

FLOWERING PLANTS AND ENTOMOPHAGOUS ARTHROPODS IN THE AGRICULTURAL LANDSCAPE: A PRACTISE-ORIENTED SUMMARY OF A COMPLEX RELATIONSHIP

Zhizhi WANG^{1,2}, Pu TANG^{1,2}, Min SHI^{1,2}, Jianhua HUANG^{1,2,3}, Xuexin CHEN (✉)^{1,2,3,4}

1 Institute of Insect Science, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China.

2 Ministry of Agriculture Key Laboratory of Molecular Biology of Crop Pathogens and Insect Pests, Zhejiang University, Hangzhou 310058, China.

3 Key Laboratory of Biology of Crop Pathogens and Insects of Zhejiang Province, Zhejiang University, Hangzhou 310058, China.

4 State Key Laboratory of Rice Biology, Zhejiang University, Hangzhou 310058, China.

KEYWORDS

ecosystem services, flowering plants, natural enemies, nectar, pollen

HIGHLIGHTS

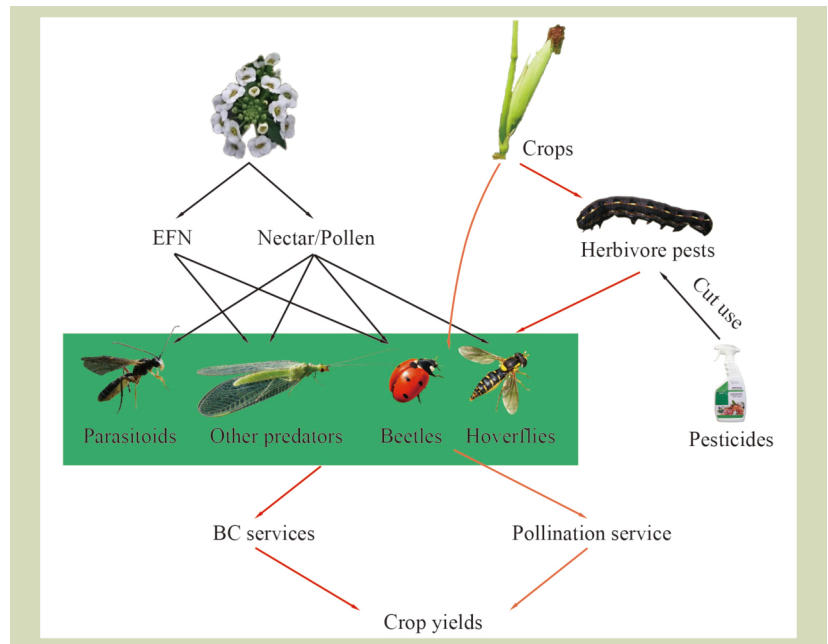
- Most entomophagous arthropods consume nectar or pollen as alternative diets.
- The attractive of floral resource with different traits varies in a wide degree.
- Floral resource plays positive effects on not only entomophagous insects but also agricultural biodiversity, multiple ecosystem services and crop production.

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Correspondence: xxchen@zju.edu.cn

GRAPHICAL ABSTRACT



ABSTRACT

There is a growing demand for high-quality agricultural products and more countries have adopted landscape management by sowing flowering plants in agricultural fields as an important branch of conservation biological control. However, there has been less concern over the interactions and trade-offs between floral plants and entomophagous arthropods. This paper review progress in pollen/nectar feeding habits of entomophagous insects including parasitoids and predators which are important natural enemies of crop pests in agricultural fields. Factors that influence the preference of different guilds of

natural enemies are reviewed to guide the selection of flowering plants in conservation biological control practices. Most studies find that floral resources have positive effects on both biological traits of natural enemies and their abundance and diversity, and this is believed to contribute greatly to pest control. Furthermore, the potential impacts of floral resources on crop yields are also discussed with an emphasis on a guild of entomophagous insects that provides both pest control and pollination services.

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1 INTRODUCTION

Entomophagous arthropods are predatory and parasitic insects. Most of these insects can be used for the control of herbivore pests and they provide valuable ecosystem services that are the multitude of benefits that humans obtain from the ecosystem^[1]. In addition to their entomophagy propensity, most taxonomic groups of entomophagous arthropods visit flowering plants to feed on nectar or pollen. The floral nectar is a fluid produced by the flower whereas pollen is the sperm cells of the plant. Many plants have extrafloral nectar, a fluid from nectar-producing glands physically separated from the flower, helpful to beneficials. Nectar is important primarily as an energy source for many entomophagous arthropods. The main components in most nectars are glucose, fructose and sucrose. Also, about 10% of nectar dry weight is represented by many classes of non-sugar metabolites including amino acids, vitamins, alkaloids, phenolics, terpenoids, lipids, metal ions, hormones and proteins, which have diverse functions in attracting mutualists while at the same time deterring exploitative visitors^[2]. In contrast, pollen is rich in proteins, lipids, carbohydrates (mainly starch) and minerals, and consequently is one of the most nutritious non-host food sources^[3]. The detailed chemical composition of nectar and its nutritional value have been extensively reported^[4]. These floral resources are vital to the energetic and nutritional requirements of entomophagous insects. The benefits of floral resources have inspired much research on the relationship between flowering plants and entomophagous arthropods which covers a wide range of topics such as rewards provided by flower visiting, factors that influence the flower preferences of entomophagous species, and the implications of multitrophic interaction in biological control practices^[5–8]. However, many scientists note that flowering plants not only benefit natural enemies but can also have other positive effects on the life history of many agricultural pests^[9–14]. Here, we review research progress on the relationships between flowering plant and arthropods, especially entomophagous species, aiming to provide useful information for the

application of flowering plants in habitat management practices and thus improve the reliability of conservation biological control in agricultural ecosystems.

2 ENTOMOPHAGOUS ARTHROPODS THAT REQUIRE FLORAL RESOURCES

It is estimated that about 30% of arthropod species (> 350,000 described species) regularly use flowers to feed, find a mate, or obtain other resources, and the actual number would be much larger if global species diversity were taken into account^[15]. Despite the well-documented pollinators, many other flower-visiting arthropods may have been largely ignored in the study of pollination biology. Here, we attempt to present an overview of the taxonomic range of flower-visiting entomophagous arthropods and their feeding requirements (Table 1).

The flower-visiting entomophagous arthropods can be grouped into two categories according to their requirements for floral resources. Species that require floral resources for at least part of their life-cycle are defined as obligate flower-visitors. Examples of this category are found in groups of the Diptera (Bombyliidae, Conopidae, Phoridae, Syrphidae and Tachinidae)^[15] and certain Hymenoptera (Chalcidoidea)^[29]. Species defined as facultative occasionally consume floral resources but are not obviously dependent on them. Examples include most predacious Coleoptera, Hemiptera, Mantodea, Neuroptera and Thysanoptera, as well as some parasitic Hymenoptera, and some other flower-visiting invertebrates (Acari and Araneae).

Most dipteran adults visit flowers to feed primarily on nectar but the ability to feed on pollen has been described for some species including the hoverflies (Empididae and Syrphidae). All adults of the Syrphidae are believed to use nectar and pollen as principal foods^[20]. Field observations strongly suggest that most hymenopterous parasitoids feed on nectar, particularly sugars and free amino acids^[30]. Although the pollen feeding

Table 1 Entomophagous arthropods and their preference for floral resources and extrafloral nectar (EFN)

Order	Family	Predators or parasitoids	Obligate flower-visitors or not	Pollinators or not	Type of non-prey food	Reference	
Araneae	Oxyopidae	Predators			Nectar/pollen/EFN	[16]	
	Thomisidae	Predators			Nectar /pollen/EFN		
Mesostigmata	Phytoseiidae	Predators			Nectar /pollen	[17,18]	
Neuroptera	Hemerobiidae	Predators			Nectar	[19]	
	Chrysopidae	Predators			Nectar		
	Coniopterygidae	Predators			Nectar		
Diptera	Syrphidae	Predators	Yes	Yes	Nectar/pollen	[20]	
	Dolichopodidae	Predators			Nectar		
	Empididae	Predators		Yes	Nectar/pollen		
	Asilidae	Predators			Nectar		
	Cecidomyiidae	Predators			Nectar		
	Tachinidae	Parasitoids	Yes	Yes	Nectar		
	Phoridae	Parasitoids	Yes		Nectar		
	Bombyliidae	Parasitoids	Yes	Yes	Nectar/pollen		
	Conopidae	Parasitoids	Yes	Yes	Nectar		
	Coleopteran	Meloidae	Predators	Yes	Yes	Nectar/pollen	[21,22]
Cantharidae		Predators		Yes	Nectar/pollen/EFN		
Carabidae		Predators			Pollen/EFN		
Coccinellidae		Predators		Yes	Nectar/pollen/EFN		
Staphylinidae		Predators			Pollen/EFN		
Cleridae		Predators		Yes	Nectar/pollen		
Cucujidae		Predators			Unknown		
Rhipiphoridae		Predators			Unknown		
Hemiptera		Anthocoridae	Predators		Yes	Nectar/pollen/EFN	[23,24]
		Nabidae	Predators			Nectar/pollen/EFN	
	Pentatomidae	Predators			Nectar/pollen/EFN		
	Geocoridae	Predators			Nectar		
	Reduviidae	Predators			Nectar/pollen/EFN		
	Phymatidae	Predators			Nectar		
Thysanoptera	Aeolothripidae	Predators			Nectar/pollen	[25]	
Mantodea	mantidae	Predators			Pollen	[26]	
Hymenoptera	Orussidae	Parasitoids			Nectar	[20]	
	Trigonalyidae	Parasitoids			Nectar		
	Megalyridae	Parasitoids			Nectar		
	Evaniidae	Parasitoids			Nectar		
	Aulacidae	Parasitoids			Nectar		
	Gasteruptionidae	Parasitoids			Nectar		
	Stephanidae	Parasitoids			Nectar		
	Cynipidae	Parasitoids			Nectar		
	Liopteridae	Parasitoids			Nectar		

(Continued)

Order	Family	Predators or parasitoids	Obligate flower-visitors or not	Pollinators or not	Type of non-prey food	Reference
	Figitidae	Parasitoids			Nectar	
	Ibaliidae	Parasitoids			Nectar	
	Eurytomidae	Parasitoids	Yes		Nectar	
	Pteromalidae	Parasitoids	Yes		Nectar	
	Trichogrammatidae	Parasitoids			Nectar/pollen	[27]
	Megastigmidae	Parasitoids	Yes		Nectar	
	Rotoitidae	Parasitoids	Yes		Nectar	
	Signiphoridae	Parasitoids	Yes		Nectar	
	Perilampidae	Parasitoids	Yes		Nectar	
	Ormyridae	Parasitoids	Yes		Nectar	
	Tetracampidae	Parasitoids	Yes		Nectar	
	Encyrtidae	Parasitoids	Yes		Nectar	
	Eupelmidae	Parasitoids	Yes		Nectar	
	Aphelinidae	Parasitoids	Yes		Nectar	
	Chalcididae	Parasitoids	Yes		Nectar	
	Eucharitidae	Parasitoids	Yes		Nectar	
	Mymaridae	Parasitoids	Yes		Nectar	
	Eulophidae	Parasitoids	Yes		Nectar/pollen	
	Tanaostigmatidae	Parasitoids	Yes		Nectar	
	Pelecinidae	Parasitoids	Yes		Nectar	
	Torymidae	Parasitoids	Yes		Nectar	
	Leucospidae	Parasitoids	Yes		Nectar	
	Mymarommatidae	Parasitoids			Nectar	
	Austroniidae	Parasitoids			Nectar	
	Heloridae	Parasitoids			Nectar	
	Diapriidae	Parasitoids			Nectar	
	Vanhorniidae	Parasitoids			Nectar	
	Maamingidae	Parasitoids			Nectar	
	Proctotrupidae	Parasitoids			Nectar	
	Monomachidae	Parasitoids			Nectar	
	Proctorenyxidae	Parasitoids			Nectar	
	Roproniidae	Parasitoids			Nectar	
	Peradeniidae	Parasitoids			Nectar	
	Platygastridae	Parasitoids			Nectar	
	Megaspilidae	Parasitoids			Nectar	
	Ceraphronidae	Parasitoids			Nectar	
	Ichneumonidae	Parasitoids			Nectar/pollen	
	Braconidae	Parasitoids			Nectar/pollen	
	Sapygidae	Parasitoids			Nectar	

(Continued)

Order	Family	Predators or parasitoids	Obligate flower-visitors or not	Pollinators or not	Type of non-prey food	Reference
	Vespoidea	Parasitoids			Pollen	
	Eucoilidae	Parasitoids			Nectar	
	Chrysididae	Parasitoids			Nectar	
	Scoliidae	Parasitoids			Nectar/pollen	
	Tiphidae	Parasitoids			Pollen	
	Mutillidae	Parasitoids			Pollen	
	Scelionidae	Parasitoids			Nectar	
	Bethylidae	Parasitoids			Nectar	
	Pompilidae	Predators			Nectar	
	Sphexidae	Predators			Nectar	
	Formicidae	Predators	Yes/F	Yes	Nectar/EFN	[28]
	Nyssonidae	Predators			Nectar	
	Bradynobaenidae	Parasitoids			Nectar	
	Embolemyidae	Parasitoids			Nectar	
	Scolebythidae	Parasitoids			Nectar	
	Sclerogibbidae	Parasitoids			Nectar	
	Dryinidae	Parasitoids			Nectar	

Note: Animals with an unclear status were excluded from this analysis.

habit of parasitoids has been partly investigated, it is usually considered less valuable and several species including the trichogrammatid and braconid parasitoids are reported to use pollen as an alternative source of food^[31,32]. Although both sexes were found on flowers and other plant parts, females were observed feeding most often. In addition to frequently feeding on floral nectar sources, there is direct evidence that predaceous coleopterans exploit pollen and extrafloral nectar as alternative diets^[21,22]. Among the Hemiptera, predaceous species are phytophagous to varying degrees and members of the Anthocoridae, Geocoridae, Nabidae, Pentatomidae (Asopinae), Phymatidae and Reduviidae all feed on nectar. Some species of the Anthocoridae, Reduviidae and Pentatomidae also feed on pollen and extrafloral nectar^[23,24]. Mantids (Mantodea) are frequently seen on flowers waiting for potential prey, and several species have been observed feeding on pollen, including Chinese mantids (*Tenodera aridifolia*)^[26]. Among the Neuroptera, adults of the Chrysopidae, Hemerobiidae and Mantispidae feed on sugar sources of various classes under field conditions. Most adults of some genera (*Eremochrysa*, *Hypochrysa*, *Kimochrysa*, *Pamochrysa* and *Pimachrysa*) within the Chrysopidae (green lacewings) appear to be predominately pollinivorous^[19]. Among the Thysanoptera, many predaceous species of the Aeolothripidae

include pollen in their diets^[25]. Predaceous mites frequently feed on a range of sugar sources including nectar, honeydew and extrafloral nectar, whereas pollen feeding has been reported in several families (Araneidae, Erythraeidae, Phytoseiidae, Stigmaeidae and Thomisidae)^[24]. It is reported that predatory mite species differ greatly in their ability to use pollen^[17,18]. The degree of pollen consumption is used to classify Phytoseiid mites into four groups, and members of Group IV (e.g., *Euseius* spp.) can complete their development by feeding on pollen in the absence of prey^[33]. Spiders (Arachnida: Araneae) have been generally regarded as strict carnivores but it is now widely known that nectar and pollen are of dietary importance for at least a small number of species. Also, extrafloral nectar is also frequently consumed by spiders^[16].

3 IMPACTS OF FLORAL RESOURCES ON ENTOMOPHAGOUS INSECTS

Resources derived from flowering plants such as nectar and pollen provide many essential nutrients for the growth and development of entomophagous arthropods, especially when prey is scarce or of low quality. The positive effects of floral

resources on entomophagous arthropods have been well-studied in the field of conservation biological control, especially on increased longevity, fecundity, searching and parasitism/predation rate as well as the female ratio^[5]. However, the impacts of nectar/pollen feeding depend on the interactions between entomophagous species and the characteristics of floral resources.

Parasitic wasps often obtain nutrients by feeding in or on the bodies of other arthropods, ultimately killing them. The adults are typically free-living and most parasitic wasps are synovigenic, i.e., adults emerge with an immature reproductive system and undergo a pre-maturation period before being capable of mating^[34]. The life span, mating ability, fertility, fecundity and sex ratio of parasitoids can be affected by the quality of adult diets. In most cases the provision of carbohydrate-rich diets enhances the longevity and fecundity of parasitic wasps^[35–40]. Floral feeding experiences significantly influence the searching and dispersal behavior of some parasitoids^[41,42]. For example, *Aphidius ervi* fed with buckwheat nectar spent a higher proportion of their time actively in searching than those with access to water only, and spent almost twice as much time in attacking and carried out nearly twice as many attacks as unfed parasitoids^[43]. Siekmann et al. (2004) also found that well-fed *Cotesia rubecula* exhibited a preference for hosts while unfed individuals visited hosts and flowers in equal proportions^[44]. In the case of trophic food webs, habitat modification especially floral resources provision can alter the structure of trophic host-parasitoid food webs by enhancing abundance of parasitoids and the levels of parasitism^[45–47]. Based on these cases a parasitoid nectar-provision hypothesis seems reasonable with the presence of nectar-producing plants increasing biological control of pests by supplying parasitoids with sugars or floral sources^[48].

Most hoverfly species are life-history omnivores and synovigenic^[49]. Floral resources affect hoverfly fitness and nutritional status in different ways^[50–54]. Pollen provides essential nutrition for female ovarian maturation and egg production^[55] and nectar significantly increases the longevity and oviposition rate^[50,51]. Compared with pollen feeding, nectar accessibility is the main driver determining flower resource suitability, flower choice and hoverfly abundance in the field^[50]. Selective flowers with accessible nectar such as wild parsnip (*Pastinaca sativa*), sweet alyssum (*Lobularia maritima*), coriander (*Coriandrum sativum*), phacelia (*Phacelia tanacetifolia*), fennel (*Foeniculum vulgare*), buckwheat (*Fagopyrum esculentum*) and common mallow (*Malva sylvestris*) have been considered to be useful floral plants that enhance the longevity and fecundity of adult hoverflies^[50,53,56,57]. Also, richness and abundance of

aphidophagous syrphids are positively correlated with flower density in sample landscape^[58]. This benefit correspondingly makes an important contribution to aphid pest control^[59].

As for other natural enemies, generalist predators such as predaceous beetles, green lacewings, mantids and mites, as well as spiders are attracted to many kinds of flowering plants^[21,60,61]. They usually have broad diets and often use plant resources as supplementary food. As non-prey diets, flowering plants especially pollen can considerably prolong the longevity and increase the survival and fecundity of many flower-visiting predators when prey are absent^[62–66]. For example, when provided with both cowpea and buckwheat, *Orius insidiosus* survived 35% longer and laid 111% more eggs compared to a single-species control^[67]. In addition, the positive effects of supplemental floral diets on generalist predators usually led to population increase and a high predation rate^[64,68–70].

However, this is not always the case when considering the use of floral resources in conservation biological control. For example, sugar and flower diets increased the adult longevity of the two spotted lady beetle *Adalia bipunctata* whereas the fecundity was nil on all non-prey diets^[62]. In some predators, floral diets or sugar sources do not support juvenile molting^[62,71,72]. Also, there are studies reporting that the addition of nectar or pollen sources affects the diversity and population community of many natural enemies without increasing pest suppression^[73]. It is also reported that insect herbivores consume nectar and pollen for nutritional requirements as well, which has a strong impact on the population structure of agricultural ecosystems^[2]. Some studies have confirmed that herbivorous pests reach higher population densities and oviposition in the presence of flowering companion plants^[9–11]. Also, buckwheat flowers significantly increased the longevity and fecundity of parasitoids as well as their associated herbivorous pests^[12–14]. With the impact of biological control on herbivores as well as entomophagous insects, researchers have long been aware that the complicated interaction between the vegetation, herbivorous pests and natural enemies in the food web and the balance between top-down [refers to the action of natural enemies (third trophic level) on herbivores] and bottom-up (refers to the action on herbivore pests (second trophic level) of vegetation (first trophic level)] effects were affected by the provision of nectar or pollen. Given the reported specificity of flower exploitation patterns between pests and their natural enemies (discussed below) the relative benefits for natural enemies versus pests depend on the flowering species used in crop fields^[74]. Thus, leveraging floral resources to promote biological control

requires carefully screening flowering species for their prospective suitability for both natural enemies and also for targeted pests.

4 SELECTION OF FLOWERING PLANTS IN AGRICULTURE PRACTICES

The global diversity of flowering plants is estimated at ~ 248,000 species but it is clear that only a tiny fraction of the plants have potential use in habitat management^[75]. So far, 165 species of plants appear to have been field-tested for their utility in habitat management, of which more than 10 plant species from four families (Apiaceae, Asteraceae, Fabaceae and Lamiaceae) are the most frequently studied^[76]. Also, a number of methods have been used to access the attractiveness of flowering plant species to natural enemies and pests^[6]. Flower morphology, color, nectar accessibility and chemical composition have been recognized as important factors influencing the behavior and preference of target organisms. Surveys on visitation to flowering plants show that a large number of wasps in the family Ichneumonidae were collected on Umbelliferae due to the greater accessibility of the nectar^[30]. A 33-year survey shows that species diversity of parasitoids was highest on plant species of the Apiaceae (*Cicuta maculate*, *Heracleum maximum*, *Oxypolis rigidior*, *P. sativa*, *Perideridia americana* and *Sium suave*) and Asteraceae (*Symphotrichum pilosum*, *Eupatorium serotinum* and *Solidago canadensis*)^[77]. Subsequently, Tooker et al.^[78] reported the most preferred plant species by syrphid and tachinid species were the asteraceous *Aster pilosus* and *Heracleum maximum* and the umbellifer *P. sativa*, which matched the preference range of parasitoids. Plants in the family Polygonaceae, such as domesticated and wild buckwheat, *Fagopyrum esculentum* and *Eriogonum* spp., respectively, common knotweed, *Polygonum aviculare*, and *Sesamum indicum* (Pedaliaceae) are also reported as important honey plants presenting exposed floral nectaries in small flowers that provide easily-accessible nectar^[79]. The quality and abundance of floral resources in time and space can affect the specificity and diversity of flower-visiting insects. A study of floral attractiveness to parasitic Hymenoptera shows that the floral-area is positively associated with the abundance of Braconidae and Chalcidoidea, and plants with higher flower density also support more both predator and pest populations^[80,81]. However, the presence of flowers with certain traits can be a stronger driver for attracting parasitoids or predators compared to the high-density plantation of unattractive plants or the presence of prey, indicating that the selective effects of flowering plant species should be taken as a primary consideration when it comes to natural enemy conservation^[81–83].

Furthermore, it is important to screen flowering plant species with differing life histories and characteristics. Most efficacy studies of non-crop flowering habitats focus on only one or a few flower species^[56,64,84,85]. Alyssum flowers in vegetable fields are effective in attracting generalist predators (coccinellids, *Orius* sp., spiders and syrphids) which in turn translates into a significant reduction in vegetable pests, resulting in an enhancement of vegetable quality through elevated natural enemy fitness^[86,87]. Similarly, single-species nectar-producing plant borders added to rice paddies promote biological control, leading to a trophic cascade that increases grain yields and provides economic advantages^[88]. However, single-species nectar-producing plants may lead to pest-control problems. Therefore, mixtures of flowering species with different characteristics can be complementary in supporting a diversity of insects^[74]. After a six-year study, Cahenzli et al.^[89] successfully managed fruit damage for the first time using the rosy apple aphid *Dysaphis plantaginea* in an insecticide-free apple orchard optimized for self-regulation of pests by introduction of a series of biocontrol strategies including extensively managed strips of flowering plants. Despite no clear effects on the yield or quality of harvested apple (weight and size), flowering strips with careful selection of multiple plant species can provide floral resources for both pollinators and natural enemies in orchards, and enhance predator activity in adjacent apple trees^[90].

5 EFFECTS OF FLOWERING PLANTS IN AGRICULTURAL SYSTEMS

Flowering plants increase natural enemy biodiversity but less is known about the effects of floral resources on multitrophic interactions and other ecosystem services. However, natural enemy diversity in general enhances herbivore pest suppression in agricultural systems, although the magnitude of the effect differs substantially between studies and is often negative^[7,8]. A modeling stimulation also shows a positive response of natural enemy visitation rate of pest-colonized crops in response to increased proportion of semi-natural habitats in the landscape^[91]. The degree to which natural enemies suppress herbivore populations potentially affects net primary productivity, crop yield and plant composition. Gurr et al. reported that sesame planted around rice fields significantly reduced populations of two types of planthopper, reduced insecticide application by 70%, increased grain yields by 5% and delivered an economic advantage of 7.5%^[88]. For decades the FAO has emphasized the management of pests through good agronomy, biological diversity and ecological processes to lower the amount of pesticide required. These FAO programs

have attained pesticide cuts of 50%–80% on millions of farms without compromising productivity^[92].

Global food crops benefit from pollinating animals. In addition to bees, non-bee pollinators also contribute greatly to crop production with a total GDP of over 1.2 billion USD^[93]. In our view, some flower-visiting insects provide both biological control and pollination services. Compared to the record of non-bee pollinator taxa, several families hold great promise in provision of dual ecosystem services, including two families of flies (Syrphidae and Tachinidae) and one beetle family (Coccinelidae). The Syrphidae (hoverflies) was the most frequent non-bee family visiting over half of the crop species. Flowering plants enhance pest control and pollination in many crops by increasing the hoverfly species abundance and richness but several recent reports demonstrate that aphidphagous hoverflies significantly increase yields by 10%–29% in non-infested crop fields^[49,94,95]. However, the role of other entomophagous insects as pollinators has usually been poorly investigated.

6 CONCLUSIONS AND PERSPECTIVES

Many entomophagous insects benefit from the provision of

flowering plant strips around or in crop fields as non-crop habitats and thus enhance biological control. The establishment of strips of flowering plants combined with other environmentally friendly techniques is an important aspect of ecological intensification and generally reduces the use of pesticides and assists in meeting rising demands for high quality and security of agricultural products. However, limitations and knowledge gaps in the use of floral resources in ecological intensification and their potential contribution to crop yields still need to be addressed. Moreover, the overall outcome of the presence of floral resources relies on their intrinsic attributes, agricultural practices, and other human activities. Although scientists are increasingly highlighting the benefits of conserved biological control practices through the establishment of strips of flowering plants to support the biodiversity and abundance of natural enemies, farmers generally seem to have little interest in this topic. Strikingly, this practice, which is often eligible for subsidy support by the European Union and United States governments, is one of the practices most disliked by farmers, followed by other on-field management practices such as cover crops, conservation headlands or beetle banks^[96]. It is therefore important to consider factors such as extension services, short-term economic benefits, public attitudes and government policies, that affect the adoption of nature-based management practices by farmers.

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Compliance with ethics guidelines

Zhizhi Wang, Pu Tang, Min Shi, Jianhua Huang, and Xuexin Chen declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any study with human or animal subjects performed by any of the authors.

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