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Generalist Predators, Food Web Complexities and Biological Pest Control in Greenhouse Crops

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1. Introduction

Biological control of pest species has traditionally mainly focused on specific natural enemies for each pest (Huffaker & Messenger, 1976; Hokkanen & Pimentel, 1984; Van Lenteren & Woets, 1988; Hoy, 1994). However, pest-enemy interactions are often embedded in rich communities of multiple interacting pests and natural enemies and the interactions among these species affect the efficacy of biological pest control (Sih et al, 1985; Janssen et al, 1998; Prasad & Snyder, 2006; Evans, 2008). The effect of interactions among various species of predators and parasitoids on biological control of a shared pest species has received ample attention (see Letourneau et al., 2009), showing that it can range from larger to smaller than the effect of each enemy species separately (Rosenheim et al., 1995; Rosenheim et al., 1998; Losey and Denno, 1998; Colfer & Rosenheim, 2001; Venzon et al., 2001; Cardinale et al., 2003; Snyder & Ives, 2001, 2003; Finke & Denno, 2004; Cakmak et al., 2009). However, it is not only predator diversity, but also the diversity of herbivorous prey that may affect the suppression of a particular pest species through competition or indirect interactions mediated by host plant or shared predators (Holt,1977; Karban & Carey, 1984). Hence, designing effective biological control programs for more than one pest species requires an understanding of all interactions occurring among species within biocontrol communities, not just those among pests and their natural enemies or among different species of natural enemies.

Greenhouse crops are often considered as simple ecosystems with low biodiversity (Enkegaard & Brødsgaard, 2006). Especially modern greenhouses appear sterile compared to outdoor crops, as plants are grown on hydroponic systems in greenhouses that are closed from the environment because of modern energy saving techniques (Bakker, 2008). However, the general experience is that infestations by several small pest species cannot be avoided, and the release of natural enemies against these pests adds to the diversity (van Lenteren et al., 2000; Cock et al., 2010). Thus, apparently "clean" greenhouse crops often accommodate complex artificial communities of multiple pests and natural enemies. Furthermore, there seems to be a tendency that these communities increase in food web complexity during the last decades (Enkegaard & Brødsgaard, 2006). One reason for this increased diversity is the invasion of exotic pest species (global trade, global warming) (Roques et al., 2009). Second, more species than before develop into pests as a result of the reduced use of pesticides and the use of more selective pesticides (van der Blom et al., 2009). A third reason is that biological control programs increasingly include generalist predators (Gerson & Weintraub, 2007; Sabelis et al., 2008), and such generalists potentially interfere more with other natural enemies than specialists. Thus, recent developments further increase food web complexity in biological control programs and emphasize that such complexities need to be considered when designing biological control programs.

Here, we review the ecological theory relevant to interactions in food webs occurring within arthropod communities and we discuss the possible implications for biological control in greenhouses. This review is restricted to the most important greenhouse pests, namely aphids (Ramakers, 1989; Blümel, 2004), thrips (Lewis, 1997; Shipp and Ramakers, 2004), spider mites (Helle & Sabelis, 1995; Gillespie & Raworth, 2004) and whiteflies (Byrne & Bellows, 1991; Avilla et al., 2004), and their natural enemies.

2. Food web theory and effects in greenhouse crops

Consumption (i.e. herbivory, predation and parasitism) and competition are considered the two most important interactions determining the structure of communities (Chase et al., 2002). Within communities of natural enemies and pests, species may interact through exploitative competition, induced plant defences, apparent competition or apparent mutualism via shared natural enemies, or through predation and parasitism, which includes omnivory, intraguild predation and hyperpredation or hyperparasitism (Fig. 1). Besides these density-mediated interactions, species interactions can be modified through trait changes of the interacting individuals (which includes changes in behaviour and induced plant responses). In the following, we summarize the current theory on these interactions and their relevance for biological control.

2.1 Exploitative competition and induced plant responses

Herbivores can interact through exploitative competition for the plant (Fig. 1), but this is undesirable for biological control, because it occurs at high pest densities, which may exceed the economic damage threshold. We will therefore refrain from discussing resource competition among herbivores here. Herbivores can also interact via the plant when the presence of one species induces a defence response in the plant that also affects a second species (Karban & Carey, 1984). These plant responses can both result in increased resistance or increased susceptibility (e.g. Karban & Baldwin, 1997; Sarmento et al., 2011). Induced plant resistance against insects consists of direct defences, such as the production of toxins and feeding deterrents that reduce survival, fecundity or reduce developmental rate (Kessler & Baldwin, 2002), and indirect defences such as the production of plant volatiles that attract carnivorous enemies of the herbivores (Dicke and Sabelis, 1988; Schaller, 2008). Several biochemical pathways are involved in these processes (Walling, 2000). Recent studies have shown that plant-mediated interactions between herbivores are very common and could be important in structuring herbivore communities (Kessler et al., 2007). Models of interactions that are mediated by inducible changes in plant quality predict a range of outcomes including coexistence, multiple equilibria, dependence on initial conditions and competitive exclusion of some herbivore species (Anderson et al., 2009). However, these models assume that herbivore populations are well mixed and possible variation in induction caused by variation in population densities is ignored.

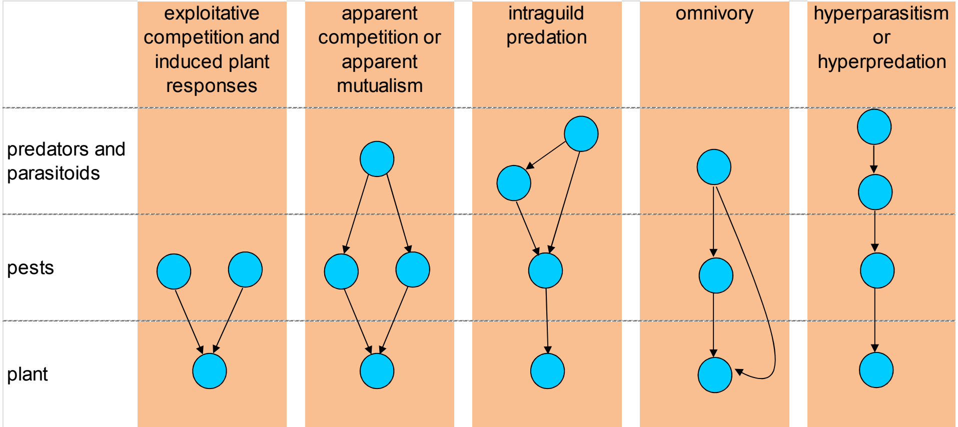

Fig. 1. Schematic diagrams of the direct and indirect interactions among plants, pests and natural enemies that will be treated in this chapter. Arrows indicate consumption. From left to right: *exploitative competition*: two pest species compete for the same plant, but also affect each other's densities through induced plant defences; *apparent competition or apparent mutualism*: indirect interactions between two prey species mediated by a shared natural enemy (with pests on the same plants this automatically includes exploitative competition and induced plant defences); *intraguild predation*: predators consume another natural enemy with whom they also compete for the same pest species; *omnivory*: consumption of species from more than one trophic level, "true" omnivores are predators that feed on both pests and plants; *hyperparasitism or hyperpredation*: the consumption of natural enemies by other natural enemies with whom they do not compete for shared prey, but they differ by the fact that hyperpredators can develop on alternative prey, whereas true hyperparasitoids are obligate. Except for induced plant responses, these interactions are density mediated.

Several studies documented indirect interactions between herbivores through induced changes in plant quality (Karban & Baldwin 1997), but studies on greenhouse crops are limited. In tomato, it has been demonstrated that infestations by caterpillars of a noctuid moth increased resistance to spider mites, aphids and another lepidopteran pest (Stout et al., 1998). Likewise, infestations by whiteflies induced resistance against leafminers (Inbar et al., 1999). Similar results were found on cucumber (Zhang et al., 2005). Induced susceptibility may also occur, for example, infestations of tomato plants by whiteflies increased susceptibility to aphids (Nombela et al., 2008). On lima bean, similar results were found for whiteflies and spider mites (Zhang et al., 2009). The spider mite *Tetranychus evansi* Baker & Pritchard was found to down-regulate plant defences (Sarmento et al., 2011), and the closely related species *Tetranychus urticae* Koch can profit from this induced susceptibility (Sarmento et al. in press). Induced resistance may also affect the behaviour of omnivores that facultatively feed on plants. The omnivorous western flower thrips switched from feeding on the host plant to feeding on spider mite eggs when defences of the plants were induced (Agrawal et al., 1999). Moreover, they performed worse on eggs of spider mites from induced plants than on eggs from spider mites on non-induced plants (Agrawal & Klein, 2000). In conclusion, plant-mediated interactions among pest species are probably a common phenomenon in greenhouse crops, where they may influence the biological control of multiple pests.

2.2 Apparent competition and apparent mutualism

Generalist predators can mediate indirect interactions among prey species that might otherwise not interact (Holt & Lawton 1994; Janssen et al., 1998; Harmon & Andow 2004; van Veen et al., 2006) (Figure 1). If, for example, the density of one prey species increases, the density of the shared predator subsequently increases and ultimately, the second prey species decreases in abundance. Holt (1977) suggested the term "apparent competition" for this interaction between prey, because the dynamics of the two species resemble that of species competing for resources, whereas in fact it is mediated by the shared predator. Apparent competition is usually defined as a reciprocal negative interaction between prey, but most empirical studies show non-reciprocal indirect interactions (Chaneton & Bonsall, 2000). Hence, only one of the two prey species is negatively affected by the predator-mediated prey interaction. Originally, the theory of apparent competition considered equilibrium densities. However, generalist predators can also cause "short-term" apparent competition between prey species when predators aggregate in habitat patches containing both prey, or when their feeding rate on one prey is enhanced by the presence of another prey (Holt & Kotler 1987, Müller and Godfray 1997).

The opposite effect may also occur between two prey that share a natural enemy, i.e. a positive indirect effect of one prey population on densities of the other (apparent mutualism). This occurs when increases in the density of one prey species result in satiation of the shared predator or in predator switching (when a predator eats disproportionately more of the most common type of prey), consequently reducing the consumption of the second prey species (Murdoch 1969; Abrams & Matsuda 1996). This effect is apparent in the short-term, when the densities have not yet reached an equilibrium (transient dynamics), because eventually, the predator populations will increase because of the higher densities of prey (Abrams & Matsuda 1996) and result in apparent competition. Apparent mutualism may also occur in the long term when population densities do not reach equilibria, but show cycles, resulting in repeated satiation of the shared predators and repeated reduced predation on the other prey (Abrams et al., 1998). Hence, depending on the time scale and on the type of dynamics, theory predicts that a shared natural enemy can generate positive or negative indirect effects between prey species.

Apparent competition and apparent mutualism are inherently related to diet choice and switching of the predators from feeding on one prey to feeding on the other or both prey, but effects of mixed diets on predator performance are also relevant. Mixed diets are known to have positive effects on reproduction in some predator species (Wallin et al., 1992; Toft 1999; Evans et al., 1999).

When generalist predators are released in greenhouse crops, pest species such as thrips, whiteflies, spider mites and aphids can be involved in apparent competition or apparent mutualism. Examples of such generalist predators are anthocorid and mirid bugs and several species of predatory mites. For example, the predatory mite *Amblyseius swirskii* Athias–Henriot is able to control both whiteflies and thrips effectively (Nomikou et al., 2002; Messelink et al., 2006). On greenhouse cucumber, it has indeed been shown this predator mediates apparent competition between the two pests: whitefly control was substantially better in the presence of thrips (Messelink et al., 2008). Moreover, better pest control was also achieved by positive effects of a mixed diet of thrips and whiteflies on juvenile survival and developmental rate (Messelink et al., 2008). So far, this aspect of mixed diets has been ignored in theoretical models about apparent competition. Not only whiteflies, but also spider mites were controlled better by the presence of thrips through apparent competition (Messelink et al., 2010). Although *A. swirskii* is not an effective predator of spider mites because it is strongly hindered by the webbing, it can prevent the formation of new colonies of spider mites when there are other prey, such as thrips, available. Thus, generalist predators can even have significant effects on prey species which they cannot suppress successfully on their own.

Although the theory of predator-mediated interactions has long been neglected in biological control, there has been a long-standing interest in the use of alternative hosts for enhancing biological control (Stacy, 1977). The method by which these alternative hosts are facilitated is based on the introduction of a non-crop plant harbouring the alternative hosts. It is often referred to as the “banker plant method” (Frank, 2010; Huang et al., 2011). A widely applied system in greenhouse crops is the use of monocotyledonous plants with grain aphids that serve as alternative hosts for parasitoids of aphids that attack the crop (Huang et al., 2011). The elegance of this system is that the grain aphids are host-specific and pose no threat to the crop. Another method is based on banker plants that provide pollen to generalist predators (Ramakers & Voet, 1995). For example, pollen can serve as food for generalist predatory mites and enhance the biological control of thrips and whiteflies (van Rijn et al., 2002; Nomikou et al., 2010). In fact, all kinds of “open rearing” systems of natural enemies in greenhouse crops (e.g. rearing sachets containing small cultures of predatory mites, bran and an astigmatic mites) are based on the principles of apparent competition, but there is little awareness that apparent mutualism may also occur.

2.3 Intraguild predation

Natural enemies can compete for the same prey species, but this is frequently combined with predation by one species of natural enemy on another (Rosenheim et al., 1995), which is called intraguild predation (IGP, Figure 1). The predator that kills and eats the other natural enemy is called the intraguild predator and the other natural enemy is the intraguild prey (Polis et al., 1989; Holt and Polis 1997). General theory predicts that IGP can only result in stable coexistence of the species when the intraguild prey is the superior competitor for the shared prey, and only in systems with intermediate levels of productivity (Holt and Polis 1997). These conditions are very restrictive and thus predict that IGP is not common in nature. However, it has become clear that IGP generally occurs in many ecosystems, including in biological control systems (Polis et al., 1989; Rosenheim et al., 1995, Janssen et al. 2006, 2007). There may be several reasons for this discrepancy between theory, predicting that systems with strong IGP will be rare, and reality, where IGP is common. Factors that can contribute to the coexistence of intraguild predators and intraguild prey are now increasingly included in theoretical models. Examples of such factors are structured populations with intraguild prey stages that are invulnerable or intraguild predator stages that do not prey on the other predator (Mylius et al., 2001), anti-predator behaviour (Heithaus, 2001), switching intraguild predators (Krivan, 2000) or alternative prey (Daugherty et al., 2007; Holt & Huxel, 2007). Based on theory, intraguild predation is expected not to benefit biological control (Rosenheim et al., 1995), but in practice, results are mixed (Janssen et al., 2006; 2007; Vance-Chalcraft et al., 2007).

Intraguild predation has been described for many natural enemies that are used for biological control in greenhouse crops (Rosenheim et al. 1995; Janssen et al., 2006). Here, we summarize the results for natural enemies of thrips, whiteflies, aphids and spider mites. The omnivorous predator *Macrolophus pygmaeus* (Rambur) (formely identified as *Macrolophus caliginosus* Wagner) is an intraguild predator of natural enemies of aphids; it consumes the eggs of the syrphid *Episyrphus balteatus* de Geer (Frechette et al., 2007) and parasitized aphids (Martinou, 2005). This predator did not prey on nymphal stages of *Orius majusculus* (Reuter), but in turn, the nymphal stages of *M. pygmaeus* were vulnerable for predation by *O. majusculus* (Jakobsen et al., 2004). Predatory bugs of the genus *Orius* act as intraguild predators of phytoseiid mites (Gillespie & Quiring, 1992; Venzon et al., 2001; Brødsgaard & Enkegaard, 2005; Chow et al., 2008), the aphidophagous predatory midge *Aphidoletes aphidimyza* (Rondani) (Hosseini et al., 2010) and aphid parasitoids (Snyder & Ives, 2003). Many generalist predatory mites are intraguild predators of other predatory mites (Schausberger & Walzer, 2001; Buitenhuis et al., 2010; Montserrat et al., 2008; Van der Hammen et al., 2010) or juvenile stages of predatory bugs (Madali et al., 2008). Finally, a number of studies show intraguild predation among specialist natural enemies of aphids. The syrphid *E. balteatus* feeds on freshly parasitized as well as unparasitized aphids (Brodeur & Rosenheim, 2000). Syrphid larvae may also consume the aphidophageous gall midge *A. aphidimyza*, but predation rates are low in the presence of aphids (Hindayana et al., 2001). In turn, this midge does not prey on *E. balteatus* (Hindayana et al., 2001), but may consume parasitized aphids (Brodeur & Rosenheim, 2000).

None of these studies demonstrates a negative effect of intraguild predation on biological control in greenhouse crops. Although the potential risk of intraguild predation disrupting biological control appears to be low in many cases (Janssen et al., 2006), there are also examples of negative effects of intraguild predation on biological control.

2.4 Omnivory

Omnivory in its broadest sense can be defined as the consumption of species of more than one trophic level. Under this definition, intraguild predators are also omnivores. Predators that feed on both animals and plants are a particular case of trophic omnivory, also referred to as “true omnivory” (Coll & Guershon, 2002). The first theoretical models on its dynamical consequences showed that omnivory destabilizes food webs (Pimm & Lawton, 1978), which is remarkable, considering the fact that omnivory is a common feature of food webs (Coll & Guershon, 2002, Polis & Strong, 1996). More specific theory for plant-feeding omnivores shows that omnivores can stabilize the dynamics and persistence of populations by switching between consuming plants and prey, especially when the searching efficiency of the predator for prey is low relative to that for plant tissue (Lalonde et al., 1999). Hence, this theory suggests that biological control with plant-feeding omnivores may stabilize pest population dynamics. The question is, whether these equilibrium densities are acceptable for pest control (Lalonde et al., 1999). Other aspects of plant-feeding omnivory, such as the persistence of predators in the absence of prey, or the nutritional benefits for predators of feeding on plants may also result in positive contributions to biological control.

Many predators that are used for biological control are true omnivores, feeding on pests and plant-provided food such as pollen, nectar and plant saps. For example, many generalist predatory mites and bugs can complete their life cycle feeding on pollen. However, not all greenhouse crops produce pollen (e.g. male-sterile cucumber) or edible pollen, but some omnivores, such as the mirid bug *M. pygmaeus*, can also live and reproduce on plant saps. Although considered as a pest species, western flower thrips, *Frankliniella occidentalis* (Pergande) are in fact omnivorous predators that feed on spider mites, predatory mites, whiteflies and plants (Trichilo & Leigh, 1986; Faraji et al., 2001; Janssen et al., 2003, van Maanen et al., in prep.). The consumption of prey in addition to plant material by mirid bugs and thrips can increase reproduction rates (Janssen et al., 2003; Perdikis & Lykouressis, 2004). The quality of the host plant can affect the predation rates of omnivores on pests (Agrawal et al., 1999; Agrawal & Klein, 2000; Magalhães et al., 2005; Hatherly et al., 2009) or the extent to which intraguild predation occurs (Janssen et al., 2003, Shakiya et al., 2009). Thus for biological control with predators that can also feed on the plant, it is important to known that the dynamics will be affected by plant quality.

2.5 Hyperpredation and hyperparasitism

In contrast to intraguild predation, natural enemies can also be consumed by other predators or parasitoids without sharing a prey with these enemies. Thus there is no competition for prey between the natural enemies. This consumption is well known for parasitoids, so-called hyperparasitism. Hyperparasitism is well-studied for its dynamical consequences, both theoretically (Beddington & Hammond, 1977; May & Hassell, 1981) and empirically (Sullivan & Völkl, 1999). These studies indicate that obligate hyperparasitoids (secondary parasitoids that can develop only in or on a primary parasitoid) always lead to an increase of the pest equilibria, which might be detrimental to biological control. In case the hyperpredator is a true predator, there is no agreement in the literature on the name of this type of interaction. Some prefer to use the term “secondary predation” (Rosenheim et al., 1995), or “higher-order predation” (Rosenheim, 1998; Symondson, 2002) for predators consuming other predators, which includes both hyperpredation and intraguild predation. Even more confusing is that some interactions are described as hyperpredation, whereas it would be more consistent to typify them as apparent competition (e.g. Courchamp et al., 2000; Roemer et al., 2001) or intraguild predation (e.g. Roemer et al., 2002). We suggest to use the term hyperpredation in cases where predators eat other predators without sharing a prey, because of its similarity to hyperparasitism. However, an important difference is that hyperpredators can develop on alternative prey or food, whereas most hyperparasitoids specifically reproduce on or in other parasitoids. In the presence of alternative prey, hyperpredation can be classified as apparent competition between the alternative prey and the specialist natural enemy. To our knowledge, no specific theory has been formulated on the effects of hyperpredation on prey populations in the presence of alternative prey. Theory on apparent competition predicts that the presence of one prey lowers the equilibrium densities of the second prey. For hyperpredation, this would mean that increases in the densities of the alternative prey will results in lower equilibrium densities of the specialist natural enemy, which would consequently release the prey of the specialist from control. In the short-term, satiation effects of the hyperpredator might result in apparent mutualism between the alternative prey and the specialist natural enemy, hence, a reduced negative effect on pest control by the specialist natural enemy.

In greenhouse crops, predatory mites that are used for control of thrips and whiteflies have been observed to be hyperpredators. They feed on eggs of predatory midge *A. aphidimyza*, but not on aphids, the pest that is controlled by predatory larvae of midges (Messelink et al., 2011). In sweet pepper, the biological control of aphids by *A. aphidimyza* was seriously disrupted through this hyperpredation by the predatory mite *A. swirskii* (Messelink et al., 2011). Hyperparasitism is common in the biological control of aphids in greenhouses and can also disrupt biological control (Messelink, personal observations).

2.6 Effect of flexible behaviour

The interactions in food webs described above all concern density-mediated interactions among species. However, it is generally recognized that traits of individuals, such as behaviour or defence levels, can change in response to the presence of individuals of other species (so-called trait-mediated interactions, Werner & Peacor, 2003). For example, anti-predator behaviour, can strengthen or weaken density-mediated effects (Prasad & Snyder, 2006; Janssen et al., 2007). Many of these behavioural changes are mediated by chemical cues, which are released or left behind by both natural enemies and prey (Dicke & Grostal, 2001). Theoretical models of community dynamics now increasingly try to study the consequences of these behavioural-mediated interactions (e.g. Holt & Kotler, 1987; Abrams, 2008). These models show that the effects of such interactions may change the dynamics substantially.

Many interactions among natural enemies and pests in greenhouses can be affected by changes in the behaviour of pest and natural enemy. First of all, it is known that pest species can avoid their enemies. For example, whiteflies can learn to avoid plants with generalist predatory mites (Nomikou et al., 2003) and spider mites avoid plants with the predator *Phytoseiulus persimilis* Athias-Henriot (Pallini et al., 1999) or with thrips, which is a competitor and intraguild predator (Pallini et al., 1997). Aphids are well-known for their antipredator responses, for example, they kick at natural enemies, or they walk away or drop off the plants when perceiving a natural enemy (Villagra et al., 2006). Aphids as well as thrips release alarm pheromones that alert conspecifics (Bowers et al., 1972; Teerling et al., 1993; de Bruijn et al. 2006). Thrips can avoid predation by predatory bugs and predatory mites by using spider mite webbing as a refuge (Pallini et al. 1998; Venzon et al. 2000). They can defend themselves against predators by swinging with their abdomen and producing defensive droplets (Bakker & Sabelis, 1989), or even by counter-attacking the vulnerable egg stages of their phytoseiid predators (Faraji et al., 2001, Janssen et al. 2002). Natural enemies also respond to threats of other (intraguild) predators or counter-attacking prey. Predatory mites avoid ovipositing near counter-attacking thrips (Faraji et al., 2001) or intraguild predators (Choh et al., 2010, van der Hammen et al., 2010), or retain eggs in the presence of intraguild predators (Montserrat et al., 2007). Aphid parasitoids are known to avoid intraguild predation once they detect the chemical cues of their predators (Nakashima et al., 2006). The effects of intraguild predation can also be changed by the prey preference of the intraguild predator. For example, the syrphid *E. balteatus* is an intraguild predator of aphid parasitoids because it consumes parasitized aphids, but when given a choice, it prefers to oviposit in aphid colonies without parasitized aphids (Pineda et al., 2007), thus weakening the effects of intraguild predation.

Interactions among species may change over time through learning or experience (Nomikou et al., 2003). For example, the predatory bug *O. majusculus* was more successful at preying on aphids after learning how to avoid the prey's kicking response (Henaut et al., 2000). Furthermore, predation rates on a specific pest might change through the presence of alternative food: the predatory bug *O. laevigatus* increased the predation rates on thrips in the presence of pollen (Hulshof & Linnamäki, 2002). Thus somehow, the pollen seemed to stimulate the feeding behaviour of these predators. In contrast, the presence of unsuitable prey may reduce the efficacy of a natural enemy for the target pest. For example, studies with parasitoids demonstrated that spending foraging time or eggs on less-suitable hosts will decrease parasitoid foraging success and ultimately decrease parasitoid population size (Meisner et al., 2007). Such "distraction" effects may also occur in greenhouses when mixtures of aphid species are present in a crop. The reason why parasitoids attack unsuitable or marginal hosts in the study by Meisner et al. (2007) is not clear, perhaps the parasitoids and marginal hosts have not coevolved and there has been no selection on the parasitoid to discriminate between the marginal host and other host species. It is also possible that the parasitoids cannot assess host suitability as this may vary through the presence of symbiotic bacteria that induce resistance to parasitoids (Oliver et al., 2003). The examples presented above show that multiple prey effects can change the behaviour of shared natural enemies and may determine the outcomes of biological control.

Summarizing, changes in interactions or interaction strengths through flexible behaviour are common among the pests and natural enemies in greenhouse crops. Thus, when designing and interpreting results of multi-species experiments, it should be realized that both density-mediated interactions and behavioural mediated interactions affect biological control. The potential diversity and complexity of an artificial food web in a greenhouse vegetable crop is presented in the next section.

3. A case study: Food web complexity in sweet pepper

The complexities of arthropod communities associated with biocontrol systems vary among crops, because crops differ in susceptibility to pests species and suitability for natural enemies. Sweet pepper is one of the crops where the release of natural enemies for biological control has resulted a complex system of multiple pests and natural enemies, including several different species of generalist predators. The most important pests in sweet pepper in greenhouses in temperate regions are western flower thrips, *F. occidentalis*, two-spotted spider mites, *T. urticae* and aphids, mostly the green peach aphid, *Myzus persicae* (Sulzer) and the foxglove aphid *Aulacorthum solani* (Kaltenbach) (Ramakers, 2004), whereas in Mediterranean countries, one of the major pest species is the tobacco whitefly, *Bemisia tabaci* Gennadius (Calvo et al., 2009). Many other pest species can attack sweet pepper, such as caterpillars of noctuid moths, broad mites, leaf miners and mirid bugs, but they are less important (Ramakers, 2004).

Anthocorid bugs are commonly used as generalist predators in sweet pepper. *Orius laevigatus* (Fieber) is most used in Europe, *O. insidiosus* (Reuter) in Northern America (Brødsgaard, 2004; Shipp and Ramakers, 2004). Although anthocorid bugs are mainly released for thrips control, they can also contribute to the control of whiteflies (Arnó et al., 2008), aphids (Alvarado et al., 1997), and spider mites (Venzon et al., 2002). The omnivorous predator *M. pygmaeus* is also released often, and is know to suppress whiteflies (Gerling et al., 2001), aphids (Alvarado et al., 1997), thrips (Riudavets & Castañé, 1998) and spider mites (Hansen et al., 1999). Finally, generalist predatory mites are commonly released in sweet pepper. The first releases started with the phytoseiid *Neoseiulus barkeri* (Hughes) (= *Amblyseius mckenziei*) for the control of thrips (Ramakers, 1980). Since then, several other phytoseiids, such as *Neoseiulus cucumeris* (Oudemans) or *Iphiseius degenerans* (Berlese), are released in sweet pepper (Ramakers, 2004). Nowadays, *A. swirskii* is a very popular species, because this predatory mite not only controls thrips (Messelink et al., 2006), but also whiteflies (Nomikou et al., 2002; Calvo et al., 2009), broad mites (van Maanen et al. 2010) and it can contribute to the control of spider mites (Messelink et al., 2010). Populations of both generalist predatory bugs and predatory mites can establish in sweet pepper crops even when prey is scarce, because of the continuous presence of flowers that produce pollen (Ramakers, 1980; Van den Meiracker & Ramakers, 1991).

Specialist predators released in sweet pepper crops are the predatory mite *P. persimilis* against spider-mites (Gillespie & Raworth, 2004), and the aphidophagous predators *A. aphidimyza* and *E. balteatus* (Ramakers, 1989; Blümel, 2004) against aphids. Furthermore, several specialist parasitoids are released: for aphids mainly *Aphidius colemani* Viereck, *Aphidius ervi* Haliday or *Aphelinus abdominalis* Dalman and for whiteflies mainly *Eretmocerus mundus* Mercet and *Er. eremicus* Rose & Zolnerowich (Cock et al., 2010).

The simultaneous occurrence and need to control several pest species in sweet pepper results in a complex food web of interacting species (Fig. 2). The presence of western flower thrips in this food web contributes strongly to the complexity. Although *F. occidentalis* is primarily considered a phytophagous species that feeds on plant tissue, plant nectar or pollen, it is actually an omnivore, feeding facultatively on spider mite eggs (Trichilo & Leigh, 1986), predatory mite eggs (Faraji et al., 2001; Janssen et al., 2003), or on whitefly crawlers (van Maanen et al., in prep.).

The food web presented in Figure 2 shows that the interactions between a certain pest and its natural enemy are often embedded in a complex web of interactions. For example, intraguild predation is often accompanied by apparent competition between the intraguild prey and several other alternative prey species. Furthermore, the intraguild predators or hyperpredators can also feed on plant-provided food, with the result that plant quality may affect intraguild predation or hyperpredation (Agrawal & Klein, 2000; Janssen et al., 2003). This emphasizes the complexity of biological control, where effects of some interactions may override the effects other interactions (Polis & Holt, 1989). Thus, the study of particular species interactions, such as those between a pest and its natural enemy, should be embedded in empirical studies and models that capture the essence of realistic food webs. Although it may be difficult to disentangle all possible interactions and their importance for biological control, the understanding of such interactions will help in designing effective communities of natural enemies for the suppression of multiple pests.

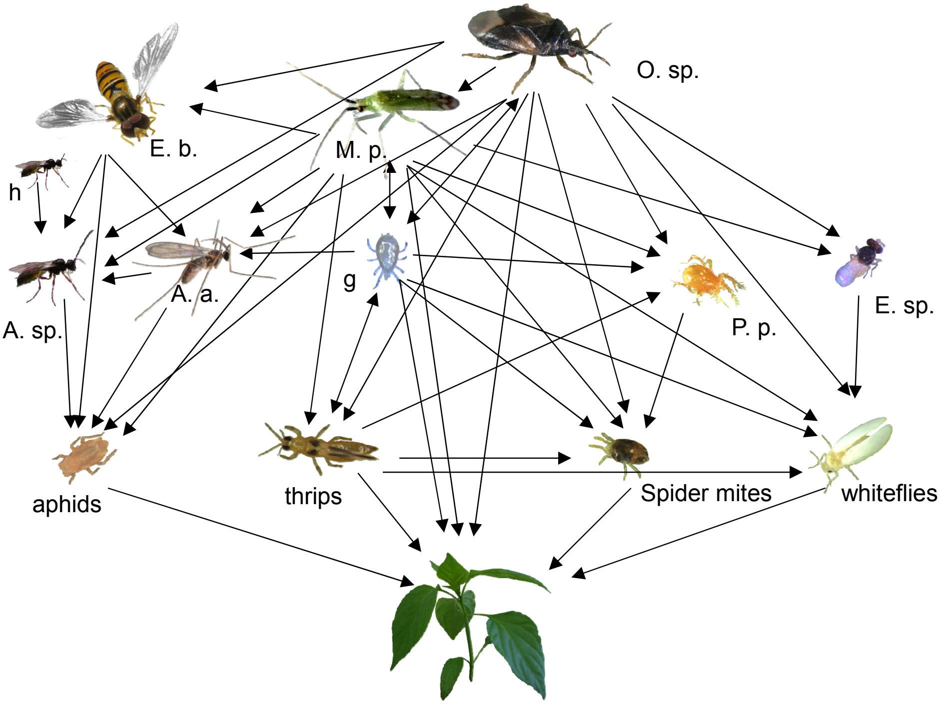

Fig. 2. A food web of pest species and their most commonly used natural enemies in sweet pepper crops. The generalist predators are bugs from the genus *Orius* (O. sp.), the mirid bug *Macrolophus pygmaeus* (M. p.) and generalist phytoseiid predatory mites (g). Specialist enemies of aphids are parasitoids from the genus *Aphidius* (A. sp.), the predatory midge *Aphidoletes aphidimyza* (A.a.) and the syrphid *Episyrphus balteatus* (E.b.). Parasitoids are commonly attacked by several species of hyperparasitoids (h). The specialist predator of spider mites is *Phytoseiulus persimilis* (P.p.). The main whitefly species in sweet pepper is *Bemisia tabaci*, which can be controlled by specialist whitefly parasitoids from the genus *Eretmocerus* (E. sp.).

4. Conclusions

Food web theory can provide insight into how various interactions between species might affect species dynamics and their possible effects on biological control. However, since models are necessarily based on simplifying assumptions, theoretical predictions are bound to differ from empirical studies (e.g. Janssen et al., 2006; Rosenheim & Harmon, 2006). For example, theory often predicts equilibrium dynamics, whereas biological control systems often concern short-term (transient) dynamics, which might differ from long-term dynamics (Bolker et al., 2003; Briggs & Borer, 2005). A second reason is that real food webs are much more complex than theoretical models assume (Rosenheim et al, 1995; May, 1999, Coll & Guershon, 2002; Bolker et al., 2003; Cardinale et al., 2003; Janssen et al., 2006, 2007; Letourneau et al., 2009). The presence of multiple pests and natural enemies will result in joint effects of several types of interactions, and there is limited theory that takes such complexity into account. Although theory is increasingly extended with aspects such as anti-predator behaviour (Heithaus, 2001), predator switching (Krivian (2000) or alternative prey (Holt & Huxel, 2007), there is still a large gap between theory and practice. Theory might be further extended by connecting different types of interactions, such as omnivory and apparent competition between prey. We further recommend to implement effects of mixed diets in the theory of apparent competition. Furthermore, no specific theory exists on hyperpredation in the presence of alternative prey. Greenhouse crops are ideally suited to test theoretical predictions, because artificially created communities in biocontrol systems can easily be manipulated. Similarly, such greenhouse experiments could give insight into short-term dynamics of interactions for which more theory is needed since current theory focuses on what happens in or near equilibrium states (Briggs & Borer, 2005).

This review shows that both density-mediated interactions and behaviour-mediated interactions are common in greenhouse crops and affect the results of biological control. Especially the use of generalist predators may give rise to several types of interactions and food web complexity. Generalist predators were long considered as less effective than specialist natural enemies (Huffaker & Messenger, 1976; Hokkanen & Pimentel, 1984; Van Lenteren & Woets, 1988; Hoy, 1994). Moreover, recent criteria for risk assessments of natural enemies consider generalist predators as less desirable than specialist natural enemies (van Lenteren et al., 2006). However, several studies show that generalists can be effective control agents, especially because populations of generalists can be established easily (Messelink et al., 2010). The role of generalist predators was recognized earlier by Murdoch et al. (1985), who argued that the biggest advantage of generalist predators is their persistence in systems (see also Chang & Kareiva, 1999; Symondson et al., 2002). In contrast, augmentative releases of specialist natural enemies often involve problems with timing, costs and quality (Bloemhard & Ramakers, 2008). Generalist predators can establish into crops prior to pest infestations, which makes the system resilient to pest invasions. Moreover, growers need to respond less to infestations with pest species. In the near future, we expect that biological control systems in greenhouses will increasingly shift from augmentative releases of specialist natural enemies to inoculative releases of generalist predators. For example, whitefly control was mainly based on releases of specialist parasitoids for decades (van Lenteren & Woets, 1988; Avilla et al., 2004). This has changed since the introduction of generalist predatory bugs and predatory mites that also feed on whiteflies. This has been so successful in some crops that most, if not all, biological control is done by means of generalist predators (Messelink, personal observations). Thrips control has a long tradition of using generalist predators, and in crops such as sweet pepper, these predators are very effective (Ramakers, 2004). So far, biological control of aphids is mainly based on frequent releases of specialist natural enemies such as parasitoids and predatory midges (Ramakers, 1989; Blümel, 2004), which is expensive and often not successful (Bloemhard & Ramakers, 2008). Recent experiments showed that inoculative releases of the generalist predator *M. pygmaeus* can also effectively control aphids in sweet pepper (Messelink, 2011). Hence, we expect that future control of aphids and other pests will increasingly be based on generalist predators. In general, we suggest that generalist predators deserve more attention in biological control programs for greenhouse crops.

An interesting aspect of using generalist predators is that pest control strongly depends on the diversity of pests in the crop (see paragraph 2.2). The fact that a mixture of two pests can increase the survival and developmental rate of a generalist predator offers new opportunities to enhance pest control by optimizing the diet for predators. Because many crops do not or hardly provide food for generalist predators, it may be possible to add food that is supplemental to the diet of a certain natural enemy species. Research should furthermore focus on ways to enhance establishment of generalist predators by offering alternative prey in open rearing systems or banker plant systems (Huang et al., 2011), by food sprays (Wade et al., 2008), or by selecting plants that provide food or shelter in the crop (Wäckers et al., 2005). Finally, it is desirable that future research focuses on selecting predators that are adapted to important crops and perform well on the pests and food sources present in these crops, rather than selecting natural enemies for any particular pest species.

Finally, we conclude that it is important to consider all possible interactions among species in arthropod food webs in order to detect interactions that are potentially detrimental or beneficial for biological control. Detrimental effects can mainly be expected from hyperpredators or hyperparasitoids, and, in theory, IGP can also disrupt biological control. Furthermore, apparent mutualism may be negative for pest control. Hence, it is clear that the results of biological control of a particular pest species may be negatively affected by the presence of other pests or natural enemies. However, this review also showed many examples of plant-mediated and predator-mediated interactions that are beneficial for pest control. Future research should focus on more complementarity and synergy among natural enemies. The literature provides interesting examples of such interactions based on predator facilitation (Losey & Denno, 1998), pest stage complementarity (Calvo et al., 2009) or microhabitat complementarity (Onzo et al., 2004).

Nowadays, there are unique possibilities to manipulate communities of natural enemies by choosing from several species that are commercially available (van Lenteren, 2000; Enkegaard & Brødsgaard, 2006). Thus, biodiversity can be created and manipulated to maximise sustainable pest control. At the same time, such systems can be used to study the manipulation of biodiversity on the dynamics of communities of plant-inhabiting arthropods under relatively controlled conditions and at larger spatial scales than can usually be realized with communities under field conditions. Based on the abundance, diversity and potential risk of pest species, it is possible to adapt the strategies of natural enemy releases. In conclusion, greenhouse experiments that evaluate multiple pest control with diverse assemblages of natural enemies are not only needed to further develop biological control strategies, but also offer excellent opportunities to test and extend theories on multispecies interactions.

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