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Predators and Parasitoids-in-First: From Inundative Releases to Preventative Biological Control in Greenhouse Crops

Juliette Pijnakker, Dominiek Vangansbeke, Marcus Duarte, Rob Moerkens and Felix L. Wäckers*

R&D Department, Biobest Group NV, Westerlo, Belgium

Repeated mass introductions of natural enemies have been widely used as a biological control strategy in greenhouse systems when the resident population of natural enemies is insufficient to suppress the pests. As an alternative strategy, supporting the establishment and population development of beneficials can be more effective and economical. The preventative establishment of predators and parasitoids, before the arrival of pests, has become a key element to the success of biological control programs. This "Predators and parasitoids-in-first" strategy is used both in Inoculative Biological Control (IBC), and in Conservation Biological Control (CBC). Here, we provide an overview of tools used to boost resident populations of biocontrol agents.

Keywords: biological control, conservation, standing army, bodyguards, predators, factitious prey, pollen, nectar

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***Correspondence:**
Juliette Pijnakker
juliette.pijnakker@biobestgroup.com

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INTRODUCTION

Biological control in greenhouses dates back almost 100 years, when Speyer (1927) at the Cheshunt Experimental Station first described the control of greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) by the specialist parasitoid *Encarsia formosa* Gahan (Hussey et al., 1969). This example was followed in the fifties by the use of the natural enemies against mealybugs (Doutt, 1951) and in the sixties, by the introductions of the specialist predatory mite *Phytoseiulus persimilis* Athias-Henriot for the control of spider mites (Bravenboer and Dosse, 1962). Biological control in greenhouses has since been extended by the addition of generalist biocontrol agents to complement the specialist beneficials (Janssen and Sabelis, 2015). The release of generalists, that can feed on a range of prey, but may also exploit non-prey food, made it possible to maintain populations of natural enemies in crops in absence of the target pest, thus facilitating the preventative use of natural enemies.

Thirty years ago, Ramakers (1990) proposed the concept of "predator-in-first" and stated that the availability of supplementary foods, such as pollen and nectar, is essential for early establishment of generalist natural enemies. However, many cropping systems lack these floral resources (Wäckers et al., 2005). As a result, most biological control programmes rely on inundative release strategies, where natural enemies are periodically introduced in large numbers to control pest problems (Stinner, 1977; Van Lenteren et al., 2003; Collier and Van Steenwyk, 2004). The pest control in inundative strategies often relies on the released individuals, rather than their progeny (De Bach, 1964). In ornamentals especially, cheap predators and parasitoids are released weekly in crops without necessarily accomplishing establishment (Hoddle et al., 1997, 1998; Buitenhuis et al., 2014, 2015). Manual and automatized blowers of beneficials have been specially designed for that purpose

(Van Schelt et al., 2008). Inundative biological control strategies have among others the drawback to exclude more clostly, but more efficient natural enemies, like predatory bugs.

In recent years, there has been an increased interest in strategies to allow a preventative establishment of natural enemies (standing army) (Messelink et al., 2014; Pijnakker et al., 2017). Both Inoculative Biological Control (IBC), which aims at establishing mass-reared natural enemies, and Conservation Biological Control (CBC), that seeks to conserve or enhance naturally occurring biocontrol organisms, can benefit by providing natural enemies with missing resources (Hagen, 1986; Zemek and Prenerová, 1997; Wäckers, 2005). In biological control programs substantial advancements have been made in the use of factitious prey, pollen (extrafloral) nectar, and honeydew as food supplements (Van Rijn et al., 2002; Wäckers et al., 2005; Lundgren, 2009; Messelink et al., 2014). In addition, some predators can feed on plant tissues, which facilitates their establishment in periods of prey scarcity or in the absence of prey (Eubanks and Denno, 1999; Lucas and Alomar, 2001; Pappas et al., 2017). Besides the role of non-prey food, establishment of predators can also be supported through the provisioning of additional non-food resources, like shelter and oviposition sites (Messelink et al., 2014; Pekas and Wäckers, 2017). The advances in the use of supplementary resources to support early establishment of natural enemies in greenhouse crops are the focus of this review. Microbial control is not developed in this review, as preventative use of insect-pathogenic and antagonistic fungi is complex, there are few studies and results are inconsistent (Elliot et al., 2000).

PLANT-TISSUE FEEDING

While plant feeding by omnivorous biocontrol organisms can potentially cause plant damage (see below), using tissue-feeding omnivores as biological control agents has many advantages. They have been traditionally underestimated in inundative release biocontrol strategies (Castañé et al., 2011); however, several recent studies emphasize its importance (Coll and Guershon, 2002; Eubanks and Styrsky, 2005; Wäckers et al., 2005; Castañé et al., 2011; Pappas et al., 2017). Plant-tissue feeding plays a major role in the survival of several omnivores, as it has been shown to occur broadly in heteropterans (Ridgway and Jones, 1968; Naranjo and Gibson, 1996), as well as in a number of phytoseiid mites (Tanigoshi et al., 1993). In Heteroptera it provides nutrients that are essential to successful development (Gillespie and McGregor, 2000; Sinia et al., 2004) and may help them persist in periods of drought. Plant-tissue feeding is also assumed to provide some crucial resources that facilitate prey consumption. When consuming prey, some predatory Heteroptera require a source of water to dilute the digestive enzymes they inject into their prey (Cohen, 1985). Plant-tissue feeding may allow the Heteroptera to balance nutrients, proteins, carbohydrates, vitamins and minerals that would otherwise be restricted in a carnivorous diet (Polis et al., 1989; Coll, 1998). Particular plant species allow a full development of omnivorous Heteroptera in absence of prey. As omnivores can rely on tissue feeding, the risk of dying or leaving the crop at low prey densities is probably limited (Crawley, 1975; Pimm and Lawton, 1978), but will depend on the plant species.

While the induction of plant resistance mechanisms in response to herbivore feeding has been widely studied, few studies have addressed the effect of plant-tissue feeding by omnivore natural enemies in terms of plant defense induction (Stout et al., 1997; Agrawal et al., 1999; Agrawal and Klein, 2000; Agrawal, 2005a,b; Pappas et al., 2017). Induced plant resistance mechanisms include the production of secondary metabolites, part of which are released as volatile chemicals (Herbivore-induced plant volatiles, HIPVs) (Paré and Tumlinson, 1999). HIPV's play an important role in protecting the damage sites against entry by pathogens. The induced change in plant chemistry can reduce plant attractiveness to herbivores, as well as herbivore performance (Turlings et al., 1990, Bolter et al., 1997; Karban and Baldwin, 1997; De Moraes et al., 2001; Kalberer et al., 2001; Wakefield et al., 2005), thus representing an important example of direct plant defense. An indirect defense mechanism is involved when HIPV's are used by the herbivore's natural enemies to locate their prey/hosts (Turlings and Wäckers, 2004). In addition, plant-tissue feeding also elicits the production of extrafloral nectar, an indirect defensive trait which allows plants to recruit ants and other nectar feeding omnivores, which in turn protect the plants by attacking the herbivores (Wäckers and Bonifay, 2004; Kost and Heil, 2005). Several studies have now demonstrated that plant-tissue feeding by predators also activates plant defense mechanisms (Pérez-Hedo et al., 2015a,b; Naselli et al., 2016; Pappas et al., 2016; Zhang et al., 2018). Plants with activated defense systems are less attractive to the tobacco whitefly *Bemisia tabaci* (Gennadius), but more attractive to the whitefly parasitoid *E. formosa*. Pappas et al. (2015) showed that the zoophytophagous predator *Macrolophus pygmaeus* Rambur induces defense of tomato plants, making them less susceptible to the two-spotted spider mite *Tetranychus urticae* Koch, but without affecting the greenhouse whitefly *T. vaporariorum*. Zhang et al. (2018) demonstrated that *T. urticae* and Western flower thrips *Frankliniella occidentalis* (Pergande) laid fewer eggs on sweet pepper plants previously inoculated with *M. pygmaeus*. As this also applied to newly produced leaves, which were not directly exposed to the omnivore, this suggests that the induced plant response is systemic. The development time of *F. occidentalis* larvae feeding on leaves previously exposed to *M. pygmaeus* was also prolonged.

The introduction of omnivores as biological control agents can create complex interactions. The ability of omnivores to feed on multiple trophic levels may not improve biological control. The possible benefits of plant-tissue feeding are omnivore specific and dependent on the developmental stage, prey availability and plant nutritional composition (Naranjo and Gibson, 1996). The complexity of food choice by omnivores remains poorly understood: in some cases, prey consumption is reduced when both prey and plant diets are available (Crum et al., 1998, Kiman and Yeargan, 1985, Weiser and Stamp, 1998). Feeding on high-quality plant food may provide a highly nutritious preferred food source and decrease the consumption of a particular prey species (Abrams, 1987). Omnivorous bugs consumed fewer prey on plants presenting lima bean pods in a study by Eubanks and Denno (1999). Plant-tissue feeding often facilitates survival rather than reproduction probably because of low nitrogen contents (De Clercq and Degheele, 1992). Population dynamics can be strongly influenced by the developmental stage (Coll and Guershon, 2002), the period of phytophagy of the omnivores (Cisneros and Rosenheim, 1997) or by the competition for plant food between omnivores and prey (Polis and Holt, 1992; Coll and Izraylevich, 1997).

Concerning the impact of induced changes in host plant chemistry on pests and beneficials, Ode (2006) underlined that this aspect has been insufficiently explored and reviewed negative tritrophic effects of inducible plant defenses on natural enemies. In a study by Agrawal et al. (2002), predatory mites were less attracted to plants that produced cucurbitacins than cucurbitacin-free plants and had a reduced fecundity when feeding on herbivores that feed on defended plants when compared to those that fed on plants free of cucurbitacins. Induced plant resistance is thus not always favorable to biological control.

Using phytophagous beneficials also has the consequence that their plant feeding exposes them to systemic pesticides (Coll, 1998; Smith and Krischik, 1999, Arnó and Gabarra, 2011; Prabhaker et al., 2011; Put et al., 2015). Plant feeding by omnivores can also result in crop damage or reduced crop growth, in particular at high omnivore populations. Omnivores can cause direct mechanical feeding injuries, injuries to plant vascular tissues or damage through the salivary enzymes killing plant cells (Castañé et al., 2011). Plant-tissue feeding heteropterans can also disturb plant hormonal balances (Zhang et al., 2018). In tomatoes, fruit damage by heteropterans is often reported, reflecting a preference for the more nutritious tomato fruit (Salamero et al., 1987; Alomar et al., 1991; Lucas and Alomar, 2002; Albajes et al., 2006; Castañé et al., 2011). *Nesidiocoris tenuis* (Reuter) is known to cause injuries on the aerial parts of tomato plants (necrotic rings on stems, shoots, leaf petioles and flower stalks), leading to flowers and fruits abortion, and, reduced growth (Arnó et al., 2010). Gillespie et al. (2007) reported damage on gerbera flowers, Castañé et al. (2003) and Sengonça et al. (2003) on cucumber and zucchini fruit.

Despite the above negative aspects, omnivores are crucial elements in biological control strategies, especially mirids in tomato crops and anthocorids in sweet pepper crops. Current biological control programmes are supported with different tools like smart-phone applications to register and follow crop injuries and sticky traps to monitor omnivores and the pests. This allows growers to maximize benefits of omnivores and avoid risks. Omnivorous predators are commonly used in greenhouse crops and their establishment is even stimulated by provision of alternative food (Lenfant et al., 2000; Castañé et al., 2006; Put et al., 2012; Moerkens et al., 2017; Brenard et al., 2019; Sade et al., 2019). Growers try to avoid applications of systemic pesticides, which are not compatible with omnivores. Resistance breeding does not yet take plant suitability for omnivores into account, but this might change as we gain further insights in the complex interactions involving omnivores.

PEST FEEDING (PEST-IN-FIRST)

The “pest-in-first” (PIF) strategy is one of the oldest strategies to allow the establishment of a biocontrol “standing army” in greenhouses. Here an early introduction of natural enemies is combined with a controlled (pre-) release of the pest. This concept can also be used to allow early establishment of specialist natural enemies, which cannot be supported by factitious prey or pollen. One of the first examples of a successful PIF strategy is the release of two-spotted spider mites to reinforce the establishment of the predatory mite *P. persimilis* (Hussey et al., 1965; Gould et al., 1969; Markkula and Tiittanen, 1976; Havelka and Kindlmann, 1984; Waite, 2001; Bolckmans and Tetteroo, 2002). Other pest-in-first strategies have been evaluated, such as the introduction of low numbers of greenhouse whitefly *T. vaporariorum* in tomato followed by timed releases of its parasitoid *E. formosa* (Parr et al., 1976). Growers, however, are typically reluctant to release pests due to the risks of causing crop damage (Parr et al., 1976; Stacey, 1977, Starý, 1993). Instead, they prefer to wait until the pest develops naturally before introducing biocontrol, as releasing *P. persimilis* in naturally occurring *T. urticae* hot spots is often cheaper. Alternatively, they opt for calendar introductions of biocontrol agents.

FACTITIOUS PREY

To allow early establishment of generalist predators, growers can use factitious prey (i.e., foods which the predators usually do not encounter in their natural habitat). Some factitious prey, such as eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller, decapsulated cysts of the brine shrimp *Artemia* spp. and astigmatid mites (Hoogerbrugge et al., 2008; Midthassel et al., 2013; Nguyen et al., 2014a; Delisle et al., 2015a; Labbé et al., 2018) can be excellent food sources for a wide range of generalist predators. Studies on these supplemental foods are summarized in **Table 1**. Some of these factitious prey, especially *E. kuehniella* eggs and astigmatid prey mites, are also used in the commercial production of biological control agents.

Astigmatid Prey Mites

In greenhouses, breeding sachets of *Neoseiulus cucumeris* Athias-Henriot have been developed to allow slow releases of predatory mites in the crop and thus reduce handling costs (Sampson, 1998). These rearing systems consist of predators, astigmatid mites as food and carrier material. They allow for a release of predators for periods up to four (sometimes even eight) weeks. In crops like roses or potted plants, that do not feature pollen, astigmatid prey mites do not establish on the plant, and where pests cannot be tolerated, predatory mite populations cannot build up on the crop and sachets need to be renewed regularly.

In potted plants, the spread of the predatory mites released from the breeding sachet is limited because plants are widely spaced; the majority of the predators remain on the plant, which received the sachet (Buitenhuis et al., 2010, 2014). To tackle these problems, strategies like using one (small) sachet per plant have been developed to provide each plant an open rearing system (Valentin, 2017) or predators and prey are blown over the crop

TABLE 1 | Examples of facticious prey.

Factitious prey	**Category natural enemy**	**Natural enemy**	**Source**
Astigmatids: *Carpoglyphus lactis* L.; *Tyrophagus putrescentiae* (Schrank)	Anthocorids	*Orius naivashae* (Poppius); *Orius thripoborus* (Hesse)	Bernardo et al., 2017; Bonte et al., 2017
Astigmatids: *Aleuroglyphus ovatus* (Troupeau); *Austroglycyphagus lukoschusi* (Fain); *Blomia tropicalis*; *Carpoglyphus lactis* L.; *Suidasia medanensis* (Oudemans); *Thyreophagus cracentiseta* Barbosa	Predatory mites	*Amblydromalus limonicus* Garman and McGregor; *Amblyseius eharai* Amitai and Swirski; *Amblyseius tamatavensis* Blommers; *Amblyseius swirskii* (Athias-Henriot); *Gaeolaelaps aculeifer* (Canestrini); *Neoseiulus cucumeris* (Oudemans)	Hoogerbrugge et al., 2008; Xia et al., 2012; Midthassel et al., 2013; Nguyen et al., 2013; Vangansbeke et al., 2014a; Barbosa and de Moraes, 2015; Ji et al., 2015; Ferrero et al., 2016; Massaro et al., 2016; Muñoz-Cárdenas et al., 2017; Rueda-Ramírez et al., 2018
Cysts of *Artemia* spp.	Anthocorids	*Orius laevigatus* (Fieber); *Orius majusculus* (Reuter); *Orius naivashae* (Poppius); *Orius strigicollis* (Poppius); *Orius thripoborus* (Hesse)	Arijs and De Clercq, 2001; De Clercq et al., 2005a; Riudavets et al., 2006; Bonte and De Clercq, 2008; Bonte et al., 2012; Nishimori et al., 2016; Oveja et al., 2016; Sade et al., 2019
Cysts of *Artemia* spp.	Coccinellids	*Harmonia axyridis* (Pallas); *Coleomegilla maculata* (DeGeer)	Hongo and Obayashi, 1997; Riddick and Wu, 2015; Seko et al., 2019
Cysts of *Artemia* spp.	Mirids	*Dicyphus errans* (Wolff); *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter)	Tavella and Arzone, 1996; Callebaut et al., 2004; Castañé et al., 2006; Riudavets et al., 2006; Vandekerkhove et al., 2006, 2009; Messelink et al., 2015; Hilgers et al., 2016; Oveja et al., 2016; Moerkens et al., 2017; Arvaniti et al., 2018; Brenard et al., 2018, 2019; Ghasemzadeh and Gharekhani, 2019; Owashi et al., 2020
Cysts of *Artemia* spp.	Predatory mites	*Amblydromalus limonicus* Garman and McGregor; *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus bicaudus* (Wainstein); *Neoseiulus cucumeris* (Oudemans)	Vantornhout et al., 2004; Oveja et al., 2012; Audenaert et al., 2013; Nguyen et al., 2014b, 2015; Vangansbeke et al., 2014b,c, 2016a,b; Leman and Messelink, 2015; Su et al., 2019
Sterilized eggs of *Ephestia kuehniella* Zeller	Anthocorids	*Orius* spp.; *Orius albidipennis* Reuter; *0rius insidiosus* (Say); *Orius laevigatus* (Fieber); *Orius majusculus* (Reuter); *Orius naivashae* (Poppius); *Orius niger* Wolff; *Orius sauteri* (Poppus); *Orius strigicollis* (Poppius); *Orius thripoborus* (Hesse); *Orius tristicolor* (White)	Salas-Aguilar and Ehler, 1977; Richards, 1992; Tommasini and Nicoli, 1993; Chyzik et al., 1995; Richards and Schmidt, 1995; Schmidt et al., 1995; Cocuzza et al., 1997; Arijs and De Clercq, 2001, 2004; Van Lenteren and Tommasini, 2003; De Clercq et al., 2005a; Riudavets et al., 2006; Ferkovich et al., 2007; Bonte and De Clercq, 2008; Yano et al., 2009; Vandekerkhove and De Clercq, 2010; Bonte et al., 2012, 2017; Oveja et al., 2012; Pumariño and Alomar, 2012, 2014; Nishimori et al., 2016; Bernardo et al., 2017; Sade et al., 2019
Sterilized eggs of *Ephestia kuehniella* Zeller	Chrysopids	*Chrysoperla carnea* (Stephens); *Chrysoperla externa* (Hagen); *Chrysoperla rufilabris* (Burmeister)	Zheng et al., 1993; Kathiar et al., 2015; Bezerra et al., 2017
Sterilized eggs of *Ephestia kuehniella* Zeller	Coccinellids	*Adalia bipunctata* L.; *Coleomegilla maculata* DeGeer; *Cryptolaemus montrouzieri* Mulsant; *Harmonia axyridis* (Pallas)	Hongo and Obayashi, 1997; De Clercq et al., 2005b; Berkvens et al., 2007; Riddick, 2009; Attia et al., 2011; Maes et al., 2014; Riddick and Wu, 2015
Sterilized eggs of *Ephestia kuehniella* Zeller	Mirids	*Campyloneuropsis infumatus* (Carvalho); *Dicyphus errans* (Wolff); *Dicyphus hesperus* Knight; *Dicyphus tamaninii* Wagner; *Engytatus varians* (Distant); *Macrolophus basicornis* (Stal); *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter)	Fauvel et al., 1987; Grenier et al., 1989; Constant et al., 1996; Tavella and Arzone, 1996; Gillespie and McGregor, 2000; Iriarte and Castañé, 2001; Sanchez et al., 2003, 2004; Callebaut et al., 2004; Castañé and Zapata, 2005; Messelink et al., 2005; Alomar et al., 2006; Castañé et al., 2006; Riudavets et al., 2006; Vandekerkhove et al., 2006, 2009; Oveja et al., 2012; Put et al., 2012; Mollá et al., 2014; Van Holstein and Messelink, 2014; Hilgers et al., 2016; Perdikis and Arvaniti, 2016; Moerkens et al., 2017; Arvaniti et al., 2018; Brenard et al., 2018; Bueno et al., 2018; Ghasemzadeh and Gharekhani, 2019; Owashi et al., 2020
Sterilized eggs of *Ephestia kuehniella* Zeller	Lygids	*Geocoris varius* (Uhler); *Geocoris proteus* Distant	Oida and Kadono, 2012; Igarashi and Nomura, 2013
Sterilized eggs of *Ephestia kuehniella* Zeller	Predatory mites	*Amblydromalus limonicus* Garman and McGregor; *Amblyseius swirskii* (Athias-Henriot); *Euseius scutalis* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus barkeri* (Hughes)	Romeih et al., 2004; Vantornhout et al., 2004; Momen and El-Laithy, 2007; Audenaert et al., 2013; Nguyen et al., 2014a; Vangansbeke et al., 2014a,b,c; Leman and Messelink, 2015

with purpose built automatized blowers. Supplying predatory mites with factitious (astigmatid) prey mites as food has recently gained popularity among growers. The following feeding mites could be used to improve the reproduction and survival of predatory mites: *Tyrophagus putrescentiae* (Schrank) (Pirayeshfar et al., 2020), *Carpoglyphus lactis* (L.) (Nguyen et al., 2013), *Thyreophagus entomophagus* (Laboulbene), *Suidasia medanensis* (Oudemans) (Sánchez et al., 2019), and *Aleuroglyphus ovatus* (Troupeau) (Xia et al., 2012; Ferrero et al., 2016; Rueda-Ramírez et al., 2018). However, very few trials have been performed at plant level (Hoogerbrugge et al., 2008; Vila et al., 2017; Pirayeshfar et al., 2020) and studies on the actual effect of these strategies on pest control are limited. Pirayeshfar et al. (2020) succeeded in increasing *Amblyseius swirskii* Athias-Henriot numbers on chrysanthemum plants by providing living *T. putrescentiae* per plant, but failed to do so using frozen *T. putrescentiae*. Pirayeshfar et al. (2020) suggested that the different diets used to rear the prey mites may have an influence on the population increase of the predatory mites. Nowadays, some growers disperse the astigmatid mites *C. lactis* or *T. entomophagus* to supplement the released predatory mites with food. Ferrero et al. (2016) developed a gel product protecting astigmatid mites' eggs when they are dispersed, and increasing their shell-life on the crops. This product resulted in high population levels of A. swirskii on cucumber plants and a better biological control of sweet potato whitefly than with the use of breeding sachets. Using astigmatid mites as food supplement has the advantage that they are relatively cheap (Ramakers and van Lieburg, 1982; Castagnoli, 1989). The main drawback of mass application of astigmatid mites lies in the fact that they can cause health issues for users including dermatitis, allergies and anaphylaxis (Iglesias-Souto et al., 2009; Fernández-Caldas et al., 2014; Liu and Zhang, 2017; Mullen and O'Connor, 2019; Pirayeshfar et al., 2020). Furthermore, Tyrophagus spp. can cause plant damage (Czaikowska et al., 1988; Buxton, 1989; Fischer, 1993; Fan and Zhang, 2007; Yasukawa et al., 2011).

Muñoz-Cárdenas et al. (2017) proposed another approach using astigmatid mites in combination with mulch layers to provide food to crop-inhabiting predatory mites. Prey mites were introduced in the litter to stimulate the predatory mite *A. swirskii* on aboveground plant parts. In cage experiments with rose plants this increased predatory mite numbers 4-fold, as compared to control plants. Thrips control was increased and leaf- and flower damage was reduced as a result. It was shown that A. swirskii, which is usually considered to be a leaf-inhabiting species, actually moved between rose foliage and mulch to feed on the astigmatid mites. Similarly, Grosman et al. (2014) increased biocontrol of thrips and whiteflies with *A. swirskii* using mulch layers in different ornamental crops. Adding mulches with, for example bran, yeast or Biotop®, waste product of the potato industry (Grosman and de Groot, 2011), organic matter (Settle et al., 1996; Neves Esteca et al., 2020), animal manure (Navarro-Campos et al., 2012) to boost fungi, decomposers and plankton feeders can increase predators' population levels. Despite promising results in small-scale experiments, this strategy has not been adopted by growers. This is probably due to the increased labor when mulching, and the fact that the system is often effective on the short term only. Grosman et al. (2014) found that this approach produced predators for up to 6 weeks, which is comparable to the longevity of breeding sachets. These methods carry also the risk that the predators switch from feeding on herbivores to soil organisms (apparent mutualism, Holt, 1977) as reported by Birkhofer et al. (2008), or, are out-competed by other soil predators, that also benefit from the substrate manipulation (Messelink and Van Holstein-Saj, 2007, 2011).

Mediterranean Flour Moth Eggs

To support establishment of predatory bugs, growers mainly use eggs of the Mediterranean flour moth *E. kuehniella*. The high nutritional value of *E. kuehniella* eggs ensures development, reproduction and survival of many arthropods (**Table 1**). In *M. pygmaeus*, higher reproduction rates were found when the mirids were fed on the moth eggs, as compared to whitefly pupae (Fauvel et al., 1987; Alomar et al., 2006). Sprinkling of *E. kuehniella* eggs on crop plants was the first supplemental food strategy widely adopted by growers on a large scale. They are typically used on the points where predatory bugs *Orius* spp. (sweet pepper) and mirid bugs *M. pygmaeus*, *N. tenuis*, and *Tupiocoris cucurbitaceus* (Spinola) (mainly tomato) are introduced (Put et al., 2012; Moerkens et al., 2017; Brenard et al., 2018).

The main factor limiting the use of *E. kuehniella* eggs is their cost, with prices of 400 EUR/kg (Nguyen et al., 2014a). They also need to be kept frozen. Furthermore, the eggs tend to dry out once applied on the crop, or when the relative humidity is too high, they become moldy on the leaves. Due to their cost, *E. kuehniella* eggs are not used to feed predatory mites. However, this food source was found to be suitable for oviposition of *Iphiseius degenerans* (Berlese) (Vantornhout et al., 2004), *A. swirski* and *Amblydromalus limonicus* Garman and McGregor (Nguyen et al., 2014a; Vangansbeke et al., 2014c), *Gaeolaelaps aculeifer* Canestrini and *Stratiolaelaps scimitus* (Womersley) (Navarro-Campos et al., 2016), as well as for the pest *F. occidentalis*. The performance of predatory mites on *E. kuehniella* eggs can vary (Vangansbeke et al., 2014c; Leman and Messelink, 2015) depending on egg storage conditions and ambient humidity in the crop. Liu and Zhang (2017) observed that immatures of *A. limonicus* exhibited difficulties to pierce the chorion of *E. kuehniella* eggs that hardened at low ambient humidity.

Cysts of the Brine Shrimp

Several cheaper options have been investigated to replace the use of *Ephestia* moth eggs in commercial production as well as in field applications (**Table 1**). Out of the options tested, the most promising substitute of flour moth eggs for feeding generalist predators was found to be dry cysts of the brine shrimp *Artemia* spp. Having been used widely as fish food, *Artemia* cysts have the advantage that they can be stored for years in dry form, and do not require freezing as required for *E. kuehniella* eggs (Arijs and De Clercq, 2001). They keep their nutritional value longer than *E. kuehniella* eggs when applied on crops (De Clercq et al., 2005a; Messelink et al., 2016; Moerkens et al., 2017), they do not become moldy on plants (Vandekerkhove et al., 2009) and are, depending on the quality, up to 30 times cheaper than flour moth eggs (Nguyen et al., 2014a). However, *Artemia* cysts vary substantially in nutritional quality, and the high quality product is roughly the same price as *E. kuehniella* eggs. When used at high densities, *Artemia* cysts can leave a "fishy smell" on the crop. Brine shrimp cysts have been tested as prey for several natural enemies for production purposes (**Table 1**).

In field crops, Hoogerbrugge et al. (2008) and Leman and Messelink (2015) found either no or poor establishment of *A. swirskii* when fed with a commercial strain of *Artemia* sp. cysts alone in a chrysanthemum crop. In contrast, Vantornhout et al. (2004), Nguyen et al. (2014a) and Vangansbeke et al. (2014c, 2016b) showed in laboratory studies complete development of, respectively, I. degenerans, *A. swirskii* and *A. limonicus* on a diet of decapsulated cysts of a non-commercial *Artemia franciscana* Kellogg strain. Vangansbeke et al. (2016a) succeeded in establishing *A. swirskii* on chrysanthemum and ivy plants using this *Artemia* strain, but not when using a commercial decapsulated *Artemia* cyst product. Inconsistent results between studies might be explained by the incomplete decapsulation of the cysts or their level of hydration (Castañé et al., 2006) and by the substantial variation in *Artemia* product quality. De Clercq et al. (2005a) showed differences of composition and nutritional quality between *Artemia* cysts of diverse origins, which can have an impact on the nutritional value as well (Bloemhard et al., 2018; Sade et al., 2019). Overall, *Artemia* cysts have become a valuable complement in biological control programs in greenhouse vegetable crops, as most tomato and sweet pepper growers release *M. pygmaeus* with this alternative food, either by itself or in combination with *E. kuehniella*.

The provision of brine schrimp cysts and Mediterranean flour moth eggs is now a common practice on introduction points of predatory bugs in vegetable crops. As astigmatid prey mites are concerned, only ornamental growers release them weekly or biweekly, but generally additionally to predatory mites. They tend to use them within their inundative release strategies of predatory mites instead of seeking for an early establishment of predators after a few release. Besides their use to stimulate predatory mites, astigmatid mites might also hold potential to support field populations of predatory bugs, as they were found to be a suitable food source for *Orius* spp. (El-Husseiniak and Sermann, 1992; Husseini et al., 1993; Nagai et al., 1998; Gomaa and Agamy, 2002; Yang et al., 2009; Bernardo et al., 2017; Bonte et al., 2017; Song et al., 2018). This application is still at an experimental stage at growers.

BANKER PLANT SYSTEMS

Supplementation of food resources and oviposition places for natural enemies can be done by providing secondary plants, so-called "banker plants" or "open rearing systems" (Bennison, 1992; Bennison and Corless, 1993). The principle of the banker plant system is the use of plants, usually different from the crop, to provide beneficials with alternative (non-pest) prey and/or plant-provided food resources. This method was developed for the introduction of parasitoid wasps to control aphids (Starý, 1969; Lyon, 1973) and whiteflies (Stacey, 1977). The banker plant method is often seen as a further development of the "Pest-in-first" method in greenhouses as the initial banker plant systems introduced additional crop plants carrying the target pest (**Table 2**) (Parr and Stacey, 1975; Stacey, 1977).

The advantages of using banker plants have been widely described. They aid survival, reproduction and development of naturally occurring or introduced natural enemies even in absence of pests (Pratt and Croft, 2000). When introducing beneficials, they can be released onto the banker plants where they find essential resources for survival and reproduction. Once the target pest appears, they then move from the banker plants into the crop. Successful banker plant systems allow for early season augmentation of beneficials and can replace "repeated inundative releases" (Hansen, 1983) thereby reducing costs (Huang et al., 2011). Furthermore, when using potted banker systems, these banker plants can be moved for "hot spot treatment" of pest colonies (Ramakers and Voet, 1995). When selecting banker plants, one should consider the natural enemies' affinity for the plant, as well as the plant's capacity to carry suitable alternative prey or other (food) resources (Jacobson and Croft, 1998; Goolsby and Ciomperlik, 1999). Nutritional, allelochemical and plant morphological traits (Price et al., 1980; Grevstad and Klepetka, 1992, Desneux and Ramirez-Romero, 2009) are taken into account when selecting candidate banker plant-prey combinations. It is known that morphological plant characteristics (e.g., toughness of leaves and stems, number of nectar glands, flowering period, number of flowers, plant pubescence, acarodomatia, trichomes) can be correlated with the dispersal, oviposition, developmental and reproductive success of arthropods (Walter and O'Dowd, 1992a,b; Pfannenstiel and Yeargan, 1998; Lucas and Brodeur, 1999, Lundgren et al., 2008; Parolin et al., 2012a). In addition, banker plants must be capable to survive temperatures and light conditions as the ones used in greenhouse production (Van der Linden, 1992).

Banker plant systems can be divided into two groups: (1) plants providing non-pest prey/host (2) plants producing non-prey food sources (pollen and nectar). Diverse publications provide complete inventories of the banker plant systems and their potential (Osborne et al., 2005; Frank, 2010; Huang et al., 2011; Ying et al., 2012; Miller et al., 2017; Miller, 2018; Payton Miller and Rebek, 2018). An overview of banker plant systems is given in **Tables 2–4**.

Banker Plant Systems (Non-pest Prey)

Most banker plant systems using alternative prey/hosts (**Table 3**) were designed to control aphids, such as *Myzus persicae* Sulzer on sweet peppers or *Aphis gossypii* Glover on cucumbers. Hansen (1983) first evaluated a banker plant system using broad bean infected with *Megoura viciae* Bucken, to rear *Aphidoletes aphidimyza* (Rondani). Other banker plant systems consist of sorghum, rye, barley or wheat seedlings infested with cereal aphids which are harmless to greenhouse crops, such as *Rhopalosiphum padi* Linnaeus, *Sitobion avenae* Fabricius, *Metopolophium dirhodum* (Walker), *Melanaphis sacchari* (Zehntner), or *Schizaphis graminum* (Rondani) (Kuo-Sell, 1987; Abe et al., 2011; Nagasaka et al., 2011; Yano et al., 2011).

TABLE 2 | Examples of (pest prey) banker plant systems.

Banker plant (common name)	Banker plant (Latin name)	Prey/host	Category natural enemy	Natural enemy	Source
Borage	*Borago officinalis* L.	*Myzus persicae* (Sulzer)	Parasitoids	*Aphidius colemani* Viereck	Fujinuma et al., 2010
Bush bean	*Phaseolus vulgaris* L.	*Tetranychus urticae* Koch	Mites	*Phytoseiulus persimilis* Athias-Henriot	Matteoni, 2003
Castor bean	*Ricinus communis* L.	*Bemisia tabaci* (Gennadius)	Parasitoids	Eretmocerus hayati (Zolnerowich and Rose); *Encarsia sophia* (Girault and Dodd)	Kidane et al., 2018
Corn	*Zea mays* L.	*Tetranychus urticae* Koch	Mites	*Phytoseiulus persimilis* Athias-Henriot	Miller et al., 2017; Miller, 2018
Kidney bean	*Phaseolus vulgaris* L.	*Tetranychus urticae* Koch	Mites	*Amblyseius fallacis* Garman	Lester et al., 2000
Laurustinus	*Viburnum tinus* L.	*Tetranychus urticae* Koch	Mites	*Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot	Parolin et al., 2013; Bresch et al., 2015
Melon	*Cucumis melo* L.	*Bemisia tabaci* (Gennadius)	Parasitoids	*Encarsia sophia* (Girault and Dodd); *Eretmocerus* spp.; *Eretmocerus hayati* (Zolnerowich and Rose)	Goolsby and Ciomperlik, 1999; Pickett et al., 2004; Kidane et al., 2018
Pumpkin	*Cucurbita maxima* "Uchiki Kuri"	*Trialeurodes vaporariorum* Westwood	Parasitoids	*Encarsia tricolor* Foërster	Laurenz and Meyhöfer, 2017
Rhododendron	*Rhododendron* sp. "Ana Kruschke"	*Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi)	Mites	*Neoseiulus fallacis* (Garman)	Pratt and Croft, 2000
Riverbank grape	*Vitis riparia* (Michx.)	*Tetranychus urticae* Koch	Mites	*Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot	Parolin et al., 2013; Bresch et al., 2015
Rose	*Rosa* sp.	*Macrosiphum rosae* L.	Parasitoids	*Praon volucre* Haliday	Maisonneuve, 2002
Swedes	*Brassicae napus rapifera* Metzg.	*Myzus persicae* (Sulzer)	Parasitoids	*Ephedrus cerasicola* Starý	Hågvar and Hofsvang, 1994
Sweet pepper	*Capsicum annuum* L.	*Myzus persicae* (Sulzer)	Parasitoids	*Ephedrus cerasicola* Starý	Hofsvang and Hågvar, 1979
Sweet pepper	*Capsicum annuum* L.	Aphids	Parasitoids	*Aphidius colemani* Viereck; *Aphidius ervi* Haliday	Matteoni, 2003
Sweet pepper	*Capsicum annuum* L.	Aphids	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Matteoni, 2003
Tobacco	*Nicotiana tabacum* L.	*Trialeurodes vaporariorum* Westwood	Parasitoids	*Encarsia formosa* (Gahan)	Schmidt, 1996
Tomato	*Lycopersicon esculentum* Mill.	*Trialeurodes vaporariorum* Westwood	Parasitoids	*Encarsia formosa* (Gahan)	Parr and Stacey, 1975; Stacey, 1977; Rumei, 1991
Watermelon	*Citrullus lanatus* (Thunb.)	*Bemisia tabaci* (Gennadius)	Parasitoids	*Eretmocerus hayati* (Zolnerowich and Rose)	Goolsby and Ciomperlik, 1999

Parasitoids, such as *Aphidius colemani* Viereck, *Aphidius ervi* Haliday, and *Aphidius matricariae* Haliday, and, the predatory gall midge *A. aphidimyza* can reproduce on these banker plant systems and thus be pre-established once crop aphids appear (**Table 3**). Abe et al. (2011) succeeded in maintaining *A. aphidimyza* for at least 3 months with such a system. Banker plant systems with non-pest prey used to be broadly implemented (Walters and Hardwick, 2000; Nagasaka and Oya, 2003; Yano, 2006). Some growers produce the banker plants themselves. However, a majority of growers are reluctant to adopt

TABLE 3 | Examples of (non-pest prey) banker plant systems.

Banker plant (common name)	Banker plant (Latin name)	Prey/host	Category natural enemy	Natural enemy	Source
Arborvitae	*Thuja occidentalis* L.	*Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi)	Predatory mites	*Neoseiulus fallacis* (Garman)	Pratt and Croft, 2000
Barley	*Hordeum vulgare* L.	*Rhopalosiphum padi* L.	Coccinellids	*Scymnus creperus* Mulsant	Miller et al., 2017
Barley	*Hordeum vulgare* L.	*Rhopalosiphum padi* L.	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Ramakers and Maaswinkel, 2002; Yano et al., 2009; Nagasaka et al., 2010; Hemerik and Yano, 2012; Higashida et al., 2016; Miller et al., 2017
Barley	*Hordeum vulgare* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Vierec, *Aphidius matricariae* Haliday; *Syrphophagus* sp.; *Alloxysta* sp. nr victrix (Westwood); *Dendrocerus laticeps* (Hedicke)	Goh et al., 2001; Matsuo, 2003; Nagasaka and Oya, 2003; Ode et al., 2005; Saito, 2005 Van Driesche et al., 2008; Nagasaka et al., 2010, 2011; Jandricic et al., 2014; Prado and Frank, 2014; Miller et al., 2017; Miller, 2018
Barley	*Hordeum vulgare* L.	*Rhopalosiphum padi* L.	Syrphids	Several hoverflies species	Pineda and Marcos-García, 2008
Barley	*Hordeum vulgare* L.	*Rhopalosiphum maidis* (Fitch)	Parasitoids	*Aphidius colemani* Viereck; *Aphidius gifuensis* (Ashmead)	Goh et al., 2001; Ohta and Honda, 2010
Barley	*Hordeum vulgare* L.	*Schizaphis graminum* (Rondani)	Parasitoids	*Aphidius colemani* Viereck; *Aphidius gifuensis* (Ashmead)	Kim, 2003; Kim and Kim, 2004; Ode et al., 2005; Sun et al., 2017
Barley	*Hordeum vulgare* L.	*Sitobion akebiae* (Shinji)	Parasitoids	*Aphidius gifuensis* (Ashmead)	Ohta and Honda, 2010
Black elder	*Sambucus nigra L.*	*Aphis sambuci L.*	Syrphids	Several hoverflies species	Bribosia et al., 2005; Wojciechowicz-Żytko and Jankowska, 2016
Bluegrass	*Poa* spp.	*Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani)	Parasitoids	*Lysiphlebus testaceipes* (Cresson)	Miller et al., 2017; Miller, 2018
Broad bean	*Vicia faba* L.	*Acyrthosiphon pisum* (Harris)	Parasitoids	*Aphidius gifuensis* (Ashmead)	Ohta and Honda, 2010
Broad bean	*Vicia faba* L.	*Megoura viciae* Bucken	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Hansen, 1983
Buckwheat	*Fagopyrum esculentum* Moench	*Sitobion avenae* (Fabricius)	Syrphids	Several hoverflies species	Fischer, 1997
Corn	*Zea mays* L.	*Oligonychus pratensis* (Banks)	Gall midges	*Feltiella acarisuga* (Vallot)	Xiao et al., 2011b
Corn	*Zea mays* L.	*Oligonychus pratensis* (Banks)	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot	Parker and Popenoe, 2008; Popenoe and Osborne, 2010
Corn	*Zea mays* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck	Jacobson and Croft, 1998; Payton Miller and Rebek, 2018
European columbine	*Aquilegia vulgaris*	*Aleyrodes lonicerae* Walker	Parasitoids	*Encarsia tricolor* Foërster	Laurenz and Meyhöfer, 2017
European black nightshade	*Solanum nigrum* L.	*Aphis fabae solanella* Theobald	Mirids	*Macrolophus pygmaeus* Rambur	Lykouressis et al., 2008
Finger millet	*Eleusine coracana* Gaertn.	*Sitobion avenae* (Fabricius)	Parasitoids	*Aphelinus abdominalis* Dalman; *Aphidius ervi* Haliday; *Praon volucre* Haliday	Fischer, 1997; Fischer in Huang et al., 2011

(Continued)

TABLE 3 | Continued

Banker plant (common name)	Banker plant (Latin name)	Prey/host	Category natural enemy	Natural enemy	Source
Finger millet	*Eleusine coracana* Gaertn.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck; *Lysiphlebus testaceipes* (Cresson)	Delgado, 1997; Fischer and Leger, 1997; Schoen and Martin, 1997; Vergniaud, 1997; Martin et al., 1998; Schoen, 2000; Boll et al., 2001a,b
Finger millet	*Eleusine coracana* Gaertn.	*Sitobion avenae* (Fabricius)	Syrphids	*Episyrphus* sp.	Fischer, 1997
Greater celandine	*Chelidonium majus* L.	*Aleyrodes proletella* L.	Parasitoids	*Encarsia formosa* Gahan	Van der Linden and van der Staaij, 2001
Kale	*Borecole oleracea* L.	*Aleyrodes proletella* L.	Parasitoids	*Encarsia formosa* Gahan	Laska and Zelenkova, 1988
Lucerne	*Medicago sativa* L.	*Acyrthosiphon pisum* (Harris)	Parasitoids	*Aphidius ervi* Haliday	Cameron et al., 1984
Melon	*Cucumis melo* L.	*Bemisia tabaci* (Gennadius)	Parasitoids	*Encarsia sophia* (Girault and Dodd); *Eretmocerus* spp.; *Eretmocerus hayati* (Zolnerowich and Rose)	Goolsby and Ciomperlik, 1999; Pickett et al., 2004; Kidane et al., 2018
Nipplewort	*Lapsana communis* L.	*Aleyrodes proletella* L.	Parasitoids	*Encarsia formosa* Gahan	Van der Linden and van der Staaij, 2001
Oat	*Avena sativa* L.	*Metopolophium dirhodum* (Walker)	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Götte and Sell, 2002
Oat	*Avena sativa* L.	*Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani)	Parasitoids	*Aphelinus abdominalis* Dalman; *Aphidius colemani* Viereck	Andorno and López, 2014; Miller et al., 2017; Miller, 2018
Papaya	*Carica papaya* L.	*Trialeurodes variabilis* (Quaintance)	Coccinellids	*Delphastus pusillus* (LeConte)	Osborne et al., 2005
Papaya	*Carica papaya* L.	*Trialeurodes variabilis* (Quaintance)	Parasitoids	*Encarsia transvena* Timberlake; *Encarsia sophia* (Girault and Dodd)	Osborne et al., 2005; Xiao et al., 2011a
Persian buttercup	*Ranunculus asiaticus* L.	*Phytomyza caulinaris* Hering	Parasitoids	*Dacnusa sibirica* Telenga; Diglyphus isaea Walker	Van der Linden, 1992
Potato	*Solanum tuberosum* L.	*Macrosiphum euphorbiae* (Thomas)	Parasitoids	*Aphelinus abdominalis* Dalman	Blümel and Hausdorf, 1996
Rhododendron	*Rhododendron* sp.	*Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi)	Predatory mites	*Neoseiulus fallacis* (Garman)	Pratt and Croft, 2000
Rye	*Secale cereale* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck	McClure, 2014; McClure and Frank, 2015
Rye	*Secale cereale* L.	*Rhopalosiphum maidis* (Fitch)	Parasitoids	*Aphidius colemani* Viereck; *Aphidius ervi* Haliday	Matteoni, 2003
Rye	*Secale cereale* L.	*Rhopalosiphum maidis* (Fitch)	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Matteoni, 2003
Ryegrass	*Lolium multiflorum* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck	Jacobson and Croft, 1998);
Ryegrass	*Lolium multiflorum* L.	*Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani)	Parasitoids	*Lysiphlebus testaceipes* (Cresson)	Miller et al., 2017; Miller, 2018
Savoy cabbage	*Brassica oleracea* L.	*Brevicoryne brassicae L.*	Parasitoids	*Diaeretiella rapae* McIntosh	Freuler et al., 2001, 2003
Sorghum	*Sorghum bicolor* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck	Payton Miller and Rebek, 2018
Sorghum	*Sorghum bicolor* L.	*Rhopalosiphum maidis* (Fitch)	Parasitoids	*Diaeretiella rapae* McIntosh	Ceballos et al., 2011
Sorghum	*Sorghum bicolor* L.	*Schizaphis graminum* (Rondani)	Parasitoids	*Lysiphlebus testaceipes* (Cresson)	Rodrigues and Bueno, 2001; Miller et al., 2017; Miller, 2018

(Continued)

TABLE 3 | Continued

Banker plant (common name)	Banker plant (Latin name)	Prey/host	Category natural enemy	Natural enemy	Source
Sorghum	*Sorghum bicolor* L.	*Melanaphis sacchari* (Zehntner)	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Abe et al., 2011; Yano et al., 2011; Higashida et al., 2017
Switchgrass	*Panicum virgatum* L.	*Rhopalosiphum padi* L.	Parasitoids	*Aphidius colemani* Viereck	Payton Miller and Rebek, 2018
Triticale	*Triticosecale rimpaui* Wittm.	*Sitobion avenae* (Fabricius)	Parasitoids	*Aphidius ervi* Haliday	Jansson in Huang et al., 2011
Triticale	*Triticosecale* sp.	*Metopolophium dirhodum* (Walker)	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Götte and Sell, 2002
Turnip	*Brassica rapa* L.	*Brevicoryne brassicae L.*	Parasitoids	*Diaeretiella rapae* McIntosh	Freuler et al., 2001, 2003
Wheat	*Triticum aestivum* L.	*Diuraphis noxia* (Mordvilko)	Parasitoids	*Aphidius matricariae* Haliday	Miller and Gerth, 1994
Wheat	*Triticum aestivum* L.	*Rhopalosiphum padi* L.	Parasitoids	*Alloxysta sp. nr victrix (Westwood); Aphidius colemani* Viereck; *Dendrocerus laticeps* (Hedicke); *Aphidius matricariae* Haliday; *Syrphophagus* sp.	Bennison, 1992; Lamparter, 1992; Albert, 1995; Conte, 1998; Jacobson and Croft, 1998; Van Schelt, 1999; Nagasaka and Oya, 2003; Saito, 2005 Nagasaka et al., 2010, 2011; Jandricic et al., 2014; McClure, 2014; McClure and Frank, 2015; Miller et al., 2017; Miller, 2018; Payton Miller and Rebek, 2018
Wheat	*Triticum aestivum* L.	*Rhopalosiphum padi* L.	Coccinellids	*Scymnus creperus* Mulsant	Miller et al., 2017
Wheat	*Triticum aestivum* L.	*Rhopalosiphum padi* L.	Gall midges	*Aphidoletes aphidimyza* (Rondani)	Bennison, 1992; Bennison and Corless, 1993; Albert, 1995; Miller et al., 2017
Wheat	*Triticum aestivum* L.	*Schizaphis graminum* (Rondani)	Parasitoids	*Aphidius gifuensis* (Ashmead); *Aphidius colemani* Viereck; *Lysiphlebus testaceipes* (Cresson)	Starý, 1993; Miller et al., 2017; Sun et al., 2017; Miller, 2018
Wheat	*Triticum aestivum* L.	*Sitobion avenae* (Fabricius)	Parasitoids	*Aphidius ervi* Haliday; *Aphidius gifuensis* (Ashmead); *Aphelinus asychis* Walker	Van Schelt, 1999; Wang et al., 2016; Miller et al., 2017; Miller, 2018; Sun and Song, 2019
Wheat	*Triticum aestivum* L.	*Sitobion avenae* (Fabricius)	Syrphids	*Episyrphus balteatus* DeGeer	Ankersmit et al., 1986

the system, due to inconsistent efficacy, labor (handling and maintenance), sink effects, and/or issues with hyperparasitoids (Jacobson and Croft, 1998; Van Driesche et al., 2008; McClure and Frank, 2015; Payton Miller and Rebek, 2018). Furthermore, the parasitoid species reared on banker plant systems are not necessarily efficient against all occurring target pest species, such as the potato aphid, *Macrosiphum euphorbiae* (Thomas), and the foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Van Driesche et al., 2008; Nagasaka et al., 2010; Prado et al., 2015). Development of parasitoid wasps (Jandricic et al., 2014) on the banker plant systems may be insufficient due to the provided aphids being of insufficient size. This can lead to a reduction of survival and male biased sex ratio of the parasitoids (Hoddle et al., 1998; Chau and Mackauer, 2001; Henry et al., 2005). Gall midges produced on aphid species of poor nutritional value can also suffer in terms of size and fecundity (Kuo-Sell, 1989). Natural enemies may be reluctant to switch from aphids on the banker plant to the crop aphids (Lester et al., 2000; Coyle et al., 2011) which can hamper the establishment of beneficials on the crop. This can be due to an acquired adaptation to the banker plant aphid through associative learning processes (Hoddle et al., 1998, Keasar et al., 2001, Ode et al., 2005, Prado and Frank, 2014). For all these reasons, the use of non-pest prey banker plant systems is relatively limited, relative to other methods supporting preventative establishment.

Banker Plant Systems (Nectar and Pollen)

Natural enemies can also be boosted by banker plants providing pollen and nectar (**Table 4**). The use of castor beans as banker plants has been based on this principle, as it provides a copious and steady supply of pollen and extra-floral nectar, making it a suitable host plant for generalist phytoseiid predatory mites, such as *I. degenerans* and *Euseius* spp. (Van Rijn and Tanigoshi, 1999b). Castor bean bankers hosting about 2000 predatory mites have been used by growers allowing growers to move the plants to crop spots where pests were detected or where predatory mites

TABLE 4 | Examples of (nectar-pollen) banker plant systems.

Banker plant (common name)	Banker plant (Latin name)	Category natural enemy	Natural enemy	Source
African marigold	*Tagetes erecta* L.	Anthocorids	*Orius insidiosus* say	Bueno et al., 2009
Apple mint	*Mentha suaveolens* Ehrh.	Anthocorids	*Orius laevigatus* (Fieber)	Cano et al., 2009, 2012
Basil	*Ocimum basilicum* L.	Anthocorids	*Orius* spp.	Cano et al., 2012
Bishop's weed	*Ammi majus* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Brown hemp	*Crotolaria juncea* L.	Anthocorids	*Orius* spp.	Calvert et al., 2019
Buckweat	*Fagopyrum esculentum* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Buckweat	*Fagopyrum esculentum* L.	Syrphids	Several hoverflies species	Colley and Luna, 2000; Wäckers and van Rijn, 2012
Borage	*Borago officinalis* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Borage	*Borago officinalis* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Castor bean	*Ricinus communis* L.	Anthocorids	*Orius insidiosus* Say	Waite et al., 2014
Castor bean	*Ricinus communis* L.	Predatory mites	*Amblyseius andersoni* (Chant); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans)	Ramakers and Voet, 1995; Van Rijn and Tanigoshi, 1999b; Miller et al., 2017; Miller, 2018
Chamomile	*Matricariae camomilla* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Chamomile	*Matricariae camomilla* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Chenille bush	*Acalypha hispida* Burm. f.	Anthocorids	*Orius laevigatus* (Fieber)	Armando and Yates, 2011
Chrysanthemum	*Chrysanthemum segetum* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Chrysanthemum	*Chrysanthemum segetum* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Cilantro	*Coriandrum sativum* L.	Syrphids	Several hoverflies species	Colley and Luna, 2000
Coriander	*Coriandrum sativum* L.	Syrphids	Several hoverflies species	Pineda and Marcos-García, 2008
Corn	*Zea mays* L.	Mites	*Amblyseius andersoni (Chant); Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans)	Miller et al., 2017; Miller, 2018
Corn flower	*Centaurea cyanus* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Corn flower	*Centaurea cyanus* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
False yellowhead	*Dittrichia* (= *Inula*) *viscosa* L.	Mirids	*Macrolophus melanotoma* Costa; *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter)	Vila, 2004; Perdikis et al., 2007; Cano et al., 2012
Feverfew	*Tanacetum parthenium L.*	Anthocorids	*Orius insidiosus* Say	Waite, 2012; Waite et al., 2014
Field Marigold	*Calendula arvensis* L.	Mirids	*Nesidiocoris tenuis* (Reuter)	Vila, 2004
Floss flower	*Ageratum mexicanum* Sims	Predatory mites	Several predatory mite species	Huang et al., 2011
French marigold	*Tagetes patula* L.	Anthocorids	*Orius* spp.	Imura and Kamikawa, 2012
Geranium	*Geranium* sp.	Mirids	*Nesidiocoris tenuis* (Reuter)	Vila, 2004; Cano et al., 2012
Gerbera daisy	*Gerbera jamesonii* L. "Festival"	Anthocorids	*Orius insidiosus* Say	Waite, 2012, Waite et al., 2014
Golden Crownbeard	*Verbesina encelioides* Benth and Hook	Anthocorids	*Orius laevigatus* (Fieber)	Armando and Yates, 2011

(Continued)

TABLE 4 | Continued

Banker plant (common name)	Banker plant (Latin name)	Category natural enemy	Natural enemy	Source
Great basil	*Ocimun basilicum* L.	Anthocorids	*Orius laevigatus* (Fieber)	Cano et al., 2012
Gypsophila	*Gypsophila elegans* M. Bieb.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Gypsophila	*Gypsophila elegans* M. Bieb.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Hidalgo Stachys	*Stachys albotomentosa* L.	Mirids	*Dicyphus hesperus* Knight	Sanchez et al., 2004
Kale	*Brassica oleracea* L. var. Acephala	Parasitoids	*Diadegma insulare* (Cresson)	Gourdine et al., 2003
Lance-leaf Coreopsis	*Coreopsis lanceolata* L.	Anthocorids	*Orius laevigatus* (Fieber)	Armando and Yates, 2011
Male trees of blush macaraga	*Macaranga tanarius* Müll. Arg	Anthocorids	*Orius laevigatus* (Fieber)	Armando and Yates, 2011
Marigold	*Tagetes patula L. "Lemon Gem'*	Anthocorids	*Orius insidiosus* Say	Waite, 2012; Waite et al., 2014
Mint	*Mentha* sp.	Mirids	*Nesidiocoris tenuis* (Reuter)	Vila, 2004
Mullein	*Verbascum thapsus* L.	Anthocorids	*Orius insidiosus* Say	Miller et al., 2017
Mullein	*Verbascum thapsus* L.	Mirids	*Dicyphus hesperus* Knight	Matteoni, 2003; Sanchez et al., 2003, 2004; Lambert et al., 2005; Gillespie et al., 2012; Nguyen-Dang et al., 2016; Miller et al., 2017
Mustard	*Brassica juncea* L.	Syrphids	Several hoverflies species	Colley and Luna, 2000
Ornamental pepper	*Capsicum annuum* L. "Black Pearl," "Purple Flash"	Anthocorids	*Orius insidiosus* Say	Valentin, 2011; Wong and Frank, 2012, 2013; Brownbridge et al., 2013; Waite et al., 2014; Miller et al., 2017
Ornamental pepper	*Capsicum annuum* L. "Masquerade," "Red Missile," "Explosive Ember," "Balck pearl"	Predatory mites	*Amblyseius andersoni* (Chant); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Amblyseius swirskii* (Athias-Henriot)	Popenoe and Osborne, 2010; Xiao et al., 2012; Avery et al., 2014; Kumar et al., 2014, 2015; Miller et al., 2017; Miller, 2018
Parasol leaf tree	*Macaranga tanarius* L.	Anthocorids	*Orius* spp.	Calvert et al., 2019
Parsnip	*Pastinaca sativa* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Parsnip	*Pastinaca sativa* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
Phacelia	*Phacelia tanacetifolia* Benth.	Syrphids	Several hoverflies species	Wnuk and Wojciechowicz-Zytko, 2007; Wojciechowicz-Zytko and Wnuk, 2012
Perennial alyssum	*Aurinia saxitalis* L.	Syrphids	Several hoverflies species	Colley and Luna, 2000
Pot marigold	*Calendula officinalis* L.	Anthocorids	*Orius sauteri* (Poppius)	Zhao et al., 2017
Pot marigold	*Calendula officinalis* L.	Syrphids	Several hoverflies species	Colley and Luna, 2000
Sage-leaved rock-rose	*Cistus salviifolius* L.	Mirids	*Nesidiocoris tenuis* (Reuter)	Vila, 2004
Sesame	*Sesamum indicum L.*	Mirids	*Nesidiocoris tenuis* (Reuter)	Nakaishi et al., 2011; Biondi et al., 2016
Sowthistle	*Sonchus* spp.	Anthocorids	*Orius* spp.	Ferragut and González-Zamora, 1994
Spanish lupine	*Lupinus hispanicus* (Boiss and Reuter)	Anthocorids	*Orius majusculus* (Reuter)	Alomar et al., 2006
Sunflower	*Helianthus annuus* L. "Choco sun"	Anthocorids	*Orius insidiosus* Say	Waite, 2012; Waite et al., 2014
Sunflower	*Helianthus annus* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Sunflower	*Helianthus annus* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012

(Continued)

TABLE 4 | Continued

Banker plant (common name)	Banker plant (Latin name)	Category natural enemy	Natural enemy	Source
Sweet alyssum	*Lobularia maritima* (L.) Desv.	Anthocorids	*Orius* spp.; *Orius laevigatus* (Fieber); *Orius majusculus* (Reuter)	Picó and Retana, 2000; Alomar et al., 2008; Bennison et al., 2011; Hogg et al., 2011; Pumariño and Alomar, 2012, 2014
Sweet alyssum	*Lobularia maritima* (L.) Desv.	Parasitoids	*Dolichogenidea tasmanica* (Cameron)	Berndt and Wratten, 2005
Sweet alyssum	*Lobularia maritima* (L.) Desv.	Syrphids	Several hoverflies species, *Eupeodes fumipennis* (Thomson)	Colley and Luna, 2000; Pineda and Marcos-García, 2008; Hogg et al., 2011
Sweet alyssum	*Lobularia maritima* (L.) Desv.	Parasitoids	Several parasitoids, *Cotesia marginiventris* (Cresson); *Diadegma insulare* (Cresson); *Trissolcus* spp.; *Gyron obesum* Masner	Johanowicz and Mitchell, 2000; Berndt and Wratten, 2005; Begum et al., 2006; Pease and Zalom, 2010
Sweet pepper	*Capsicum annuum* L.	Anthocorids	*Orius laevigatus* (Fieber)	Van den Meiracker and Ramakers, 1991
Tamarillo	*Cyphomandra betacea* (Cav.) Sendtn.	Mirids	*Macrolophus pygmaeus* Rambur	Fischer and Terrettaz, 2003
Tobacco	*Nicotiana tabacum* L.	Mirids	*Dicyphus hesperus Knight; Macrolophus pygmaeus* Rambur	Arnó et al., 2000; Ridray et al., 2001; Fischer, 2003; Fischer and Terrettaz, 2003; Schoen, 2003; Sanchez et al., 2004; Bresch et al., 2014
Tree marigold	*Tithonia diversifolia* (Hemsl.)	Anthocorids	*Orius laevigatus* (Fieber)	Armando and Yates, 2011
Vetch	*Vicia sativa* L.	Anthocorids	*Orius majusculus* (Reuter)	Alomar et al., 2006
Vetch	*Vicia sativa* L.	Parasitoids	Several species	Wäckers and van Rijn, 2012
Vetch	*Vicia sativa* L.	Syrphids	*Episyrphus balteatus* (De Geer)	Wäckers and van Rijn, 2012
White rocket	*Diplotaxis erucoides* L.	Anthocorids	*Orius* spp.	Ferragut and González-Zamora, 1994
Wild carrot	*Daucus carota* L.	Parasitoids	*Diadegma insulare* (Cresson)	Idris and Grafius, 1995, 1996; Johanowicz and Mitchell, 2000
Wild carrot	*Daucus carota* L.	Chrysopids	*Chrysoperla carnea* (Stephens)	Wäckers and van Rijn, 2012
Wild mustard	*Brassica kaber* L.	Parasitoids	*Diadegma insulare* (Cresson)	Idris and Grafius, 1995, 1996; Johanowicz and Mitchell, 2000
Yellow rocket	*Barbarea vulgaris* R. Br.	Parasitoids	*Diadegma insulare* (Cresson)	Idris and Grafius, 1995, 1996

were scarce (Ramakers and Voet, 1995). However, this banker plant requires a lot of maintenance due to its rapid growth and the predatory mites do not always move into the crop. Additionally, castor bean can become a source of certain pests. The usefulness of castor bean plants was also limited in sweet pepper crops, as pepper produces pollen and floral nectar. Only a limited number of ornamental growers is still using castor bean plants. Many banker plant systems were developed to maintain predatory bugs, especially the anthocorid *Orius* spp., primarily used for the control of thrips. Establishing this predator requires prey, and a range of plant derived food, including pollen (Kiman and Yeargan, 1985; Richards and Schmidt, 1996; Corey et al., 1998), nectar (Yokoyama, 1978), and plant sap (Kiman and Yeargan, 1985; Richards and Schmidt, 1996; Lundgren et al., 2008). In addition, the plant structures need to be acceptable as oviposition substrate (Lundgren et al., 2008). The predator establishes easily in sweet pepper crops where it utilizes the floral resources of the pepper plants. However, most ornamental crops lack these resources. This hampers establishment of beneficials as well as the short crop cycle of many ornamentals. As repeated introductions of *Orius* spp. are too onerous and expensive for growers, a range of banker plant systems have been designed to support establishment of the predator. Several studies have used ornamental peppers "Black pearl" or "Purple Flash" and the perennial Sweet Alyssum (Valentin, 2011; Wong and Frank, 2013). The use of Sweet Alyssum with its long lasting flowering period results not only in higher densities of *Orius* spp. (Picó and Retana, 2000; Alomar et al., 2008; Bennison et al., 2011; Hogg et al., 2011; Pumariño and Alomar, 2014), but also benefits hoverflies, predatory Heteroptera (Pease and Zalom, 2010) and several parasitoids (Johanowicz and Mitchell, 2000; Berndt and Wratten, 2005; Begum et al., 2006). However, the adoption of this method has been limited due to the fact that Sweet Alyssum is also exploited by pollen-feeding pest species, such as thrips. Several banker plant systems have also been designed to attract and sustain reproductive populations of predatory mirids. These include tobacco plants for *M. pygmaeus*, mullen for *Dicyphus hesperus* Knight and sesame for *N. tenuis* (**Table 4**). Fischer and Terrettaz (2003) managed even to successfully overwinter *M. caliginosus* on tobacco and tamarillo as banker plants, thus allowing the establishment of the predatory bug into the new tomato crops the next spring. Other examples of banker plant systems maintaining predatory bugs are summarized in **Table 4**. Addition of factitious prey on banker plants, as discussed earlier, is often suggested to increase survival, longevity and fecundity of the predatory bugs (Pumariño and Alomar, 2012, 2014).

The complexity of banker plant systems in greenhouse crops limited their adoption. Since the last decade, more straightforward methods have been developed to support the establishment and retention of beneficials in greenhouse. However, some sweet pepper growers still use them against aphids before the appearance of hyperparasitoids and there is an increased interest for banker plants to maintain predatory bugs in ornamental crops. Few attempts were made to use cover crops in or next to greenhouses and to grow combined crops, alternating rows of tomato, sweet pepper and egg plants in one greenhouse (Janmaat et al., 2014) to benefit from the vegetational diversity (Letourneau, 1983, 1990). Despite good technical results, these strategies failed in practice because of the complexity of their management. In open fields, we recently see an increased interest for the use of banker plant systems.

POLLEN

Providing pollen as a protein rich food in crops is another approach to boost establishment of pollen-feeding natural enemies, especially predatory mites. Pollen has been used extensively to support populations of generalist predatory mites (McMurtry and Scriven, 1966; Kennett et al., 1979; Van Rijn and Sabelis, 1990, 1993; Van Rijn and Tanigoshi, 1999a; Messelink et al., 2009; Nomikou et al., 2010; Hoogerbrugge et al., 2011; Maoz et al., 2014; Ranabhat et al., 2014, Vangansbeke et al., 2016a).

In greenhouse crops, bee-collected pollen has been tested in a number of studies, either as dry pellets or in suspension (Ramakers, 1995; Kolokytha et al., 2011; Goleva and Zebitz, 2013; Montserrat et al., 2013; Duarte et al., 2015). However, as the grains absorb water and become moldy, bee pollen was judged inappropriate by growers for crop applications (Ramakers, 1995). Attempts of using pollen providing banker plant systems, like castor beans (Ramakers and Voet, 1995; Van Rijn and Tanigoshi, 1999b), also failed, for reasons described previously. Pollen started to be used on a large scale by growers in July 2013, when commercial supplements based on narrowleaf cattail pollen were made available for crops where pollen sources are lacking (Pijnakker et al., 2014). This allowed preventative establishment of predatory mites in crops like cucumbers (which are parthenocarp and do not produce pollen), as well as ornamentals where no pests are tolerated.

Pollen can provide proteins, free amino acids, lipids, and phytosterols, nitrogen, carbohydrates, vitamins, and other inorganic minerals for many arthropods (Goss, 1968; Standifer et al., 1968; Stanley and Linskens, 1974; Rabie et al., 1983; Day et al., 1990; Roulston and Cane, 2000; Patt et al., 2003; Somerville and Nicol, 2006; Li et al., 2007; You et al., 2007; Campos et al., 2008; Lundgren, 2009). Pollen supports development, survival, and longevity of a range of natural enemies (Fauvel, 1974; Overmeer, 1985; Wäckers and van Rijn, 2005). Many studies (**Table 5**) show that several natural enemies are capable of reproducing and developing solely on pollen or in combination with other plant material in the absence of prey (Cocuzza et al., 1997; Beckman and Hurd, 2003; Berkvens et al., 2007; Carrillo et al., 2010). Among many studies on predatory mites, Onzo et al. (2005) showed increased survival and longevity of predatory mites when corn pollen was supplemented to the prey diet. Cloutier and Johnson (1993) and Buitenhuis et al. (2014) suggested that pollen feeding can benefit juvenile stages of predatory mites, since it is more difficult for them to attack thrips larvae, which usually show aggressive defensive behavior (Bakker and Sabelis, 1989). The nutritional value of the pollen depends on the pollen type (Todd and Bretherick, 1942; Saito and Mori, 1975; Van Rijn and Tanigoshi, 1999a; Goleva and Zebitz, 2013) and can differ between pollen consumers (Van Rijn and Tanigoshi, 1999a; Delisle et al., 2015a,b). Lundgren and Wiedenmann (2004) demonstrated that pollen quality can also vary within a given plant species. Van Rijn and Tanigoshi (1999a) showed the benefits of feeding on different pollen for predatory mites in the absence of prey. Pollen of Betulaceae, Euphorbiaceae, Leguminosae, Rosaceae, and Typhaceae seem, in general, to be suitable food sources for predatory mites (**Table 5**). The variations in nutritional value of pollen can be partly explained by the differences in the content of amino acids and lipids of pollen (Stanley and Linskens, 1974, Wäckers, 2005; Goleva and Zebitz, 2013). Also, pollen may contain secondary metabolites, that can reduce their suitability as food sources for arthropods (Rivest and Forrest, 2020); some types of pollen can even be toxic (Ranabhat et al., 2014; Goleva et al., 2015; Rivest and Forrest, 2020). In addition to variation in pollen nutrient composition, differences exist between natural enemies in their utilization of pollen from different plant species (McMurtry and Scriven, 1964; Van Rijn and Tanigoshi, 1999a; Adar et al., 2012). Part of this variation can be explained by the degree in which the phytoseiids have adapted to pollen feeding. While some predatory mites are specialized pollen feeders; others use it to complement their diet, while some specialist predators like *Phytoseiulus* do not consume pollen (McMurtry and Croft, 1997). Van Rijn and Tanigoshi (1999a) showed that *I. degenerans* could develop and reproduce on Betulaceae pollens whereas N. cucumeris failed to do so. Both predatory species did not perform on pollen from the conifer Pinopsida, but reproduced well on common cattail pollen. Goleva and Zebitz (2013) suggested that the morphology of the different pollens and their odor (Dobson and Bergström, 2000) are likely to influence their acceptance as food by a predator. Among insects, the coccinellids *Coleomegilla maculata* (DeGeer) and *Harmonia axyridis* (Pallas) use pollen as a supplemental food, allowing the ladybugs to survive during prey scarcity (Smith, 1960a,b; Koch, 2003; Lundgren and Wiedenmann, 2004; Lundgren et al., 2005; Michaud and Grant, 2005; Berkvens et al., 2007; Hodek and Honěk, 2013). The predatory bug *Orius* spp. has been frequently shown to be able to reproduce and develop on a sole diet of specific pollen (Fauvel, 1974; Naranjo and Gibson,

TABLE 5 | Examples of suitable pollen types.

Plant (common name)	Plant (Latin name)	Category natural enemy	Natural enemy	Source
African oil palm	*Elaeis guinensis* Jacq.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Alfafa	*Medicago sativa* L.	Predatory mites	*Euseius scutalis* (Athias-Henriot)	Al-Shammery, 2011
Almond	*Prunus amygdalis* Batsch; *Prunus dulcis* (Mill.) D.	Predatory mites	*Iphiseius degenerans* (Berlese); *Euseius stipulatus* (Athias-Henriot); *Euseius tularensis* (Congdon); *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Khanamani et al., 2017
Amazonian palm	*Euterpe oleracea* Mart.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Aninga	*Montrichardia linifera* (Arr.) Schott	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Annual mercury	*Mercurialis annua* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Apple	*Malus domestica* L.; *Malus sylvestris* Mill.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Euseius finlandicus* Oudemans; *Euseius tularensis* (Congdon); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Delisle et al., 2015a,b
Apricot	*Prunus armeniaca* L.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Euseius finlandicus* Oudemans; *Euseius stipulatus* (Athias-Henriot); *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Fadaei et al., 2018; Soltaniyan et al., 2018
Avocado	*Persea americana* Mill.	Predatory mites	*Euseius hibisci* (Chant)	McMurtry and Scriven, 1964
Bermuda buttercup	*Oxalis pes-caprae* L.; *Oxalis* sp.	Predatory mites	*Typhlodromus pyri* (Sheuten); *Cydnodromus picanus* Ragusa	Ragusa et al., 2000; Bermúdez et al., 2010
Betulaceous plants (e.g., alder, birch and hazel)	*Alnus incana* (L.) Muench; *Betula pubescens* Ehrh., *Betula pendula* Roth.; *Carpinus betulus* L., *Corylus avellana* L.; *Corylus americana* Marsh.; *Alnus rubra* Bong.; *Turnera ulmifolia* L.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor); *Amblyseius andersoni* Chant; *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Euseius addoensis* (Van der Merwe and Rijke); *Euseius finlandicus* (Oudemans); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus pyri* (Scheuten)	Saito and Mori, 1975; Overmeer, 1981; Englert and Maixner, 1988; Grout and Richards, 1992; Engel and Ohnesorge, 1994; Kostiainen and Hoy, 1994; Schausberger, 1997; Van Rijn and Tanigoshi, 1999a; Addison et al., 2000; Goleva et al., 2015; Ferreira et al., 2020
Bitter melon	*Momordica charantia* L.	Anthocorids	*Orius sauteri* (Poppius)	Zhou and Wang, 1989
Brazilian oil palm	*Elaeis oleifera* Cort.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Broad bean	*Vicia fabae* L.	Predatory mites	*Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans)	Van Rijn and Sabelis, 1990; Van Rijn and Tanigoshi, 1999a; Nomikou et al., 2001
Castor bean	*Ricinus communis* L.	Predatory mites	*Amblyseius gossypi* Elbadry; *Amblyseius herbicolus* (Banks); *Amblyseius idaeus* (Denmark and Muma); *Amblyseius largoensis* (Muma); *Amblyseius zaheri* Yousef and El-Borolossy; *Euseius hibisci* (Chant); *Euseius mesembrinus* (Dean); *Euseius scutalis* (Athias-Henriot); *Euseius tularensis* (Congdon); *Euseius yousefi* Zaher and El-Borolossy; *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Phytoseius plumifer* (Canestrini and Fanzago); *Typhlodromalus aripo* DeLeon; *Typhlodromus negevi* Swirski and Amitai; *Typhlodromus pyri* Scheuten	Dosse, 1961; McMurtry and Scriven, 1964; McMurtry and Johnson, 1965; Rasmy and El-Banhawy, 1975; Momen and El-Saway, 1993; Tanigoshi et al., 1993; Yue et al., 1994; Ramakers and Voet, 1995; Yue and Tsai, 1996; Van Rijn and Tanigoshi, 1999a; Van Rijn et al., 2002; Momen, 2004; Gnanvossou et al., 2005; Skirvin et al., 2006; Momen et al., 2009; Al-Shammery, 2011; Rodríguez-Cruz et al., 2013
Cat grass	*Dactylis glomerata* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994

(Continued)

TABLE 5 | Continued

Plant (common name)	Plant (Latin name)	Category natural enemy	Natural enemy	Source
Cattail	*Typha* spp.*: Typha angustifolia* L.; *Typha domingensis* Pers.; *Typha latifolia* L.; *Typha orientalis* Presl.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor); *Amblyseius andersoni* Chant; *Amblyseius herbicolus* (Banks); *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Euseius concordis* (Chant); *Euseius finlandicus* (Oudemans); *Euseius gallicus* (KreiterandTixier), *Euseius hibisci* (Chant); *Euseius ovalis* (Evans); *Euseius stipulatus* (Athias-Henriot); *Euseius mesembrinus* (Dean); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Proprioseiopsis asetus* Muma; *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa	Kennett et al., 1979; Ouyang et al., 1992; Kostiainen and Hoy, 1994; Yue et al., 1994; Yue and Tsai, 1996; Van Rijn et al., 1999; Nomikou et al., 2002; Nomikou, 2003; Emmert et al., 2008; Messelink et al., 2008; Park et al., 2010, 2011; Tuovinen and Lindqvist, 2010; Kolokytha et al., 2011; Goleva and Zebitz, 2013; Nguyen et al., 2013, 2014a,b; Pijnakker et al., 2014, 2016; Vangansbeke et al., 2014a, 2016a; Nguyen et al., 2015; Duarte et al., 2015; Leman and Messelink, 2015; Samaras et al., 2015; Massaro et al., 2016; Beltrà et al., 2017; Liu and Zhang, 2017; Muñoz-Cárdenas et al., 2017; De Figueiredo et al., 2018; Liu et al., 2019; Ferreira et al., 2020; Pascua et al., 2020
Cherry (sweet)	*Prunus avium* L.	Predatory mites	*Iphiseius degenerans* (Berlese); *Euseius concordis* (Chant); *Euseius finlandicus* Oudemans; *Euseius stipulatus* (Athias-Henriot); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008
Chili pepper	*Capsicum frutescens* L.	Predatory mites	*Amblyseius herbicolus* (Banks)	Duarte et al., 2015
China rose	*Rosa chinensis* Rehder and Wils.	Anthocorids	*Orius sauteri* (Poppius)	Zhou and Wang, 1989
Coconut	*Cocos nucifera* L.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma; *Neoseiulus paspalivorus* DeLeon; *Proctolaelaps bickleyi* Bram	Lawson-Balagbo et al., 2007; Ferreira et al., 2020
Common henbit	*Lamium amplexicaule* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Common meadow-grass	*Poa pratensis* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Common mugwort	*Artemisia vulgaris* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Common sowthistle	*Sonchus oleraceous* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Common wild poppy	*Papaver rhoeas* L.	Predatory mites	*Euseius finlandicus* Oudemans	Broufas and Koveos, 2000
Corn	*Zea mays* L.	Anthocorids	*Orius insidiosus* (Say); *Orius sauteri* (Poppius)	Richards, 1992; Funao and Yoshiyasu, 1995; Richards and Schmidt, 1995
Corn	*Zea mays* L.	Coccinellids	*Coleomegilla maculata* (De Geer)	Smith, 1960a,b; Hodek et al., 1978; Lundgren and Wiedenmann, 2004; Lundgren et al., 2005; Michaud and Grant, 2005
Corn	*Zea mays* L.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor)*; Amblyseius swirskii* (Athias-Henriot); *Euseius concordis* Chant; *Euseius hibisci* (Chant); *Euseius fustis* Pritchard and Baker; *Euseius scutalis* (Athias-Henriot); *Iphiseiodes zuluagai* Denmark and Muma; *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Phytoseius plumifer* (Canestrini and Fanzago); *Typhlodromalus aripo* DeLeon; *Typhlodromalus manihoti* Moraes; *Typhlodromus pyri* Scheuten	McMurtry and Scriven, 1964; Engel and Ohnesorge, 1994; Gnanvossou et al., 2005; Weintraub et al., 2009; Onzo et al., 2012; Saber, 2012, 2013; Goleva and Zebitz, 2013; Khodayari et al., 2013; Adar et al., 2014; Vieira Marques et al., 2014; Leman and Messelink, 2015; Samaras et al., 2015; Palevsky, 2016; Rezaie and Askarieh, 2016; Khanamani et al., 2017; Rezaie, 2017
Corn	*Zea mays* L.	Trichogrammatids	*Trichogramma brassicae* Bezdenko	Zhang et al., 2004

(Continued)

TABLE 5 | Continued

Plant (common name)	Plant (Latin name)	Category natural enemy	Natural enemy	Source
Date palm	*Phoenyx dactylifera* L.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Euseius scutalis* (Athias-Henriot); *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Proprioseiopsis asetus* (Chant)	Fouly, 1997; Al-Shammery, 2011; Abou-Elella et al., 2013; Rezaie and Askarieh, 2016; Rezaie, 2017
Echinocereus	*Echinocereus* sp.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot)	Goleva and Zebitz, 2013
Eucalyptus	*Eucalyptus* spp.	Predatory mites	*Euseius hibisci* (Chant)	McMurtry and Scriven, 1964
False oat-grass	*Arrhenatherum elatius* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Field bindweed	*Convolvulus arvensis* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Fireweed	*Epilobium angustifolium* L.	Predatory mites	*Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans)	Van Rijn and Tanigoshi, 1999a
Foxglove-tree	*Paulownia tomentosa* Steud.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot)	Goleva and Zebitz, 2013
Galega	*Galega officinalis* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Hazel	*Corylus avellana* L.	Coccinellids	*Adalia bipunctata* L.	Blackman, 1967
Henbit dead-nettle	*Lamium amplexicaule* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Hoary mustard	*Hirschfeldia incana* (L.) Lagr.-Foss.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Bermúdez et al., 2010
Honey bee pollen	different plants	Anthocorids	*Orius laevigatus* (Fieber); *Orius albidipennis* (Reuter)	Cocuzza et al., 1997
Honey bee pollen	(mainly Brassicaceae+Verbascum spp.)	Coccinellids	*Harmonia axyridis* (Pallas)	Berkvens et al., 2007
Horse-chestnut	*Aesculus hippocastanum* L.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Neoseiulus cucumeris* (Oudemans)	Goleva and Zebitz, 2013; Ranabhat et al., 2014; Goleva et al., 2015
Ice plant	*Carpobrotus edulis* (L.); *Malephora crocea* (Jacq.); *Mesembrianthemum* sp.	Predatory mites	*Amblyseius similoides* Buchelos and Pritchard; *Cydnodromus californicus* (McGregor); *Euseius hibisci* (Chant); *Euseius mesembrinus* (Dean); *Euseius stipulatus* (Athias-Henriot); *Euseius tularensis* (Congdon); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus exhilaratus* Ragusa; *Typhlodromus phialatus* Athias-Henriot	McMurtry and Scriven, 1964, 1966; Ferragut et al., 1987; Van Rijn and Sabelis, 1990; Castagnoli and Liguori, 1991; Flechtmann and McMurtry, 1992; Ouyang et al., 1992; Yue et al., 1994; Van Rijn et al., 2002; Villanueva and Childers, 2004; Ragusa et al., 2009; Pina et al., 2012
Maple (honey bee pollen)	*Acer* spp.	Anthocorids	*Orius insidiosus* (Say)	Kiman and Yeargan, 1985
Meadow foxtail	*Alopecurus pratensis* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Nettle-leaved Figwort	*Scrophularia peregrina* L.	Predatory mites	*Cydnodromus californicus* (McGregor)	Ragusa et al., 2009
Norway spruce	*Picea abies* L.	Predatory mites	*Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994
Oak	*Quercus* spp.: *Quercus agrifolia* Nee., *Quercus ilex* L.; *Quercus ithaburensis* L.; *Quercus virginiana* Mill.; *Quercus macranthera* Fisch. and Mey; *Quercus robur* L.	Predatory mites	*Amblyseius andersoni* (Chant); *Amblyseius herbicolus* (Chant); *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (chant); *Euseius mesembrinus* (Dean); *Euseius scutalis* (Athias-Henriot); *Euseius tularensis* (Congdon); *Metaseiulus occidentalis* (Nesbitt); *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Neoseiulus longispinosus* (Evans); *Neoseiulus paraki* (Ehara); *Typhlodromus cryptus* Athias-Henriot; *Typhlodromus exhilaratus* Ragusa; *Typhlodromus pyri* (Sheuten)	McMurtry and Scriven, 1964; Swirski, 1967; Calvert and Huffaker, 1974; Saito and Mori, 1975 Castagnoli and Liguori, 1986; Duso and Camporese, 1991; Ouyang et al., 1992; Engel and Ohnesorge, 1994; Yue et al., 1994; Hodek and Honěk, 1996; Yue and Tsai, 1996; Castagnoli and Simoni, 1999; Preverieri et al., 2006; Carrillo et al., 2010; Adar et al., 2014; Goleva et al., 2015
Oak	*Quercus* spp.	Coccinellids	*Adalia bipunctata; Harmonia axyridis* (Pallas)	Hodek and Honěk, 1996; Koch, 2003

(Continued)

TABLE 5 | Continued

Plant (common name)	Plant (Latin name)	Category natural enemy	Natural enemy	Source
Oil palm	*Elaeis guineensis* Jacq.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Olive	*Olea europaea* L.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Euseius tularensis* (Congdon); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Neoseiulus cucumeris* (Oudemans)	Ouyang et al., 1992; Matsuo et al., 2003; Kolokytha et al., 2011; Kumar et al., 2014; Samaras et al., 2015
Passion fruit	*Passiflora edulis* Sims	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Peach	*Prunus persica* L.	Predatory mites	*Euseius tularensis* (Congdon)	Ouyang et al., 1992
Pear	*Pyrus communis* L.	Predatory mites	*Iphiseius degenerans* (Berlese); *Euseius finlandicus* Oudemans; *Euseius tularensis* (Congdon); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Matsuo et al., 2003; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011
Peltaea riedelii	*Peltaea riedelii* (Gürke) Standl.	Predatory mites	*Iphiseiodes zuluagai* Denmark and Muma; *Euseius concordis* Chant	Vieira Marques et al., 2014
Pine (black, turkish, calabrian)	*Pinus* sp.; *Pinus brutia* Ten.; *Pinus nigra* L.	Predatory mites	*Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus pyri* (Sheuten)	Engel and Ohnesorge, 1994; Van Rijn and Tanigoshi, 1999a; Samaras et al., 2015; Kütük, 2018
Pistachio	*Pistachio vera* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Soltaniyan et al., 2018
Plum	*Prunus domestica* L.	Predatory mites	*Euseius stipulatus* (Athias-Henriot); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman	Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011
Pygmy date palm	*Phoenix roebelenii* O'Brien	Predatory mites	*Amblyseius largoensis* (Muma)	Yue and Tsai, 1996
Small nettle	*Urtica urens* L.	Predatory mites	*Neoseiulus californicus* (McGregor)	Gugole Ottaviano et al., 2015
Sour orange	*Citrus aurantium* L.	Predatory mites	*Euseius scutalis* (Athias-Henriot)	Al-Shammery, 2011
Spanish needle	*Bidens pilosa* L.	Predatory mites	*Euseius mesembrinus* (Dean)	Yue et al., 1994
Spring crocus	*Crocus vernus* (L.) Hill	Predatory mites	*Amblyseius swirskii* (Athias-Henriot)	Goleva and Zebitz, 2013
Squash	*Curcubita pepo* L.	Predatory mites	*Iphiseiodes zuluagai* Denmark and Muma; *Euseius concordis* Chant	Vieira Marques et al., 2014
Strawberry	*Fragaria x ananassa* (West.)	Predatory mites	*Iphiseius degenerans* (Berlese); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans)	Van Rijn and Tanigoshi, 1999a; Shakya et al., 2009; Gugole Ottaviano et al., 2015
Sunflower	*Helianthus annuus* L.	Predatory mites	*Amblyseius zaheri* Yousef and El-Borolossy; *Euseius yousefi* Zaher and El-Borolossy; *Iphiseius degenerans* (Berlese); *Neoseiulus barkeri* Hugues	Van Rijn and Tanigoshi, 1999a; Momen, 2004; Rezaie and Askarieh, 2016; Ferreira et al., 2020
Sunnhemp	*Crotalaria juncea* L.	Predatory mites	*Amblyseius herbicolus* (Banks)	Rodríguez-Cruz et al., 2013
Sweet orange	*Citrus sinensis* L.	Predatory mites	*Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma	Ferreira et al., 2020
Sweet pepper	*Capsicum annuum* L. cv. Mazurka	Anthocorids	*Orius albidipennis* Reuter; *Orius laevigatus* (Fieber)	Vacante et al., 1997
Sweet pepper, ornamental pepper, peper	*Capiscum annum* L.; *Capsicum frutescens* L.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (Chant); *Neoseiulus cucumeris* (Oudemans)	McMurtry and Scriven, 1964; Van Rijn and Sabelis, 1990; Kumar et al., 2014
Tea	*Camellia sinensis* L.	Predatory mites	*Amblyseius sojaensis* Ehara; *Neoseiulus cucumeris* (Oudemans)	Osakabe et al., 1986; Matsuo et al., 2003
Tulip	*Tulipa* sp.; *Tulipa gesneriana* L.	Predatory mites	*Neoseiulus cucumeris* (Oudemans); *Amblyseius swirskii* (Athias-Henriot)	Ranabhat et al., 2014; Goleva et al., 2015
Turkish pine	*Pinus brutia* (Ten.)	Predatory mites	*Amblyseius swirskii* (Athias-Henriot)	Kütük and Yigit, 2011

(Continued)

TABLE 5 | Continued

Plant (common name)	Plant (Latin name)	Category natural enemy	Natural enemy	Source
Walnut	*Juglans regia* L.	Predatory mites	*Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (Chant); *Euseius finlandicus* Oudemans; *Neoseiulus barkeri* Hugues, *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudemans; *Typhlodromus pyri* (Sheuten)	McMurtry and Scriven, 1964; Engel and Ohnesorge, 1994 Broufas and Koveos, 2000; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Rezaie and Askarieh, 2016; Rezaie, 2017; Fadaei et al., 2018
Willow	*Salix* sp.	Coccinellids	*Adalia bipunctata* L.	Blackman, 1967

1996; Cocuzza et al., 1997; Coll, 1998; Lundgren, 2009). However, the development of *Orius* spp. was prolonged and reproduction and survival reduced on pollen only diet (Salas-Aguilar and Ehler, 1977; Kiman and Yeargan, 1985; Funao and Yoshiyasu, 1995; Richards and Schmidt, 1996; Cocuzza et al., 1997; Vacante et al., 1997,?). As with the phytoseiids, *Orius* performance is dependent on pollen type (Vacante et al., 1997). Pollen feeding also provides benefits for *M. pygmaeus* (Perdikis and Lykouressis, 2000; Vandekerkhove and De Clercq, 2010; Portillo et al., 2012; Put et al., 2012). Cattail pollen doubled the longevity of *M. pygmaeus* females compared to bugs provided only broad beans (Portillo et al., 2012) and promoted its establishment on tomato plants (Put et al., 2012). Also larvae of green lacewings can benefit from (bee) pollen (Patt et al., 2003). For syrphids, sexual maturation requires proteins that can be provided by pollen, allowing the females to mature successive batches of eggs (Schneider, 1948; Pineda and Marcos-García, 2008).

In biological control, pollen has been reported to support population densities of natural enemies when prey densities are low and improve control efficacy against pests. Most of these studies concern predatory mites. In the presence of pollen, predatory mites provided better control of phytophagous mites (McMurtry and Scriven, 1966; Kennett et al., 1979; Ferragut et al., 1987; Pina et al., 2012, 2015; Saber, 2013; Maoz et al., 2014; Duarte et al., 2015; Pijnakker et al., 2016), thrips (Ramakers, 1990; Van Rijn and Sabelis, 1993; Van Rijn et al., 1999) and whiteflies (Nomikou et al., 2001, 2002, 2010; Nomikou, 2003). Van Rijn et al. (1999) were the first to provide clear experimental evidence that supplementing pollen can be an efficient strategy to boost the biological control potential of predatory mites. By supplying the predatory mite species *A. limonicus* and *I. degenerans* with cattail pollen they were able to enhance population levels of the predatory mites, which resulted in increased thrips control and reduced plant damage. Kütük and Yigit (2011) succeeded in pre-establishing *A. swirskii* on sweet pepper by spraying suspensions of pine pollen, thereby maintaining *F. occidentalis*-numbers under the desired threshold. Provision of cattail or corn pollen increased densities of *A. swirskii* and improved thrips control on potted chrysanthemum (Leman and Messelink, 2015). Muñoz-Cárdenas et al. (2017) succeeded in establishing *A. swirskii* in roses before thrips release by weekly provision of cattail pollen and thus managed to realize a decrease of thrips numbers and damage. Nomikou et al. (2002, 2010) showed improved suppression of tobacco whitefly populations by *A. swirskii* on single cucumber plants treated with cattail pollen. Skirvin et al. (2006) achieved a higher density of *N. cucumeris* on chrysanthemum plants with an application of castor bean pollen. Still, it led to an increased infestation of western flower thrips, as only a few predatory mites were recovered. These examples give an idea of the potential of pollen as alternative food but the studies were often performed over short temporal scales and at pest densities higher than those found in commercial greenhouses. Since cattail pollen has been made commercially available in 2013, growers can now apply pollen as part of biocontrol programs. They typically apply pollen weekly (blown at 250 g/ha) or biweekly (at 500 g/ha) (Pijnakker et al., 2016). These dosages correspond to 2.5 to 20 mg per plant. Various devices are available to apply pollen to enhance the establishment of predatory mites on crops (Gan-Mor et al., 2003, 2011; Weintraub et al., 2009; Pijnakker et al., 2016). Other arguments in favor of the use of cattail pollen, next to its high nutritional value, are its low allergenic character (Weber and Nelson, 1985), its relatively low attractiveness to pests and poor nutritional suitability for thrips (Hulshof et al., 2003). The fact that cattail pollen is not attractive to (bumble) bees, means that it does not distract pollinators used in the crop (Schmidt et al., 1989).

However, the use of pollen can have some drawbacks as it can also benefit herbivores (Kirk, 1987; Van Rijn et al., 2002; Chitturi et al., 2006; Wäckers et al., 2007, Leman and Messelink, 2015; Vangansbeke et al., 2016b). Hulshof et al. (2003) showed at laboratory scale that *F. occidentalis* feeds on pollen, resulting in an enhancement of its growth rate and fecundity. Van Rijn et al. (2002), using simulation models, showed that availability of pollen benefits predators more than thrips and improved predator-prey ratios resulting in enhanced thrips control. This has since been repeatedly confirmed in studies showing the efficacy of the pollen supplementation at plant or crop level (see above). The high reproduction by *A. swirskii* on plants treated with pollen prevented the pest from developing, even if they can feed on the pollen. This represents an example of apparent competition, where the population development of a prey is suppressed by a shared predator when an additional prey or food supplement is present (Nomikou et al., 2010). Despite the fact that *Typha* pollen has been widely shown to be effective in supporting biological control, growers could still run a risk of damage when thrips are too numerous at the start of the crop or when predators do not establish because of pesticide residues. When applying any food supplement, including pollen, predation per predatory mite will go down due to satiation effects (Skirvin et al., 2007). In addition to predator satiation (Holt and Lawton, 1993, 1994; Shakya et al., 2009) a feeding-switch to pollen may occur. Both mechanisms may result in a temporary reduction in predation rate of the pest (so-called apparent mutualism, Abrams and Matsuda, 1996). High dosage of cattail pollen reduced the predation of thrips by individual *A. swirskii* by 50% on laboratory scale (Leman and Messelink, 2015). However, these effects are typically short term and are soon outbalanced by the augmentation of natural enemy numbers (Van Rijn et al., 1999).

The use of supplementary food, and pollen in particular, is a powerful tool to help establish predatory mites and improve biocontrol efficacy. The application of exogenous pollen as supplemental food source can be optimized by avoiding excessive doses, as overly high pollen levels may result in satiation of predatory mites and stimulation of thrips (Sabelis and van Rijn, 2006). The choice of the pollen type and the match with the predatory mite can also affect the outcome. However, *Typha* pollen has proved to be suitable for a broad range of predatory mites (**Table 5**). Growers succeed in building strong populations of predatory mites with feeding their predators before pest appearance and performing adjustments in their irrigation systems and their spraying data. Some persue the development of the application by automatizing the blowing of this alternative food.

NECTAR/SUGAR SOLUTION

Many natural enemies depend on sugars as their main source of energy. This includes a.o. parasitoids (Wäckers, 2001), syrphids (Van Rijn and Wäckers, 2016), gall midges (Fratoni et al., 2020), chrysopids (Stelzl, 1991; Hogervorst et al., 2007), coccinellids (Pemberton and Vandenberg, 1993), mirids (Portillo et al., 2012), and phytoseiids (Van Rijn and Tanigoshi, 1999b). Natural enemies can feed from a range of carbohydrate sources. Besides floral nectar, they can also exploit extrafloral nectar, as well as honeydew.

Floral nectar has evolved as a food reward in the mutualism between plants and their pollinators. Even though natural enemies, with a few noticeable exceptions (Pekas et al., 2020), are most likely not necessarily effective in pollinating flowers, they, nevertheless, can collect floral nectar to provide for their energetic needs. As natural enemies tend to have short mouthparts, their nectar foraging is restricted to those plant species with open and exposed floral nectaries, such as Apiaceae, Euphorbiaceae, or buckwheat (Campbell et al., 2012; Wäckers and van Rijn, 2012; Van Rijn and Wäckers, 2016).

While accessibility of floral nectar can be a bottleneck for natural enemies, some plants also produce nectar outside of the flowers. These so-called extrafloral nectaries tend to be exposed and thus highly accessible. Furthermore, the nectar is often secreted over prolonged periods of time (Wäckers and Bonifay, 2004). These adaptations fit their ecological function, as extrafloral nectar is part of a defensive strategy, allowing plants to recruit ants and other sugar feeding natural enemies. They, in turn, protect the plants when attacking herbivores. Extrafloral nectaries have been described in more than thousand plant species, including a number of important crops, such as cotton, cassava, peaches, plums, cherries, pumpkins, roses, field beans. In a number of plant systems, it has been demonstrated that the presence of extrafloral nectar can translate into both reduced plant damage and increased plant reproductive fitness (Heil, 2015).

Honeydew is a generic term for sugar-rich excretions of phloem-feeding Sternorrhyncha. In agricultural ecosystems, honeydew is often the most prevalent sugar source (Wäckers and Steppuhn, 2003; Hogervorst et al., 2007; Tena et al., 2015). However, honeydew differs from the above-mentioned sugar sources, as it is primarily a waste product. This can reduce the nutritional value of honeydew (Wäckers et al., 2008).

Overall, the nutritional suitability of the above sugar sources depends on composition and concentration of carbohydrates (Wäckers, 2001; Azzouz et al., 2004; Fratoni et al., 2020). Sugar concentration is an important factor determining sugar uptake. At low concentrations, gustatory perception might be impeded (Wäckers, 1999), whereas viscosity at high sugar concentrations can interfere with sugar uptake (Wäckers, 2000; Winkler et al., 2009). Upon the time of nectar secretion, sugar concentrations can already range from 5 to 75% (Dafni, 1992). Environmental conditions may further affect nectar concentrations both indirectly through their effects on the nectar producing plant, and directly through evaporation, hygroscopy or rain dilution (Winkler et al., 2009). Sugar concentrations of undiluted extrafloral nectar range from 5 to more than 80% (Koptur, 1992a,b; Wäckers, 2001). In general, extra floral nectar shows much more variation in terms of sugar concentration than floral nectar from the same plant. Extrafloral nectar tends to be more concentrated, probably due the fact that its exposed nature increases evaporation. The fact that honeydew is typically available as little droplets or as a thin film on the substrate, means that it is even more subjected to evaporation. As a result, sugar concentrations are often at saturation. This is likely to be a limiting factor in honeydew uptake. This problem is accentuated by the specific tendency of the honeydew sugars: raffinose and melezitose, to crystallize rapidly (Wäckers, 2000).

Providing Sugar Sources to Boost Biological Pest Control

It has long been recognized that the lack of sugar sources in agricultural systems can strongly undermine the efficacy of biological control. This problem could be overcome by introducing food sources into our agricultural systems. Recently, we have seen an increasing interest in the use of (flowering) non-crop plants in field margins as a tool to sustain predators and parasitic wasps. Specifically selected seed mixtures are available that are intended to attract natural enemies and provide them with nectar sources. When introducing nectar plants, the use of sugar sources is not restricted to beneficial insects. Many pest insects thrive on sweets as well (Wäckers et al., 2007). By choosing plants that primarily benefit natural enemies, the positive impact on pest control can be maximized (Gurr, 2005; Winkler et al., 2010). Banker plants can also be used to provide sugar sources, either in the form of (extra-) floral nectar as in the case of castor bean or broad bean or by providing honeydew (considering the caveats mentioned above). As an alternative to the introduction of nectar- or honeydew providing plants, sugar can also be applied as such. Sugar can be either sprayed onto the crop, or provided in so-called "feeding stations." Spraying sugar has the advantage that it is an easy and cheap application method resulting in an even coverage and providing an easily accessible sugar source for the predators and parasitoids. The quantity of the sugar applied can be controlled through the choice of sugar concentration, by adjusting the spray volume/spray nozzle, and by varying the walking/driving speed. Yet, there are also obvious drawbacks to the use of sugar sprays. Blanket sprays quickly result in the crop getting sticky. Certain sugars can cause phytotoxicity when sprayed directly on the foliage. In addition, sugars on the plant surface are prone to growth of sooty mold. These drawbacks can be avoided, either by using very weak sugar concentrations (e.g., 0.1–1%) or by applying a higher concentrated solution in a very fine and light mist. For the target arthropods, having minute sugar droplets is often better than having to deal with a sticky sugar layer, as the latter interferes with arthropod mobility. Biological control practitioners have attempted to incorporate artificial sugar sprays as a strategy to cater to the nutritional needs of parasitoids (Mandour et al., 2007; Wade et al., 2008). However, the efficacy of this form of sugar provisioning in biological control programmes has been limited and inconsistent (Heimpel and Jervis, 2005; Wade et al., 2008). Tena et al. (2015) studied the use of sugar sprays in combination with the release of the parasitoid *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) for the control of the California red scale *Aonidiella aurantii* in a commercial citrus orchard. They demonstrated that sugar supplementation increased the parasitoid population density 2-fold. Parasitoid fecundity on sugar treated trees was shown to be enhanced as well. Higher population densities and the increase in realized fecundity translated in a 2-fold increase in parasitism under crop conditions. The successful examples show that under certain conditions the use of sugars can be an effective element in a conservation biological control strategy.

DOMATIA

Shelter and oviposition substrates are other resources that can be essential to successful establishment and efficacy of natural enemies (Gurr et al., 2017). Providing sites of refuge can support reproduction (Pemberton and Turner, 1989; O'Dowd and Willson, 1991; Grostal and O'Dowd, 1994; Walter, 1996) and development, overwintering or aestivation and can protect them from cannibalism (Ferreira et al., 2008; Lee and Zhang, 2016, 2018), predation (Roda et al., 2000; Norton et al., 2001; Faraji et al., 2002a,b; Romero and Benson, 2005; Seelmann et al., 2007; Ferreira et al., 2011) and unfavorable climatic conditions (Walter and O'Dowd, 1992a,b; Grostal and O'Dowd, 1994; Walter, 1996; Sabelis et al., 1999; Norton et al., 2001).

Some plants have special morphological structures, called domatia (from the Latin for home "domus"), that are targeted to either ants, or predatory/fungivorous mites. Ant domatia are represented by hollow thorns or stems and rolled leaf margins. Acarodomatia may take the form of either pits or (dense) tufts of leaf hairs, in which small arthropods may reside (Romero and Benson, 2005). Many studies have demonstrated that the presence of domatia increases the population of predators, that in turn protect the plant against herbivores and in some instances pathogens and weeds (Lundstrom, 1887; Rozario, 1995; Kreiter et al., 2003; Ferreira et al., 2008, 2011; Shenoy and Borges, 2010; Parolin et al., 2013). Predatory mites tend to occur more abundantly on plants bearing acarodomatia (O'Dowd and Willson, 1997; Norton et al., 2000; Roda et al., 2001; Romero and Benson, 2005; Avery et al., 2014) and their survival and reproduction on such plants is enhanced (Pemberton and Turner, 1989; Karban et al., 1995; Agrawal, 1997; Agrawal et al., 2000; Cortesero et al., 2000; Avery et al., 2014; Bresch et al., 2015, 2018). Domatia also act as oviposition substrate. Many predatory mite species show a preference to lay eggs on trichomes. Egg clusters can be frequently seen inside domatia, where predatory mites can molt protected from predators. Besides serving as shelters and oviposition sites, the hair-tufts may trap pollen and fungal spores that the mites can then consume (Roda et al., 2000; Romero and Benson, 2005; Loughner et al., 2008). Thus, acarodomatia can serve a function in providing food as well. Pekas and Wäckers (2017) showed a strong synergistic effect between the availability of fibers and food (pollen and sugar water) in affecting population growth of predatory mites on citrus plants. Romero and Benson (2004) demonstrated the protective role of domatia on the tropical tree *Cupania vernalis* L. By blocking domatia on part of the experimental trees, they showed that domatia increased predatory mite abundance and lowered herbivore damage from eriophyid mites. However, very few studies have investigated their long-term effect on predatory mites, pest or fungi under natural conditions (Norton et al., 2000; Monks et al., 2007; Ferreira et al., 2010). Norton et al. (2000) showed that acarodomatia increased the abundance of the mycophagous tydeid mite, *Orthotydeus lambi* (Baker), which resulted in the reduction of 48% of grape mildew infestation on the riverbank grape.

Domatia can be provided to beneficials by (1) selecting crop variety with the appropriate properties, (2) by adding suitable non-crop plants to crops (Skirvin and Fenlon, 2001; Van Rijn et al., 2002; Osborne and Barrett, 2005; Frank, 2010; Huang et al., 2011; Parolin et al., 2012b; Kumar et al., 2015), (3) or by using artificial structures (Loughner et al., 2011; Adar et al., 2014; Pekas and Wäckers, 2017). Crop varieties can differ substantially in domatia characteristics. Choosing crop varieties for their domatia traits could thus help to support establishment of natural enemies. Breeding programmes have actually started to include traits that determine suitability for beneficial organisms (Bottrell et al., 1998; English-Loeb et al., 1999). Some tomato varieties, for example, have been selected for their distorted trichomes to facilitate biological control of tomato russet mites (Van Houten et al., 2013; Legarrea et al., 2020). Another method for applying domatia can be the interplanting of domatia bearing banker plants between crop plants lacking domatia. Parolin et al. (2013) showed an increased spider mite control in roses using the predatory mites *P. persimilis* and *Neoseiulus californicus* (MCGregor) when adding lauristinus and frost grape bearing acarodomatia as bankerplants. Adding the banker plants in this system enhanced the establishment of predatory mites and increased their efficacy. The method can only be successful if natural enemies disperse from the manipulated habitat to the crop. In practice, growers tend to focus on commercial crops and are reluctant to introduce non-crop (banker) plants. A further strategy could be to use artificial domatia. Various types of artificial domatia have been used in studies to assess the benefits of natural dolmatia, but also, to improve biological control on crops (Loughner et al., 2010, 2011; Pekas and Wäckers, 2017). Rozario (1994) brought tufts of polyester fibers to grape varieties with low natural domatia to augment populations of *Galendromus occidentalis* Nesbitt. Agrawal and Karban (1997) supplemented cotton plants with artificial domatia, which enhanced spider mite control and fruit yields. However, thrips numbers were also shown to benefit from domatia. Kawashima et al. (2006a) reported laboratory experiments showing that textured urethane foam and polyethylene shading nets were suitable sites for the reproduction of *N. californicus*. Kawashima and Jung (2011) suggested using urethane foam as ground cover in apple orchards to increase the survival of *N. californicus* populations during the winter. Loughner et al. (2011) mimicked domatia on glabrous beans seedlings and Impatiens plants by adding cotton fiber patches and chopped acrylic yarn fibers and found more *A. swirskii* on plants provided with pollen and artificial domatia than on plants given solely pollen or fibers. In this study, cotton patches and paper pulp supplements augmented and maintained *A. swirskii* populations, whereas jute and celluflo were not effective. Adar et al. (2014) tested the "pollen on-twine" method (Gan-Mor et al., 2011), using fibers (rayon/viscose 80% and jute 20%) coated with pollen and succeeded in enhancing *E. scutalis* populations. Oviposition occurred on rayon rather than on jute. Bresch et al. (2018) found wool, silk, polyamide, viscose and polyester to be equally suitable as natural domatia for oviposition by N. californicus. However, none of them improved spider mite control by N. californicus and polyamide even benefitted the pest. Pekas and Wäckers (2017) showed that the combined use of fibers, pollen, and sugar generate synergistic benefits to population growth of *Euseius stipulatus* (Athias-Henriot) on bitter orange. In orchards, Koike et al. (2000) designed a Phyto trap, which contains wool yarn mimicking the microstructure of spider mites colonies. This tool aims at collecting predatory mites in pear trees to monitor their densities during the seasons and maintain populations (Kawashima and Amano, 2006; Kawashima et al., 2006b). This tool inspired Messelink et al. (2016) to test among others further material with Velcro tape in greenhouse crops, but found that using millet husk or jute both combined with pollen were more effective to enhance the establishment of *A. limonicus* on anthurium. In spite of these examples showing the potential of using artificial domatia, there are no commercial applications of these artificial domatia yet.

CONCLUSIONS

This review presents the potential, advantages and risks of the concept of "beneficials-in-first" over augmentative biological control in greenhouses and aims at discussing tools thought to preserve natural enemies in biological control programmes. The studies described show that natural enemies' survival, development, reproduction and efficacy can be enhanced with the use of factitious prey, banker plant systems, pollen, sugars and manipulated habitats. This concept of "beneficials-in-first" is no longer a focus of researchers only, but has been explored by commercial growers over the past two decades. However, despite the trials demonstrating their benefit, some methods to enhance natural enemies' establishment are still excluded from biological strategies in practice, as they often lead to other issues at large scale. The development of hyperparasitoids or pests on banker plant systems, the possible molting of *Ephestia* eggs and *Artemia* cysts, the lack of survival of living factitious prey, the damages caused by *Tyrophagus putrescentiae* or by mirid predatory bugs when they are too numerous, are such examples. Overhead irrigation can hamper the application of alternative food and artificial domatia in some crops. Artificial domatia are also difficult for growers to introduce in their crop.

Further increasing the adoption of the "beneficials-in-first" concept by growers can be achieved by:

1. Clearly demonstrating efficacy on a larger scale and communicate if the selected resources benefit more natural enemies than the antagonists or pests, decrease pest damage and increase production quality or yield;
2. Increasing the involvement of growers in the process of such large-scale experiments, including costs and handling times;
3. Fine-tuning the amount of supplemental resources, the release techniques, the timing and the frequency with which the tools should be employed (Janssen and Sabelis, 2015; Madadi, 2018);
4. Automatization as it will be the key in expanding the scope of inoculative biological control, both in protected and open-field crops.

In the coming decade, we foresee more applications of feeding stations and nectar plants in crops to enhance the survival of natural enemies. Beside the tools of enhancement of beneficials, the use of methods limiting pest activity in greenhouses will gain more importance like tools of sexual confusion, distraction of pests such as "push-pull systems" or the use of "repellent substances."

AUTHOR CONTRIBUTIONS

JP: conceptualization, supervision, writing original draft, review, and editing. FW: conceptualization, supervision, writing draft, review, and editing. DV, RM, and MD: review and editing. All authors contributed to the article and approved the submitted version.

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