biological management programme requires careful planning and consideration of multiple programmatic steps (Hoddle et al., 2015). These steps include (1) accurate identification of the target pest (see Chapter 1) (and associated natural enemies found during foreign exploration (see Section 3)); (2) determining the origin and, if possible, a more specific source region within the larger native range of the introduced pest; (3) executing extensive surveys for natural enemies of the target pest within the home range, often referred to as foreign exploration, and returning selected agents under appropriate permits to an approved quarantine facility; (4) conducting rigorous host range (i.e. determination of the number of species a natural enemy can use for food and/or reproduction and an indication of host use breadth) and

host specificity (i.e. characterized by the natural enemy's prey/reproductive preferences for different species, both target and non-target) testing in a quarantine facility to ascertain the risk natural enemies may pose to non-target species, should they be released from quarantine. These safety tests are not required in all countries, but in countries where legislation regulates the introduction of new organisms, these data are needed before release permits will be issued to establish classical biological control agents in a new geographical area; (5) mass production, liberation and establishment of natural enemies approved for release from quarantine by regulatory authorities for control of the target pest; (6) conducting post-release evaluations on the spread and impact of the natural enemy/enemies on target pest densities to assess the long-term benefit of the investment in the biocontrol programme (Godfray and Waage, 1991; Mills and Kean, 2010; Barratt et al., 2010; Latham and Mills, 2010).

This chapter summarizes developments in classical biological control programmes targeting invasive pests to support IPM programmes. Here we review 'tools' that can help guide emerging biocontrol programmes with a particular focus on pests of perennial crops. Perennial cropping systems typically lack large perturbative activities (e.g. habitat destruction after harvest), as opposed to annual agricultural environments, which results in stable environments for the long-term coexistence of both pests and natural enemies (Kogan et al., 1999; Zeddies et al., 2001; Mills, 2005; Gutierrez et al., 2008; Cullen et al., 2008; Esser et al., 2015).

2 Developing a classical biological control programme for managing invasive insect pests

2.1 Pest and natural enemy identifications

The success and failure of developing a classical biological control programme for an invasive pest can pivot on the accurate taxonomic identification of the target. Errors at this early stage of the programme can cause significant time delays and depletion of resources (Schlinger and Doult, 1964; Room et al., 1981; Sands, 1983; Gordh and Beardsley, 1999; see also Chapter 1). If the identity of the pest is unknown, taxonomic identification (i.e. new species descriptions or revisions of outdated taxonomic placements) and phylogenetic position of a target species coupled with host plant preferences may help delineate bio-geographic regions that potentially encompass the home range of the pest and its natural enemies (Hoddle et al., 2002).

Species identifications for incipient biocontrol projects may present significant challenges as species of interest may be undescribed, or taxonomic placements may be poorly resolved (e.g. uncertainty over genus or tribe-level placements) or the target pest or natural enemies may be cryptic species that are

indistinguishable morphologically (Rugman-Jones et al., 2010, 2013; Gebiola et al., 2016). Molecular analyses (i.e. DNA-level analyses such as 'barcoding') offer powerful diagnostic tools for identifying pests (Rugman-Jones et al., 2010, 2013, 2017), natural enemy species (Lozier et al., 2008) and separating cryptic species (Szűcs et al., 2011), and this approach can be highly complementary with morphological identifications (Hoddle et al., 2008).

2.2 Foreign exploration for natural enemies

Foreign exploration for natural enemies for use in a classical biological control programme requires accurate delineation of the pest's home range. If the pest is a known entity it is likely that part or the entire geographic area of the native range is known. On the other hand, if the pest is a species new to science, and its area of origin is unknown, then a critical first step is the naming of the species and then executing a foreign exploration programme to delineate the home range while simultaneously surveying for natural enemies. Attempts at prescribing the tentative home range for a previously unknown pest may be based on taxonomic relatedness to other known species in the genus, study of previously unidentified material in museum collections for which locality data are available (this information may be discovered when species descriptions are being developed and materials loaned from museums are reviewed), its association with preferred host plants (this can be useful if the pest is monophagous/oligophagous) and climatic preferences which may also affect the preferred phenological stages of host plants (Hoddle et al., 2002).

Sourcing natural enemies from the pest's home range can present significant ecological issues that need consideration. Biocontrol theory suggests that an important factor pertains to matching the climate from the area of origin to the intended area of introduction (Goolsby et al., 2005; Van Driesche et al., 2008) and genetic matching of the invasive biotype with populations in the home range that have similar molecular identities (Lara et al., 2017). Using these two selection criteria either individually or together has the potential to significantly reduce the geographic area that needs to be searched for natural enemies while increasing the possibility that natural enemies sourced from foreign exploration efforts will be pre-adapted to the climate in the intended receiving area and the biotype of the pest being targeted (Hoddle et al., 2015).

Empirical studies have quantified the effects of regional climatic differences (especially extremes of summer heat and winter cold, low relative humidity, photoperiod and seasonal rainfall patterns) on establishment, spread, population dynamics and impact of natural enemies (Thomson et al., 2010). Biocontrol practitioners speculate that a likely reason for the failure (i.e. no establishment or patchy establishment of prospective agents throughout the intended release area results in little or no observable effect

on pest population densities) of classical biological control programmes is poor climate matching (Bartlett and van den Bosch, 1964; Stiling, 1993; Syrett et al., 2000; Hoelmer and Kirk, 2005; Van Driesche et al., 2008; Sexton et al., 2009; Thomas, 2010; Daane et al., 2012). It has been estimated that 35% of biocontrol introductions have been unsuccessful because of climate-related factors (Stiling, 1993).

Bioclimatic species distribution models (e.g. BIOCLIM, bioSIM, CLIMATE, CLIMEX, DOMAIN, GARP, HABITAT and MaxEnt) can be used to assess the invasive potential of species of interest (i.e. distribution of a species) and incursion vulnerability of areas of concern (Baker, 2002; Worner, 2002; Peterson, 2003; Sutherst, 2003; Hannaway et al., 2005; Stone et al., 2008; Peterson et al., 2008; Lozier and Mills, 2011; Fiaboe et al., 2012; Ge et al., 2015; Milosavljević et al., 2016a, 2017b; Kistner, 2017; see also Chapter 2). Model outputs may help guide searches for natural enemies in specific donor regions within the pest's native range that are climatically similar to the receiving area of interest (Hoelmer and Kirk, 2005; Senaratne et al., 2006; Phillips and Dudík, 2008; Robertson et al., 2008; Ulrichs and Hopper, 2008). These models (e.g. CLIMEX) can be applied deductively and in doing so they make use of laboratory-derived biological and life history data for the target pest (e.g. temperature-driven effects on development and population growth) to parameterize variables (see, for example, Sutherst and Maywald, 2005; Yonow et al., 2016; Kriticos et al., 2017; Kistner, 2017). This approach attempts to construct a model that best describes the effect of these variables on the distribution of a target and natural enemy species in the home and invaded range (Hoddle et al., 2002; Baker, 2002; Pilkington and Hoddle, 2006, 2007; Wang et al., 2012). In the absence of climate-driven biological data, an alternative approach to using climate matching models deductively is an inductive approach, in which model parameters are 'tweaked' iteratively until the model simulates the known distribution in both the home and invaded range. Climate data for the native and invaded range can be used as 'kernels' for initial parameterization of models (Baker, 2002). With respect to CLIMEX for example, the goodness of fit for a particular model is defined by the ecoclimatic index (EI). The larger the EI value, on a scale from 0 to 100, the better the climatic conditions and model fit for the species of concern.

In addition, geographic information system (GIS) models driven by natural enemy degree-day data may help predict geographic overlap between an invasive target and key biocontrol agents, and climatic match values of ~75% suggest a strong climate match between native and introduced ranges (Pilkington and Hoddle, 2006, 2007). However, high climatic match indices, as high as 80%, do not guarantee establishment or high impact of biological control agents (Goolsby et al., 2005). In these instances, factors other than climate (e.g. impoverished habitat, insufficient numbers of natural enemies

released, lack of genetic diversity or interference by resident natural enemies) can negatively affect establishment, spread and impact of introduced natural enemies even though suitable agents with good climatic tolerance were identified (Van Klinken et al., 2003; Goolsby et al., 2005).

Molecular data from invasive pest populations, such as the use of mitochondrial DNA markers and microsatellites, can be useful for identifying the origin and invasion history of exotic pests (e.g. avocado thrips (Rugman-Jones et al., 2005, 2006, 2007, 2009), invasive palm weevils (Rugman-Jones et al., 2013, 2017) and avocado lace bug (Rugman-Jones et al., 2012)). A potential benefit from identifying the area of origin(s) for an invasive population is that it may enable prospecting in parts of the pest's native range for natural enemies best adapted to the genetic structure (i.e. collection of natural enemies specific to the target pest's haplotype) of the invasive target population (Rugman-Jones et al., 2005; Lara et al., 2017). At this stage, this concept of 'molecular matching' for guiding natural enemy prospecting has little empirical support from field studies. However, this approach could be very important for programme success if target pest species are protected by defensive endosymbionts and closely co-evolved natural enemies are needed to counter these mutualists (Hoddle et al., 2015).

2.3 Evaluating host specificity and host range of natural enemies in quarantine

After foreign exploration trips, prospective biocontrol agents are returned to a secure quarantine facility where they are reared to confirm their identity and to remove unwanted 'hitchhikers' (i.e. pathogens and hyperparasitoids). Colonies of natural enemies are propagated from this initial stock that was collected overseas. Before natural enemies can be deliberately released in a new area, pre-release host specificity and host range assessments are recommended and these 'safety' tests may be mandatory in some countries (e.g. New Zealand, Australia, Canada and the United States). If such testing is not mandatory in the country of release it is highly recommended that such tests be conducted in advance of natural enemy introductions and codes of good practice and experimental design are available for review (Schulten, 1997; Schaffner, 2001; Kuhlmann et al., 2006; Van Driesche and Murray, 2004). The fundamental approaches underlying safety test designs used by classical biocontrol programmes targeting arthropods have been adopted and modified from existing methods used in weed biological control programmes (Kuhlmann et al., 2006).

Establishment of host-specific natural enemies with a narrow host range may be more likely to provide effective control of the target because of tight biological, behavioural and ecological linkages to the pest (Hoddle, 2004;

Kimberling, 2004; Hoddle et al., 2013; Rossinelli and Bacher, 2014). An additional benefit to high host specificity is the assumption that specialized biocontrol agents would be less likely to attack non-target species.

In an attempt to measure host specificity and host range of natural enemies, non-target species need to be selected for testing, and two types of experimental tests are commonly employed in quarantine to determine host use: (1) no-choice and (2) choice tests (or variants of these basic tests) (Van Driesche and Murray, 2004; Van Lenteren et al., 2006; Barratt et al., 2010; Van Driesche and Hoddle, 2017).

No-choice tests are those in which only one species of host or prey is presented to the natural enemy and its ability to reproduce and sustain itself on this host is assessed. No-choice tests can expose either the target pest (this is a test of the natural enemy's competency under quarantine conditions) or a non-target species (e.g. a native species of concern) to the natural enemy and outcomes of interactions, especially mortality rates, are recorded and compared to control populations not exposed to the natural enemy (Hoddle and Pandey, 2014; Bistline-East et al., 2015). No-choice tests may either be static where the natural enemy is presented to the host or non-target species once and it is not assessed further, or they can be sequential where the natural enemy is exposed to non-target, target and so on in an alternating pattern (Withers and Mansfield, 2005). The strength of sequential no-choice testing is that the competency of the natural enemy used in experiments is confirmed by exposure to the presumably preferred target. Sequential no-choice tests also assess the possibility as to whether or not exposure to the preferred host (i.e. target species) 'primes' the natural enemy to attack a non-target species it encounters later. No-choice tests simulate conditions under which the target pest is absent and the natural enemy is encountering non-target species under highly artificial conditions and its ability to successfully exploit non-targets is assessed. No-choice experiments in quarantine may overestimate the range of non-target species attacked under field conditions because the natural enemy is unable to abandon the patch to search elsewhere and confined conditions in vials or small cages may modify host utilization behaviours resulting in attacks that would not normally occur under less restrictive conditions (Balciunas et al., 1997). Lack of attack on certain species under no-choice conditions may strongly suggest that those species would be immune from attacks in the field (Hill, 1999).

Under choice conditions, two or more hosts, of which one is usually the target species while the remainder are non-target species, are presented to the agent simultaneously in the same arena, and preference responses (i.e. host utilization) across test species are assessed. This method is used for direct comparison of the acceptance (i.e. oviposition or feeding preference) and development on the target pest and non-target species when both co-occur

contemporaneously. Both no-choice and choice experiments in quarantine estimate to varying degrees the 'physiological host range' of the natural enemy, that is, the hosts on which the agent can develop. Choice tests attempt to mimic the 'realized host range' (i.e. the host range that may occur under field conditions) by lessening restrictions on host choice by natural enemies (Balciunas et al., 1997). Well-designed quarantine experiments may allow estimation of the agent's 'true' or 'ecological' host range (Balciunas et al., 1997) from which tentative conclusions on specificity (i.e. the natural enemy is either a specialist or generalist, or exhibits intermediate preferences on this continuum (van Klinken, 1999)) can be made (Schaffner, 2001; Sands and Van Driesche, 2002; Hoddle et al., 2015).

Non-target species used for natural enemy evaluations may be selected from three categories based on (1) phylogenetic relatedness to target species; (2) occurrence of target and non-targets in the same ecological niche; and (3) unrelated 'safeguard' species such as beneficial species (e.g. weed biological control agents) (Van Lenteren et al., 2006; Kuhlmann et al., 2006). A standardized exposure period for tests is recommended to accommodate host use behaviours that may be specific to certain times of the day, and for minimizing the possibility of increased attacks on less preferred hosts because of excessive time exposure under confined conditions (e.g. a 4 h vs. 24 h exposure window) (Hoddle and Pandey, 2014).

2.4 Preserving genetic variation of natural enemies collected from foreign exploration

During the importation-rearing process in quarantine, continuous mass inbreeding of commingled populations collected from different areas within the native range may reduce the fitness of natural enemies as they adapt to quarantine conditions and genetic diversity is reduced (Hopper et al., 1993; Roush and Hopper, 1995; Woodworth et al., 2002). Genetic variation could be preserved in laboratory populations with the establishment of single family lines (referred to as isocage (i.e. a small population from one location and collection time is continuously inbred) or isofemale lines (i.e. colonies are started from one mated female and progeny are inbred)). Although isocage lines become inbred and lose some genetic variability over time, traits (alleles) become fixed because of homozygosity (Roush and Hopper, 1995). Inbreeding results in reduced genetic variation in isocage or isofemale lines for natural selection to act upon and this counteracts the presumed negative fitness effects of laboratory selection and subsequent 'domestication' of natural enemies to prevailing quarantine conditions.

Genetic variation is assumed to be reconstituted to some unknown degree, and fitness is presumably increased, when inbred males and females

from each isocage or isofemale line are introduced into a panmictic mating cage and random male-female pairings result in heterozygote hybrid offspring which are released into the field. It is assumed that this interbreeding restores to some unknown degree the genetic variation that was originally captured during foreign exploration (Roush and Hopper, 1995; Hoddle and Hoddle, 2013). Following liberation of offspring resulting from panmictic mating into the field, natural selection acts on these hybrids selecting for genetic make ups that are best adapted to prevailing conditions in release areas (Hoddle and Hoddle, 2013). Although there are no field data to support the putative benefits of isocage or isofemale lines for maintaining and restoring genetic diversity of natural enemies in continuously bred colonies, this approach is intellectually appealing and could minimize the adverse genetic consequences of population bottlenecks and subsequent low fitness of 'domesticated' biocontrol agents released from quarantine.

2.5 How many natural enemy species should be released?

The number of natural enemy species to be released against an invasive arthropod target to maximize the probability of effective biological control is controversial (Denoth et al., 2002; Stephens et al., 2013). While empirical studies of natural enemy diversity and consumption of insect herbivores in both managed and natural ecosystems have identified both species complementarity (i.e. more diverse communities of natural enemies typically use more resources by occupying unique nutritional niches) and identity effects (i.e. more diverse natural enemy communities are expected to contain highly impactful species, resulting in greater resource consumption) (Snyder and Ives, 2003; Snyder et al., 2006; Straub and Snyder, 2006; Letourneau et al., 2009), meta-analyses of biological control programmes indicate that significant population suppression of an arthropod pest is often achieved by a single natural enemy species (i.e. identity effects) and not introduced guilds of natural enemies (Denoth et al., 2002; Cardinale et al., 2006; Crowder and Jabbour, 2014).

Therefore, instead, releasing multiple agents with the aim of increasing the probability that a single, effective agent is fortuitously introduced amongst several species, a strategy referred to as the 'lottery' or 'shotgun' approach, may result in effects on the target being less than additive due to possible antagonistic interactions between natural enemies (e.g. interspecific competition). This could occur if the same resource (e.g. host life stage) is preferred by competing species (Rosenheim et al., 1995; Stephens et al., 2013). Thus, prioritizing natural enemy species for release is recommended and precautions should be considered if releases of additional species of natural enemies are planned to minimize unintended detrimental impacts.

Robust selection of appropriate natural enemy species from the complex of interest for classical biological control may require laboratory and/or field assessment of their contribution to population regulation, preferably in the home range rather than under highly artificial conditions in a quarantine facility. One approach to evaluating competitive exclusion among natural enemies is to quantify the ecological niche space or 'niche breadth' available to each species (Northfield et al., 2010). The greater niche overlap, the more intense competition amongst species will be. Another approach is to directly manipulate niche complementarity (i.e. niche overlap and diversity) independently within the natural enemy communities, and experimentally determine the effect of functional complementarity between species (Finke and Snyder, 2008; Gable et al., 2012). Both of these approaches require complex experimental designs to capture details of the ecological interactions underpinning the intricate dynamics of particular systems. A more pragmatic approach is to compare resource consumption of the natural enemy species that causes the greatest amount of pest mortality with that of a guild that constitutes the multi-consumer community within which the target pest operates (Ramirez and Snyder, 2009; Milosavljević et al., 2016b). With this food-web approach, if a single natural enemy species significantly depletes resource levels below that of a multi-enemy community, it is identified as the keystone species regulating pest population growth (Ramirez and Snyder, 2009). If a single consumer species doesn't dominate, then complementarity amongst members of the consumer guild is responsible for regulating population growth (Loreau and Hector, 2001; Petchey, 2003).

Other approaches for assessing the impacts of individual or guilds of dominant natural enemy species include life table analyses. Life table results can be used to design experiments that manipulate host-natural enemy populations, to confirm the most susceptible life stages of the target and to quantify natural enemy impacts in a given system (Briggs et al., 1995; Jervis et al., 1996; Van Driesche, 1993; Bellows and Van Driesche 1999; Kistner et al., 2016b, 2017). Life table analyses can include multiple-decrement forms which can be used to partition death rates across competing contemporaneous mortality factors to better identify contributions to pest mortality by different natural enemy species (Carey, 1993, 2001; Elkinton et al., 1992; Peterson et al., 2009; Buteler et al., 2015; Varella et al., 2015).

2.6 Planning release and establishment programmes

The likelihood of establishing natural enemies in a new environment can be enhanced by evaluating factors likely to affect establishment success. Mass production of natural enemies for release programmes is necessary if sufficient numbers are to be released through time and across sites and the

fitness of released natural enemies must be as optimal as possible given rearing restrictions in quarantine facilities (see above for details on theoretical approaches for preserving and reconstituting fitness of laboratory-reared natural enemies).

Three important factors that influence establishment likelihood are selection of release sites (i.e. number of sites, their temporal and spatial stability, host availability and climate), the frequency of releases and the number of natural enemies released each time (Beirne, 1975). With respect to release sites, these should consist of multiple separate areas spanning a variety of climatic zones (e.g. cool coastal areas, hot interior desert regions) with long-term access that won't be subject to unfavourable management practices (e.g. pesticide applications or host plant removal), or vulnerable to catastrophic stochastic events (e.g. flooding or wildfires). The release sites should collectively form a receiving ecosystem that should be large enough to contain a stable metapopulation of the target pest to indefinitely support populations of candidate biocontrol agents (Van Driesche, 1993; Van Driesche and Bellows, 1996).

Theory from invasion biology and manipulative field studies have verified the importance of introduction pressure on establishment rates. Biological control introductions are carefully planned invasions and natural enemy release patterns and subsequent establishment frequency have been assessed to identify factors that affect successful colonization. Propagule pressure, a combination of the number of individuals introduced and introduction frequency affect establishment rates. A general rule of thumb suggests that the more agents that are released the greater the likelihood of the natural enemy establishing itself in a locality (Beirne, 1975; Memmott et al., 1998; Grevstad, 1999; Shea and Possingham, 2000; Lockwood et al., 2005; Simberloff, 2009; Brockerhoff et al., 2014). This can be achieved via a few large releases or multiple small releases (Beirne, 1975; Ehler and Hall, 1982). Timing of these releases is critical as they must coincide with favourable conditions in the receiving environment such as the availability of hosts, a suitable climate (e.g. selection of a specific time during the day for release such as mornings when temperatures and light intensity are relatively low) and the possible need for additional resources (e.g. access to pollen, nectar or shelter). Lack of consideration of these factors or failure to incorporate practices to mitigate potentially adverse impacts on newly released natural enemies may contribute to establishment failure (Hoddle et al., 2015). The last step in this process is confirmation of establishment. A rule of thumb that indicates establishment has likely occurred is recovery of natural enemies at release sites after the first winter that the agents experienced. A further sign of establishment and indicator of natural spread is recovery of natural enemies at non-release sites (Hoddle et al., 2016b).

3 Case study: classical biological control of Asian citrus psyllid in California

California is a large agricultural state in the United States and collectively this industry is worth an estimated US\$47–54 billion each year (CDFA 2016a,b). California's position on the Pacific Rim, its high rates of international, national and regional trade and tourism, extremely varied climatic zones, and high floral diversity (i.e. native and exotic (urban landscape and agricultural) plants) make it vulnerable to invasion by non-native species which may become significant pests and diseases, the economic cost of which may exceed US\$6 billion per year (CISR, 2017). High economic costs associated with invasive pests are not unique to California. For the United States as a whole (and other regions such as Europe and Asia) the environmental and economic losses, and associated management costs, for non-native pest invertebrates have been estimated to be in billions of dollars per year (Pimentel et al., 2005; Xu et al., 2006; Vilà et al., 2010; Naranjo et al., 2015).

Non-native invertebrates (~84% are insects) either enter California directly from overseas points of origin (~45% of introduced non-native species) or via invasion bridgeheads established elsewhere in the United States (~44% of introductions). Dowell et al. (2016) estimate that about nine new macro-invertebrate species (i.e. insects, mites, snails, spiders, mites etc.) establish each year in California, of which ~33% (i.e. roughly three species per year) become pests requiring some form of management.

The predominant group of insect invaders in California are hemipterans with representatives from the Auchenorrhyncha (e.g. leafhoppers, planthoppers, spittlebugs) and Sternorrhyncha (e.g. scales, aphids, psyllids, whiteflies, mealybugs) (Dowell et al., 2016). This group of invasive hemipterans, especially Sternorrhyncha, is typically comprised of small, cryptically concealed, hard to identify sap sucking bugs that have high pest potential. Even though hemipterans are a well-recognized pest group they are frequently moved internationally via trade in live plants (Liebhold et al., 2012).

One particularly devastating exotic hemipteran pest of citrus in California is the Asian citrus psyllid, *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae) (Milosavljević et al., 2017a, 2018a) (Fig. 1). The general native range is large and thought to include parts of the Indian subcontinent (Beattie et al., 2009). *D. citri* has since emerged as a dominant economically important pest species of citrus worldwide because of its ability to acquire and vector the phloem-dwelling bacterium, *Candidatus Liberibacter asiaticus* (CLAs), the putative causative agent of a lethal citrus disease, huanglongbing (HLB, also known as citrus greening disease) (Bové, 2006; Pelz-Stelinski et al., 2010; Halbert and Manjunath, 2004; Hall et al., 2013; Grafton-Cardwell et al., 2013). CLAs-infected citrus trees show reduced vigour and yield and die prematurely (Gottwald,



Figure 1 Asian citrus psyllid life stages: (left) gravid adult *D. citri* female feeding on young tissue and eggs on citrus flush, (right) nymphs producing white sugary secretions. Photos: Mike Lewis, Center of Invasive Species Research, UC Riverside.

2010) (Fig. 2). Though there are some differences in susceptibility amongst commercial citrus varieties, there are almost no exceptions to vulnerability to infection by CLAs (Yang et al., 2006).

Together, *D. citri* and CLAs pose a serious threat to California's ~US\$2.7 billion-a-year citrus industry. The first detections of *D. citri* and CLAs in California were in 2008 and 2012, respectively (Leavitt, 2012; Kumagai et al., 2013). Following detections of *D. citri*, the California Department of Food and Agriculture (CDFA) initiated urban insecticide treatments and monitoring programmes in attempt to eradicate the pest (Hoddle, 2012). By 2012, the CDFA spray programme was terminated, in part, because of cost (it was estimated at ~US\$4.7 million with treatments costing more ~US\$100



Figure 2 Huanglongbing or citrus greening disease symptoms: (left) irregular blotchy yellowing or mottling of leaves, (right) citrus trees in advanced stages of decline because of CLAs infection. Photos: Mark Hoddle, Center of Invasive Species Research, UC Riverside.

per residence) and increasing and widespread detections of *D. citri* outside of treatment areas (Hoddle and Pandey, 2014). Detections of *D. citri* are being made with increasing frequency in residential areas in the San Joaquin Valley (SJV). Around 77% of California citrus is grown in the SJV on ~84 000 ha, and in this production area harvested fruit is worth about US\$1.6 billion each year (USDA NASS, 2016).

As of spring 2018, CLas infections were limited to citrus growing in residential areas in southern California with over 530 trees confirmed as being infected and subsequently destroyed (David Morgan, CDFA, *pers. comm.*, 2018). As CLas is known to spread rapidly through *D. citri* populations, one way to minimize pathogen transmission rates across citrus bearing landscapes is to reduce vector densities (Boina et al., 2009; Lewis-Rosenblum et al., 2015).

Backyard citrus is ubiquitous in southern California, and some estimates conservatively suggest that ~36% of California residences have at least one citrus tree (Hoddle and Pandey, 2014). Urban citrus is largely unmanaged and has potential to harbour large *D. citri* populations, which increases the likelihood of CLas acquisition and transmission to uninfected trees. Surveys of *D. citri* populations following initial detections of this pest in southern California failed to detect significant natural enemy activity, especially parasitism of nymphs. Consequently, 'enemy release' may have been one reason for high urban *D. citri* populations and this may have facilitated rapid population increases and subsequent range expansion of *D. citri* throughout southern California (Hoddle and Pandey, 2014). *D. citri* suppression was urgently needed to protect commercial citrus production areas, yet large-scale urban chemical control programmes are prohibitively expensive, largely ineffective and legal action has stopped applications (Mohan, 2018). Therefore classical biological control with specialist natural enemies was an obvious and publically acceptable long-term management option for *D. citri* control in urban areas.

3.1 Selecting host-specific natural enemies, preserving natural enemy genetic diversity in quarantine and release strategies

The classical biological control programme targeting *D. citri* in California has focused on two primary parasitoids, *Tamarixia radiata* (Waterston, 1922) (Hymenoptera: Eulophidae) and *Diaphorencyrtus aligarhensis* (Shafee, Alam and Argarwal, 1975) (Hymenoptera: Encyrtidae) (Figs. 3 and 4), both of which are well-recognized natural enemies that attack nymphs of this pest in the regions of origin (Halbert and Majunath, 2004). The development of this programme required coordinated and collaborative efforts of federal and state agencies (i.e. United States Department of Agriculture (USDA), University of California at Riverside (UCR) and CDFA), international collaborators (i.e. Department of Entomology at University of Agriculture, Faisalabad (UAF), Punjab, Pakistan) and grower groups (e.g. Citrus Research Board) (Hoddle, 2012).



Figure 3 The developmental biology of *Tamarixia radiata*: (left) gravid female laying an egg underneath a psyllid nymph, (right) *T. radiata* is a specific ectoparasitoid of immature *D. citri* (attacks fourth and fifth stage nymphs) and *T. radiata* larvae feed and develop externally on its hosts. Photos: Mike Lewis, Center of Invasive Species Research, UCR.

Natural enemy prospecting was conducted in Punjab, Pakistan, as CLIMEX modelling indicated a ~70% match with major citrus growing regions in the SJV in California. As mentioned earlier, biocontrol theory suggests that natural enemies for use in classical biological control should be sourced from regions with climates similar to the receiving range so they are pre-adapted to prevailing climates in the intended release areas (Hoddle, 2012; Hoddle and Hoddle, 2013). Over the course of a 2.5-year period, six foreign exploration trips to citrus production areas (e.g. Gujranwala, Sargodha and Toba Tek Singh) in Punjab, Pakistan, were made to collect *D. citri* natural enemies (Hoddle, 2012; Hoddle and Hoddle, 2013; Khan et al., 2014; Hoddle et al., 2014). A total of 3675 parasitoids were reared out in quarantine at UC Riverside from material imported under USDA-APHIS permits from Pakistan over the period from 2011 to 2013, and 13 potential natural enemy species associated with collected *D. citri* were identified (Hoddle et al., 2014). The two



Figure 4 The developmental biology of *Diaphorencyrtus aligarhensis*: (left) gravid female lays an egg within (parasitizing) an *D. citri* nymph, (right) *D. aligarhensis* is a specific endoparasitoid of immature *D. citri* (attacks second through fourth stage nymphs) and *D. aligarhensis* larvae feed and develop within a host. Photos: Mike Lewis, Center of Invasive Species Research, UCR.

primary parasitoids of *D. citri*, *T. radiata* and *D. aligarhensis*, represented the majority of collected specimens at 55% and 28%, respectively. In addition to *T. radiata* and *D. aligarhensis*, eleven other hymenopteran species associated with *D. citri*-infested foliage were collected. Subsequent biological studies in quarantine indicated that five species were obligate hyperparasitoids of immature *T. radiata* and *D. aligarhensis* and these were eliminated from quarantine colonies, while the remainder were contaminants associated with cryptic life stages of other insects (e.g. parasitoids of hemipteran eggs laid inside citrus stems) (Hoddle et al., 2014; Bistline-East and Hoddle, 2014, 2015). In an attempt to preserve genetic diversity of imported parasitoids, a total of seventeen *T. radiata* and five *D. aligarhensis* isocage breeding lines representing different collection localities and dates were maintained in quarantine at UC Riverside (see above for rationale on maintaining isocage lines) (Hoddle and Hoddle, 2013).

Following the completion of host specificity and host range tests (sequential and static no-choice and choice experiments) in quarantine (Hoddle and Pandey, 2014; Bistline-East et al., 2015), permits were issued by USDA-APHIS authorizing the release of *T. radiata* and *D. aligarhensis* from quarantine as it was concluded that these two natural enemy species posed no significant threat to non-target species in California, especially indigenous species closely related to the target (e.g. native California psyllids) and beneficial psyllids used for weed biocontrol.

T. radiata and *D. aligarhensis* have been released in California because, combined, they may be more effective in suppressing *D. citri* populations than either parasitoid species alone (i.e. complementarity may be possible) (Milosavljević et al., 2017a, 2018a). Both natural enemy species have been reported to have contributed to decreased densities of *D. citri* in Pakistan (Khan et al., 2014). As of early 2018, more than 9 million *T. radiata* and 500 000 *D. aligarhensis* have been released at more than 1500 sites covering over 10500 km² across eight counties (Imperial, Los Angeles, Orange, Riverside, San Bernardino, San Diego, Santa Barbara and Ventura) in urban California to control *D. citri* (David Morgan, CDFA, *pers. comm.*, 2018).

T. radiata has established at more than 95% of release sites spread over a range of climates in southern California (which included both release and non-release sites (n = 100)). Recoveries have been made in localities distant from release sites (with some finds at least 13 km from the nearest release site) indicating extensive natural dispersal (Hoddle et al., 2016b). Parasitism of *D. citri* by *T. radiata* has been regularly observed across survey sites (Kistner et al., 2016a). Molecular testing of field-recovered *T. radiata* conclusively demonstrated that recovered parasitoids had genetic signatures unique to the Pakistani populations released in southern California (Paul Rugman-Jones, UC Riverside, *pers. comm.*).

T. radiata and *D. aligarhensis* attack different *D. citri* host stages and have preferences for differing pest densities. *D. aligarhensis* (an endoparasitoid) lays eggs within second through fourth stage nymphs and performs better under lower pest densities, whereas *T. radiata* (an ectoparasitoid) lays eggs under fourth and fifth stage nymphs and prefers higher *D. citri* densities (Milosavljević et al., 2017a). Furthermore, *D. aligarhensis* and *T. radiata* may have subtly different climate and habitat preferences, and heterogeneous climates and variations in citrus production habitat across major citrus production areas may favour establishment of one parasitoid species in parts of southern California that could be unfavourable for the other. Although complementarity in the field is speculative at this stage, laboratory studies suggest that both parasitoids may have potential to be complementary (Vankosky and Hoddle, 2017a,b) and both species could simultaneously contribute to *D. citri* control in California, perhaps through resource, geographic or habitat partitioning. An example of this type of complementarity is the successful biocontrol of cottony cushion scale, *Icerya purchasi* Mulsant, 1850 (Hemiptera: Monophlebidae), in citrus by the parasitic fly, *Cryptochaetum iceryae* (Williston, 1888) (Diptera: Cryptochaetidae) (prefers cooler coastal climates) and the coccinellid, *Rodolia cardinalis* Mulsant, 1850 (Coleoptera: Coccinellidae) (dominates in hotter interior areas) in California (Quezada and DeBach, 1973).

Post-release monitoring in southern California indicates that average year-round parasitism by *T. radiata* is moderate at about 21%, varying greatly across locations and over time. However, it is likely that *Tamarixia*-inflicted mortality on *D. citri* is underestimated because mortality from host feeding and loss of parasitized *D. citri* nymphs through intraguild predation are very hard to quantify in the field (Kistner et al., 2016b). Moreover, the combination of *T. radiata* and attacks by native predators, such as syrphid fly larvae (Diptera: Syrphidae) and lacewings (Neuroptera: Chrysopidae), which utilize *D. citri* nymphs for food, are having a substantial impact, reducing urban *D. citri* populations by more than 90% at some locations at certain times of year (Kistner et al., 2016b, 2017). Ironically, field measures of *T. radiata* efficacy in terms of percentage parasitism estimates decline as *D. citri* populations decrease. This occurs because females preferentially host feed when *D. citri* patches are small and there may be too few hosts of appropriate life stages to parasitize after host feeding (Tena et al., 2017).

Similarly, post-release monitoring of *D. aligarhensis* in southern California demonstrates that average year-round parasitism varies greatly across localities and time of the year (up to 37.5% at certain locations). Evidence of *D. aligarhensis* activity has been found at more than 80% of surveyed sites, indicating that *D. aligarhensis* can find and reproduce on *D. citri*-infested citrus. Interestingly, significantly higher rates of parasitism by *D. aligarhensis*

are observed on orange trees when compared to lemons, which tentatively suggests this parasitoid may have host plant preferences when searching for *D. citri* patches (Milosavljević et al., 2017c).

3.2 Synergizing the impacts of natural enemies attacking *D. citri* in California: disrupting ant-psyllid mutualism

Ants that tend honeydew producing hemipterans (HPH) infesting citrus (Schall and Hoddle, 2017) and other perennial crops (e.g. grapes (Tollerup et al., 2004; Daane et al., 2007)) disrupt natural enemy activity directed towards these pests. This occurs because ants that tend HPH are rewarded with a carbohydrate source, honeydew, which is harvested and shared amongst nest mates. In return for this reward, ants protect HPHs from their natural enemies allowing populations to increase in density. Because ants provide sanitation services by removing honeydew they lower disease incidence in HPH colonies, ants may herd and move HPH from infestation foci to other areas of orchards causing infestations to spread, and by harvesting honeydew they increase pest vigour (decreased developmental times and increased reproductive outputs) as feeding rates increase (Lehouck et al., 2004). Consequently, a positive feedback loop is developed that results in pest infestations building in severity and ant populations increasing as a result of increasing HPH densities that provide ever-increasing amounts of honeydew.

With respect to the *D. citri* biological control programme in California, the invasive Argentine ant, *Linepithema humile* (Mayr, 1868) (Hymenoptera: Formicidae), is the dominant natural enemy antagonist in southern California because of the food-for-protection mutualisms it forms with a variety of HPHs (e.g. *D. citri*, mealybugs, softscales, aphids and whiteflies) infesting citrus (Schall and Hoddle, 2017; Milosavljević et al., 2017a). *L. humile* has thrived in southern California's natural, urban and agricultural systems for more than a century, with populations reaching exceptionally high densities in citrus groves with abundant food supplies and irrigation runoff (Cook, 1953; Holway et al., 2002). Some estimates suggest that individual citrus trees may receive more than one million ant visits in a single day (Schall and Hoddle, 2017).

Surveys of urban citrus in southern California have indicated that more than 90% of trees have *L. humile* activity and more than half (~55%) of *D. citri* colonies are tended by *L. humile*. As a result *D. citri* parasitism by *T. radiata* is significantly reduced because of ants tending patches of *D. citri* nymphs (Tena et al., 2013). Field trials in commercial citrus groves in southern California have supported observations from studies in urban citrus. Control of *L. humile* in citrus groves using either liquid baits or sticky barriers that exclude ants from

D. citri colonies, resulted in significantly higher levels of parasitism by *T. radiata* (up to 8-fold increase when compared to untreated controls where ants could access *D. citri* colonies) and generalist natural enemies (e.g. lacewing larvae, spiders, hover fly larvae and lady beetles) were considerably more abundant (~1–4 times greater) in *D. citri* colonies where *L. humile* was absent (Schall and Hoddle, 2017). Similarly, suppression of HPH tending ant species substantially improved *D. citri* biocontrol by *T. radiata* in Florida (Navarrete et al., 2013). When taken together, these results strongly suggest that the ant-*D. citri* mutualisms are directly responsible for observed declines in biocontrol efficacy by *T. radiata* and generalist predators.

Low-toxicity insecticide liquid bait mixtures can be used to control HPH tending ant species in managed ecosystems (e.g. citrus orchards, vineyards) where ant pests present a perennial management problem (Rust et al., 2004, 2015). There are several major drawbacks to liquid bait for ant control. These include cost in terms of bait dispensers, the liquid bait carrying the insecticide and labour associated with deployment, cleaning and reloading of dispensers. Additionally, high densities of dispensers (i.e. hundreds) need to be deployed in orchards to inflict sufficient mortality (Cooper et al., 2008; Buczkowski et al., 2014; Nelson and Daane, 2007; Rust et al., 2015; Tay et al., 2017).

To overcome the limitations of conventional liquid baiting, hydrogels applied to soil under trees may be used for the cost-effective localized delivery of a sucrose liquid bait with ultra-low concentrations of pesticide (i.e. 0.0001% of thiamethoxam in 25% sucrose solution), without the need for bait stations (Rust et al., 2015; Tay et al., 2017). Field trials evaluating biodegradable hydrogels in commercial citrus orchards have shown ant suppression comparable to conventional ant control practices (Schall et al., 2018).

4 Benefits of classical biological control for IPM of insect pests in perennial crops

Biological control is a well-recognized pest suppression tool that has central importance for IPM programmes that aim to reduce pesticide use (Mills and Daane, 2005). In well-managed perennial tree crop systems, natural enemies may be highly effective for managing native and non-native insect pests (Naranjo and Ellsworth, 2009; Hoddle et al., 2015). However, the arrival and establishment of new pests may cause significant disruption to well-established and stable IPM programmes in the invaded area (Pimentel et al., 2005; Cock et al., 2012). Exotic insects that vector invasive pathogens that cause disease (e.g. *D. citri*-CLAs) are particularly troublesome for IPM programmes because of the lethal aspect of the disease which drives increased pesticide use to mitigate vector densities (Milosavljević et al., 2017a).

Citrus production (and other tree crops) in California, for example, has a long tradition of successful classical biological control programmes that started in the late 1880s with the successful suppression of the invasive cottony cushion scale, *I. purchasi*, by an imported ladybird (the vedalia beetle, *R. cardinalis*) and dipteran parasitoid (*C. iceryae*) (DeBach and Schlinger, 1964; Quezada and DeBach, 1973; Caltagirone and Doutt, 1989). In addition to this programme, there have been numerous subsequent classical biocontrol successes in California citrus, including the suppression of invasive armoured scales (Hemiptera: Diaspididae), whiteflies (Hemiptera: Aleyrodidae) and mealybugs (Hemiptera: Pseudococcidae) (Luck and Forster, 2003; Mills and Daane, 2005). Collectively, the use of introduced natural enemies for biological control of citrus pests in California has resulted in significant economic savings and decreased reliance on broad-spectrum chemicals (Habeck et al., 1991; Orr, 2009; Warner et al., 2011; Naranjo et al., 2015; Kenis et al., 2017). The importance of natural enemies for supporting IPM programmes in perennial crops is not limited to California. Successes have been achieved globally (DeBach and Schlinger, 1964; Bellows and Fisher, 1999; Greathead, 1976), with highly notable programmes being the development of successful biological control programmes targeting invasive pests of walnuts and pears in California (Mills and Daane, 2005), apples in New Zealand (Wearing et al., 1978, 2010) and Europe (Greathead, 1976), papaya in the Republic of Palau (Muniappan et al., 2006) and citrus in Spain and Mediterranean Europe (Bale et al., 2008).

5 Future trends and conclusion

Classical biological control programmes developed to support IPM programmes are benefitting from technological and theoretical advances in supporting disciplines (e.g. molecular biology) that are providing 'new tools' which may increase the efficacy of this approach for managing invasive pests in perennial agricultural crops. For example, molecular tools are being used to evaluate impacts of natural enemies (e.g. generalist predators) on herbivorous pests by analysing gut contents (Hosseini et al., 2008; Krey et al., 2017) which helps identify natural enemy-prey interactions that may be impossible to detect with other methods (e.g. unknown sources of mortality in life table analyses). These molecular approaches can be extended further to analyse food webs which identify interactions between hosts, primary parasitoids and hyperparasitoids, thereby providing insight into trophic linkages and their relative importance for suppressing targets of interest (Ye et al., 2017). Molecular genetics can help disentangle uncertainty over identities of pests and natural enemies especially when cryptic species complexes may be involved (Heraty et al., 2007; Rugman-Jones et al., 2009, 2010). This step is especially critical at the initial stages of developing a classical biological control programme as projects have either

stalled or failed because of taxonomic misidentifications that relied solely on morphology (Sands, 1983; Rosen, 1986).

Emerging methods that rely on technology for monitoring invasive pest populations through time may exploit the Internet of Things (IoT), drones or micro-video cameras. Rapid advances in IoT and wireless technologies has the potential to automatically collect pest count data which is then transmitted in near real time to computers or smart devices via the cloud. This approach has tremendous potential to significantly reduce monitoring costs and to provide pest count data for specific areas of orchards that would allow initiation of precisely deployed management tactics (Potamitis and Rigakis, 2015; Potamitis et al., 2017; Al-Saraj et al., 2017). Responses could include releases of natural enemies or application of highly targeted sprays that are limited just to areas of an orchard where pest densities have crossed the action threshold. Highly localized pesticide applications would help preserve natural enemy populations in orchards and would be very compatible with IPM programmes (Matthews, 2008). Low-cost drones outfitted with high-resolution cameras represent a cheap and powerful way to digitally collect data over large areas that can then be processed to assess plant health which can guide management decisions (Hogan et al., 2017). For example, data from drone surveillance could be used to deploy drones customized to aurally release natural enemies in areas of orchards where resident populations need augmenting (Li et al., 2013). Cheap micro-video cameras that record pest and natural enemy activity over a 24 h period can provide deep insight into natural enemy complexes attacking pests of economic concern, periodicity of pest and natural enemy activity, and their relative abundance across sites and through time (Kistner et al., 2017). These data can be used to assess natural enemy impacts and if necessary management practices can be modified to enhance biocontrol efficacy.

Other IPM-compatible approaches under development that may have potential for enhancing natural enemies by reducing reliance on pesticides for pest control are molecular alterations of host plants (e.g. genetically modified crops (Ballester et al., 2007)), gene silencing (e.g. plant genome editing with CRISPR/Cas9) and RNA interference (RNAi) (Niblett and Bailey, 2012; Sattar et al., 2017). These molecular modifications of crop plants may provide cost-effective control of a variety of pests infesting perennial crops, thereby reducing reliance on pesticides which in turn increases natural enemy activity (Ballester et al., 2007; Lu et al., 2012). The human population is estimated to reach 9.1 billion by 2050 and global food production may need to increase by 70% to minimize food insecurities (Godfray et al., 2012; Tscharnke et al., 2012; Rayl et al., 2018). Destabilization of cropping systems by invasive pests will likely continue unabated and proven pest suppression technologies, like classical biological control, as a key component of IPM programmes will be needed, perhaps even more so than now.

6 Where to look for further information

6.1 Journals

A standard introduction to the subject is Van Driesche and Bellows, *Steps in Classical Arthropod Biological Control* (see Van Driesche and Bellows (1993) for full details).

Further information on invasion biology, emerging protocols and legislation for assessing natural enemy specificity and safety can be found in several published texts, including:

- Van Driesche, R. G. (2002), *Proceedings of the 1st International Symposium on Biological Control of Arthropods*, Washington, DC, USA: United States Department of Agriculture, Forest Service.
- Hoddle, M. S. (2005), *Second International Symposium on Biological Control of Arthropods*, Washington, DC, USA: United States Department of Agriculture, Forest Service.
- Mason, P. G., Gillespie, D. R. and Vincent, C. (2009), *Proceedings of the 3rd International Symposium on Biological Control of Arthropods*, Morgantown, WV, USA: United States Department of Agriculture, Forest Health Technology Enterprise Team.
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- Mason, P. G., Gillespie, D. R. and Vincent, C. (2017), *Proceedings of the 5th International Symposium on Biological Control of Arthropods*, Wallingford, UK: CAB International.

6.2 Books

We direct the interested reader to the books of Hajek (2004) and Jervis (2007) to learn about 'biological control'. As a textbook on 'classical biological control', we suggest DeBach and Schlinger (1964), while more advanced safeguarding decisions and resulting actions for exotic pests are found in Van Driesche and Reardon (2004), Wäckers et al. (2005), Bigler et al. (2006), Sithanatham et al. (2013), Van Driesche et al. (2008, 2016) and Heimpel and Mills (2017):

- Bigler, F., Babendreier, D. and Kuhlmann, U. (2006), *Environmental Impact of Invertebrates for Biological Control of Arthropods: Methods and Risk Assessment*, Wallingford, UK: CABI Publishing.
- DeBach, P. and Schlinger, E. I. (1964), *Biological Control of Insect Pests and Weeds*, New York, NY, USA: Reinhold Publishing Company.

- Hajek, A. E. (2004), *Natural Enemies: An Introduction to Biological Control*, Cambridge, UK: Cambridge University Press.
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- Wäckers, F. L., van Rijn, P. C. J. and Bruin, J. (2005), *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*, Cambridge, UK: Cambridge University Press.

6.3 Websites

Further information regarding appropriate safeguarding decisions and resulting actions for exotic plant pests can be found on institutional websites such as Center of Invasive Species Research (<http://cisr.ucr.edu>), Integrated Pest Information Platform for Extension and Education (<http://www.ipipe.org>), International Organization for Biological Control (<http://www.lobc-global.org>), Pest Lens (<https://pestlens.info>), The Western Integrated Pest Management Center (<http://westernipm.org>) and University of California Agriculture and Natural Resources Statewide Integrated Pest Management Program (<http://ipm.ucanr.edu>).

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