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# **Aromatic plants of East Asia to enhance natural enemies towards biological control of insect pests. A review**

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## **Abstract**

Introducing flowering plants in fields may attract and benefit predators and parasitoids of insect pests and potentially enhance biological control. Through a vote counting analysis, the present review aims at evaluating whether aromatic plants of East Asia could be used in this purpose. A systematic search of the scientific literature was conducted and 64 papers published worldwide were identified, considering 32 aromatic plant species. A significant number of studies reported that Apiaceae aromatic plants attract and benefit insect predators. Constrasting results were found for parasitoids, as well as with plant species from other families (mostly Asteraceae and Lamiaceae). These results are discussed by considering plant and insect traits. Moreover, there are not a significant number of studies reporting an enhancement of biological control in crop or fruit trees adjacent to aromatic plants. However, the number of studies was limited, highlighting the need for further field-based research in various types of agricultural landscapes.

**Keywords:** Syrphidae; Coccinellidae; Chrysopidae; parasitoid; nectar; pollen; volatile; functional trait; intercropping; insectary plant

## **1. Introduction**

Simplification of agricultural landscape and high in-field management intensity are major causes of biodiversity loss in farmed environment (Bengtsson et al. 2005; Gamez-Virués et al. 2015) and may consequently be responsible for disturbances in ecosystem functioning (Tschamtké et al. 2005; Cardinale et al. 2012). Hence, there is a rising interest for increasing plant diversity in agroecosystems to enhance the delivery of multiple ecosystem services, among others the natural regulation of insect pests by their natural enemies (i.e., predators, parasitoids) (Hatt et al. 2018; Muneret et al. 2018). At the farm scale, mixing crops (i.e., intercropping), crop with non-crop plants (i.e., cover cropping) and introducing trees (i.e., agroforestry) are practices to increase plant diversity within fields (Malézieux et al. 2009; Médiène et al. 2011). Additionally, semi-natural habitats can be managed at field margins by sowing wildflower strips, planting hedgerows and maintaining woodlots (Holland et al. 2016; Uyttenbroeck et al. 2016). Increasing plant diversity at the local scale is recognized to support populations of natural enemies while reducing the abundance of insect pests and their damages to crops (Letourneau et al. 2011). A reason is that spatial diversification would offer shelters and food resources to natural enemies (Gurr et al. 2017). Especially, several natural enemies are flower visitors which feed on pollen and nectar to enhance their longevity and fecundity (Wäckers and Van Rijn 2012). Nevertheless, simply sowing flowering plants may not support natural enemies. Flowering plants must be attractive (Farré-Armengol et al. 2013), bloom at the time when natural enemies need their resources (Fiedler and Landis 2007), these resources must be accessible (Van Rijn and Wäckers 2016) and be of high nutritional quality (Lu et al. 2014). Hence, interest for trait-based studies have arose in order to understand how insects interact with plants with the aim of predicting ecosystem services delivery (Gardarin et al. 2018; Perovic et al. 2018).

In Europe, the agri-environmental policy subsidizes the sowing of wild flower species in fields or at field margins to conserve insects (Haaland et al. 2011). Additionally research, also conducted in North America and New Zealand, assessed the ability of flowering strips to enhance natural enemies towards biological control of insect pests (Berndt et al. 2006; Blaauw and Isaacs 2015; Tschumi et al. 2016; Hatt et al. 2017a, 2017b). In East Asia, agri-environmental policies are scarcer but being developed these last years (Nomura et al. 2013; Zhang et al. 2015). However in China notably, the pressure on land for producing enough biomass for a very large population may hinder dedicating productive arable lands to plants that are not consumed (Liu et al. 2013). Meanwhile in these regions, small scale farming associated with very biodiverse landscapes has a long tradition. In China, terraces, multi-layers home gardens, as well as intercropping and agroforestry systems, have shaped agricultural landscapes through time (Min and He 2014). In Japan, the traditional *satoyama* agricultural landscape 'is composed of several habitat types, including paddy fields, secondary forests, secondary grasslands, ponds, and streams' (Kato et al. 2009) and intercropping has been a main agricultural practice to control pests in these landscapes before the adoption of chemical pesticides (McGreevy 2012). Finally, *Maeul* is the equivalent of such landscapes in Korea (Kim and Hong 2011). The modernization of agriculture from the mid-twentieth century has led to an important rural exodus and as a result, many of these agroecosystems have been gradually abandoned (McGreevy 2012). However, today's need of developing sustainable agricultural systems has renewed the interest for these managed landscapes and the ecosystem services they can deliver (Liu et al. 2013; Takeuchi et al. 2016; Wu et al. 2016), among others the support of natural enemies and the regulation of insect pests (Taki et al. 2013; Tabuchi et al. 2014). Some research specifically focused on how to manage plant diversity at the field/farm scale. A careful management of weeds in rice fields surrounded by wood patches was for example recommended to prevent the development of

mirid bugs (Hemiptera: Miridae) (Takada et al. 2012). Meanwhile nectar producing plants were introduced adjacent to rice fields to enhance the biological control of rice planthoppers (Hemiptera: Delphacidae) by parasitoids (Gurr et al. 2016). Nectar plants were selected in consultations with farmers, who—in the case reported from China—chose sesame *Sesamum indicum* (Pedaliaceae) and soybean *Glycine max* (Fabaceae) (i.e., setting intercropping systems based on economically viable flowering plants). In this same vein, flowering aromatic plants could be considered.

‘Aromatic plants’ is not a clearly botanically defined group of plants, but are commonly viewed as those plants cultivated and consumed for their chemical properties (i.e., phenolic acids, flavonoids and aromatic compounds like terpenoids, steroids, alkaloids and organic cyanides), providing them olfactory attributes used in food, medicine and plant protection (Schippmann et al. 2002; Gahukar 2012). These potential uses distinguish aromatic plants from other wildflower plants, in that they can provide economic benefits to farmers. However, could they also be used as insectary plants (i.e., ‘flowering plant which attracts and possibly maintains, with its nectar and pollen resources, a population of natural enemies which contribute to biological pest management on crops’, Parolin et al. 2012)? Because there is no specific definition of aromatic plants to our knowledge, aromatic plants have been identified from any other plants through a systematic search of published research that studied various properties of plants considered as being aromatic plants (see Methods).

By focussing on aromatic plants growing in East Asia, the aim of the present paper is to review the scientific literature published worldwide (not only in East Asia) which reported interactions between these aromatic plants and natural enemies of insect pests. More specifically, the present review aims at answering the following questions: what are the aromatic plant species that attract and benefit natural enemies, and enhance biological control of pests when sown in fields? Are there common trends among plant and insect families? Are

there differences between predators and parasitoids? A trait-based approach is proposed to discuss the reviewed results. This overview is expected to help practitioners to select the appropriate species to sow in fields and scientists to identify the needs for further research.

## 2. Methods

### 2.1 Systematic search of the literature

#### 2.1.1 Identification of aromatic plants

The search of literature was conducted by using Web of Science Core Collection (version 5.25.1). A first search was conducted on 6 October 2017 to identify the aromatic plants studied in East Asia. The following terms were used: ("aromatic plant\*" OR "aromatic herb\*" OR "aromatic tree" OR "aromatic shrub" OR "aromatic grass\*" OR "aromatic forb" OR "aromatic flower\*"). The search was restricted to studies from China, Taiwan, Korea and Japan by adding these countries/regions in the query and additional options allowed retrieving only peer-reviewed articles written in English. This search selected 158 papers and based on their abstracts, or in case of doubts the full papers, 190 aromatic plant species were identified (Tab. S1). Three additional aromatic species, known to grow in East Asia from our knowledge and personal observations, were added to the list: *Anethum graveolens* (L.) (Lamiaceae), *Calendula officinalis* (L.) (Asteraceae) and *Coriandrum sativum* (L.) (Lamiaceae).

#### 2.1.2 Identification of papers studying natural enemy - aromatic plant interactions

A second search was conducted on 11-12 October 2017 to identify the papers that studied interactions between the listed aromatic species and natural enemies of insect pests (i.e., predatory ladybeetles (Coleoptera: Coccinellidae), hoverflies (Diptera: Syrphidae), lacewings

(Neuroptera: Chrysopidae) and parasitoids). 193 queries were successively introduced by using the following terms: ["*aromatic species*" AND (coccinellid\* OR ladyb\* OR syrphid\* OR hoverfly OR chrysopidae OR lacewing OR "hymenopter\* wasp" OR parasitoid)], where '*aromatic species*' was one of the listed plants. Additional options allowed retrieving only peer-reviewed articles written in English. From these searches, 244 unique papers were obtained, to which nine relevant papers to our knowledge were added.

### *2.1.3 Selection of relevant papers*

From their abstracts, or in case of doubts the full papers, a selection was made based on the following criteria. First, papers had to be research articles. Review papers were excluded because they are based on other studies. Second, they had to assess a paired interaction between an aromatic plant and an insect natural enemy. Studies addressing for instance the effect of a plant on a natural enemy through its pest/prey-host (tritrophic interaction) were excluded. Indeed, pests/prey-hosts on plants can be responsible for herbivore induced plant volatiles that affect natural enemy behaviour (Zhu and Park 2005) whereas the present review aims at identifying aromatic insectary plants (i.e., directly enhancing natural enemies). Third, they had to specify at least the family taxa of the insect natural enemy. Studies only specifying 'predator' as functional group were excluded but some studies mentioning only 'parasitoids' were conserved when they were considered relevant. Fourth, in the specific case of intercropping studies, the aromatic species had to be the associated plant. Studies where the aromatic plant was the main crop were rejected. It resulted in a selection of 64 papers, involving 32 aromatic plant species, constituting the core of studies used for the present review (Table S2).



## 2.2 Description of the selected papers

In the event that a single paper reported several tests, all instances were considered, hereafter termed ‘responses’. For each response, the family and species names of the aromatic plants and of the natural enemies, as well as natural enemy functional group (predator, parasitoid), were noted. The responses were classified according to the indicator used to assess the interaction between natural enemies and plants, following Wäckers and Van Rijn (2012). One response was described by one indicator only. Indicators evaluating the attractiveness of plants were whether the natural enemy (1) chose the plant (i.e., the whole plant or parts of it), (2) visited its flowers, (3) chose the plant based on its volatiles only (i.e., the whole plant or parts of it in laboratory conditions using olfactometer), (4) consumed plant resources and (5) the morphometric compatibility between the natural enemy and the plant. Indicators assessing the benefits for natural enemies were natural enemy (6) longevity and (7) fecundity. Finally indicators assessing the enhancement of biological control were (8) pest parasitisation or predation, and (9) whether the natural enemy colonizes an associated crop in the case of intercropping. The score ‘1’ was given when a significant positive effect was reported (higher attractiveness, flower visit, consumption of the plant pollen and/or nectar, morphometric compatibility, increased longevity or fecundity of the natural enemy, parasitisation or predation of pests, or increased colonization of the adjacent crop), and a ‘0’ in case of negative or neutral effect. This scoring method allowed to get binary data to perform statistical analyses (see below) and highlighted the potential positive effects of aromatic plants versus non- or negative effects. Negative effects were negligible here, as they represented less than 0.03% of the obtained responses (8 out of 314 responses). Both absolute (when compared to a control) and relative (when compared to other plant species) effects were considered, but only absolute effects were kept when a study assessed both. For studies numbering plant choices or flower

visitations without conducting statistical analyses, only the main conclusions (i.e., the most attractive or visited plant species according to the authors of the study) were kept. Finally, the type of experiment (field, greenhouse, laboratory) and the country in case of field experiment were described.

## 2.4 Statistical analyses

Studies (i.e., responses) were grouped according to the indicator used: (i) studies assessing attractiveness of plants to natural enemies (indicators 1 to 5), (ii) studies assessing benefits for natural enemies (indicators 6 and 7) and (iii) studies assessing an enhancement of biological control (indicators 8 and 9). First, Exact Bernoulli tests ( $P < 0.05$ ) were used to assess whether, for each group of indicators, there is a significant number of studies showing a positive effect (i.e., attractiveness, benefits, enhancement of biological control, respectively). Second, Generalized Linear Models (GLM) with binomial error distribution (logit link function) were fitted to identify which variables affect attractiveness, benefits for natural enemies and enhancement of biological control. Explanatory variables, introduced in the models as fixed factors, were (i) plant family, (ii) insect functional group (predator, parasitoid), (iii) predator family (for predators) or parasitoid family (for parasitoids), as well as interactions between plant family and the other variables. The models were tested using likelihood ratio tests ( $P < 0.05$ ). Third, when a significant effect was reported for a variable, Exact Bernoulli tests ( $P < 0.05$ ) were used on each of the variable component (e.g., on each plant family or each parasitoid family). Analyses were performed by using R (v. 3.4.1) software (R Core Team 2017).

### 3. Results

#### 3.1 Selected papers

##### 3.1.1 Aromatic plants

The 32 selected species of aromatic plants belonged to eight different families. The most studied (number of responses / number of papers) were Lamiaceae (19 species, 112/23), followed by Apiaceae (three species, 99/34), Asteraceae (three species, 74/20), Fabaceae (two species, 14/6), Brassicaceae (one species, 8/2), Rosaceae (one species, 3/2), Solanaceae (one species, 3/3) and Pinaceae (one species, 1/1). All the species are flowering herbaceous plants, except for *Pinus massoniana* (Lamb.) (Pinaceae) which is a tree plant. The most studied plant species were *Coriandrum sativum* (L.) (Apiaceae) (40/22), *Anethum graveolens* (L.) (Apiaceae) (32/15), *Centaurea cyanus* (L.) (Asteraceae) (32/13), *Tagetes patula* (L.) (Asteraceae) (28/10), *Foeniculum vulgare* (L.) (Apiaceae) (27/12) and *Ocimum basilicum* (L.) (Lamiaceae) (26/6), totalizing together more than 60 % of all the responses through 49 different papers.

##### 3.1.2 Insect natural enemies

For natural enemies, Coccinellidae (nine species, 75/23) were the most studied predators, followed by Chrysopidae (five species, 56/10) and Syrphidae (four species, 50/16). The most studied predatory species were *Episyrphus balteatus* (Diptera: Syrphidae) (16/4), *Ceraeochrysa cubana* (Neuroptera: Chrysopidae) (16/2), *Harmonia axyridis* (Coleoptera: Coccinellidae) (15/5), *Coccinella septempunctata* (Coleoptera: Coccinellidae) (12/4) and *Chrysoperla externa* (Neuroptera: Chrysopidae) (12/3), totalizing together more than 50 % of responses (when the species name of the insect was specified) through 14 papers. Braconidae

(10 species, 41/16) were the most studied parasitoids, followed by Ichneumonidae (four species, 21/9), Trichommatidae (three species, 17/4), Encyrtidae (three species, 13/4), Eulophidae (three species, 10/3), Platygasteridae (one species, 10/2), Figitidae (one species, 6/1), Mymaridae (four species, 4/2), Scelionidae (one species, 4/1) and Bothriideridae (one species, 1/1). The most studied parasitoid species were *Trissolcus basalis* (Hymenoptera: Platygasteridae) (10/2), *Microplitis mediator* (Hymenoptera: Braconidae) (7/4), *Cotesia glomerata* (Hymenoptera: Braconidae) (6/2), *Trybliographa rapae* (Hymenoptera: Figitidae) (6/1), *Trichogramma carverae* (Hymenoptera: Trichogrammatidae) (6/1) and *Edovum puttleri* (Hymenoptera: Eulophidae) (2/5), totalizing together more than 50 % of the responses (when the species name of the insect was specified) through 12 papers.

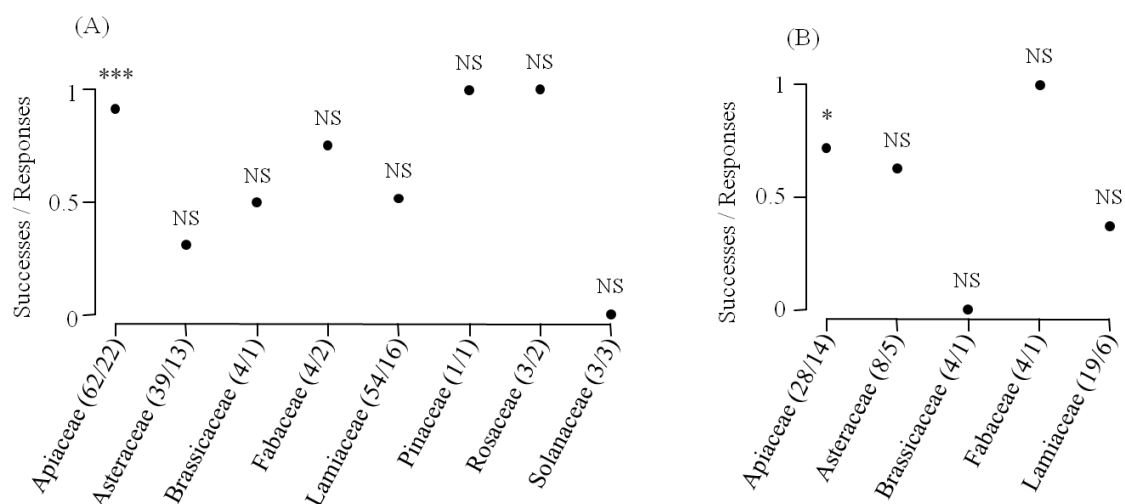
### 3.1.3 Indicators and experimental methodologies

Assessing visitation of flowers by natural enemies (58/13) was the most used approach to evaluate plant attractiveness to natural enemies. Most assessments of flower visitations were conducted in fields (e.g., Martínez-Uña et al., 2013; Tavares et al., 2015) and few in laboratories (Wanner et al. 2006), while Van Rijn and Wäckers (2016) did both. Assessments of plant choices (44/7) (without specifying flower visitations) were conducted by trapping natural enemies in sown monospecific plots (Frank et al. 2008; Tang et al. 2013) or by using potted plants (Sivinski et al. 2011) in fields, and in laboratories through for example ‘release-recapture experiment’ in cages (Batista et al. 2017). In order to understand the mechanisms involved in plant attractiveness and resource consumption, plant traits were isolated and confronted to natural enemies. Choice tests evaluated plant volatile attractiveness (27/14) by using H-tube (Song et al. 2017) or Y-tube (as described by Belz et al., 2013) olfactometers. The whole plant was mostly used to conduct the choice tests (16/8), but sometimes only the flower parts were considered (6/3), and rarely the leaf parts only (3/3). Two responses

compared flower volatiles to leaf volatiles resulting in neutral effects (Foti et al. 2017). Also, the morphometric compatibility (11/2) between the shape of the inflorescence (corolla width and depth) and the head of the insects was measured (Vattala et al. 2006; Nave et al. 2016). Some studies went further by establishing the consumption of floral resources (nectar and/or pollen) by natural enemies (30/10). Insects were for example dissected to count ingested pollens (Laubertie et al. 2012; D'Ávila et al. 2016; Resende et al. 2017), consumed fructose from nectar was detected with the anthrone test (Laubertie et al. 2012), insects were weighted before and after consumption of pollen or nectar (Wäckers 2004; Nilsson et al. 2011), or plants were marked with an isotope that was found back in insects (Pollier et al. 2016).

Benefits of consuming flower resources were evaluated by measuring natural enemy longevity or survival (45/17) and fecundity (15/7). Measurements were mostly performed in laboratories; only Begum et al. (2006) performed experiments in a greenhouse. Measuring longevity consisted in counting the number of days insects lived in the presence of flowers, compared to a control (e.g., Furtado et al., 2016; Walton and Isaacs, 2011). For fecundity, number of oviposited eggs of predators (Laubertie et al. 2012; Togni et al. 2016; Batista et al. 2017; Resende et al. 2017) and number of parasitised eggs and/or emerged adults of parasitoids (Begum et al. 2006; Witting-Bissinger et al. 2008; Foti et al. 2017) were counted.

Parasitisation (4/3) was used as an indicator of biological control enhancement. Host eggs fixed on cards (Balmer et al. 2014) or host larvae placed on plants (Géneau et al. 2013) were offered to parasitoids and the number of parasitised individuals were counted after a time delay. A molecular approach also consisted in identifying parasitoid DNA through PCR from larvae collected in fields (Juric et al. 2015). Assessing the abundance of natural enemies found in crops or fruit trees intercropped with—or sown adjacent to—aromatic plants was a more indirect indicator of biological control enhancement in fields (80/12) (e.g., Ramalho et al., 2012; Wan et al., 2015; Winkler et al., 2010; Zhang et al., 2017).



**Figure 1.** Ratio of the number of successes on the total number of responses reporting an (A) attractiveness of aromatic plants on pest natural enemies and (B) benefits provided by aromatic plants on pest natural enemies, according to plant families. The ratio given in brackets corresponds to the number of responses/number of papers. Exact Bernoulli test. \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ ; NS: non-significant.

### 3.2 Natural enemy – aromatic plant interactions

#### 3.2.1 General effects of aromatic plants on predators and parasitoids

Exact Bernoulli tests show that there is a significant number of studies reporting the attractiveness of aromatic plants to natural enemies (mean = 0.62;  $P < 0.001$ ), but it is not the case for the benefits provided (mean = 0.55;  $P = 0.26$ ). GLM and  $\chi^2$  analyses show that attractiveness of aromatic plants significantly varies among plant families, insect functional groups and parasitoid families (Tab. 1). Exact Bernoulli tests performed on predators and parasitoids separately show that a significant number of studies reported the attractiveness of aromatic plants to predators (mean = 0.74;  $P < 0.001$ ) but not to parasitoids (mean = 0.52;  $P = 0.377$ ). When parasitoid families are considered separately, Exact Bernoulli tests indicate that there is not a significant number of studies reporting aromatic plant attractiveness to any of the families (Tab. S3). Furthermore, GLM and  $\chi^2$  analyses indicate that benefits for natural

enemies of consuming floral resources vary among plant families and parasitoid families (Tab. 1). However, similarly to attractiveness, no significant results of Bernoulli tests have been found when considering each parasitoid family separately (Tab. S3).

### 3.2.2 Positive effects of Apiaceae

Exact Bernoulli tests performed on each family of plants show that a significant number of studies reported an attractiveness of Apiaceae aromatic plants to natural enemies (Fig. 1a) and increased benefits for natural enemies when they feed on them (Fig. 1b). *Anethum graveolens*, *C. sativum* and *F. vulgare* are the three Apiaceae aromatic species considered in the present review. There are also among the most studied plants of the present selection.

Regarding predators, ladybeetles and hoverflies were the most studied natural enemies to test the attractiveness of Apiaceae species while the benefits Apiaceae provide in terms of longevity and fecundity were mostly explored on lacewings. Studies showed that Apiaceae flowers were significantly more visited than those of other plant families by ladybeetles and hoverflies in fields, and by hoverflies in laboratory (Tab. 2). Volatiles from Apiaceae were found to significantly attract predators: the ladybeetles *H. axyridis* to *A. graveolens* (Adedipe and Park 2010), *Cycloneda sanguinea* (Coleoptera: Coccinellidae) to *C. sativum* (Togni et al. 2016) and the lacewing *Chrysoperla externa* (Neuroptera: Chrysopidae) to *C. sativum* (Salamanca et al. 2015). However, it remains to assess if volatiles of Apiaceae aromatic plants also attract hoverflies. The pollen of these three Apiaceae species can be consumed by *Coleomegilla maculata* (Coleoptera: Coccinellidae) (D'Ávila et al. 2016) and an increased longevity, but not fecundity, of *C. sanguinea* was observed when it fed on *C. sativum* (Togni et al. 2016). In this last study, fecundity increased when aphids were added to *C. sanguinea* diet, recalling that ladybeetles need prey food for laying eggs (Lundgren 2009). Conversely fecundity, in addition to longevity, of the lacewing *C. externa* significantly increased when it

consumed pollens of the three Apiaceae species (Resende et al. 2017), which is consistent with *C. externa* biology (i.e., its dependence on plant-based diet at the adult stage). Moreover, it suggests that pollens of these Apiaceae contain sufficient carbohydrates, that are macro nutrients which significantly affect lacewing fecundity (Venzon et al. 2006). The longevity of the hoverfly *E. balteatus* was increased when it fed on *C. sativum* or *F. vulgare* (Van Rijn and Wäckers 2016) but its fecundity was not the highest when it fed on *C. sativum* compared to other plants (Laubertie et al. 2012). According to these authors, quality of floral resource rather than quantity of nectar and pollen ingested determines *E. balteatus* fitness. However, criteria defining a high quality of nectar and pollen for hoverflies remain limitedly known to our knowledge.

Regarding parasitoids, Braconidae and Ichneumonidae were found to visit Apiaceae flowers and to consume their nectar which led to an increased longevity (Tab. 3) (e.g., *C. glomerata* with *A. graveolens*, Wanner et al. 2006). However, when parasitoids are considered together as one functional group, there are not a significant number of studies reporting the attractiveness of aromatic plants and the provision of benefits. Instead, contrasted results were reported depending on plant species, parasitoid family or parasitoid species (Tab. 1 and 3). For example, Eulophidae (Hymenoptera) species *Edovum puttleri* and *Pediobius foveolatus* were both attracted by nectary volatiles of *A. graveolens* (Patt et al. 1999), they both consumed *A. graveolens* nectar but only *P. foveolatus* consumed *C. sativum* nectar (Patt et al. 1997). Patt et al. suggested a morphometrical incompatibility as the partly hidden nectaries of *C. sativum* prevented *E. puttleri* to feed on this flower. *Trybliographa rapae* (Hymenoptera: Figitidae) also did not feed on *C. sativum* nectar, but in this case because it was repelled by coriander volatiles; however it fed on *A. graveolens* even if it was not especially attracted by *A. graveolens* volatiles (Nilsson et al. 2011). A last example is *Trichogramma exiguum*



(Hymenoptera: Trichogrammatidae), which longevity was significantly increased when it fed on *F. vulgare*, nevertheless it was not the case of its fecundity (Witting-Bissinger et al. 2008).

**Table 1.** Effect (increased attractiveness, benefits and biological control enhancement) of aromatic plants on natural enemies according to the plant family, the insect group (predator or parasitoid) and the insect family. Likelihood ratio tests on GLMs with binomial error distribution. Degree of freedom (df),  $\chi^2$ -values and *P*-values are provided. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . A dash indicates that it was not possible to perform the analysis.

	<b>df</b>	<b><math>\chi^2</math></b>	<b><i>P</i>-value</b>
<b>Attract natural enemies</b>			
Plant family	7	54.5	<b>&lt; 0.001</b> ***
Insect group	1	9.01	<b>0.003</b> **
Predator family	2	2.14	0.343
Parasitoid family	9	27.8	<b>0.001</b> **
Plant family : Insect group	5	10.1	0.072
Plant family : Predator family	6	9.89	0.129
Plant family : Parasitoid family	8	6.31	0.612
<b>Benefit natural enemies</b>			
Plant family	4	13.5	<b>0.009</b> **
Insect group	1	1.03	0.311
Predator family	2	0.53	0.768
Parasitoid family	6	12.8	<b>0.047</b> *
Plant family : Insect group	2	3.45	0.178
Plant family : Predator family	1	6.49	<b>0.011</b> *
Plant family : Parasitoid family	2	2.36	0.306
<b>Enhance biological control</b>			
Plant family	3	2.72	0.437
Insect group	1	0.66	0.418
Predator family	2	3.14	0.209
Parasitoid family	1	< 0.001	1
Plant family : Insect group	3	3.89	0.273
Plant family : Predator family	5	14.8	<b>0.011</b> *
Plant family : Parasitoid family	-	-	-

### 3.2.3 Contrasted effects among the other plant families

Regarding aromatic plants from families other than Apiaceae, Exact Bernoulli tests show that there is nor a significant number of studies reporting an attractiveness of these plants to

natural enemies (Fig. 1a), neither a significant number of studies reporting increased benefits for natural enemies when they feed on them (Fig. 1b).

Concerning predators, few studies reported that Asteraceae *C. cyanus* and *T. patula* were more visited relatively to other species by ladybeetles and hoverflies in fields (Tab. 2). Still, the ladybeetle *H. axyridis* was found to be attracted by *T. patula* volatiles (Song et al. 2017) and the hoverfly *E. balteatus* to feed on *C. cyanus* flowers which increased its longevity (Van Rijn and Wäckers 2016). For Lamiaceae, totally 11 plant species were tested. Six of them were significantly more visited by hoverflies compared to other plants (Tab. 2). The lacewing *C. cubana* had different behavior from a species to another: it was significantly more attracted by *O. basilicum* than by *Mentha piperita* (L.) (Lamiaceae) or *Melissa officinalis* (L.) (Lamiaceae), the consumption of *O. basilicum* flowers increased its longevity but not its fecundity, while it was not the case with the other plant species (Batista et al. 2017). Few studies tested the interactions between ladybeetles and Lamiaceae. *Harmonia axyridis* was attracted by the volatiles of *Ajuga reptans* (L.) (Lamiaceae) (Adedipe and Park 2010) and *Hippodamia convergens* (Coleoptera: Coccinellidae) lived longer when it fed on *Monarda fistulosa* (L.) (Lamiaceae) (Walton and Isaacs 2011). With plants from other families, *H. axyridis* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) were attracted by the Rosaceae *Rosa multiflora* (Thunb.) in fields (Finlayson et al. 2010). Also, *C. septempunctata*, *Coccinella transversoguttata* (Coleoptera: Coccinellidae) and *H. convergens* consumed the pollen of the Fabaceae *Medicago sativa* (L.) (Davidson and Evans 2010) making alfalfa a potential source of non-prey food for ladybeetles in fields.

The preference of parasitoids when choosing plants was assessed on three Asteraceae and six Lamiaceae aromatic species in fields (Sivinski et al. 2011; Tang et al. 2013). These observations highlight that only Ichneumonidae generally chose these species, except *Ageratum houstonianum* (Mill.) (Asteraceae) and *Monarda punctata* (L.) (Lamiaceae).

Conversely Braconidae chose none of them and Encyrtidae only *Ocimum citriodorum* (Vis.) (Lamiaceae). However, various other observations conducted in laboratory showed positive interactions between several Braconidae species and Lamiaceae or Asteraceae plants (Tab. 3). For example, *Microplitis mediator* (Hymenoptera: Braconidae) was attracted by the volatiles of both *Origanum vulgare* (L.) (Lamiaceae) and *C. cyanus* (Belz et al. 2013) and the consumption of *C. cyanus* nectar increased its longevity (Géneau et al. 2012). *Diaeretiella rapae* (Hymenoptera: Braconidae) consumed *C. cyanus* nectar (Pollier et al. 2016) and *C. glomerata* consumed *O. vulgare* nectar (but not *Heterospilus prosopidis* [Hymenoptera: Braconidae]) (Wäckers 2004). *Aphidius colemani* (Hymenoptera: Braconidae) lived longer when feeding on *M. fistulosa* (Walton and Isaacs 2011) as well as *C. glomerata* when feeding on *O. vulgare* (Wanner et al. 2006). These results gathered from several papers recall that interactions in controlled conditions may not necessarily be observed in fields where other environmental variables may affect parasitoid behaviour. Also, assessments at the species level are needed because contrasted results may occur between insects belonging to a same family.

### 3.3 Enhancing biological control

Exact Bernoulli test shows that there is not a significant number of studies reporting an enhancement of biological control when aromatic plants are sown adjacent to crops (mean = 0.42;  $P = 0.949$ ). GLM and  $\chi^2$  analyses indicate that the enhancement of biological control by aromatic plants is not affected by the tested variables; only a significant interaction between plant family and predator family is observed (Tab. 1). Indeed Coccinellidae and Chrysopidae have been found more abundant in crops adjacent to Apiaceae (*C. sativum*, *F. vulgare*) (Ramalho et al. 2012; Salamanca et al. 2015; Jankowska and Wojciechowicz-Żytko 2016),

while Syrphidae have been found more abundant in crops adjacent to Asteraceae (*T. patula*) and Lamiaceae (*O. basilicum*, *Satureja hortensis* (L.)) (Song et al. 2013; Jankowska and Wojciechowicz-Żytka 2016). Almost all studies were conducted in fields; only Salamanca et al. (2015) conducted an experiment in a greenhouse and Généau et al. (2013) assessed the parasitism of *M. mediator* in laboratory conditions. The majority of studies used the presence of natural enemies in the main crop as an indirect proxy to assess the enhancement of biological control by aromatic plants. Parasitism from parasitoids was only evenly measured (Tab. 4).

**Table 2.** Effect of aromatic plant species on predators. Studies are sorted by indicators related to attractiveness (if the predator chose the plant, visited its flowers, chose its volatiles, consumed its resources, has a morphological compatibility with the flower) and benefits (longevity, fecundity). The ratio between brackets is the number of responses / number of paper in case of similar effects among or within papers for a given plant species-insect species/family interaction. A dash indicates that the information was not specified in the paper.

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	References	
				(+)	(O/-)				
<b>Chose plant</b>									
Lamiaceae	Melissa officinalis (L.)	Chrysopidae	Ceraeochrysa cubana		◇	Lab	Relative	(Batista et al. 2017)	
	Mentha piperita (L.)	Chrysopidae	Ceraeochrysa cubana		◇	Lab	Relative	(Batista et al. 2017)	
	Ocimum basilicum (L.)	Chrysopidae	Ceraeochrysa cubana	◇		Lab	Relative	(Batista et al. 2017)	
Rosaceae	Rosa multiflora (Thunb.)	Coccinellidae	Harmonia axyridis	◇		Field	Absolute	(Finlayson et al. 2010)	
		Coccinellidae	Propylea quatuordecimpunctata	◇		Field	Absolute	(Finlayson et al. 2010)	
<b>Visited flower</b>									
Apiaceae	Anethum graveolens (L.)	Coccinellidae	-	◇ (2/2)	◇	Field	Relative	(Al-Doghairi and Cranshaw 1999; Kopta et al. 2012; Tavares et al. 2015)	
		Syrphidae	-	◇ (2/2)		Field	Relative	(Al-Doghairi and Cranshaw 1999; Kopta et al. 2012)	
		Syrphidae	Toxomerus marginatus	◇		Field	Relative	(Tavares et al. 2015)	
	Coriandrum sativum (L.)	Coccinellidae	-	◇ (2/2)		Field	Relative	(Ambrosino et al. 2006; Tavares et al. 2015)	
		Syrphidae	-	◇ (3/3)		Field	Relative	(Al-Doghairi and Cranshaw 1999; Colley and Luna 2000; Ambrosino et al. 2006)	
		Syrphidae	Episyrphus balteatus	◇		Lab	Relative	(Van Rijn and Wäckers 2016)	
		Syrphidae	Sphaerophoria rueppellii	◇		Field	Relative	(Martínez-Uña et al. 2013)	
	Foeniculum vulgare (L.)	Foeniculum vulgare (L.)	Syrphidae	Sphaerophoria scripta	◇		Field	Relative	(Martínez-Uña et al. 2013)
			Syrphidae	Sphaerophoria spp.	◇		Field	Relative	(Barbir et al. 2015)
			Syrphidae	Toxomerus marginatus	◇		Field	Relative	(Tavares et al. 2015)
			Coccinellidae	-	◇ (3/3)		Field; Lab	Relative; Absolute	(Maingay et al. 1991; Al-Doghairi and Cranshaw 1999; Kopta et al.

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	References	
				(+)	(O/-)				
		Syrphidae	-	◇ (4/4)		Field	Relative; Absolute	2012) (Maingay et al. 1991; Colley and Luna 2000; Kopta et al. 2012; Van Rijn and Wäckers 2016)	
Asteraceae	Calendula officinalis (L.)	Syrphidae	Episyrphus balteatus	◇		Lab	Relative	(Van Rijn and Wäckers 2016)	
		Syrphidae	-		◇	Field	Relative	(Colley and Luna 2000)	
		Syrphidae	Episyrphus balteatus		◇	Field	Relative	(Carreck and Williams 2002)	
		Syrphidae	Sphaerophoria scripta	◇		Field	Relative	(Carreck and Williams 2002)	
	Centaurea cyanus (L.)	Chrysopidae	-			◇	Field	Relative	(Fitzgerald and Solomon 2004)
		Coccinellidae	-		◇ (2/2)		Field	Relative	(Fitzgerald and Solomon 2004; Kopta et al. 2012)
		Coccinellidae	Coccinella septempunctata			◇	Field	Relative	(Barbir et al. 2015)
		Syrphidae	-			◇ (2/2)	Field	Relative; Absolute	(Kopta et al. 2012; Van Rijn and Wäckers 2016)
	Tagetes patula (L.)	Syrphidae	Episyrphus balteatus			◇	Field	Relative	(Carreck and Williams 2002)
		Syrphidae	Sphaerophoria scripta			◇	Field	Relative	(Carreck and Williams 2002)
		Syrphidae	Sphaerophoria spp.			◇	Field	Relative	(Barbir et al. 2015)
		Coccinellidae	-			◇	Field	Relative	(Kopta et al. 2012)
		Coccinellidae	Heliotaurus ruficolis			◇	Field	Relative	(Barbir et al. 2015)
		Syrphidae	-			◇	Field	Relative	(Colley and Luna 2000; Kopta et al. 2012)
Syrphidae		Sphaerophoria spp.			◇	Field	Relative	(Barbir et al. 2015)	
Lamiaceae		Agastache rugosa (Kuntze)	Syrphidae	-	◇		Field	Relative	(Colley and Luna 2000)
	Ajuga reptans (L.)	Syrphidae	-	◇		Field	Relative	(Al-Doghairi and Cranshaw 1999)	
	Lavandula angustifolia (Mill.)	Syrphidae	-	◇		Field	Relative	(Al-Doghairi and Cranshaw 1999)	
	Mentha piperita (L.)	Syrphidae	-	◇		Field	Relative	(Al-Doghairi and Cranshaw 1999)	
	Mentha spicata (L.)	Syrphidae	-	◇		Field	Absolute	(Maingay et al. 1991)	
	Stachys officinalis (L.)	Syrphidae	-	◇		Field	Relative	(Al-Doghairi and Cranshaw 1999)	
Rosaceae	Rosa multiflora (Thunb.)	Syrphidae	-	◇		Field	Absolute	(Jesse et al. 2006)	

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	References
				(+)	(O/-)			
<b>Chose volatiles</b>								
Apiaceae	Anethum graveolens (L.)	Coccinellidae	Harmonia axyridis	◇		Lab	Absolute	(Adedipe and Park 2010)
	Coriandrum sativum (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Salamanca et al. 2015)
		Coccinellidae	Cycloneda sanguinea	◇		Lab	Absolute	(Togni et al. 2016)
Asteraceae	Tagetes patula (L.)	Coccinellidae	Harmonia axyridis	◇		Lab	Relative	(Song et al. 2017)
Brassicaceae	Brassica juncea (L.)	Chrysopidae	Ceraeochrysa cubana		◇	Lab	Absolute	(da Silva et al. 2016)
		Chrysopidae	Chrysoperla externa		◇	Lab	Absolute	(da Silva et al. 2016)
		Coccinellidae	Cycloneda sanguinea	◇		Lab	Absolute	(da Silva et al. 2016)
Lamiaceae	Ajuga reptans (L.)	Coccinellidae	Harmonia axyridis	◇		Lab	Absolute	(Adedipe and Park 2010)
	Nepeta cataria (L.)	Coccinellidae	Harmonia axyridis		◇	Lab	Relative	(Song et al. 2017)
Solanaceae	Capsicum annuum (L.)	Coccinellidae	Cycloneda sanguinea		◇	Lab	Absolute	(Oliveira and Pareja 2014)
<b>Established consumption</b>								
Apiaceae	Anethum graveolens (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)
		Coccinellidae	Coleomegilla maculata	◇ (2/1)		Lab	Absolute	(D'Ávila et al. 2016)
	Coriandrum sativum (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)
		Coccinellidae	Coleomegilla maculata	◇ (2/1)		Lab	Absolute	(D'Ávila et al. 2016)
	Foeniculum vulgare (L.)	Syrphidae	Episyrphus balteatus	◇		Lab	Absolute	(Laubertie et al. 2012)
		Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)
		Coccinellidae	Coleomegilla maculata	◇ (2/1)		Lab	Absolute	(D'Ávila et al. 2016)
Asteraceae	Calendula officinalis (L.)	Syrphidae	Episyrphus balteatus	◇		Lab	Absolute	(Laubertie et al. 2012)
Fabaceae	Medicago sativa (L.)	Coccinellidae	Coccinella septempunctata	◇		Field	Absolute	(Davidson and Evans 2010)
		Coccinellidae	Coccinella transversoguttata	◇		Field	Absolute	(Davidson and Evans 2010)
		Coccinellidae	Hippodamia convergens	◇		Field	Absolute	(Davidson and Evans 2010)

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	References	
				(+)	(O/-)				
<b>Morphometric compatibility</b>									
Apiaceae	Foeniculum vulgare (L.)	Chrysopidae	Chrysoperla carnea	◇		Lab	Absolute	(Nave et al. 2016)	
Lamiaceae	Lavandula stoechas (L.)	Chrysopidae	Chrysoperla carnea	◇		Lab	Absolute	(Nave et al. 2016)	
<b>Fecundity</b>									
Apiaceae	Anethum graveolens (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)	
	Coriandrum sativum (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)	
Asteraceae	Foeniculum vulgare (L.)	Coccinellidae	Cycloneda sanguinea		◇	Lab	Absolute	(Togni et al. 2016)	
		Syrphidae	Episyrphus balteatus		◇	Lab	Relative	(Laubertie et al. 2012)	
	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)		
	Calendula officinalis (L.)	Syrphidae	Episyrphus balteatus		◇	Lab	Relative	(Laubertie et al. 2012)	
	Lamiaceae	Melissa officinalis (L.)	Chrysopidae	Ceraeochrysa cubana		◇	Lab	Absolute	(Batista et al. 2017)
	Mentha piperita (L.)	Chrysopidae	Ceraeochrysa cubana		◇	Lab	Absolute	(Batista et al. 2017)	
Ocimum basilicum (L.)	Chrysopidae	Ceraeochrysa cubana		◇ (2/1)	Lab	Absolute	(Batista et al. 2017)		
<b>Longevity</b>									
Apiaceae	Anethum graveolens (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)	
	Coriandrum sativum (L.)	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)	
Asteraceae	Foeniculum vulgare (L.)	Coccinellidae	Cycloneda sanguinea	◇		Lab	Absolute	(Togni et al. 2016)	
		Syrphidae	Episyrphus balteatus	◇	◇	Lab	Absolute; Relative	(Laubertie et al. 2012; Van Rijn and Wäckers 2016)	
	Chrysopidae	Chrysoperla externa	◇		Lab	Absolute	(Resende et al. 2017)		
	Syrphidae	Episyrphus balteatus	◇		Lab	Absolute	(Van Rijn and Wäckers 2016)		
	Centaurea cyanus (L.)	Syrphidae	Episyrphus balteatus	◇		Lab	Absolute	(Van Rijn and Wäckers 2016)	
	Calendula officinalis (L.)	Syrphidae	Episyrphus balteatus		◇	Lab	Relative	(Laubertie et al. 2012)	
Fabaceae	Medicago sativa (L.)	Syrphidae	Episyrphus balteatus	◇		Lab	Absolute	(Van Rijn and Wäckers 2016)	
Lamiaceae	Melissa officinalis(L.)	Chrysopidae	Ceraeochrysa cubana		◇ (2/1)	Lab	Absolute	(Batista et al. 2017)	
	Mentha piperita (L.)	Chrysopidae	Ceraeochrysa cubana		◇ (2/1)	Lab	Absolute	(Batista et al. 2017)	



Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	References
				(+)	(O/-)			
	Monarda fistulosa (L.)	Coccinellidae	Hippodamia convergens	◇		Lab	Absolute	(Walton and Isaacs 2011)
	Ocimum basilicum (L.)	Chrysopidae	Ceraeochrysa cubana	◇ (2/1)	◇ (2/1)	Lab	Absolute	(Batista et al. 2017)

**Table 3.** Effect of aromatic plant species on parasitoids. Studies are sorted by indicators related to attractiveness (if the predator chose the plant, visited its flowers, chose its volatiles, consumed its resources, has a morphometrical compatibility with the flower) and benefits (longevity, fecundity). The ratio between brackets is the number of responses / number of papers in case of similar effects among or within papers for a given plant species-insect species/family interaction. A dash indicates that the information was not specified in the paper.

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference
				(+)	(O/-)			
<b>Chose plant</b>								
Asteraceae	Ageratum houstonianum (Mill.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
Centaurea cyanus (L.)	Centaurea cyanus (L.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
Tagetes patula (L.)	Tagetes patula (L.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
Lamiaceae	Mentha haplocalyx (Bricq.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference
				(+)	(O/-)			
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
	Monarda punctata (L.)	Braconidae	-		◇	Field	Absolute	(Sivinski et al. 2011)
		Chalcidoidea	-	◇		Field	Absolute	(Sivinski et al. 2011)
		Ichneumonidae	-		◇	Field	Absolute	(Sivinski et al. 2011)
	Nepeta cataria (L.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
	Ocimum basilicum (L.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
	Ocimum citriodorum (Vis.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
	Satureja hortensis (L.)	Braconidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Encyrtidae	-		◇	Field	Absolute	(Tang et al. 2013)
		Ichneumonidae	-	◇		Field	Absolute	(Tang et al. 2013)
		Trichogrammatidae	-		◇	Field	Absolute	(Tang et al. 2013)
Pinaceae	Pinus massoniana (D.Don)	Bothrideridae	Dastarcus helophoroides	◇		Lab	Absolute	(Li et al. 2016)
Solanaceae	Capsicum annuum (L.)	Mymaridae	Anagrus atomus		◇	Lab	Relative	(Agboka et al. 2003)
<b>Visited flower</b>								
Apiaceae	Anethum graveolens (L.)	Braconidae	Cotesia glomerata	◇		Lab	Relative	(Wanner et al. 2006)
			-		◇	Field	Relative	(Al-Doghairi and Cranshaw 1999)

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference
				(+)	(O/-)			
		Ichneumonidae	-	◇		Field	Relative	(Kopta et al. 2012)
	Foeniculum vulgare (L.)	Ichneumonidae	-	◇		Field	Relative	(Kopta et al. 2012)
Asteraceae	Centaurea cyanus (L.)	Ichneumonidae	-		◇	Field	Relative	(Kopta et al. 2012)
	Tagetes patula (L.)	Ichneumonidae	-		◇	Field	Relative	(Kopta et al. 2012)
Lamiaceae	Mentha piperita (L.)	Braconidae	-	◇		Field	Relative	(Al-Doghairi and Cranshaw 1999)
	Origanum vulgare (L.)	Braconidae	Cotesia glomerata		◇	Lab	Relative	(Wanner et al. 2006)
<b>Chose volatiles</b>								
Apiaceae	Anethum graveolens (L.)	Eulophidae	Edovum puttleri	◇		Lab	Absolute	(Patt et al. 1999)
			Pediobius foveolatus	◇		Lab	Absolute	(Patt et al. 1999)
		Figitidae	Trybliographa rapae		◇	Lab	Absolute	(Nilsson et al. 2011)
	Coriandrum sativum (L.)	Figitidae	Trybliographa rapae		◇	Lab	Absolute	(Nilsson et al. 2011)
Asteraceae	Centaurea cyanus (L.)	Braconidae	Microplitis mediator	◇		Lab	Relative	(Géneau et al. 2013)
			Microplitis mediator	◇		Lab	Absolute	(Belz et al. 2013)
	Tagetes patula (L.)	Platygastridae	Trissolcus basalis	◇		Lab	Absolute	(Foti et al. 2017)
			Trissolcus basalis		◇	Lab	Relative	(Foti et al. 2017)
Brassicaceae	Brassica juncea (L.)	Braconidae	Aphidius colemani	◇		Lab	Absolute	(da Silva et al. 2016)
Fabaceae	Medicago sativa (L.)	Ichneumonidae	Bathyplectes curculionis		◇	Lab	Absolute	(Jacob and Evans 2001)
Lamiaceae	Ocimum basilicum (L.)	Platygastridae	Trissolcus basalis	◇		Lab	Absolute	(Foti et al. 2017)
			Trissolcus basalis		◇	Lab	Relative	(Foti et al. 2017)
	Origanum vulgare (L.)	Braconidae	Heterospilus prosopidis	◇		Lab	Absolute	(Wäckers 2004)
			Microplitis mediator	◇		Lab	Absolute	(Belz et al. 2013)
		Figitidae	Trybliographa rapae		◇	Lab	Absolute	(Nilsson et al. 2011)
		Ichneumonidae	Pimpla turionellae	◇		Lab	Absolute	(Wäckers 2004)
Solanaceae	Capsicum annuum (L.)	Trichogrammatidae	Trichogramma ostrinae		◇	Lab	Absolute	(Yong et al. 2007)

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference	
				(+)	(O/-)				
<b>Established consumption</b>									
Apiaceae	Anethum graveolens (L.)	Braconidae	Cotesia glomerata	◇		Lab	Absolute	(Wanner et al. 2006)	
		Eulophidae	Edovum puttleri	◇		Lab	Relative	(Patt et al. 1997)	
			Pediobius foveolatus	◇		Lab	Relative	(Patt et al. 1997)	
		Figitidae	Trybliographa rapae	◇		Lab	Absolute	(Nilsson et al. 2011)	
		Ichneumonidae	Diadegma semiclausum	◇		Field	Absolute	(Winkler et al. 2009b)	
		Coriandrum sativum (L.)	Eulophidae	Edovum puttleri		◇	Lab	Relative	(Patt et al. 1997)
			Pediobius foveolatus	◇		Lab	Relative	(Patt et al. 1997)	
	Figitidae		Trybliographa rapae		◇	Lab	Absolute	(Nilsson et al. 2011)	
		Foeniculum vulgare (L.)	Eulophidae	Edovum puttleri	◇		Lab	Relative	(Patt et al. 1997)
	Asteraceae	Centaurea cyanus (L.)	Braconidae	Diaeretiella rapae	◇ (2/1)		Lab; Field	Absolute	(Pollier et al. 2016)
Lamiaceae	Mentha spicata (L.)	Eulophidae	Edovum puttleri		◇	Lab	Absolute	(Patt et al. 1997)	
	Origanum vulgare (L.)	Braconidae	Cotesia glomerata	◇	◇	Lab	Absolute	(Wäckers 2004; Wanner et al. 2006)	
			Heterospilus prosopidis			◇	Lab	Absolute	(Wäckers 2004)
		Ichneumonidae	Pimpla turionellae	◇		Lab	Absolute	(Wäckers 2004)	
<b>Morphometric compatibility</b>									
Apiaceae	Coriandrum sativum (L.)	Braconidae	Microctonus hyperodae	◇		Lab	Relative	(Vattala et al. 2006)	
			Apanteles xanthostigma	◇		Lab	Absolute	(Nave et al. 2016)	
	Foeniculum vulgare (L.)		Chelonus elaeaphilus	◇		Lab	Absolute	(Nave et al. 2016)	
		Encyrtidae	Ageniaspis fuscicollis	◇		Lab	Absolute	(Nave et al. 2016)	
		Eulophidae	Elasmus flabellatus	◇		Lab	Absolute	(Nave et al. 2016)	
Lamiaceae	Lavandula stoechas (L.)	Braconidae	Apanteles xanthostigma	◇		Lab	Absolute	(Nave et al. 2016)	

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference	
				(+)	(O/-)				
			Chelonus elaeaphilus	◇		Lab	Absolute	(Nave et al. 2016)	
		Encyrtidae	Ageniaspis fuscicollis	◇		Lab	Absolute	(Nave et al. 2016)	
		Eulophidae	Elasmus flabellatus	◇		Lab	Absolute	(Nave et al. 2016)	
<b>Fecundity</b>									
Apiaceae	Foeniculum vulgare (L.)	Trichogrammatidae	Trichogramma exiguum		◇	Lab	Absolute	(Witting-Bissinger et al. 2008)	
Asteraceae	Tagetes patula (L.)	Platygastridae	Trissolcus basalis		◇	Lab	Absolute	(Foti et al. 2017)	
Brassicaceae	Brassica juncea (L.)	Trichogrammatidae	Trichogramma carverae		◇ (2/1)	Greenhouse	Absolute	(Begum et al. 2006)	
Lamiaceae	Ocimum basilicum (L.)	Platygastridae	Trissolcus basalis	◇		Lab	Absolute	(Foti et al. 2017)	
<b>Longevity</b>									
Apiaceae	Anethum graveolens (L.)	Braconidae	Cotesia glomerata	◇		Lab	Absolute	(Wanner et al. 2006)	
		Encyrtidae	Copidosoma aretas	◇	◇	Lab	Absolute	(Baggen and Gurr 1998; Sigsgaard et al. 2013)	
		Figitidae	Trybliographa rapae	◇		Lab	Absolute	(Nilsson et al. 2011)	
		Mymaridae	Gonatocerus ashmeadi	◇		Lab	Absolute	(Irvin et al. 2007)	
			Gonatocerus fasciatus		◇	Lab	Absolute	(Irvin et al. 2007)	
			Gonatocerus triguttatus	◇		Lab	Absolute	(Irvin et al. 2007)	
		Coriandrum sativum (L.)	Braconidae	Microctonus hyperodae	◇		Lab	Absolute	(Vattala et al. 2006)
			Encyrtidae	Copidosoma koehleri	◇		Lab	Absolute	(Baggen and Gurr 1998)
			Scelionidae	Trissolcus basalis	◇		Lab	Absolute	(Rahat et al. 2005)
			Trichogrammatidae	Trichogramma carverae		◇ (2/1)	Greenhouse	Absolute	(Begum et al. 2006)
Foeniculum vulgare (L.)	Braconidae	Cotesia congregata	◇		Lab	Absolute	(Witting-Bissinger et al. 2008)		
		Psytalia concolor	◇		Lab	Absolute	(Furtado et al. 2016)		
	Trichogrammatidae	Trichogramma	◇		Lab	Absolute	(Witting-Bissinger et al.		

Plant family	Plant species	Insect family	Insect species	Effect		Exp. type	Type of effect	Reference
				(+)	(O/-)			
			exiguum					2008)
Asteraceae	Centaurea cyanus (L.)	Braconidae	Microplitis mediator	◇		Lab	Absolute	(Géneau et al. 2012)
		Ichneumonidae	Diadegma fenestratale	◇		Lab	Absolute	(Géneau et al. 2012)
	Tagetes patula (L.)	Platygastridae	Trissolcus basalis	◇ (2/1)		Lab	Absolute	(Rahat et al. 2005)
Brassicaceae	Brassica juncea (L.)	Trichogrammatidae	Trichogramma carverae		◇ (2/1)	Greenhouse	Absolute	(Begum et al. 2006)
Lamiaceae	Calamintha nepeta (L.) Savi	Braconidae	Psytalia concolor		◇	Lab	Absolute	(Furtado et al. 2016)
	Monarda fistulosa (L.)	Braconidae	Aphidius colemani	◇		Lab	Absolute	(Walton and Isaacs 2011)
	Ocimum basilicum (L.)	Scelionidae	Trissolcus basalis	◇		Lab	Absolute	(Rahat et al. 2005)
	Origanum vulgare (L.)	Braconidae	Cotesia glomerata	◇		Lab	Absolute	(Wanner et al. 2006)
	Rosmarinus officinalis (L.)	Braconidae	Psytalia concolor		◇	Lab	Absolute	(Furtado et al. 2016)

**Table 4.** Effect of aromatic plant species on biological control enhancement by predators and parasitoids. The presence of natural enemies in the main crop associated to an aromatic plant species is the main indirect proxy to evaluate an enhancement of biological control. Parasitism rate by parasitoids is evenly provided. The ratio between brackets is the number of responses / number of papers in case of similar effects among or within papers for a given plant species-insect species/family interaction. A dash indicates that the information was not specified in the paper.

Plant family (aromatic)	Plant species (aromatic)	Main crop	Insect family	Insect species	Effect		Country	Reference
					(+)	(O/-)		
<b>PREDATORS</b>								
<b>Found in intercrop</b>								
Apiaceae	Coriandrum sativum (L.)	Brassica oleracea (L.)	Syrphidae	-		◇ (2/1)	Japan	(Morris and Li 2000)
		Daucus carota (L.)	Coccinellidae	-		◇	Poland	(Jankowska and Wojciechowicz-Żytko 2016)
			Syrphidae	-		◇	Poland	(Jankowska and Wojciechowicz-Żytko 2016)
		Lactuca sativa (L.)	Syrphidae	-		◇	Spain	(Pascual-Villalobos et al. 2006)
		Rosa hybrida (L.)	Chrysopidae	Chrysoperla externa		◇	Brazil	(Salamanca et al. 2015)

Plant family (aromatic)	Plant species (aromatic)	Main crop	Insect family	Insect species	Effect		Country	Reference
					(+)	(O/-)		
Asteraceae	Foeniculum vulgare (L.)	Gossypium hirsutum (L.)	Chrysopidae	Chrysoperla carnea	◇		Brazil	(Ramalho et al. 2012)
			Coccinellidae	Cycloneda sanguinea	◇		Brazil	(Ramalho et al. 2012)
	Ageratum houstonianum (Mill.)	Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica		◇	China	(Wan et al. 2015)
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata	◇		China	(Wan et al. 2015)
			Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
	Centaurea cyanus (L.)	Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysoperla sinica		◇	China	(Wan et al. 2015)
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata	◇		China	(Wan et al. 2015)
	Tagetes patula (L.)	Brassica oleracea (L.)	Coccinellidae	-	◇		India	(Muthukumar and Sharma 2009)
			Chrysopidae	Chrysopa formosa	◇		China	(Song et al. 2013)
Malus domestica (Miller)		Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysoperla sinica	◇		China	(Song et al. 2013)
			Coccinellidae	Coccinella septempunctata	◇		China	(Song et al. 2013)
			Coccinellidae	Harmonia axyridis	◇		China	(Song et al. 2013)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Song et al. 2013)
			Syrphidae	Episyrphus balteatus	◇		China	(Song et al. 2013)
			Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
Chrysopidae		Chrysoperla sinica	◇		China	(Wan et al. 2015)		

Plant family (aromatic)	Plant species (aromatic)	Main crop	Insect family	Insect species	Effect		Country	Reference
					(+)	(O/-)		
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
Fabaceae	Cassia tora (L.)	Camellia sinensis (L.)	Chrysopidae	-	◇		China	(Zhang et al. 2017)
			Coccinellidae	-		◇	China	(Zhang et al. 2017)
	Medicago sativa (L.)	Brassica oleracea (L.)	Coccinellidae	-	◇		India	(Muthukumar and Sharma 2009)
			Chrysopidae	-		◇	China	(Zhang et al. 2017)
		Camellia sinensis (L.)	Coccinellidae	-		◇	China	(Zhang et al. 2017)
			Chrysopidae	-	◇		Australia	(Mensah 1999)
Lamiaceae	Leonurus artemisia (Lour.)	Camellia sinensis (L.)	Coccinellidae	-		◇	Australia	(Mensah 1999)
			Chrysopidae	-		◇	China	(Zhang et al. 2017)
	Mentha haplocalyx (Bricq.)	Camellia sinensis (L.)	Coccinellidae	-		◇	China	(Zhang et al. 2017)
			Chrysopidae	-		◇	China	(Zhang et al. 2017)
		Pyrus pyrifolia (Burm.)	Coccinellidae	-		◇	China	(Zhang et al. 2017)
			Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica	◇		China	(Wan et al. 2015)
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
	Nepeta cataria (L.)	Pyrus pyrifolia (Burm.)	Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica	◇		China	(Wan et al. 2015)
Coccinellidae			Coccinella septempunctata		◇	China	(Wan et al. 2015)	
Coccinellidae			Harmonia axyridis		◇	China	(Wan et al. 2015)	



Plant family (aromatic)	Plant species (aromatic)	Main crop	Insect family	Insect species	Effect		Country	Reference
					(+)	(O/-)		
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
	Ocimum basilicum (L.)	Malus domestica (Miller)	Chrysopidae	Chrysopa formosa		◇	China	(Song et al. 2013)
			Chrysopidae	Chrysoperla sinica		◇	China	(Song et al. 2013)
			Coccinellidae	Coccinella septempunctata		◇	China	(Song et al. 2013)
			Coccinellidae	Harmonia axyridis		◇	China	(Song et al. 2013)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Song et al. 2013)
			Syrphidae	Episyrphus balteatus		◇	China	(Song et al. 2013)
		Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica		◇	China	(Wan et al. 2015)
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
	Ocimum citriodorum (Vis.)	Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica		◇	China	(Wan et al. 2015)
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
	Satureja hortensis (L.)	Daucus carota (L.)	Coccinellidae	-		◇	Poland	(Jankowska and Wojciechowicz-Żytko 2016)
			Syrphidae	-		◇	Poland	(Jankowska and Wojciechowicz-Żytko 2016)
		Pyrus pyrifolia (Burm.)	Chrysopidae	Chrysopa formosa		◇	China	(Wan et al. 2015)
			Chrysopidae	Chrysoperla sinica		◇	China	(Wan et al. 2015)

Plant family (aromatic)	Plant species (aromatic)	Main crop	Insect family	Insect species	Effect		Country	Reference
					(+)	(O/-)		
			Coccinellidae	Coccinella septempunctata		◇	China	(Wan et al. 2015)
			Coccinellidae	Harmonia axyridis		◇	China	(Wan et al. 2015)
			Coccinellidae	Propylaea quatuordecimpunctata		◇	China	(Wan et al. 2015)
<b>PARASITOIDS</b>								
<b>Found in intercrop</b>								
Apiaceae	Anethum graveolens (L.)	Brassica oleracea (L.)	Ichneumonidae	Diadegma semiclausum		◇	The Netherlands	(Winkler et al. 2010)
Asteraceae	Centaurea cyanus (L.)	Brassica oleracea (L.)	Ichneumonidae	Diadegma spp.		◇	Switzerland	(Juric et al. 2015)
<b>Parasitisation</b>								
Asteraceae	Centaurea cyanus (L.)	Brassica oleracea (L.)	Braconidae	Microplitis mediator		◇	Switzerland	(Balmer et al. 2014)
					◇	◇	Switzerland	(Géneau et al. 2012, 2013)

## 4. Discussion

### 4.1 The role of functional traits in attracting and benefiting natural enemies

#### 4.1.1 Apiaceae aromatic plants

A significant number of studies showed that Apiaceae aromatic plants attract natural enemies and the consumption of their floral resources leads to an increased longevity and/or fecundity (especially predators). *Anethum graveolens*, *C. sativum* and *F. vulgare* are all classified as ‘flowers with open nectar’ by Müller (1881) cited in the BIOLFLOR database of plant traits (Kolz et al. 2002). In this database, it is specified that ‘beetles, flies, syrphids, wasps, medium tongued bees’ are the main pollinators of these flowering species. The present results confirm this assessment for several flower visitors but highlight that it depends on the insect species in the case of the hymenopteran wasps. The relation between corolla morphology and resource consumption by insects is assessed through the morphometrical compatibility between the two. For example, the mouthparts of *Chrysoperla carnae* (Neuroptera: Chrysopidae) and the corolla width of *F. vulgare* were found to be compatible, which suggests that this lacewing species has the ability to feed on its nectar (Nave et al. 2016). Nave et al. reported similar findings for several parasitoid species to *C. sativum* and *F. vulgare* (Tab. 3). Morphometrical compatibility can also be measured by relating insect fitness with flower morphology. Van Rijn and Wäckers (2016) reported that Apiaceae plants have the lowest flower depth and provide the highest longevity to *E. balteatus*, compared to Asteraceae and Fabaceae. They concluded that ‘fitness, as well as flower choice, is resulting from the accessibility of the nectar as defined by the morphology of flowers’. Accessibility to pollen, especially when nectar is not accessible, can also significantly affect fitness of *E. balteatus*, especially its fecundity (Laubertie et al. 2012). More generally, flowers with deep corolla may not be

exploitable by zoophagous hoverflies as the proboscis of most of these species is relatively short (Gilbert 1985). It is also the case of ladybeetles which main mouthparts are short mandibles (Lundgren 2009).

In addition to corolla morphology, color is an important trait involved in plant attractiveness. *Anethum graveolens* and *F. vulgare* have yellow flowers while *C. sativum* is mainly white, which may also explain the attractiveness of predators in the selected experiments. Indeed, yellow, and in some extent white, are known to be attractive to hoverflies (Sutherland et al. 1999; Laubertie et al. 2006; Lunau 2014) and the ladybeetle *H. axyridis* (Mondor and Warren 2000; Adedipe and Park 2010). For lacewings, recent findings showed that *C. carnea* was not sensitive to any color in fields (Koczor et al. 2017) and it may vary among species for parasitoids (Hatt et al. 2017c).

Volatile composition emitted by the plants is another trait involved in attractiveness, as the several retrieved studies show (Tab. 2 and 3). Various volatile compounds produced by Apiaceae have been identified, among them terpenes (e.g.,  $\alpha$ -Pinene, linalool, carvone, p-Cymene, estragole and t-anethole) (Nehlin et al. 1996; Thiéry and Marion-Poll 1998; Gross et al. 2009). These compounds are not specific to Apiaceae plants (Foti et al. 2017) and some natural enemies are sensitive to them, like the predator *E. balteatus* (Verheggen et al. 2008) or the parasitoid *D. rapae* (Kos et al. 2012). Monitoring the blend composition of *A. graveolens*, *C. sativum* and *F. vulgare*, and relating them to natural enemy behaviour, would allow confirming the role of terpenes in the attractiveness of natural enemies to these aromatic plants.

#### 4.1.2 Other aromatic plants

Asteraceae and Lamiaceae were the most studied plants after Apiaceae. There are not a significant number of studies showing that Asteraceae, Lamiaceae, or any other family of

aromatic plants attract natural enemies and provide them benefits in terms of longevity and fecundity. Many Asteraceae and Lamiaceae are classified as ‘flowers with totally hidden nectar’ by Müller (1881) cited in the BIOLFLOR database (Kolz et al. 2002). Asteraceae considered in the present review (i.e., *A. houstonianum*, *C. officinalis*, *C. cyanus*, *T. patula*) have relatively deep corolla (Adrienne et al. 1985; Winkler et al. 2009a; Van Rijn and Wäckers 2016), with nectaries ‘at the base of the narrow tubular corollas of the disc flowers’ (Patt et al. 1997). This morphology prevents the accessibility of nectar to visitors with short mouthparts, which may partly explain the limited attractiveness of these plant species to the studied natural enemies and consequently the limited benefits they provide to them. However, Jervis (1998) highlighted that not all the species of parasitoids have short mouth parts and among those with elongated mouth parts are species of Braconidae and Ichneumonidae. Moreover, some plant species like *C. cyanus* and *T. patula* (Rahat et al. 2005; Van Rijn and Wäckers 2016) offer extrafloral nectar allowing a diversity of nectar feeders to benefit from this resource despite their hidden floral nectaries (Bugg et al. 1989; Wäckers 2004; Géneau et al. 2012, 2013). Regarding Lamiaceae, it must be recalled that some species do not have hidden nectaries: lavender such as *Lavandula stoechas* (L.) is classified as ‘hymenoptera flowers’ which is consistent with Nave et al. (2016) who reported the morphometric compatibility of four parasitoid species with this flower. This variability in corolla morphology and the availability of nectar partly explain the variability of the results obtained between studies (Tab. 3).

Several studies reported the attractiveness of volatiles from Lamiaceae and Asteraceae species to some parasitoids and the ladybeetle *H. axyridis* (Tab. 2 and 3). Interestingly, volatile compounds were identified. Phenylpropanoid estragole and terpenoids (including linalool, (E)- $\alpha$ -bergamotene, c-amorphene and b-copaene) were identified as the dominant components of *O. basilicum* volatiles and terpinolene, (Z)-3-hexen-1-ol, (Z)-3-hexenyl acetate and

benzeneacetaldehyde as the main components of *T. platula*'s (the whole plants were used so the extracted volatiles were a mix of floral and vegetative compounds) (Foti et al. 2017). Foti et al. moreover showed an antennal response of the parasitoid *T. basalis* to (Z)-3-hexenyl acetate specifying the importance of this compound in the attractiveness of *O. basilicum*. With a similar approach, D-limonene and terpinolene were identified as major components of both *T. patula* and *Nepeta cataria* (L.) (Lamiaceae) volatiles and D-limonene at low concentration, but not terpinolene alone, attracted the ladybeetle *H. axyridis* (Song et al. 2017). These studies are recent, hence continuing the identification of the volatile compounds from aromatic plants involved in the attractiveness of natural enemies would help, along with the knowledge on other functional traits, to identify the plant species that may be used to support predators and parasitoids, and potentially enhance biological control in agricultural fields.

## 4.2 Enhancing biological control

### 4.2.1 The role of prey/host identity

Asteraceae and Lamiaceae were the most studied aromatic plants (Tab. 4). Their ability to favour the presence of predators was especially studied in pear *Pyrus pyrifolia* (Burm.) (Rosaceae) (Wan et al. 2015), apple *Malus domestica* (Miller) (Rosaceae) (Song et al. 2013) and tea *Camellia sinensis* (L.) (Theaceae) (Zhang et al. 2017) plantations in China. Compared to clean tillage in pear orchards, Asteraceae *A. houstonianum* and *C. cyanus* enhanced the abundance of the ladybeetle *P. quatuordecimpunctata* (in this study: syn. *P. japonica*), while *T. platula* along with the Lamiaceae *Mentha haplocalyx* (Bricq.), *N. cataria*, *O. basilicum* and *O. citriodorum*, supported the lacewing *Chrysoperla sinica* (Neuroptera: Chrysopidae) and both *Ocimum* sp. increased *Chrysopa formosa* (Neuroptera: Chrysopidae) (Wan et al. 2015). In this same study, none of the tested aromatic plants favoured ladybeetles *H. axyridis* and *C.*

*septempunctata*. Conversely, the same predatory species, along with the hoverfly *E. balteatus*, were enhanced in apple trees adjacent to *T. platula* and *O. basilicum* compared to naturally developed grass plants (Song et al. 2013). These studies show that *H. axyridis* and *C. septempunctata* are differently affected by the aromatic plants when they are in apple orchard infested by aphids (*Aphis citricola* [Hemiptera: Aphididae]) or pear orchards infested by mealybugs (*Pseudococcus comstocki* [Hemiptera: Pseudococcidae]). It suggests that not only the chosen aromatic plant but also the crop and/or the prey species affect the abundance of these ladybeetles. *Harmonia axyridis* and *C. septempunctata* can both colonize orchard ecosystems (Vandereycken et al. 2012) (even if they have their own habitat preferences, Osawa, 2011). Regarding their feeding preferences, Lucas et al. (1997) showed that both *H. axyridis* and *C. septempunctata* prey more on *A. citricola* than on a non-aphid prey. Moreover, *H. axyridis* life cycle is known to be related to aphid population dynamic (Osawa 2000). This preference for aphids may partly explain the presence of ladybeetles in the apple orchards infested by aphids. Finally, Song et al. (2017) showed that the combination of volatiles from *T. platula* and aphid-infested apple trees was particularly attractive to *H. axyridis*, suggesting that both an attractive aromatic plant and a preferred prey may be determinant to attract natural enemies in agroecosystems.

#### 4.2.2 The role of environmental factors

Apiaceae were studied in fields associated with a diversity of crops (Tab. 4). Especially *C. sativum* was associated with four different cultivated species and variable results were found concerning the abundance of predators in these crops. It may be surprising since a number of studies showed that predators are attracted by *C. sativum* volatiles, visit its flowers, consume its resources and, for some of them, get benefits in terms of longevity and fecundity (Tab. 2). Pascual-Villalobos et al. (2006) studying lettuce *Lactuca sativa* (L.) (Asteraceae) reported

experimental protocol limitations (i.e., treatment plots were too close) to explain that predatory hoverflies were found both in control plots and in plots bordered with *C. sativum*. Morris and Li (2000) also pointed that *C. sativum* blooming duration was not long enough (only three weeks in their experiment) to significantly support hoverflies in adjacent cabbage *Brassica oleracea* (L.) (Brassicaceae). Moreover, inconsistent effect through years may occur (Balmer et al. 2014), which highlights uncertainties in the efficiency of aromatic plants to enhance biological control when associated to crops. In fields, environmental factors varying through time such as climatic conditions or the landscape composition can affect the yearly abundance and diversity of insects (Vandereycken et al. 2013; Schneider et al. 2015). The temporal overlap between the occurrence of prey/hosts and their natural enemies may also be disrupted (Evans et al. 2013) with detrimental consequences on the expected service of biological control (Welch and Harwood 2014; Cohen and Crowder 2017). Additionally, landscape composition at a given time can affect the abundance and diversity of pests, natural enemies and biological control in fields (Chaplin-Kramer et al. 2011; Veres et al. 2013), with existing interactions between the local management (e.g., sowing of flowering plants) and the landscape heterogeneity (Jonsson et al. 2015). None of the reviewed studies considered the effect of the landscape composition and configuration when evaluating the introduction of aromatic plants in intercropping systems to enhance biological control, despite this landscape effect may be responsible for the variability of results observed in fields (Tschardt et al. 2005; Isaacs et al. 2009).

## **5. Conclusions and perspectives**

The present review shows that Apiaceae *A. graveolens*, *C. sativum* and *F. vulgare* aromatic species attract and benefit a diversity of natural enemies, mostly predators. However, further



studies assessing applications in fields towards biological control of insect pests are needed. Concerning Asteraceae and Lamiaceae species, contrasting results among plant and insect species ask for caution when these species are chosen to be sown in fields. The other plant families (i.e., Brassicaceae, Fabaceae, Pinaceae, Rosaceae, Solanaceae) have been only evenly studied. Further research could consider a diversity of plant species belonging to these families and evaluate the interactions between them and natural enemies by using the same kind of indicators reviewed here. Still, species proposing large amount of pollens, such as the Fabaceae *M. sativa*, are promising to support pollen feeders like ladybeetles but also hoverflies.

Aromatic plants are known to be fragrant and odours produced by plants are one of the traits involved in the attraction of insects. Volatiles are produced by different organs of the plant (i.e., flowers, leaves) and most of studies used the whole plant to assess the attractiveness of volatiles. Using flowers or leaves only (Yong et al. 2007; Adedipe and Park 2010; Belz et al. 2013), and even comparing the attractiveness of flowers to the attractiveness of leaves (Foti et al. 2017), provides useful information to understand the role of volatiles in natural enemy-flowering plant interactions. Moreover, the present review shows that, despite many studies tested the attractiveness of aromatic plant volatiles to insects, few went further by identifying what are the chemical compounds involved, the effect of compound associations and the effects of their concentrations. Hence, the recent studies of Foti et al. (2017) and Song et al. (2017) could pave the way for future research.

Whereas the present review focused on natural enemies, attention must be paid to verify that the selected aromatic plants do not support pests that would also feed on flower resources. Indeed Winkler et al. (2009a) showed that *A. graveolens* and *F. vulgare* support the longevity of *Plutella xylostella* (Lepidoptera: Plutellidae) and that *O. vulgare* supports the longevity of both *P. xylostella* and *Pieris rapae* (Lepidoptera: Pieridae), which are pests of various

Brassicaceae crops. Baggen and Gurr (1998) also showed that the fecundity of *Phthorimaea operculella* (Lepidoptera: Gelechiidae), a pest of potatoes (*Solanum tuberosum* L.; Solanaceae), was enhanced when it fed on *C. sativum* flowers. Relatively few studies conducted such assessments, compared to those studying natural enemies. Moreover, it is needed to know if the benefits pest species could get from flowering plants would result in higher infestations of crops and damages in adjacent fields. Indeed, aromatic plants attractive to pests could also serve as trap crops, and if they are not suitable for the survival of their larvae, they could even be seen as dead-end trap crops (Shelton and Badenes-Perez 2006). Alternatively, aromatic plants could also repel pests or mask the odours of their host plant, thus protecting the target crop without natural enemy control (Thiery and Visser 1986). Finally, aromatic plants could host alternative prey or hosts that would attract and support natural enemies when prey are scarce in adjacent crops (i.e., aromatic plants as banker plants, Huang et al. 2011).

The present review highlights a recent interest for sowing aromatic plants in fields towards biological control of insect pests in East Asia, especially in China (Tab. 4). However, only a limited number of plant species have been studied and a long list of species deserves to be considered (Tab. S1). A priority could be given to those being commonly used as food and/or medicine by people in these regions. Indeed, social relevance and economic viability of diversified cropping systems and landscapes are the keys to encourage and consolidate the development of a sustainable agriculture (Hatt et al. 2016).

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