REVIEW

Approaches to conserving natural enemy populations in greenhouse crops: current methods and future prospects

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Abstract Biological pest control in greenhouse crops is usually based on periodical releases of mass-produced natural enemies, and this method has been successfully applied for decades. However, in some cases there are shortcomings in pest control efficacy, which often can be attributed to the poor establishment of natural enemies. Their establishment and population numbers can be enhanced by providing additional resources, such as alternative food, prey, hosts, oviposition sites or shelters. Furthermore, natural enemy efficacy can be enhanced by using volatiles, adapting the greenhouse climate, avoiding pesticide side-effects and minimizing disrupting food web complexities. The special case of high value crops in a protected greenhouse environment offers tremendous opportunities to design and manage the system in ways that increase crop resilience to pest infestations. While we have outlined opportunities and tools to develop such systems, this review also identifies knowledge gaps, where additional research is needed to optimize these tools.

Keywords Biological control · Functional biodiversity · Open rearing systems · Food sprays · Mulch layers · Mixed diets · Pest-in-first techniques · Greenhouse climate · Pesticide side-effects

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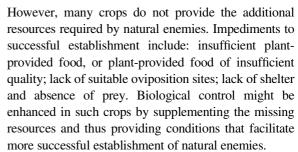Lancaster Environment Centre, Lancaster University, Lancaster L41 4YQ, UK

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Introduction

Biological control of arthropod pests has a long tradition in greenhouse crops. Both the area on which it is used and the number of available biological control agents are still expanding (Pilkington et al. 2010; van Lenteren 2012). Biological control programmes in greenhouses are often based on periodical releases of natural enemies, also referred to as augmentative biological control (van Lenteren 2012). Although biological control has proven to be successful in many greenhouse crops, efficacy can be insufficient in other crops such as ornamentals plants (Heinz et al. 2004). Poor establishment and persistence of natural enemies in certain crops can be one of the main problems in biological pest control, which is partly due to the types of natural enemies used. The selection of natural enemies for augmentative biological control was traditionally focused on specialist natural enemies that were released to obtain rapid control of the pests (van Lenteren and Woets 1988). Well-known examples are the spider mite predator *Phytoseiulus persimilis* Athias-Henriot, the whitefly parasitoid *Encarsia formosa* Gahan and the aphid parasitoids *Aphidius* spp., which are still successfully used in many crops and countries (van Lenteren 2012). Although, these specialists are well adapted to their host and can be very effective, they often disappear when prey densities have been reduced. As they are used mainly to obtain rapid control of specific pests, their efficacy requires high quantity and quality of released natural enemies and intensive monitoring to assure accurate timing of the intervention. To overcome the problem of establishment and monitoring, some specialist natural enemies (e.g. aphid and whitefly parasitoids) are released routinely (e.g. weekly) as an "insurance policy". However, this method is not always economically viable.

Methods that will increase the persistence of natural enemies in crops could greatly enhance the efficacy, robustness and cost-effectiveness of biological pest control. The establishment and persistence of generalist predators compared to specialist natural enemies may provide more sustainable biological control, as their broader diet range enables them to persist or even reproduce on alternative prey or plant-provided food sources in the absence of pest organisms (Symondson et al. 2002). This offers the opportunity to inoculate crops that provide such food sources with generalist predators before pest invasions (preventive biological control).

However, many crops do not provide the additional resources required by natural enemies. Impediments to successful establishment include: insufficient plant-provided food, or plant-provided food of insufficient quality; lack of suitable oviposition sites; lack of shelter and absence of prey. Biological control might be enhanced in such crops by supplementing the missing resources and thus providing conditions that facilitate more successful establishment of natural enemies.

Conservation of naturally occurring natural enemies (conservation biological control) is well developed in outdoor crops where various techniques of habitat modifications are used such as flowering strips, cover crops that provide windborne pollen or mulching (Landis et al. 2000; Maoz et al. 2011; Wäckers and van Rijn 2012). Biological control in greenhouse crops might be enhanced by using similar methods, but the cost-intensive production of many greenhouse crops means that conservation methods that compromise valuable cropping areas are usually not feasible. Preventive biological control through conservation techniques may help overcome many problems of greenhouse biological control, like the issues of adequate timing, pest detection, the high quantity of natural enemies required, and the labour and knowledge requirements. In this review, we summarize the current methods that are being used or studied to enhance the establishment and persistence of natural enemies in greenhouse crops and present recommendations for future research.

Methods

The methods reviewed here can be subdivided into providing alternative food, prey or hosts; providing oviposition sites or shelters; using volatiles; avoiding pesticide side-effects; adapting the greenhouse climate and avoiding disrupting food web complexities. The currently applied methods for providing alternative food, prey or hosts and oviposition sites or shelters are summarized in Table 1. It was not our aim to analyse trends in research, but rather to present an overview of tools that have been developed for enhancing biological control in greenhouse crops.

Plant-provided foods

Plants can provide nectar, pollen and plant sap as food sources for natural enemies, but the contribution of

Table 1 Conservation techniques commonly used for natural enemies in greenhouse crops

Natural enemy	Target pest	System for enhancement	Crops where applied	Reference
Phytoseiulus persimilis (specialist predatory mite)	Spider mites	Pest-in-first	Sweet pepper	Adapted from Markkula and Tiittanen (1976)
Encarsia formosa (parasitoid)	Whiteflies	Banker plants	Ornamentals and vegetables	Huang et al. (2011)
Aphidius spp. and *Aphelinus* spp. (parasitoids)	Aphids	Banker plants	Ornamentals and vegetables	Frank (2010); Huang et al. (2011)
Aphidoletes aphidimyza (gall midge)	Aphids	Banker plants	Ornamentals and vegetables	Frank (2010); Huang et al. (2011)
Episyrphus balteatus (syrphid)	Aphids	Nectar plants	Sweet pepper	Pineda and Marcos-García (2008)
Atheta coriaria (soil-dwelling rove beetle)	Shore flies, fungus gnats, thrips	Open rearing system	Herbs and ornamentals	Bennison et al. (2008)
Euseius ovalis (generalist phytoseiid predatory mite)	Thrips, whiteflies	Banker plant *Ricinus communis*	Roses	Adapted from Ramakers and Voet (1995)
Generalist phytoseiid predatory mites	Thrips, whiteflies	Rearing sachets	Ornamentals, soft fruit and vegetables	Sampson (1998)
Generalist phytoseiid predatory mites	Thrips, whiteflies	Food sprays (pollen)	Ornamentals	Adapted from van Rijn et al. (2002); Nomikou et al. (2010)
Orius spp. predatory bugs	Thrips	Banker plants, flowering plants	Strawberry, chryanthemum	Huang et al. (2011)
Orius spp. predatory bugs	Thrips	Refuge plants	Sweet pepper	Bosco et al. (2008); Cano et al. (2009)
Omnivorous mirid bugs	Whiteflies, spider mites, aphids, caterpillars	Food sprays (Ephestia eggs, Artemia cysts)	Tomato, sweet pepper	Calvo et al. (2012); van Holstein-Saj and Messelink (2014)
Omnivorous mirid bugs	Whiteflies, spider mites, aphids, caterpillars	Banker plants	Tomato	Sanchez et al. (2003)
Omnivorous mirid bugs	Whiteflies, spider mites, aphids, caterpillars	Refuge plants	Tomato	Arnó et al. (2000); Ingegno et al. 2008; Cano et al. (2009)

these food sources to their performance depends on the type of predator/parasitoid. Specialist natural enemies only reproduce in the presence of their (specific) prey/host species. However, most other natural enemies are omnivores feeding on both plant and prey (Coll and Guershon 2002). Temporal omnivores supplement their carnivorous diet with plant food during a part of their life cycle only (Wäckers et al. 2005), or they shift completely to non-prey food during part of their life cycle, often the adult stage, which has been referred to as "life history omnivores" (Polis and Strong 1996).

For example, adults of parasitoids, syrphids and gall midges can increase their longevity, flight activity and oviposition by feeding on nectar (Wäckers et al. 2005) and adults of many lacewings are herbivorous and feed on pollen and nectar (Bozsik 1992). Generalist predators consume multiple prey and may supplement their diet with plant-provided food sources (Symondson et al. 2002). True omnivores are generalist predators that feed on both prey and plants (Coll and Guershon 2002). Some of them can successfully complete their development on plant sap, such as the

mirid predatory bug *Macrolophus pygmaeus* (Rambur) (Perdikis and Lykouressis 2000). Nectar feeding can further improve this vegetarian diet (Portillo et al. 2012). Generalist phytoseiid mites and anthocorid bugs reproduce very well on pollen (Lundgren 2009). Other predatory mites, such as *Euseius scutalis* Athias-Henriot, will feed on plant sap even when pollen grains are abundant, by puncturing and feeding on the epidermal cells suggesting a close association between these predators and its plant host (Adar et al. 2012).

In those greenhouse crops where plant-provided food resources are lacking or are of insufficient quality, nutritional resources can be supplemented by planting insectary plants that provide these food sources for natural enemies. A study in greenhouses showed that adding selected flowering plants (sweet alyssum and coriander) to a sweet pepper crop results in higher densities of hoverflies, even though this crop already provides pollen and nectar itself (Pineda and Marcos-García 2008). Plants that produce a lot of pollen, like *Ricinus communis* L., can be used in greenhouses to provide fresh pollen to generalist predatory mites (Ramakers and Voet 1995). Flowering alyssum does provide resource subsidies for the maintenance of the predatory bugs *Orius laevigatus* (Fieber) and *Orius majusculus* (Reuter) during times of prey scarcity (Bennison et al. 2011; Pumariño and Alomar 2012). However, this plant is also a suitable host plant for the pest thrips itself, thus some caution is always needed. Flowering ornamental pepper plants can support and increase populations of *Orius insidiosus* (Say) in ornamental crops in commercial greenhouses (Waite et al. 2014).

Another approach can be to select crop varieties with increased levels of plant-provide food resources. A large number of plants produce so-called extrafloral nectaries and selecting varieties that produce higher nectar levels, or extrafloral nectar of a particular composition may better sustain the establishment of some species of natural enemies (Koptur 2005). For example, in greenhouse roses it has been shown that the predatory gall midge *Feltiella acarisuga* (Vallot) controlled spider mites better in rose varieties that produced higher levels of nectar in the extrafloral nectaries located on the leaf rim and stipules (Wäckers unpublished results), confirming earlier observations that availability of sugars enhances egg production of this species (Gillespie et al. 2000). Thus, the availability of plant-provided food can be a driving force in the success or failure of biological control programmes.

Food sprays

Artificial or natural food supplements can be sprayed or dusted onto the crop to support natural enemies in crops where nectar and pollen are absent or only present at low densities (Wade et al. 2008). For example, pollen sprays can serve as food for generalist predatory mites and enhance the biological control of thrips and whiteflies on cucumber (van Rijn et al. 2002; Nomikou et al. 2010). So far, pollen has not been commonly applied in greenhouses, mainly because suitable pollen was not commercially available and hand collecting pollen is labour-intensive and thus expensive. Recently, *Typha angustifolia* L. pollen has been made available commercially (sold as Nutrimite® by Biobest NV) and growers have started to use this to promote population increases of pollen feeding predatory mites. Corn pollen is also suitable for enhancing populations of *A. swirskii* and *E. scutalis* and can be mechanically harvested in large quantities, which makes it a feasible option from the economic perspective (Adar et al. 2014). Some other types of pollen are commercially available for pollination, such as apple pollen. Application of this pollen on vegetative chrysanthemum plants was found to increase the establishment of *A. swirskii* (Delisle 2013). An alternative for expensive pollen could be to use bee-collected pollen, which is available at low prices (Ramakers 1995). A disadvantage of bee-collected pollen is the fact that bees mix the pollen with enzymes and sugars to form larger clumps. This makes the pollen less accessible and nutritionally less suited for the predatory mites. Due to the added sugar, it can also be a substrate for growth of unwanted fungi in humid greenhouses (Ramakers 1995).

A potential risk of applying pollen to crops is that it could increase densities of pollen feeding thrips species such as the omnivorous western flower thrips *Frankliniella occidentalis* (Pergande), which is a major pest in greenhouse crops (Hulshof et al. 2003). However, a study with predatory mites showed that adding *Typha latifolia* L. pollen to a crop clearly enhances the biological control of thrips, even though the pollen is edible for thrips itself (van Rijn et al. 2002). This may not be the case for other pollen types,

which are more suitable for thrips (Hulshof et al. 2003). In order to minimize the potential risk of promoting thrips with pollen, it might be useful to select food sources that are more suitable for predators than for thrips.

Many artificial food sources other than pollen seem to have potential for enhancing establishment of natural enemies (Lundgren 2009). Sterilized eggs of the flour moth *Ephestia kuehniella* Zeller and decapsulated cysts of the brine shrimp *Artemia franciscana* Kellogg are two very suitable food sources for both generalist predatory bugs (Castañé et al. 2006; Bonte and de Clercq 2008) and predatory mites (Vangansbeke et al. 2014). These two food sources are now increasingly being used to boost densities of the predatory bug *M. pygmaeus* in tomato and sweet pepper crops (Calvo et al. 2012; van Holstein-Saj and Messelink 2014). Sterilized eggs of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) are currently being explored for supporting anthocorid predatory bugs in ornamentals (Anonymous 2013; Steinberg, Biobee, personal communication).

The development of inexpensive alternative food sources is one of the major opportunities and challenges for enhancing biological control in greenhouse crops in the near future. Many artificial diets have been tested with the aim of developing less expensive mass rearing techniques (e.g. Castañé and Zapata 2005; Bonte and de Clercq 2008; Nguyen et al. 2013), but these diets are currently not applied to support predator populations in commercial crops. Applying inexpensive artificial diets on crops to support predator populations have been explored only on a limited scale, but initial results seem promising (Messelink et al. 2009; Igarashi et al. 2013). Simple mixtures of yeast, sugars and proteins increased population densities of the predatory mite *A. swirskii* on chrysanthemum plants (Messelink et al. 2009). A powdered diet, based on proteins, sugars and vitamins, promoted the development of the predatory bug *Geocoris varius* (Uhler) on strawberry plants in greenhouses (Igarashi et al. 2013).

Alternative prey/hosts

The use of alternative prey/host species for the conservation of released natural enemies in greenhouse crops has been of long-standing interest for biological control of greenhouse pests (Huang et al. 2011). The method by which these alternative prey/host species are made available is based on the introduction of a non-crop plant harbouring the alternative prey species, often referred to as the "banker plant method". A widely applied system in greenhouse crops has been the use of monocotyledonous plants with cereal aphids that serve as alternative hosts for parasitoids of aphids that attack the crop (Huang et al. 2011). The advantage of this system is that the grain aphids are specific to monocotyledons and pose no threat to crops that are dicotyledon. Banker plants can also be established in the edges of the greenhouse to bridge crop-free periods and contribute to the conservation of predators (Arnó et al. 2000). The types and use of different banker plant systems have been evaluated in two recent review papers: Frank (2010) and Huang et al. (2011). These papers show that many banker plant systems have been developed, but only a limited number are currently applied due to a range of practical problems such as the risk of hyperparasitism of the parasitized aphids (Nagasaka et al. 2010; Jacobson 2011). However, banker plant systems show enormous potential for conservation of released natural enemies, if the practical problems can be overcome. For example, banker plants could be developed that specifically support aphid predatory midges by selecting aphids which are not suitable hosts for parasitoids. The negative effects of increased hyperparasitism through banker plants could then be prevented (Nagasaka et al. 2010).

Some alternative prey species are not harmful to the crop and establishment of these prey species in the crop may support their natural enemies. In chrysanthemum, the application of yeast and sugars has been shown to maintain populations of astigmatic mites that are suitable prey for phytoseiid predatory mites (Messelink et al. 2009). Another method for providing alternative prey species can be based on mulch layers. Recent developments in chrysanthemum show that such layers support the establishment of astigmatic mites and, as a result, increase densities of soil-dwelling predatory mites (Grosman et al. 2011). Similar methods have been tested to support the generalist hunter fly *Coenosia attenuata* Stein (Kühne 1998). Hence, developing mulch layers for supporting predators in greenhouse crops seems to be a promising method.

Artificial open rearing systems

The idea of rearing natural enemies in greenhouse crops on banker plants has for some natural enemies

been further developed into artificial rearing units. The best known and most widely applied system is based on a rearing sachet containing a small breeding ecosystem of bran with saprophytic fungi, fungal-feeding astigmatic mites (prey) and predatory mites (Sampson 1998). Several modifications with different types of astigmatic mites, predatory mites, food sources for astigmatic mites such as sugars, starch, yeast and types of sachets have been developed and patented by the biological control industry (Wright 2006; Baxter et al. 2011; Bolckmans et al. 2013). Such units, in general, produce predatory mites for 3–6 weeks (Baxter et al. 2011). This can be optimized by balancing the initial rate of predator, prey and food in the rearing unit. The production period can now be prolonged (7–12 weeks) by combining astigmatic mites with low and high intrinsic growth rates, for example a combination of *Lepidoglyphus destructor* (Schrank) and *Carpoglyphus lactis* (L.) (Bolckmans et al. 2013). Application of rearing sachets are particularly useful in non-flowering crops, or in crops with flowers that do not produce pollen (e.g. cucumber), or in crops such as strawberry before the first flush of open flowers.

Another type of open rearing system that has been developed for the generalist rove beetle *Atheta coriaria* (Kraatz) is based on boxes containing a poultry-feed diet (Bennison et al. 2008). The reason for using such a system is not only to support *A. coriaria* establishment, but also to provide growers with an inexpensive method for releasing high numbers of the predators when needed. This system is currently used by UK ornamental growers, usually in propagation houses for control of sciarid and shore flies. Artificial rearing units may be a useful tool to support natural enemies in greenhouse crops. However, they need to be assessed critically, as eventually it is not the production, but the establishment and survival of predators in the crop which is important for pest control.

Pest-in-first techniques

A more risky method to support natural enemies is the deliberate release of pest species into crops. This approach has been developed for spider mites as a food source for the specialist predatory mite *P. persimilis*. Normally, this predator is applied after the detection of hotspots of spider mites in the crop, but this requires intensive crop monitoring and the release needs to be in time and at sufficient densities to prevent crop damage. Instead of applying predatory mites as "living pesticides" after the development of a natural infestation of spider mites, it is also possible to inoculate plants with a low level of spider mites early in the growing season and release predators shortly afterwards or a few days later. This "pest-in-first" technique (Markkula and Tiittanen 1976) allows the predator *P. persimilis* to establish in the crop and give protection against subsequent spider mite invasions. Currently, this method is mainly used in sweet pepper crops. The method was not adopted immediately, but it promoted another way of thinking about pest control, based on living with the pest rather than trying to eliminate it. For generalist predatory mites, it has clearly been shown that pest diversity increases the population densities of generalist predatory mites (Messelink et al. 2010). Thus, allowing low levels of several species of pests, in numbers insufficient to risk crop damage, might be considered for the conservation of generalist predators.

Mixed diet effects

In addition, the reproduction of generalist predators in crops can be increased by providing mixed diets of prey, or mixes of prey and non-prey food sources. Survival and reproduction of the predator *O. insidiosus* were enhanced when diets of aphids were supplemented with thrips as a prey source (Butler and O'Neil 2007). Generalist predatory mites also benefit from mixed prey diets: juvenile development of the predatory mite *A. swirskii* was significantly improved on a mixed diet of thrips and whiteflies compared to a single pest diet (Messelink et al. 2008). Similar results were found for a red velvet mite predator, *Balaustium* sp.: this predator developed much better on a mixed diet of whitefly eggs and spider mites than on a diet of each prey alone (Muñoz-Cárdenas et al. 2014). Mixing diets of generalist predators may not only affect reproduction and survival, but also their behaviour. For example, supplementing a diet of thrips with pollen did not increase egg production by the predator *O. laevigatus*, but surprisingly increased predation rates of thrips larvae (Hulshof and Linnamäki 2002). Thus, supplementing diets of single pest species for generalist predators with alternative prey or food may be a useful method to increase predator densities and enhance pest control.

Oviposition sites and shelters

The establishment and reproduction of released natural enemies in greenhouse crops strongly depends on the plant characteristics of that specific crop. Suitable oviposition sites are crucial for reproduction of many predators. Important generalist predatory bugs such as *Orius* spp. and *M. pygmaeus* lay their eggs into soft plant parts and ovipositional acceptance of the host plant depends on the morphological characteristics such as epidermal thickness or trichome density (Lundgren et al. 2008). The woody plant parts of some crops, such as roses, are not very suitable for this specific oviposition behaviour of predators and may explain the poor establishment in roses (Chow et al. 2008). Another problem in many ornamental crops is that suitable oviposition sites (softer stems of flowers) are harvested, which removes a potential new generation of natural enemies from the greenhouse. The same problem can also occur on tomato with the de-leafing practice (a common horticultural practice consisting of removing lower leaf strata), that has a strong negative influence on the development of mirid populations (Bonato and Ridray 2007) and *E. formosa* (by removing parasitized whitefly scales, van Lenteren et al. 1996). These problems may be solved by adapting the de-leafing strategy. It may be possible to simply delay the de-leafing time, to spare parts of the plants from de-leafing or just to retain the de-leafed material in the greenhouse for a specific time period to allow for the natural enemies to emerge or move. Another option for mirid predatory bugs is to offer special non-crop plants that provide suitable oviposition sites for the mirid predators (Sanchez et al. 2003), which can be combined with plants that also provide alternative food sources (see the sections on insectary plant and alternative prey/hosts).

Predatory mites prefer plants with trichomes to attach their eggs (Loughner et al. 2010; Schmidt 2014). However, not all trichomes are favourable for natural enemies: tomato plants produce glandular trichomes which strongly hamper the movement of predatory mites (Simmons and Gurr 2005; Koller et al. 2007), as well as *Orius* spp. (Coll and Ridgway 1995). Trichomes can be completely absent in some ornamental crops. This lack of non-glandular leaf trichomes may be compensated by applying fibres to a crop that mimic the function of trichomes. The abundance of the predatory mite *A. swirskii* increased when cotton fibre patches were added to leaves with no trichomes (Loughner et al. 2011). Adar et al. (2014) enhanced predator populations of *E. scutalis* by adding pollen and rings of horticultural twine (80 % rayon and 20 % jute) for providing oviposition sites to young pepper plants before flowering. In sweet pepper, jute fibres are preferred over plant leaves as oviposition sites by the lacewing *M. variegatus,* and also provided refuges for emerging larvae to protect them from cannibalism (Messelink, personal observations).

A number of plants have independently evolved refuges for natural enemies, the so-called domatia (Walter 1996). For example, sweet pepper plants have tuft domatia in the vein axils that are used by predatory mites for oviposition. These domatia may reduce cannibalism or predation by other predators and increase survival by providing a suitable microclimate (Walter 1996). Such specific domatia are absent in most other greenhouse crops. It might be possible to provide these refuge sites to predatory mites with banker plants. A study in roses showed enhanced spider mite control by predatory mites when plants containing numerous domatia (*Viburnum tinus* L. and *Vitis riparia* Michx) were added to the rose plants (Parolin et al. 2013). Shelters for natural enemies can also be facilitated by mulch layers that increase pore size in the substrate. This is not only useful for ground-dwelling predators that use such small spaces for shelter and feeding on mycophageous mites (Vreeken-Buijs et al. 1998), but also for natural enemies that migrate between the substrate layer and the plant, such as some generalist phytoseiid predatory mites and chrysopid larvae (Szentkirályi 2001; Messelink and van Holstein-Saj 2006). This flexible migration behaviour is so far underestimated and hardly exploited, yet it may be used when applying mulch layers to enhance predator survival.
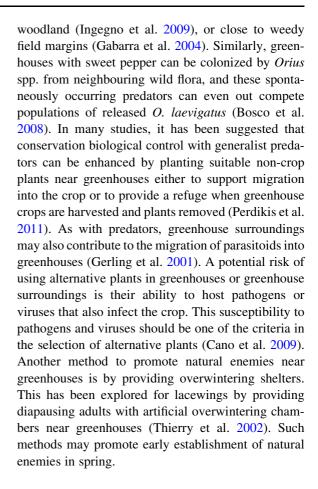
Vegetation diversity

Natural enemies may benefit from increasing vegetation diversity through the plant-provided resources such as pollen, nectar, a favourable microclimate and alternative prey species (Landis et al. 2000). However, it is important to realize that not all plant species are suited to support predators, and that it is critical to select the right plant species rather than increasing diversity per se (Wäckers and van Rijn 2012). This principle has become popular in outdoor crops where

several levels of vegetation diversity are applied with flowering strips, pollen-producing plants, beetle banks or crop mixtures (Maoz et al. 2011; Gurr et al. 2012). Increasing plant diversity allows predators to optimize their fitness by exploiting various plant-based resources such as nutrition and oviposition sites (Lundgren et al. 2008). However, such practices are probably difficult to apply in greenhouse crops when the maximum cultivation area needs to be used for crop production in order to make the production units economically viable. It might be useful to investigate whether the benefits of plant diversity for pest control can be achieved by mixing economically important crops. However, modern greenhouse crops are often monocultures in highly specialised production units where not only crop cultivation, but also harvest and packaging techniques are specialised. Greenhouse crops are not mixed specifically with the aim to enhance pest control, but plant diversity can be applied on a smaller scale with banker plants, trap plants or companion plants (Huang et al. 2011; Parolin et al. 2012; Xu et al. 2012). Even the application of such plants remains limited, because they require separate care. More experimental data that show the potential benefits of using crop diversity in greenhouse crops may promote this idea to growers and biological control advisors.

Conservation of naturally-occurring natural enemies in greenhouse surroundings

Conservation biological control can also be useful in greenhouse areas where naturally occurring natural enemies are able to migrate into greenhouses from non-crop plants outside. In fact, such background biocontrol can help make augmentative releases economical (Gerling et al. 2001). In the Mediterranean region, generalist mirid predators often migrate from outdoor non-crop plants into tomato greenhouses, where they contribute to the control of important pests such as whiteflies, leaf miners and *Tuta absoluta* (Meyrick) (Castañé et al. 2004; Perdikis et al. 2011; Ingegno et al. 2013). The natural presence of predatory bugs in tomato greenhouses seems to be strongly related to the surrounding landscape. For example, mirid predators are found mainly in agroecosystems characterized by a high environmental complexity, i.e. a patchy landscape where greenhouses are surrounded by natural vegetation corridors, wasteland and woodland (Ingegno et al. 2009), or close to weedy field margins (Gabarra et al. 2004). Similarly, greenhouses with sweet pepper can be colonized by *Orius* spp. from neighbouring wild flora, and these spontaneously occurring predators can even out compete populations of released *O. laevigatus* (Bosco et al. 2008). In many studies, it has been suggested that conservation biological control with generalist predators can be enhanced by planting suitable non-crop plants near greenhouses either to support migration into the crop or to provide a refuge when greenhouse crops are harvested and plants removed (Perdikis et al. 2011). As with predators, greenhouse surroundings may also contribute to the migration of parasitoids into greenhouses (Gerling et al. 2001). A potential risk of using alternative plants in greenhouses or greenhouse surroundings is their ability to host pathogens or viruses that also infect the crop. This susceptibility to pathogens and viruses should be one of the criteria in the selection of alternative plants (Cano et al. 2009). Another method to promote natural enemies near greenhouses is by providing overwintering shelters. This has been explored for lacewings by providing diapausing adults with artificial overwintering chambers near greenhouses (Thierry et al. 2002). Such methods may promote early establishment of natural enemies in spring.

Induced plant responses

Induced plant resistance against insects consists of direct traits, such as the production of toxins and feeding deterrents that reduce survival, host plant preference, fecundity or developmental rate of pests, and indirect traits, that attract and/or retain carnivorous enemies of the herbivores (Paré and Tumlinson 1999; Turlings and Wäckers 2004). The latter category includes traits such as the production of plant volatiles and extrafloral nectar. Both types of resistance mechanisms can affect the conservation of natural enemies in greenhouse crops. For example, secondary plant metabolites induced by pests can also reduce the reproduction rate of the natural enemies of that prey (Koller et al. 2007). These effects will negatively affect the establishment of natural enemies into crops. Pests might even adapt to these plant responses, whereas the natural enemies still encounter negative effects (Ode 2006). Herbivore induced plant volatiles (HIVs) help natural enemies to detect their prey/hosts

in a crop (Paré and Tumlinson 1999), whereas extrafloral nectar production is increased locally in response to herbivory, guiding natural enemies to the feeding herbivore (Wäckers and Bonifay 2004). Conservation of natural enemies might be enhanced in greenhouse crops by breeding cultivars that give increased HIV or extrafloral nectar production (Turlings and Wäckers 2004; Kappers et al. 2005), but such techniques are, so far, not included in commercial breeding programmes.

Induced plant responses can also affect other plant traits, such as trichomes. On tomato, it has been observed that the tomato russet mite *Aculops lycopersici* (Massee) induces a plant response which locally causes the collapse of glandular trichomes (van Houten et al. 2013). In future work, it will be interesting to determine whether these plant responses can be triggered and used to promote the establishment of predators on tomato plants.

Semiochemicals

Behaviour of natural enemies is largely guided by semiochemicals, and these volatile signals can be applied to manipulate their behaviour. Attraction of natural enemies with synthetic compounds, similar to HIVs, is increasingly being tested in outdoor crops (Kaplan 2012). Natural enemies may also respond to odours that are produced by their prey/host species, such as sex pheromones or alarm pheromones. Sex pheromone lures are commonly used to monitor for certain pest species in greenhouse crops and in some cases to contribute to control when used with trapping systems. However, volatiles for enhancing natural enemy establishment are so far not applied in greenhouse crops. Such techniques seem at first not to be relevant for greenhouse crops, because most natural enemies are released and retained by the closed system, so there is limited need to lure them into crops. However, some released natural enemies tend to fly out of the greenhouse and retaining them in the crop may increase their efficacy. For example, aphid parasitoids can be triggered to search more actively for aphids when the aphid sex pheromone is present (Powell and Pickett 2003). Main chemical components of this pheromone could possibly be used to treat clusters of aphid infested plants in greenhouses, which might increase efficacy of released parasitoids (Glinwood et al. 1998). Lures may also be used to attract released

natural enemies to alternative food sources in order to help them establish (attract & reward, Simpson et al. 2011). In fact, parasitoids and predators may very quickly learn to associate certain odours with a reward (Turlings et al. 1992). Finally, lures may be a useful tool to stimulate oviposition of released natural enemies. For example, releases of adult chrysopids in greenhouse crops often fail, probably because of an obligatory migration flight before oviposition (Duelli 1980). The use of attractants in combination with food sprays may stimulate oviposition of released chrysopid females into the target crop (Kunkel and Cottrell 2007).

Pesticide side-effects

Conservation of natural enemies should ideally not be combined with the use of pesticides, as most pesticides have lethal effects on natural enemies (summarized in Table 2). However, the use of pesticides is often inevitable for pests and diseases that lack effective non-chemical control measures. Mitigation of undesired side-effects on conservation of natural enemies can be achieved by selecting pesticides that are compatible or as close to compatible as possible with natural enemies. However, most insecticides have a broad spectrum of action affecting both pest and beneficial arthropods, and very few are completely selective (an overview of side-effects on main natural enemy families with simplified toxicity classes of principal pesticides is presented in Table 2). Moreover, pesticides can have underestimated sub-lethal effects affecting the physiology and behaviour of natural enemies and reducing their viability (Stark et al. 2004; Desneux et al. 2007). A careful assessment of overall side-effects (including sub-lethal effects) of pesticides, both synthetic and natural, is essential to develop truly selective pesticides for the conservation of natural enemies by using active ingredients with the least non-target activity. Undesired side-effects of pesticides on natural enemies could be further reduced by adapting the timing, place and mode of application (Croft 1990). However, caution is needed especially for pesticides with a high level of persistence as these could disrupt natural enemy establishment over long periods.

Climate and light adaptations

Natural enemies, just like plants, can be impacted directly by greenhouse climate parameters, such as

Table 2 Side-effects (0 = harmless; 1 = variable harmfulness (effects depend on the species, stage and product, or results are contrasting); 2 = harmful) of pesticide classes in laboratory (L), semi-field (SF) and field (F) conditions on predators and parasitoids used in greenhouse crops (OP organophosphorus pesticides, SFB selective feeding blockers, SP synthetic pyretroids)

	Family	Insecticide, chemical class and toxicity	References
Predators	Phytoseiidae	Azadirachtin (L-1), OP (L, F-2), SP (F-2), neonicotinoids (L, F-0), SFB (L-0), oxadiazine (L, F-0), chlorantraniliprole (L-0), abamectin (L-1, F-0), spinosad (L, SF, F-0), benzoyl ureas (L, F-0), buprofezin (L-0), cyromazine (L-1, SF-0), ecdysone antagonists (L, F-0)	El-Wakeil et al. (2013); Gradish et al. (2011); Cloyd (2012)
	Anthocoridae	Azadirachtin (L, F-0), OP (L-2), carbamates (L, F-0), SP (L, F-2), etofenprox (L-1, F-2), neonicotinoids (L-1), SFB (L-1), oxadiazine (L-0), chlorantraniliprole (L, F-0), abamectin (L, F-1), spinosad (L-1, F-0), benzoyl ureas (L-1), buprofezin (L-0), juvenoids (L-0), ecdysone antagonists (L-0)	Gradish et al. (2011); Cloyd (2012); Angeli et al. (2005); Bosco et al. (2012)
	Miridae	Azadirachtin (L-1), OP (L-2), neonicotinoids (L-1), SFB (L-0), oxadiazine (L-1), abamectin (L-0), spinosad (L-1), ecdysone antagonists (L-0)	Cloyd (2012); Figuls et al. (1999); Arnó and Gabarra (2011)
	Chrysopidae	Azadirachtin (L-1, SF, F-0), neonicotinoids (L, F-2), spinosad (L-1), benzoyl ureas (L-1), buprofezin (L-0), juvenoids (L-1), ecdysone antagonists (L-0)	El-Wakeil et al. (2013); Cloyd (2012)
	Cecidomyiidae	Azadirachtin (L-0)	Cloyd (2012)
	Syrphidae	SFB (L-0)	Cloyd (2012)
	Coccinellidae	Azadirachtin (L-1, SF, F-0), OP (F-1), carbamates (L, F-1), neonicotinoids (SF-1), SFB (L-0), spinosad (L-2), benzoyl ureas (L-1), buprofezin (L-2), juvenoids (L-1)	El-Wakeil et al. (2013); Cloyd (2012)
Parasitoids	Braconidae (including Aphidiinae)	Azadirachtin (L-0), SP (L, SF-2), SFB (L-2, F-0), juvenoids (L-2, F-0)	El-Wakeil et al. (2013); Cloyd (2012)
	Aphelinidae	Azadirachtin (L-0), carbamates (L, SF, F-2), SP (SF-2), neonicotinoids (L, SF-1), SFB (L-0), oxadiazine (L, F-0), chlorantraniliprole (L, F-0), abamectin (L-1, SF, F-0), spinosad (L, F-2), benzoyl ureas (SF-0), buprofezin (L, SF-0), OP (L-1), cyromazine (SF-0), juvenoids (L-1), ecdysone antagonists (L-0)	El-Wakeil et al. (2013); Gradish et al. (2011); Cloyd (2012)
	Trichogrammatidae	Azadirachtin (L-1, F-0), OP (L-2), carbamates (L-2), SP (L, SF, F-2), etofenprox (L-2), neonicotinoids (L-2), abamectin (L-1), spinosad (L-2), benzoyl ureas (L-0), ecdysone antagonists (L-0)	El-Wakeil et al. (2013)

temperature, vapour pressure deficit (VPD), light intensity and quality, and day length. As ectotherms, natural enemies are directly affected by temperature, i.e., the higher the temperature the shorter the development period up to the upper developmental threshold for the arthropod. It is well-known that *P. persimilis* provides effective control of two spotted spider mite up to 30 °C, but above 30 °C the development time for spider mites becomes shorter than *P. persimilis* (Lindquist and Short 2004). With the concern for energy conservation, growers are moving to daily temperature integration regimes for crop production. For example, temperature integration means that higher temperatures during the day are tolerated and compensated by lower temperatures during the night. This may be detrimental for night-active natural enemies like *Aphidoletes aphidimyza* (Rondani), that may need certain temperatures to be flight-active (Markkula et al. 1979). In addition, the impact on development time for natural enemies under fluctuating temperature regimes seems to vary according to the species (Gillespie et al. 2012). With the

move to year round production and to increase yield/production per unit area, growers are increasingly using supplementary lighting in vegetable production and are extending the period of artificial lighting in ornamentals to continuous lighting in the case of rose production. By extending the photoperiod using supplemental lighting, diapause induction will be prevented in biological control agents that enter reproductive diapauses under short daylengths. However, not all natural enemies respond in the same way to supplementary lighting. Very little is known on this subject, and this is an area which needs further investigation (Johansen et al. 2011).

Optical manipulation of natural lighting can also impact the behaviour of pests and their natural enemies. Studies have shown that the use of photoselective nets can reduce the invasion of whiteflies, aphids or thrips into a tomato or pepper crop and the subsequent viral diseases that they vector (i.e., Tomato yellow leaf curl virus) (Ben-Yakir et al. 2012). This material should contain selective additives that allow photosynthetically active radiation to pass, but inhibit or reflect wavelengths that the pests perceive, such as UV (330–350 nm) and green–yellow (520–550 nm). However, their influence on natural enemies is not known and needs to be investigated. Thus, the covering may need to be adjusted according to the crop, pests and natural enemies involved. Conservation of natural enemies may also be improved by selecting natural enemies that are better adapted to the greenhouse climate, for example strains of predatory mites that are better adapted to low humidity levels and higher temperatures (Walzer et al. 2007) or are non-diapausing (van Houten et al. 1995).

Food web complexities

Methods that support the establishment of natural enemies are often associated with increased complexity within food webs of natural enemies, prey and food sources which could include potential risks for pest control (Messelink et al. 2012). For example, the provision of alternative prey or food can have negative effects on biological control should predators switch to more abundant or more preferred alternative prey or food sources, or through predator satiation (van Maanen et al. 2012). However, such effects mainly occur on the short-term and often turn soon into positive effects through a strong numerical response of the predator population (van Rijn et al. 2002; Messelink et al. 2008). Complexity increases even more when the alternative food source is also edible for the pest species. It is well-known that many herbivores also benefit from alternative food sources such as pollen and nectar (Wäckers et al. 2007). Also, the selection of nectar resources to support parasitoids needs careful consideration, as some flowering plants can be more beneficial for the targeted pest than for its natural enemies (Balzan and Wäckers 2013). As discussed before, these problems can be avoided by selecting food sources that are more suitable for predators than for the herbivore.

Providing food and shelter for natural enemies may also benefit the fourth trophic level, e.g. secondary parasitoids or so-called hyperparasitoids. Aphid parasitoids, particularly in greenhouse crops, are commonly attacked by several species of hyperparasitoids that can strongly disrupt aphid biological control (Jacobson 2011). The longevity of these hyperparasitoids is enhanced in the presence of nectar sources, thus potentially increasing the chance of disruption of aphid control (Araj et al. 2009). The benefits of conservation methods obviously must benefit the third trophic level (the natural enemies) more than it does the second (pests) or fourth (hyperparasitoids).

Finally, increased numbers of natural enemy species may also result in more interactions among natural enemies, such as intraguild predation, which could disrupt biological control in some cases (Rosenheim et al. 1995; Symondson et al. 2002; Messelink et al. 2012). However, effects of intraguild predation should not be overestimated, because most studies do not show any negative effect on biological control (Janssen et al. 2006). For example, mirid predatory bugs also feed on parasitized whiteflies, but the combination of predators and parasitoids can still be better for biological control (Castañé et al. 2004; Gabarra et al. 2006). Hyperpredation occurs when one predators feeds on another predator without sharing a prey. This can be very disruptive for biological control, as was shown for predatory mites consuming eggs of the aphid predatory midge *A. aphidimyza* (Messelink et al. 2011). Biological control of honeydew-producing pests, such as aphids and mealybugs, can be disrupted by ants defending their sugar source. Similarly, ants may prevent biological control agents from utilizing sugar rich food supplements when used in the crop. Methods that exclude or distract ants from

crops may enhance the conservation of natural enemies (Vanek and Potter 2010).

These food web complexities emphasize that a thorough understanding is needed of the direct and indirect effects of conservation methods on the total ecosystem in greenhouses in order to avoid potential negative effects on pest control. Interactions that are potentially negative for biological pest control could be avoided by selecting and releasing natural enemy communities that maximise sustainable pest control. Hence, the development of tools that support the establishment of natural enemies should go hand in hand with extending our understanding of species interactions in biological control communities.

Conclusions

Biological control in greenhouse crops has proven to be very successful (Heinz et al. 2004; Pilkington et al. 2010), but a huge challenge still exists to combat pest species that currently cannot be controlled with natural enemies or to control pest species in crops where natural enemies do not establish well. One of the underlying problems may be that natural enemies are often still applied as "biopesticides" rather than seeing them as living organisms that require appropriate resources and conditions to survive and reproduce. This review has presented several methods that can be used to support establishment of natural enemies by combining the fundamentals of conservation biological control with releases of commercially produced natural enemies. For many growers, this approach may be a paradigm shift, as it is a true evolution from simply releasing natural enemies to the active management of an ecosystem. The special case of high value crops in a protected environment of greenhouses offers tremendous opportunities to design and manage the system in such a way that increases crop resilience to pest infestations. While we have outlined opportunities and tools to develop such systems, additional research is needed to optimize these tools. We recommend further research for (1) development of alternative food sources that more specifically support natural enemies and not the pest species or hyperparasitoids, (2) identifying food sources for natural enemies that specifically supplement the nutritional value of certain pest species, (3) utilization of volatiles that retain natural enemies in

greenhouses and (4) selecting natural enemies with traits that are well-adapted to specific crops or greenhouse climates.

The conservation methods described in this review are not only important for controlling pests that currently occur in greenhouses, but also for new invasive pest species which may appear in the future. We expect that this field of research will be especially important in order to further develop biological control strategies in ornamentals, where the low tolerance for pests is currently a stumbling block for natural enemy establishment and in organic cropping systems, where pest control is mainly dependent on biological control with natural enemies.

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