Entomologia Generalis, Vol. 46 (2026), Issue 1, 5–20
Published online March 31, 2026

Steering biological control through agroecosystem diversification: the case of *Harmonia axyridis*

Séverin Hatt[1,], Xiaoling Tan[2,**], Ibtissem Ben Fekih[3], Frédéric Francis[3], Grégoire Noël[3], Naoya Osawa[4], Yunfei Pan[2], Arnaud Segers[3], Su Wang[5], Kris A. G. Wyckhuys[2,6,7], Long Yang[2], Qingxuan Xu[3,5,*]**

[1] Natagriwal asbl, Namur, Belgium
[2] State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China
[3] Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, Université de Liège, Gembloux, Belgium
[4] Laboratory of Applied Entomology, Faculty of Agriculture, Setsunan University, Osaka, Japan
[5] Key Laboratory of Environment Friendly Management on Fruit and Vegetable Pests in North China (Co-construction by Ministry and Province), Ministry of Agriculture and Rural Affairs, Institute of Plant Protection, Beijing Academy of Agriculture and Forestry Sciences, Beijing, China
[6] Chrysalis Consulting, Da Nang, Vietnam,
[7] School of the Environment, The University of Queensland, St. Lucia, Australia
* Corresponding author: xuqxfarmer@126.com
** These authors contributed equally to this work.

With 3 figures and 2 tables

Abstract: Increasing plant diversity in crop production systems has the potential to enhance natural enemies of insect pests and improve biological control. The ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) is a predator of multiple pests, mainly aphids. Native to Northeast Asia, this species was intentionally introduced into many countries during the early and mid-1900s. Its subsequent spread in Europe, Africa, and the Americas caused major concerns due to its competition with, and (intraguild) predation on, resident biota. As an eradication of *H. axyridis* in its invaded range is impossible, efforts could be made to exploit its role as a biological control agent in agricultural settings and mitigate its negative impact on biodiversity. We outline how on- and off-farm measures affect *H. axyridis* abundance and behaviour, both in its native and invasive ranges. Crop and non-crop diversification can provide shelter and nutritional resources for resident predators, reduce predation on non-target biota and thereby sustain biodiversity in farmland ecosystems. Drawing upon insights into the ecology of *H. axyridis*, we describe how annual crop successions and polycultures, companion planting, non-crop habitats, and insectary or banker plants can strengthen its role as a biological control agent in different settings. We conclude by discussing whether increasing plant diversity can potentially steer *H. axyridis* predation away from non-target biota. As such, our study provides guidance for conservation and biological control science and practice in *H. axyridis* native and invaded farmland ecosystems.

Keywords: Coccinellidae; conservation biological control; Harlequin ladybird; intraguild predation; landscape management; mixed cropping; multi-colored Asian lady beetle

1 Introduction

Integrated pest management (IPM) and agroecological crop protection (ACP) have been proposed as concepts and strategies to resolve pest issues with fewer or no use of synthetic pesticides (Barzman et al. 2015; Deguine et al. 2017). Despite a considerable gap between IPM theory and practice (Deguine et al. 2021), both highlight the necessity to strengthen agroecological or biodiversity-driven preventive measures. One of these measures, conservation biological control, consists of modifications to the agricultural environment and farming practices to enhance the abundance, activity-density, fitness and impact of pest-killing natural enemies (Barbosa 1998; Landis et al. 2000). This is often, though not always, achieved through the implementation of plant diversification tactics in space and time (Hatt et al.

DOI: 10.1127/entomologia/3703

E. Schweizerbart'sche Verlagsbuchhandlung, 70176 Stuttgart, Germany, www.schweizerbart.de

2018). This can be achieved by crop rotation schemes, crop associations such as intercropping and the management or preservation of non-crop habitats in agricultural landscape mosaics (Boeraeve & Hatt 2024; Landis et al. 2000). The use of conservation biological control is not restricted to field settings but also entails a scientifically-guided deployment of plant diversity in greenhouses (Messelink et al. 2021; Xu et al. 2020). Across cropping systems and geographies, diversification measures consistently fortify biological control by favouring natural enemy diversity without compromising primary productivity (Tamburini et al. 2020).

Harmonia axyridis Pallas (Coleoptera: Coccinellidae), commonly known as Asian, harlequin or multi-colored Asian lady-beetle, preys upon many crop pests, especially aphids (Hemiptera: Aphididae), but also Tetranichidae (Acari), Psyllidae (Hemiptera), Coccoidea (Hemiptera), and the immature stages of Chrysomelidae (Coleoptera), Curculionidae (Coleoptera) and Lepidoptera (Koch 2003). Native to Northeast Asia (Sasaji 1971), *H. axyridis* has been accidentally or intentionally introduced into many countries for aphid biological control, subsequently spreading widely in Europe, Africa, and the Americas (Roy et al. 2016; Camacho-Cervantes et al. 2017). In its introduced range, *H. axyridis* negatively affects native coccinellids through competition for prey and habitats and intraguild predation (IGP) (Brown & Roy 2018; Koch & Galvan 2008; Lamb et al. 2019; Martins et al. 2009; Roy et al. 2012). Its spread may have altered the species composition and survival of endemic ladybird beetles (Honek et al. 2016).

The biology, ecology, invasion history and dynamics, non-target impacts and contribution to IGP of *H. axyridis* have been extensively reviewed by multiple authors (Brown et al. 2011; Koch 2003; Osawa 2011; Pell et al. 2008; Roy & Brown 2015; Sloggett et al. 2011). However *H. axyridis* could also benefit agriculture (Koch & Costamagna 2017; Riddick 2017) if its non-target impacts could be mitigated. Given its role as a key predator of many crop pests, one can also leverage the presence of *H. axyridis* to advance IPM or ACP in its native and introduced range alike. Quite surprisingly, this has received only scant scientific attention up till present.

In this review, we comprehensively assess whether and how agroecosystem diversification may affect *H. axyridis* population dynamics and predation on target and non-target organisms. Following (1) an in-depth description of *H. axyridis* ecology and biological control potential, (2) we explore the population-level effects of plant diversification measures at field and farm scales both in its native and non-native range. Finally, (3) we question whether increasing plant diversity and enhancing habitat structural complexity could contribute to minimize the non-target impact that *H. axyridis* exerts on other natural enemies of pests. Although speculative at this stage, it suggests new directions to potentially turn *H. axyridis* into a partner instead of a threat, especially in its invaded range.

2 Population ecology in farming landscapes

2.1 Habitat diversity

In its native range, *H. axyridis* is recorded from a diverse range of natural (Osawa 2011) and urban habitats (Wang et al. 2011). The species makes up approx. 30% of aphidophagous predators in natural habitats in Japan (Osawa 1991) and 12–47% of predatory ladybeetles in crops such as maize (Pan et al. 2020a), or wheat (Hatt et al. 2019b), and orchard (Cai et al. 2021a, b). Locally, *H. axyridis* feeds upon a diverse set of aphids (Osawa 2000), though experiences high mortality when consuming *Aulacorthum magnoliae* Essig & Kuwana (Hemiptera: Aphididae) – which assimilates toxic compounds from its host plant *Sambucus sieboldiana* (Fukunaga & Akimoto 2007). *Harmonia axyridis* also feeds on plant-based food (pollen, nectar, fruits) providing energy which contributes to extend its longevity and increase its reproductive capacity. However, *H. axyridis* reproduction capacity is limited if it does not consume prey (Hatt & Osawa 2019; Wang et al. 2025). In natural habitats, *H. axyridis* may not be a good competitor as its abundance negatively correlates with the diversity of other aphidophagous ladybird beetles (Osawa 2011).

In its introduced range, *H. axyridis* is found in different kinds of habitats (Brown et al. 2011), and they may not be the same from an invaded region to another (Colunga-Garcia & Gage 1998; Vandereycken et al. 2013a). For instance in the UK and Belgium, coccinellid communities in rural settings or semi-natural habitats were less dominated by *H. axyridis* as in urban ones (Adriaens et al. 2008; Farrow et al. 2022). In rural areas, *H. axyridis* attained the highest abundance in man-made, disturbed ecosystems such as ephemeral agricultural crops (Fig. 1). Meanwhile, in natural habitats in the UK, *H. axyridis* preferred deciduous over coniferous woodland (Farrow et al. 2022). *Harmonia axyridis* constitutes the main aphid predator in maize in Belgium, whereas the ladybeetle community in wheat, broad bean and potato is dominated by *Coccinella septempunctata* Linnaeus (Coleoptera: Coccinellidae) (Vandereycken et al. 2013a, 2013b). In the Americas, *H. axyridis* is a dominant aphid predator on alfalfa in Chile (Grez et al. 2016) but it is less the case in USA (Forbes & Gratton 2011). There however, it feeds on *Rhopalosiphum maidis* Fitch (Hemiptera: Aphididae) on maize but not on sorghum, although it preys on *Melanaphis sorghi* Theobald (Hemiptera: Aphididae) on this crop (Uyi et al. 2022).

2.2 Resources and enemies

The landscape-level abundance of natural enemies such as *H. axyridis* is closely tied to the availability and continuity of key food and non-food resource (Schellhorn et al. 2015). As aphids constitute the primary food for *H. axyridis* (Hodek 1996), their spatiotemporal occurrence in farming landscapes will greatly determine ladybeetle population dynamics

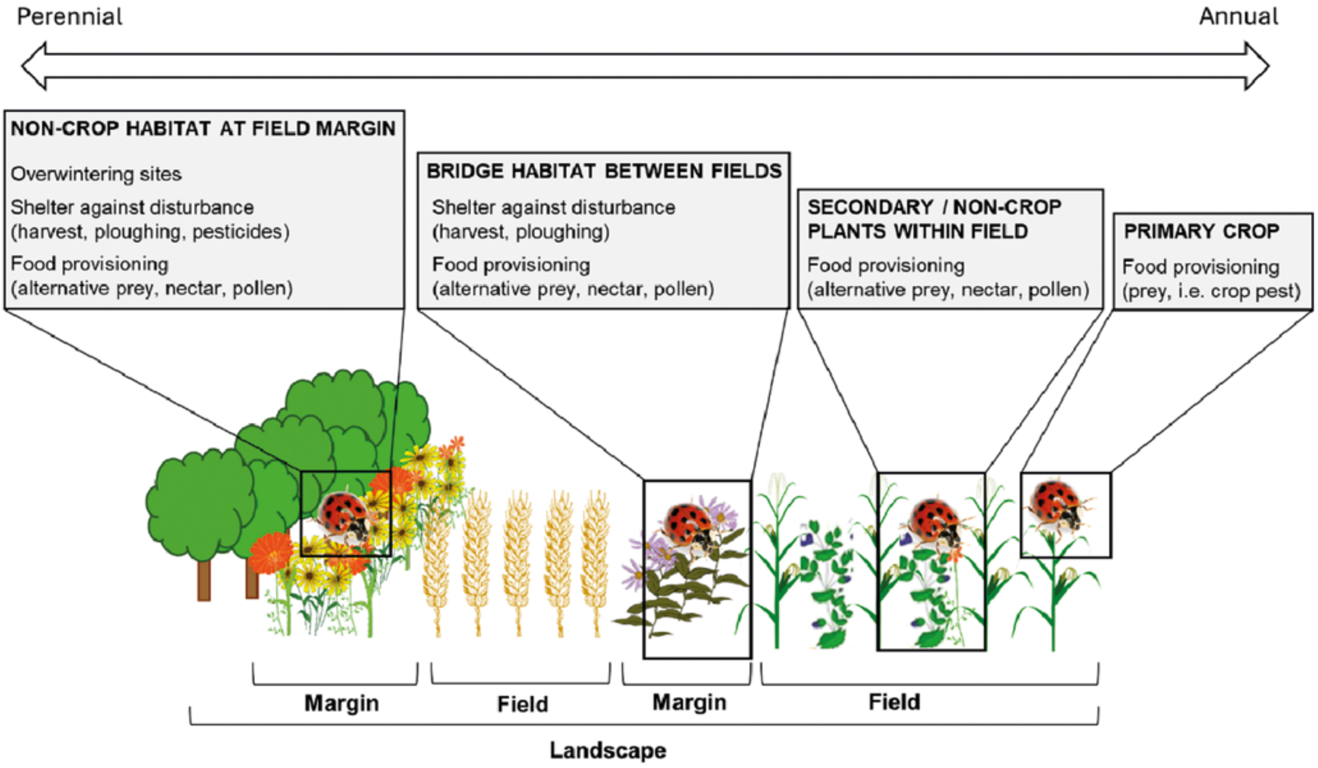

Fig. 1. Schematic representation of the spatio-temporal diversity of habitats offering suitable resources for *Harmonia axyridis* in agricultural landscapes.

(Osawa 2000). Predator-prey interactions and their overall relevance for biological control are mediated by the spatio-temporal heterogeneity of agroecosystems and the extent to which food and non-food resources are distributed (Kareiva 1987; Park & Obrycki 2004). In particular, landscapes of high heterogeneity (both compositional and configurational) increase resource continuity for *H. axyridis*, which ultimately benefit its landscape-level abundance and biological control potential (Gardiner et al. 2009b; Grez et al. 2014; Haan et al. 2020) (Fig. 1). Landscape composition shapes *H. axyridis* field colonization dynamics as much as its landscape-level abundance. Indeed, while *H. axyridis* abundance correlates with aphid numbers at small spatial scale, crop type and growing season ultimately dictate predator-prey interactions at the landscape level (Thomine et al. 2020; 2023). In the native range of *H. axyridis*, increased coverage of urban habitat and woodland at small spatial scales enhances its early-season abundance, while landscapes with high fallow, woodland, shelterbelts, and grassland cover are typified by high late-season abundance of *H. axyridis* (Dong et al. 2015; Yang et al. 2018, 2019). Ladybeetle influx into a given crop is then determined by the extent to which non-crop habitats act as sources or sinks (Gardiner et al. 2009a; Gardiner et al. 2009b; Yang et al. 2018). Similarly, configurational heterogeneity benefits *H. axyridis* by offering habitats with vital food or non-food resources at specific points in time within or beyond its dispersal radius (Lundgren 2009), leading to increasing its abundance and improving its body condition (e.g. body size, mass, lipid content) (Tiede et al. 2022).

Over time, ladybird beetles interact in a wide range of agricultural and forest habitats within a farming landscape – where they engage with (aphid) prey, conspecifics, competitors, intraguild predators and specific natural enemies. Natural enemies of *H. axyridis* include generalist predators (e.g. birds, spiders) and parasitoids such as *Phalacrotophora* spp. (Diptera: Phoridae) and *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae) (Ceryngier et al. 2018). However, their ability to control the abundance of *H. axyridis* is limited, especially in the invasive range. In Italy, the predation rate from invertebrate predators remained below 2% on *H. axyridis* eggs, below 15% on larvae, and never occurred on pupae and adults (Burgio et al. 2008). Through a meta-analysis, Ceryngier et al. (2018) reported a parasitism rate from *Phalacrotophora* spp. of 16% in the native range, against <1% in Europe on average. Parasitism rate from *D. coccinellae* is very variable in the invaded area, ranging from none in The Netherlands (Raak-van Den Berg et al. 2014) to 24% in Minnesota, USA (Hoogendoorn & Heimpel 2002). Beyond predators and parasitoids, few records reported the natural infection of *H. axyridis* by entomopathogenic fungi (EPF). To our knowledge, the first record of such lethal association was by Kuznetsov (1997), who reported few infection cases of *H. axyridis* with *Beauveria* spp. in its native range in eastern Russia. Later on, Steenberg & Harding (2009) recorded three EPF species, i.e. *Isaria farinosa, Beauveria bassiana* and *Lecanicillium* spp., infecting *H. axyridis* larvae, pupae and overwintering adults. However, the assessment of the prevalence of these species on *H. axyridis* remains to be more studied. Under laboratory setting, *H. axyridis* was less susceptible to infection with the generalist EPF *B. bassiana* (Cottrell & Shapiro-Ilan 2003; Roy et al. 2008). The most known association is with *Hesperomyces harmoniae* (Ascomycota, Laboulbeniales), identified as the unique naturally occurring obligate ectoparasitic fungus of *H. axyridis* and studies are in progress to investigate their spatiotemporal trends with its host (De Groot et al. 2024). Experiments conducted under laboratory condition to elucidate the susceptibility of *H. axyridis* and other native ladybirds to dual infection with ectoparasitic and pathogenic fungi demonstrated that *H. axyridis* did not show the same susceptibility towards EPF infection as for native *Olla v-nigrum* Mulsant (Coleoptera: Coccinellidae) (Haelewaters et al. 2020). These findings are in line with the enemy release hypothesis, which suggests that invasive alien species encounter less regulation by native natural enemies than native species in new geographic areas.

2.3 From population dynamics to biological control

Within the farming landscape, predation contributes variably to aphid suppression and can eventually enable within-season biological control (Obrycki et al. 2009). Yet, biological control outcomes are determined by a multitude of biotic and abiotic factors that act at varying spatiotemporal scales. Within given (crop or non-crop) habitats, resident natural enemies may interact with *H. axyridis* biological control to varying extent. Positive effects arise when natural enemy diversity enhances functional redundancy, response diversity or niche complementarity, whereas negative results arise when enemies interfere directly or indirectly, for instance via IGP (Straub et al. 2008). *Harmonia axyridis* can coexist with other natural enemies when they utilize the resources differentially, leading to resource partitioning, and/or when the intraguild prey has some competitive advantage over the intraguild predator (i.e. is better at exploiting the shared resources) (Rocca et al. 2022). This occurs in natural habitats in its native range, where *H. axyridis* co-exists with multiple aphid predators (Osawa 1991). Co-existence with other (ladybeetle) predators is influenced by the respective defensive traits (e.g. harmonine content in eggs, Kajita et al. 2010), the oviposition site selection of female *H. axyridis* (Sicsú et al. 2015) that is influenced by the level of plant diversity (Amaral et al. 2015). Specifically, non-crop plants can expand niche space, offer shelter opportunities or provide alternative prey which, in turn, reduce IGP. As these processes occur in crop- and non-crop habitats alike, they will ultimately dictate landscape-level performance or fitness of *H. axyridis*. Habitat fragmentation may interfere with natural enemy searching and recruitment behaviour, thereby affecting predator-prey interactions (With et al. 2002). In non-fragmented landscapes, *H. axyridis* was more efficient in searching prey than other ladybird species even in plots with low aphid abundance (With et al. 2002). Habitat fragmentation can also affect cannibalism, which plays a central role in *H. axyridis* life history especially during food shortage (Osawa 2011).

Beyond predation and parasitism, the most naturally occurring biocontrol agents of aphids are EPF, which might vary from facultative to obligate pathogenic association (Humber 1991). *Harmonia axyridis* is naturally less – or even not – susceptible to these EFP infections in its invasive habitats. Considering its great dispersal capability, it would be interesting to explore the role of *H. axyridis* in the dynamics of EPF infection among insect pests (including their prey) in both crop and non-crop habitats. Such studies would enhance knowledge about the ecosystem services provided by the ladybird species. Yet, to our knowledge, no study has investigated the role of *H. axyridis* as a vector of EPF and the cost-benefit analysis from such interactions.

Overall, habitat heterogeneity and fragmentation of agricultural landscapes may affect predator-prey dynamics and attenuate negative impacts of inter-predator interactions (but see Ortiz-Martínez et al. 2020). So far, empirical work has mainly assessed *H. axyridis* abundance within individual habitats instead of its movements between habitats. Further studies are needed to determine how *H. axyridis* populations differ in their edge responses (Grez et al. 2014; Pfister et al. 2017), and how the interrelationships between habitat size, configuration and composition at field or plot scales may favor biological control by *H. axyridis*. Analysing the effect of local-scale diversification may provide valuable insights since many landscape-level outcomes result from practices implemented at the field or farm level.

3 Steering biological control with field/farm scale diversification practices

3.1 Diversification within field

Crop diversification in space and time may increase the spatiotemporal continuity of necessary resources for *H. axyridis*, as differential crop phenology can ensure its spillover from crop habitats to others e.g., following harvest cycles, tillage or pesticide sprays (Jaworski et al. 2023; Thomine et al. 2022; Tooker et al. 2020). Cereal grains such as wheat and maize may constitute suitable rotation or inter-crops, as they provide alternative prey and a suitable micro-climatic refuge for *H. axyridis* and may enhance spillover into adjacent crop fields (but rarely wheat in North America) (Forbes & Gratton 2011; Men et al. 2004; Pan et al. 2020a) (Fig. 1). As such, early-season *H. axyridis* population build-up on maize or wheat ensures a rapid colonization of the succeeding cotton crop in the northern China plain (Jaworski et al. 2022). Thus, functional complementation among diverse crops is critical to the conservation of ladybird beetles such as *H. axyridis* in agricultural landscapes. The establishment of *Cnidium monnieri* (L.) Cuss. (Apiaceae) as a bridge crop strip between wheat and maize can provide aphid prey for resident *H. axyridis* during the period between wheat maturation and emergence of the succeeding maize crop in China (Yang et al. 2021) (Fig. 1).

In addition to diversification over time, plant diversity can also be added into a standing crop through intercropping, secondary planting or more broadly the establishment of polycultures (Hatt & Döring 2025). Intercropping refers to the joint establishment of two or more cash crop species (Lopes et al. 2016), whereas secondary planting entails pairing a cash crop with one or more non-crop plant species that fulfil specific functions (Parolin et al. 2012) (Fig. 1). Increasing spatial heterogeneity of crop stands can favour the abundance and diversity of predatory insects (Rakotomalala et al. 2023). Crop stand heterogeneity creates ecological niches offering diverse resources while reducing risks of intraguild predation (Da Silva et al. 2022). Strip intercropping of peanut (*Arachis hypogaea* L., Fabaceae) with maize increases *H. axyridis* populations compared to peanut sole cropping in China (Ju et al. 2019). Strip intercropping of pea (*Pisum sativum* L., Fabaceae) with wheat increases *H. axyridis* populations compared to a wheat monocrop in Belgium (Lopes et al. 2015). In the latter system, *H. axyridis* likely benefits from the early occurrence of aphid prey on pea before moving to the subsequent wheat crop. Insectary plants (*sensu* Parolin et al. 2012) benefit predators in the absence of prey by providing pollen and floral and extrafloral nectar (Hatt et al. 2019c; Lundgren 2009). For instance, floral and extrafloral nectar of *Hibiscus cannabinus* L. (Malvaceae) improves the survival rate of *H. axyridis* (Xiu et al. 2017). Other plant species such as *Vicia sativa* L. (Fabaceae), buckwheat *Fagopyrum esculentum* Moench (Polygonaceae), coriander *Coriandrum sativum* L. (Apiaceae) (Fig. 2a) and *Perilla frutescens* (L.) Britton (Lamiaceae) similarly enhance *H. axyridis* longevity in laboratory conditions (Hatt & Osawa 2019; Wang et al. 2020).

Within-field diversification strategies are equally important for perennial agricultural crops, where they offer spatiotemporal continuity of resources to *H. axyridis* (Jacobsen et al. 2022). Orchards in particular lend themselves to biological control, as they provide comparatively stable ecosystems (Wyckhuys et al. 2025) and ample available space for habitat management interventions (Miliczky & Horton 2005; Simon et al. 2010). *Harmonia axyridis* is as an important predator of aphids in apple (Brown & Miller 1998; Judt et al. 2023; Zhou et al. 2014), pear (Ji et al. 2022), peach (Wan et al. 2019), citrus (Michaud 2002; Niu et al. 2014), and cherry (Rosas-Ramos et al. 2020) orchards as well as in vineyards (Franin et al. 2014). In its native range (Table 2), companion planting with *Ageratum* spp. L. (Asteraceae), basil *Ocimum basilicum* L. (Lamiaceae) and French marigold *Tagetes patula* L. (Asteraceae) increases the number of *H. axyridis* in apple orchards and suppressed spirea aphid (*Aphis spiraecola* Patch, Hemiptera: Aphididae) numbers (Song et al. 2013). By establishing *C. monnieri* in apple orchards (Cai et al. 2021a, b), *H. axyridis* populations are enhanced and 24–80% of these readily spill over onto the apple trees (Cai et al. 2021a, b; Zhang et al. 2022). In peach orchards, the establishment of six plant species, i.e. *Vitex negundo* L. (Verbenaceae) (Fig. 2b), *Artemisia sieversiana* Ehrh. (Asteraceae), *Vigna unguiculata* (L.) Walp. (Fabaceae), *Cosmos bipinnata* Cav. (Asteraceae), *Z. mays* and *Helianthus annuus* L. (Asteraceae) supports population abundance of *H. axyridis* (Wu et al. 2024). Meanwhile, eight aromatic plant species including *Nepeta cataria* L. (Lamiaceae) boost *H. axyridis* numbers in pear orchards and enhance biological control of resident mealybug pests (Wan et al. 2015). Different mechanisms may underpin the enhanced *H. axyridis* recruitment or population-build up following the addition of one or more plant species (Table 1). Beyond the provision of additional food, alternative aphids on added plant species can lead to herbivore-induced or constitutively released plant volatiles attracting *H. axyridis*, for instance on *V. negundo* (Xu et al. 2023) or *C. monnieri* (Cai et al. 2020).

Several empirical works, however, report failure at enhancing *H. axyridis* and biological control with insectary plants in orchards. For instance, in US apple orchards, aphid predation by *H. axyridis* adults is not affected by the presence of flowering buckwheat (*F. esculentum*) (Spellman et al. 2006). Equally, *H. axyridis* exerts higher levels of aphid biological control in Canadian apple orchards with conventional ground cover than with flowering ground cover sown with phacelia *Phacelia tanacetifolia* Benth. (Boraginaceae) or buckwheat (Fréchette et al. 2008). In China, *H. axyridis* prefer alfalfa × ryegrass strips over flower strips of marigold *Callistephus chinensis* Cass. (Asteraceae) (Dong et al. 2021). This last case study suggests that the presence of alternative prey on companion plants over-rides that of non-food resources. More generally, it indicates that crop diversification benefits to *H. axyridis* by increasing prey diversity, while flowering resources remain useful as alternative but secondary food (Lundgren 2009).

3.2 Diversification at field margins

Non-crop or semi-natural habitats can be implemented or conserved at close proximity to agricultural fields, in order to support natural enemies such as *H. axyridis* (Landis et al. 2000). As above, these habitats can offer shelter, alternative prey or hosts and non-prey foods such as pollen and nectar (Gurr et al. 2017; Shields et al. 2019). They often constitute permanent habitats which offer stability in the highly disturbed environments of many agricultural production systems (Tooker et al. 2020) (Fig. 1). These ecological infrastructures can be composed of grass and/or forb species, i.e. 'flower strips' (Hatt et al. 2020) or 'beetle banks' (MacLeod et al. 2004) depending on their botanical composition. Compared to crop fields, grass-flower strips host a comparatively higher abundance and

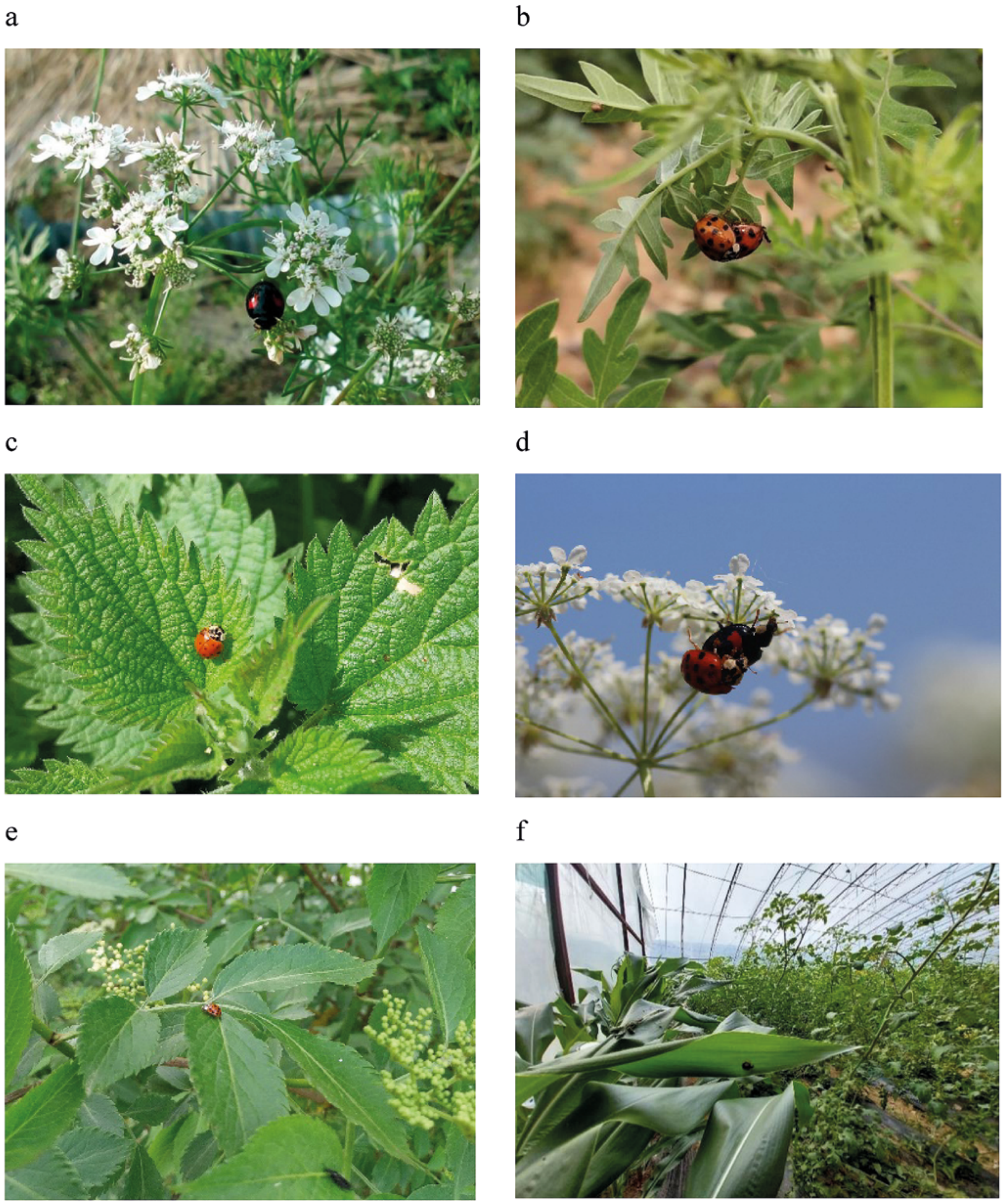

Fig. 2. Ladybird beetle *Harmonia axyridis* on non-crop plants in diversified agricultural systems. (a) Coriander *Coriandrum sativum* L. (Apiaceae) and (b) *Vitex negundo* (Verbenaceae) as companion plants, (c) nettle *Urtica dioica* L. (Urticaceae) and (d) *Heracleum sphondylium* L. (Apiaceae) as herbaceous non-crop field margins, (e) *Sambucus nigra* L. (Adoxaceae) in a hedgerow, (f) maize *Zea mays* L. (Poaceae) as a banker plant in greenhouse. (Photos: S. Hatt, Q. Xu).

Table 1. Non-exhaustive listing of plant species that benefit the ladybird beetle *Harmonia axyridis* through different mechanisms, as recorded under field or laboratory conditions. Mechanisms through which a given plant species benefit *H. axyridis* are differentiated between shelter, nectar, alternative prey or hosts, and pollen (abbreviated as SNAP; Shields et al. 2019). [1]Only indicated when reported and/or empirically demonstrated.

	Plant species (Family)	Mechanism[1]	Location	References
Field observations				
Crop rotation				
	Triticum aestivum (Poaceae)	Alternative prey	China	Men et al. 2004; Pan et al. 2020a
	Zea mays (Poaceae)	Alternative prey	USA	Forbes & Gratton 2011
Intercropping				
	Zea mays (Poaceae)	Pollen	China	Ju et al. 2019
	Zea mays (Poaceae)	Shelter	China	Pan et al. 2020b
	Pisum sativum (Fabaceae)	Alternative prey	Belgium	Lopes et al. 2015
Bridge strip in crop fields				
	Cnidium monnieri (Apiaceae)	Nectar, pollen, alternative prey	China	Yang et al. 2021, 2023
Companion plant in orchard				
	Cnidium monnieri (Apiaceae)	Nectar, pollen, alternative prey	China	Cai et al. 2021a, b; Zhang et al. 2022
	Ageratum spp. (Asteraceae)	-	China	Song et al. 2013
	Ocimum basilicum (Lamiaceae)	-	China	Song et al. 2013
	Tagetes patula (Asteraceae)	-	China	Song et al. 2013
	Vitex negundo (Verbenaceae)	Alternative prey	China	Xu et al. 2023; Wu et al. 2024
	Artemisia sieversiana (Asteraceae)	-	China	Wu et al. 2024
	Vigna unguiculata (Fabaceae)	-	China	Wu et al. 2024
	Cosmos bipinnata (Asteraceae)	-	China	Wu et al. 2024
	Helianthus annuus (Asteraceae)	-	China	Wu et al. 2024
	Zea mays (Poaceae)	-	China	Wu et al. 2024
Companion plant in greenhouse		-		
	Scaevola aemula (Goodeniaceae)	Nectar, pollen	Japan	Seko et al. 2017
	Calendula officinalis (Asteraceae)	Nectar, pollen	China	Liang et al. 2022
Banker plant in greenhouse		-		
	Vicia faba (Fabaceae)	Alternative prey	China	Wang et al. 2022
	Zea mays (Poaceae)	Alternative prey	China	Pers. observation
Grass-flower strip				
	Medicago sativa (Fabaceae)	Alternative prey	China	Dong et al. 2021
	Urtica dioica (Urticaceae)	Alternative prey	Belgium	Alhmedi et al. 2009
	Borago officinalis (Boraginaceae)	-	China	Li et al. 2021
	Centaurea cyanus (Asteraceae)	-	China	Li et al. 2021
Hedgerow				
	Populus sp. (Salicaceae)	Alternative prey	China	Dong et al. 2015; Yan et al. 2012
	Hippophae rhamnoides (Elaeagnaceae)	Alternative prey	China	Yan et al. 2012
	Rhamnus cathartica (Rhamnaceae)	Alternative prey	USA	Bahlai et al. 2008; Hesler et al. 2004
	Sambucus nigra (Adoxaceae)	-	Belgium	Adriaens et al. 2008
	Salix sp. (Salicaceae)	-	Belgium	Adriaens et al. 2008
	Acer sp. (Sapindaceae)	-	Belgium	Adriaens et al. 2008
	Tilia sp. (Malvaceae)	-	Belgium	Adriaens et al. 2008

Table 1. Continued.

	Plant species (Family)	Mechanism¹	Location	References
Laboratory experiments				
	Hibiscus cannabinus (Malvaceae)	Extrafloral nectar	China	Xiu et al. 2017
	Vicia sativa (Fabaceae)	Nectar, pollen	France (FR)	Wang et al. 2020
	Fagopyrum esculentum (Polygonaceae)	Nectar, pollen	Switzerland, FR	Wolf et al. 2018; Wang et al. 2020
	Coriandrum sativum (Apiaceae)	Nectar, pollen	Switzerland, FR	Wolf et al. 2018; Wang et al. 2020
	Perilla frutescens (Lamiaceae)	Nectar, pollen	Japan	Hatt & Osawa 2019
	Sophora japonica (Fabaceae)	Nectar, pollen	China	Zhu et al. 2023
	Ricinus communis (Euphorbiaceae)	Nectar, pollen	China	Zhu et al. 2023

diversity of beneficial insects (Haaland et al. 2011) including ladybird beetles (Meek et al. 2002; Tschumi et al. 2015; Yang et al. 2023). In grass-flower strips, *H. axyridis* often benefits from the presence of alternative prey, e.g. *Semiaphis heraclei* (Takahashi) (Hemiptera: Aphididae) on *C. monnieri* (Yang et al. 2023) or *Microlophium carnosum* (Buckton) (Hemiptera: Aphididae) on nettle *Urtica dioica* L. (Urticaceae) (Alhmedi et al. 2009) (Fig. 2c). They can also feed on nectar and pollen which allow them to bridge periods of prey scarcity and reproduce faster once prey become once more available (Wolf et al. 2018) (Fig. 2d). Forb mixtures with flowering plants tend to be more attractive to *H. axyridis*, especially those showing an ultra-violet pattern i.e. UV-reflecting peripheral flower parts and UV-absorbing centre parts (Hatt et al. 2019a).

In its native range (Table 2), monospecific strips of *C. monnieri* flowers enhance the abundance of ladybird beetles including *H. axyridis* in the adjacent cotton crop (Yang et al. 2023), and *H. axyridis* specifically by 72% in adjacent peanut crop (Ju et al. 2025). In contrast, in Europe, annual and perennial flower mixtures have limited impacts on ladybird beetle abundance in adjacent faba bean (Serée et al. 2022), wheat (Tschumi et al. 2015) or potato crops (Tschumi et al. 2016). *Harmonia axyrdis* is no exception and it is often in minority compared to the native species in fields bordered with grass-flower strips (Alhmedi et al. 2009; Hatt et al. 2017a).

Hedgerows and shelterbelts are other important non-crop habitats to conserve (beneficial) insects in agroecosystems (Thomas & Marshall 1999). They represent stable habitats used by ladybird beetles for overwintering and provide (aphid) prey especially in early season when annual crops are not yet infested (Honek & Hodek 1996). In China, *H. axyridis* and aphids attain high levels of abundance in sea-buckthorn *Hippophae rhamnoides* L. (Elaeagnaceae) and poplar *Populus* sp. L. (Salicaceae) shelterbelts, long before aphid populations build up in the adjacent wheat crop (Yan et al. 2012; cited by Riddick 2017). In the USA, *H. axyridis* and soybean aphids (*Aphis glycines* Matsumura, Hemiptera: Aphididae) sustain their populations on buckthorn *Rhamnus cathartica* L. (Rhamnaceae) trees during autumn and winter (Bahlai et al. 2008; Hesler et al. 2004). In Belgium, common hedgerow trees such as elder *Sambucus nigra* L. (Adoxaceae) (Fig. 2e), willow *Salix* sp. L. (Salicaceae), maple *Acer* sp. L., (Sapindaceae) or linden *Tilia* sp. L. (Malvaceae) host high numbers of *H. axyridis* (Adriaens et al. 2008). Tree species can also provide pollen and nectar. In the absence of aphids, flowers of *Sophora japonica* L. (Fabaceae) are attractive to *H. axyridis*, and those of *Ricinus communis* L. (Euphorbiaceae) improve survival rate of adult lady beetles (Zhu 2023). One major limitation however is that hedgerows inconsistently enhance ladybeetle spillover into the nearby crops (Albrecht et al. 2021; Morandin et al. 2014). This is possibly due to the fact that ladybeetle colonization of agricultural crops is largely determined by aphid abundance instead of extra-field features such as hedgerows (Hatt et al. 2017b).

3.3 Diversification of greenhouse environments

Greenhouses are semi-enclosed or fully-enclosed environments that lend themselves to biological control (Van Lenteren et al. 2020). The efficacy and long-term survival of released natural enemies such as *H. axyridis* can be considerably enhanced by deploying banker plants (Table 2). Banker plants are aimed at sustaining a reproducing population of natural enemies within a crop that will provide long-term pest suppression (Frank 2010). They provide alternative hosts, prey and/or food for natural enemies and can be placed throughout a greenhouse (Payton Miller & Rebek 2018). Broad bean *Vicia faba* L. (Fabaceae) infested with *Megoura japonica* Matsumura (Hemiptera: Aphididae) support *H. axyridis*-mediated biological control on bell pepper (*Capsicum annuum* L., Solanaceae) in China (Wang et al. 2022). In banker plant systems, a high density of alternative prey benefits *H. axyridis* when the density of the target pest is low, whereas low numbers of alternative prey facilitate *H. axyridis* spillover into the main crop when target prey is abundant (Wang et al. 2022). Other banker plant systems include maize infested by *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) to control *M. persicae* on greenhouse tomato (*Solanum lycopersicum* L., Solanaceae) (personal observation in China, Fig. 2f). Insectary plants are

Table 2. Examples of successful enhancement of *Harmonia axyridis* abundance through diversification practices in its native range. [a] Study reports impact on ladybird beetles, with *H. axyridis* being among the most abundant species.

Diversification practice	Treatment	Control	Impact	Location	Reference
Annual field crops					
Row intercropping	Pure stand peanut	Pure stand peanut	×25	China	Ju et al. 2019
Flower strips	Peanut + *Cnidium monnieri*	Pure stand peanut	+72%	China	Ju et al. 2025
	Cotton + *Cnidium monnieri*[a]	Pure stand cotton	×10	China	Yang et al. 2023
Orchards					
Companion planting	Apple trees + *Ageratum houstonianum*	Natural grass	+48%	China	Song et al. 2013
	Apple trees + *Tagetes patula*	Natural grass	+76%	China	Song et al. 2013
	Apple trees + *Ocimum basilicum*	Natural grass	+48%	China	Song et al. 2013
	Apple trees + *Cnidium monnieri*	Without *C. monnieri*	×2.5	China	Cai et al. 2021a
	Pear trees + *Nepeta cataria*	Clean tillage	+57%	China	Wan et al. 2015
Greenhouse					
Banker planting	Bell pepper + *Vicia faba* (400 inoculated aphids)	100 inoculated aphids	×4	China	Wang et al. 2022

also used in greenhouses. For instance, by planting fairy fan flower *Scaevola aemula* R.Br. (Goodeniaceae) together with eggplants in Japanese greenhouses, survival and long-term establishment of flightless *H. axyridis* is enhanced (Seko et al. 2017). Flightless *H. axyridis* are population strains artificially selected for greenhouse ladybird releases in augmentative biological control program (Tourniaire et al. 2000). Outside greenhouses, non-crop habitats including hedgerows and flower strips can promote biological control inside (Messelink et al. 2021; Xu et al. 2020). In flower strips sown outside Chinese greenhouses, *H. axyridis* frequently occurs on borage *Borago officinalis* L. (Boraginaceae) and cornflower *Centaurea cyanus* L. (Asteraceae) (Li et al. 2021). Presence or coverage of these two plants likely can enhance *H. axyridis* influx into the greenhouse and benefit biological control on locally grown crops.

4 Mitigating the impact on non-target biota with plant diversity?

An array of farm-scale diversification practices can enhance *H. axyridis*-mediated biological control (Tables 1 and 2). Evidence from its native range is numerous and the positive effects of diversification schemes on *H. axyridis* abundance are consistent across studies. In the invaded regions, however, evidence is scarcer and effects of diversification practices on its population abundance are unclear. In most of field-based studies, *H. axyridis* is not identified at the species level, and when it is, *H. axyridis* is often less abundant than native species (Alhmedi et al. 2009; Hatt et al. 2017a).

Intra-guild predation involving *H. axyridis* is common, and represents a sensitive issue when it is on resident (native) species in its non-native range (Pell et al. 2008). Evidence of *H. axyridis* as an asymmetric intraguild predator has been well-documented under laboratory conditions or in field cages over the past decades (Burgio et al. 2002; Katsanis et al. 2013; Rizzo et al. 2023). *Adalia bipunctata*, an endemic ladybird species in Europe, declined by 30% in Belgium and 44% in the UK over the five years following the arrival of *H. axyridis*. Hence, discussing agroecosystem designs supporting predators such as *H. axyridis* requires considering the potential risks, especially in its non-native range. Ladybird species the most at risks are primarily aphidophagous, sensitive to IGP at their immature stages, and found on deciduous trees (Kenis et al. 2017).

With the advent of high-throughput sequencing methods, DNA-based gut content analyses have been used to infer ecological interactions of *H. axyridis* in the field. Use of these tools has uncovered the extent to which habitat complexity mediates IGP (Gagnon & Brodeur 2014; Rondoni et al. 2015). However, to our knowledge, few studies have directly measured the effect of plant diversity on IGP involving *H. axyridis*. A laboratory setting using squash (*Cucurbita pepo* L., Cucurbitaceae) as a crop plant and mugwort (*Artemisia vulgaris* L., Asteraceae) as an added non-crop plant was used to analyse the effect of an increased structural complexity on the interactions between the native ladybird species *Hippodamia convergens* Guérin-Méneville and *H. axyridis* (as an exotic species in USA) (Amaral et al. 2015). Squash-mugwort combination significantly reduced the predation of *H. convergence*'s eggs by *H. axyridis* compared to settings including only squash. In addition, survival of *H. convergence* larvae in the presence of *H. axyridis* larvae was significantly increased (suggesting a lower IGP) when squash and mugwort were combined compared to when only one plant species was used. In another laboratory experiment exploring the role of nectar and pollen as a nutritive supplement to mitigate IGP, the addition of marigold (*Calendula officinalis* L., Asteraceae) flowers significantly reduced IGP between *H. axyridis* and *Propylea japonica* Thunberg (Coleoptera: Coccinellidae) in China (their native range) (Liang et al. 2022). Although obtained in microcosms highly differing from natural or agricultural contexts, these results suggest that increasing structural and resource diversity may mitigate negative interactions between ladybird species.

Prey density is a key determinant of IGP dynamics: when aphid abundance declines, IGP may increase possibly due to prey dilution effects in diversified agroecosystems (Gagnon & Brodeur 2014). Yet, to our knowledge, this ecological process has never been studied for *H. axyridis* or any other IGP predator at the landscape level and/or along a landscape complexity gradient. By designing distinct ecological niches such as arboreal and flowering habitats (Yang et al. 2021), diversification measures possibly may limit asymmetrical IGP within crops while simultaneously reducing *H. axyridis* aphidophagous activity in those same areas. However, this strategy poses risks; habitat diversification can exacerbate native coccinellid declines by increasing IGP under conditions of low prey density (Hautier et al. 2011). Introducing additional vegetation strata, such as herbaceous plants, possibly can mitigate those effects, as IGP by *H. axyridis* is less frequent in such habitats (Honek et al. 2019).

By outlining how diversification tactics may affect beneficial and deleterious impacts of *H. axyridis*, our work lays the initial groundwork for a science-based redesign of farming landscapes (Table 1). Based upon the available evidence, we are confident that plant diversity can be smartly leveraged to bolster the effectiveness of *H. axyridis* as a biological control agent in field crops and mitigate its detrimental ecological effect on endemic biota (Fig. 3). Yet, to target interventions at field, farm and landscape scales, our scientific understanding of in-field ecological interactions needs to be dramatically enhanced through large-scale and long-term observational or manipulative field studies. These eventually will lay the groundwork for a science-driven design of pest-suppressive farming landscapes in which ecological impacts of invasive biota are effectively defused.

Acknowledgements: This study was supported in part by earmarked fund for National Key Research and Development Program of China, Grant/Award Number: 2023YFD1400600 and CARS (Grant No. CARS-30) to Q. Xu, the Japan Society for the Promotion of Science to N. Osawa (No. 20205047, 24255013 & 24K08911).

Conflict of interest: XLT is Associate Editor for *Entomologia Generalis* and was not involved in the review process and decisions related to this manuscript. The authors declare no conflict of interest.

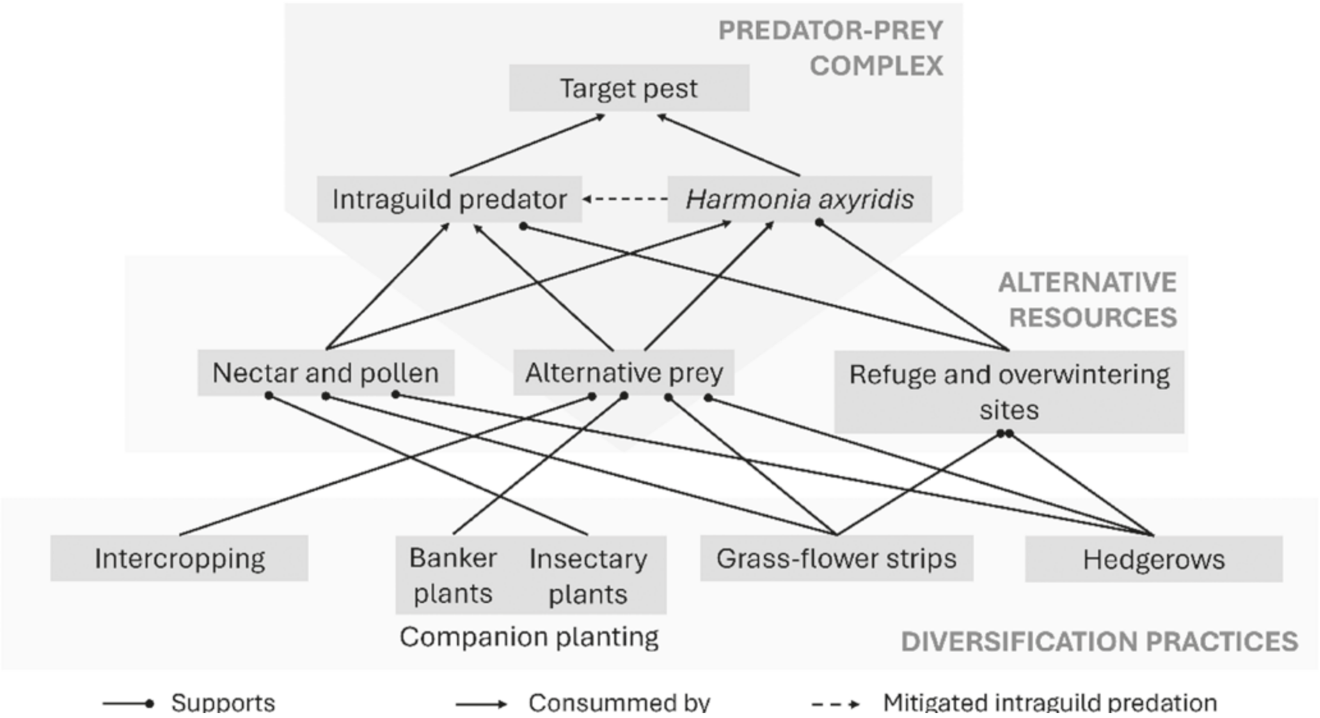

Fig. 3. Model of plant diversification practices potential to improve biological control while mitigating intraguild predation through the provisioning of alternative structural and food resources to the ladybird beetle *Harmonia axyridis*.

References

Adriaens, T., San Martin y Gomez, G., & Maes, D. (2008). Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. *BioControl, 53*(1), 69–88. https://doi.org/10.1007/s10526-007-9137-6

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., … Sutter, L. (2021). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters, 23*(10), 1488–1498. https://doi.org/10.1111/ele.13576

Alhmedi, A., Haubruge, E., & Francis, F. (2009). Effect of stinging nettle habitats on aphidophagous predators and parasitoids in wheat and green pea fields with special attention to the invader *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Entomological Science, 12*(4), 349–358. https://doi.org/10.1111/j.1479-8298.2009.00342.x

Amaral, D. S. S. L., Venzon, M., Perez, A. L., Schmidt, J. M., & Harwood, J. D. (2015). Coccinellid interactions mediated by vegetation heterogeneity. *Entomologia Experimentalis et Applicata, 156*(2), 160–169. https://doi.org/10.1111/eea.12319

Bahlai, C. A., Welsman, J. A., Macleod, E. C., Schaafsma, A. W., Hallett, R. H., & Sears, M. K. (2008). Role of visual and olfactory cues from agricultural hedgerows in the orientation behavior of Multicolored Asian Lady Beetle (Coleoptera: Coccinellidae). *Environmental Entomology, 37*(4), 973–979. https://doi.org/10.1093/ee/37.4.973

Barbosa, P. A. (1998). *Conservation Biological Control*. Academic Press. https://doi.org/10.1016/B978-012078147-8/50049-9

Barzman, M., Bàrberi, P., Birch, A. N. E., Boonekamp, P., Dachbrodt-Saaydeh, S., Graf, B., … Sattin, M. (2015). Eight principles of integrated pest management. *Agronomy for Sustainable Development, 35*(4), 1199–1215. https://doi.org/10.1007/s13593-015-0327-9

Boeraeve, F., & Hatt, S. (2024). Integrating agroecological practices to manage pests while combining organic and conservation agriculture. In J. Wang, H. Liu, I. Menzler-Hokkanen, & H. Jiang (Eds.), *The Concept of Ecostacking* (pp. 163–190). CABI. https://doi.org/10.1079/9781789248715.0013

Brown, M. W., & Miller, S. S. (1998). Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis. Entomological News, 109*, 143–151.

Brown, P. M. J., & Roy, H. E. (2018). Native ladybird decline caused by the invasive harlequin ladybird *Harmonia axyridis*: Evidence from a long-term field study. *Insect Conservation and Diversity, 11*(3), 230–239. https://doi.org/10.1111/icad.12266

Brown, P. M. J., Thomas, C. E., Lombaert, E., Jeffries, D. L., Estoup, A., & Lawson Handley, L.-J. (2011). The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): Distribution, dispersal and routes of invasion. *BioControl, 56*(4), 623–641. https://doi.org/10.1007/s10526-011-9379-1

Burgio, G., Lanzoni, A., Accinelli, G., & Maini, S. (2008). Estimation of mortality by entomophages on exotic *Harmonia axyridis* versus native *Adalia bipunctata* in semi-field conditions in northern Italy. *BioControl, 53*(1), 277–287. https://doi.org/10.1007/s10526-007-9133-x

Burgio, G., Santi, F., & Maini, S. (2002). On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control, 24*(2), 110–116. https://doi.org/10.1016/S1049-9644(02)00023-3

Cai, Z., Ouyang, F., Chen, J., Yang, Q., Desneux, N., Xiao, Y., … Ge, F. (2021a). Biological control of *Aphis spiraecola* in apples using an insectary plant that attracts and sustains predators. *Biological Control, 155*, 104532. https://doi.org/10.1016/j.biocontrol.2021.104532

Cai, Z., Ouyang, F., Su, J., Zhang, X., Liu, C., Xiao, Y., … Ge, F. (2020). Attraction of adult *Harmonia axyridis* to volatiles of the insectary plant *Cnidium monnieri*. *Biological Control, 143*, 104189. https://doi.org/10.1016/j.biocontrol.2020.104189

Cai, Z., Ouyang, F., Zhang, X., Chen, J., Xiao, Y., Ge, F., & Zhang, J. (2021b). Biological control of *Aphis spiraecola* (Hemiptera: Aphididae) using three different flowering plants in apple orchards. *Journal of Economic Entomology, 114*(3), 1128–1137. https://doi.org/10.1093/jee/toab064

Camacho-Cervantes, M., Ortega-Iturriaga, A., & del-Val, E. (2017). From effective biocontrol agent to successful invader: The harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong. *PeerJ, 5*, e3296. https://doi.org/10.7717/peerj.3296

Ceryngier, P., Nedvěd, O., Grez, A. A., Riddick, E. W., Roy, H. E., San Martin, G., … Haelewaters, D. (2018). Predators and parasitoids of the harlequin ladybird, *Harmonia axyridis*, in its native range and invaded areas. *Biological Invasions, 20*(4), 1009–1031. https://doi.org/10.1007/s10530-017-1608-9

Colunga-Garcia, M., & Gage, S. H. (1998). Arrival, establishment, and habitat use of the Multicolored Asian Lady Beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology, 27*(6), 1574–1580. https://doi.org/10.1093/ee/27.6.1574

Cottrell, T. E., & Shapiro-Ilan, D. I. (2003). Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. *Journal of Invertebrate Pathology, 84*(2), 137–144. https://doi.org/10.1016/j.jip.2003.09.003

Da Silva, A. C., Cahú, R. C., Cogitskei, M. M., Kubota, K. S. G., Sujii, E. R., & Togni, P. H. B. (2022). Intercropping collard plants with coriander modulates behavioral interactions among aphidophagous predators by altering microhabitat structure. *Biological Control, 176*, 105084. https://doi.org/10.1016/j.biocontrol.2022.105084

De Groot, M. D., Christou, M., Pan, J. Y., Adriaens, T., Maes, D., Martinou, A. F., … Haelewaters, D. (2024). Beetlehangers.org: Harmonizing host–parasite records of *Harmonia axyridis* and *Hesperomyces harmoniae*. *Arthropod-Plant Interactions, 18*(4), 665–679. https://doi.org/10.1007/s11829-023-10037-2

Deguine, J.-P., Aubertot, J.-N., Flor, R. J., Lescourret, F., Wyckhuys, K. A. G., & Ratnadass, A. (2021). Integrated pest management: Good intentions, hard realities. A review. *Agronomy for Sustainable Development, 41*(3), 38. https://doi.org/10.1007/s13593-021-00689-w

Deguine, J.-P., Gloanec, C., Laurent, P., Ratnadass, A., & Aubertot, J.-N. (Eds.). (2017). *Agroecological crop protection*. Springer Netherlands. https://doi.org/10.1007/978-94-024-1185-0

Dong, Z., Ouyang, F., Lu, F., & Ge, F. (2015). Shelterbelts in agricultural landscapes enhance ladybeetle abundance in spillover from cropland to adjacent habitats. *BioControl, 60*(3), 351–361. https://doi.org/10.1007/s10526-015-9648-5

Dong, Z., Xia, M., Li, C., Mu, B., & Zhang, Z. (2021). A comparison of flower and grass strips for augmentation of beneficial arthropods in apple orchards. *Frontiers in Sustainable Food Systems, 5*, 697864. https://doi.org/10.3389/fsufs.2021.697864

Farrow, R. A., Roy, H. E., & Brown, P. M. J. (2022). Ladybird communities in rural woodlands: Does an invader dominate? *Frontiers in Conservation Science, 3*, 759046. https://doi.org/10.3389/fcosc.2022.759046

Forbes, K. J., & Gratton, C. (2011). Stable isotopes reveal different patterns of inter-crop dispersal in two ladybeetle species. *Ecological Entomology, 36*(3), 396–400. https://doi.org/10.1111/j.1365-2311.2011.01268.x

Franin, K., Barić, B., & Kuštera, G. (2014). Fauna of Ladybugs (Coleoptera: Coccinellidae) in the vineyard agroecosystem. *Entomologia Croatica, 18*(1), 27–35.

Frank, S. D. (2010). Biological control of arthropod pests using banker plant systems: Past progress and future directions. *Biological Control, 52*(1), 8–16. https://doi.org/10.1016/j.biocontrol.2009.09.011

Fréchette, B., Cormier, D., Chouinard, G., Vanoosthuyse, F., & Lucas, É. (2008). Apple aphid, *Aphis* spp. (Hemiptera: Aphididae), and predator populations in an apple orchard at the non-bearing stage: The impact of ground cover and cultivar. *European Journal of Entomology, 105*(3), 521–529. https://doi.org/10.14411/eje.2008.069

Fukunaga, Y., & Akimoto, S. (2007). Toxicity of the aphid *Aulacorthum magnoliae* to the predator *Harmonia axyridis* (Coleoptera: Coccinellidae) and genetic variance in the assimilation of the toxic aphids in *H. axyridis* larvae. *Entomological Science, 10*(1), 45–53. https://doi.org/10.1111/j.1479-8298.2006.00197.x

Gagnon, A., & Brodeur, J. (2014). Impact of plant architecture and extraguild prey density on intraguild predation in an agroecosystem. *Entomologia Experimentalis et Applicata, 152*(2), 165–173. https://doi.org/10.1111/eea.12213

Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O'Neal, M., Chacon, J. M., … Heimpel, G. E. (2009a). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications, 19*(1), 143–154. https://doi.org/10.1890/07-1265.1

Gardiner, M. M., Landis, D. A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., … DiFonzo, C. D. (2009b). Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity & Distributions, 15*(4), 554–564. https://doi.org/10.1111/j.1472-4642.2009.00563.x

Grez, A. A., Zaviezo, T., Hernández, J., Rodríguez-San Pedro, A., & Acuña, P. (2014). The heterogeneity and composition of agricultural landscapes influence native and exotic coccinellids in alfalfa fields. *Agricultural and Forest Entomology, 16*(4), 382–390. https://doi.org/10.1111/afe.12068

Grez, A. A., Zaviezo, T., Roy, H. E., Brown, P. M. J., & Bizama, G. (2016). Rapid spread of *Harmonia axyridis* in Chile and its effects on local coccinellid biodiversity. *Diversity & Distributions, 22*(9), 982–994. https://doi.org/10.1111/ddi.12455

Gurr, G. M., Wratten, S. D., Landis, D. A., & You, M.-S. (2017). Habitat management to suppress pest populations: Progress and prospects. *Annual Review of Entomology, 62*(1), 91–109. https://doi.org/10.1146/annurev-ento-031616-035050

Haaland, C., Naisbit, R. E., & Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity, 4*(1), 60–80. https://doi.org/10.1111/j.1752-4598.2010.00098.x

Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting Landscape Configuration Effects on Agricultural Pest Suppression. *Trends in Ecology & Evolution, 35*(2), 175–186. https://doi.org/10.1016/j.tree.2019.10.003

Haelewaters, D., Hiller, T., Kemp, E. A., Van Wielink, P. S., Shapiro-Ilan, D. I., Aime, M. C., … Cottrell, T. E. (2020). Mortality of native and invasive ladybirds co-infected by ectoparasitic and entomopathogenic fungi. *PeerJ, 8*, e10110. https://doi.org/10.7717/peerj.10110

Hatt, S., Boeraeve, F., Artru, S., Dufrêne, M., & Francis, F. (2018). Spatial diversification of agroecosystems to enhance biological control and other regulating services: An agroecological perspective. *Science of the Total Environment, 621*, 600–611. https://doi.org/10.1016/j.scitotenv.2017.11.296

Hatt, S., & Döring, T. F. (2025). The interplay of intercropping, wildflower strips and weeds in conservation biological control and productivity. *Journal of Pest Science, 98*(1), 159–174. https://doi.org/10.1007/s10340-024-01801-1

Hatt, S., Francis, F., Xu, Q., Wang, S., & Osawa, N. (2020). Perennial flowering strips for conservation biological control of insect pests: From picking and mixing flowers to tailored functional diversity. In Y. Gao, H. M. T. Hokkanen, & I. Menzler-Hokkanen (Eds.), *Integrative Biological Control* (*Vol. 20*, pp. 57–71). Springer. https://doi.org/10.1007/978-3-030-44838-7_4

Hatt, S., Lopes, T., Boeraeve, F., Chen, J., & Francis, F. (2017a). Pest regulation and support of natural enemies in agriculture: Experimental evidence of within field wildflower strips. *Ecological Engineering, 98*, 240–245. https://doi.org/10.1016/j.ecoleng.2016.10.080

Hatt, S., Mouchon, P., Lopes, T., & Francis, F. (2017b). Effects of wildflower strips and an adjacent forest on aphids and their natural enemies in a pea field. *Insects, 8*(3), 99. https://doi.org/10.3390/insects8030099

Hatt, S., & Osawa, N. (2019). The role of *Perilla frutescens* flowers on fitness traits of the ladybird beetle *Harmonia axyridis. BioControl, 64*(4), 381–390. https://doi.org/10.1007/s10526-019-09937-1

Hatt, S., Uyttenbroeck, R., Lopes, T., Mouchon, P., Osawa, N., Piqueray, J., … Francis, F. (2019a). Identification of flower functional traits affecting abundance of generalist predators in perennial multiple species wildflower strips. *Arthropod-Plant Interactions, 13*(1), 127–137. https://doi.org/10.1007/s11829-018-9652-7

Hatt, S., Xu, Q., Francis, F., & Chen, J. (2019b). Intercropping oilseed rape with wheat and releasing *Harmonia axyridis* sex pheromone in Northern China failed to attract and support natural enemies of aphids. *Biotechnologie, Agronomie, Société et Environnement, 23*(3), 147–152. https://doi.org/10.25518/1780-4507.17921

Hatt, S., Xu, Q., Francis, F., & Osawa, N. (2019c). Aromatic plants of East Asia to enhance natural enemies towards biological control of insect pests. A review. *Entomologia Generalis, 38*(4), 275–315. https://doi.org/10.1127/entomologia/2019/0625

Hautier, L., San Martin, G., Callier, P., de Biseau, J.-C., & Grégoire, J.-C. (2011). Alkaloids provide evidence of intraguild predation on native coccinellids by *Harmonia axyridis* in the field. *Biological Invasions, 13*(8), 1805–1814. https://doi.org/10.1007/s10530-010-9935-0

Hesler, L., Kieckhefer, R., & Catangui, M. (2004). Surveys and field observations of *Harmonia axyridis* and other Coccinellidae (Coleoptera) in Eastern and Central South Dakota. *Transactions of the American Entomological Society, 130*, 113–133.

Hodek, I. (1996). Food relationships. In I. Hodek & A. Honek, *Ecology of Coccinellidae* (pp. 143–238). Kluwer. https://doi.org/10.1007/978-94-017-1349-8_6

Honek, A., & Hodek, I. (1996). Distribution in habitats. In I. Hodek & A. Honek, *Ecology of Coccinellidae* (pp. 95–141). Kluwer. https://doi.org/10.1007/978-94-017-1349-8_5

Honek, A., Martinkova, Z., Dixon, A. F. G., Roy, H. E., & Pekar, S. (2016). Long-term changes in communities of native coccinellids: Population fluctuations and the effect of competition from an invasive non-native species. *Insect Conservation and Diversity, 9*(3), 202–209. https://doi.org/10.1111/icad.12158

Honek, A., Martinkova, Z., Roy, H. E., Dixon, A. F. G., Skuhrovec, J., Pekár, S., & Brabec, M. (2019). Differences in the phenology of *Harmonia axyridis* (Coleoptera: Coccinellidae) and native coccinellids in Central Europe. *Environmental Entomology, 48*(1), 80–87. https://doi.org/10.1093/ee/nvy173

Hoogendoorn, M., & Heimpel, G. E. (2002). Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biological Control, 25*, 224–230.

Humber, R. A. (1991). Fungal pathogens of aphids. In D. C. Peters, J. A. Webster, & C. S. Chlouber (Eds.), *Aphid-plant interactions: Populations to molecules* (pp. 45–56). Agricultural Experiment Station, Division of Agriculture, Oklahoma State University.

Jacobsen, S. K., Sørensen, H., & Sigsgaard, L. (2022). Perennial flower strips in apple orchards promote natural enemies in their proximity. *Crop Protection, 156*, 105962. https://doi.org/10.1016/j.cropro.2022.105962

Jaworski, C. C., Thomine, E., Rusch, A., Lavoir, A.-V., Wang, S., & Desneux, N. (2023). Crop diversification to promote arthropod pest management: A review. *Agricultural Communications, 1*(1), 100004. https://doi.org/10.1016/j.agrcom.2023.100004

Jaworski, C. C., Thomine, E., Rusch, A., Lavoir, A.-V., Xiu, C., Ning, D., … Desneux, N. (2022). At which spatial scale does crop diversity enhance natural enemy populations and pest control? An experiment in a mosaic cropping system. *Agronomy, 12*(8), 1973. https://doi.org/10.3390/agronomy12081973

Ji, X., Wang, J., Dainese, M., Zhang, H., Chen, Y., Cavalieri, A., … Wan, N. (2022). Ground cover vegetation promotes biological control and yield in pear orchards. *Journal of Applied Entomology, 146*(3), 262–271. https://doi.org/10.1111/jen.12965

Ju, Q., Ouyang, F., Gu, S., Qiao, F., Yang, Q., Qu, M., & Ge, F. (2019). Strip intercropping peanut with maize for peanut aphid biological control and yield enhancement. *Agriculture, Ecosystems & Environment, 286*, 106682. https://doi.org/10.1016/j.agee.2019.106682

Ju, Q., Wei, X., Berthon, K., Zhang, Q., Ma, W., Qu, M., … Dicks, L. V. (2025). Flower strips increase natural pest control of peanut aphids, thereby enhancing crop yield. *Agriculture, Ecosystems & Environment, 388*, 109659. https://doi.org/10.1016/j.agee.2025.109659

Judt, C., Korányi, D., Zaller, J. G., & Batáry, P. (2023). Floral resources and ground covers promote natural enemies but not pest insects in apple orchards: A global meta-analysis. *Science of the Total Environment, 903*, 166139. https://doi.org/10.1016/j.scitotenv.2023.166139

Kajita, Y., Obrycki, J. J., Sloggett, J. J., & Haynes, K. F. (2010). Intraspecifc alkaloid variation in ladybird eggs and its eVects on con- and heterospecic intraguild predators. *Oecologia, 163*(2), 313–322. https://doi.org/10.1007/s00442-009-1551-2

Kareiva, P. M. (1987). Habitat fragmentation and the stability of predator–prey interactions. *Nature, 326*(6111), 388–390. https://doi.org/10.1038/326388a0

Katsanis, A., Babendreier, D., Nentwig, W., & Kenis, M. (2013). Intraguild predation between the invasive ladybird *Harmonia axyridis* and non-target European coccinellid species. *BioControl, 58*(1), 73–83. https://doi.org/10.1007/s10526-012-9470-2

Kenis, M., Adriaens, T., Brown, P. M. J., Katsanis, A., Martin, G. S., Branquart, E., … Poland, R. L. (2017). Assessing the ecological risk posed by a recently established invasive alien predator: *Harmonia axyridis* as a case study. *BioControl, 62*(3), 341–354. https://doi.org/10.1007/s10526-016-9764-x

Koch, R. L. (2003). The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science, 3*(1), 32. https://doi.org/10.1093/jis/3.1.32

Koch, R. L., & Costamagna, A. C. (2017). Reaping benefits from an invasive species: Role of *Harmonia axyridis* in natural biological control of *Aphis glycines* in North America. *BioControl, 62*(3), 331–340. https://doi.org/10.1007/s10526-016-9749-9

Koch, R. L., & Galvan, T. L. (2008). Bad side of a good beetle: The North American experience with *Harmonia axyridis*. *BioControl, 53*(1), 23–35. https://doi.org/10.1007/s10526-007-9121-1

Kuznetsov, V.N., 1997. *Lady Beetles of the Russian Far East*. Memoir no. 1, Center for Systematic Entomology. The Sandhill Crane Press, Gainesville. 248 pp.

Lamb, R. J., Bannerman, J. A., & Costamagna, A. C. (2019). Stability of native and exotic lady beetle populations in a diverse landscape. *Ecosphere, 10*(3), e02630. https://doi.org/10.1002/ecs2.2630

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology, 45*(1), 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

Li, S., Jaworski, C. C., Hatt, S., Zhang, F., Desneux, N., & Wang, S. (2021). Flower strips adjacent to greenhouses help reduce pest populations and insecticide applications inside organic commercial greenhouses. *Journal of Pest Science, 94*(3), 679–689. https://doi.org/10.1007/s10340-020-01285-9

Liang, Y., Chen, X., Dai, H., Wang, J., Guo, X., Wang, S., & Jaworski, C. C. (2022). Flower provision reduces intraguild predation between predators and increases aphid biocontrol in tomato. *Journal of Pest Science, 95*(1), 461–472. https://doi.org/10.1007/s10340-021-01396-x

Lopes, T., Bodson, B., & Francis, F. (2015). Associations of wheat with pea can reduce aphid infestations. *Neotropical Entomology, 44*(3), 286–293. https://doi.org/10.1007/s13744-015-0282-9

Lopes, T., Hatt, S., Xu, Q., Chen, J., Liu, Y., & Francis, F. (2016). Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control: A review. *Pest Management Science, 72*(12), 2193–2202. https://doi.org/10.1002/ps.4332

Lundgren, J. G. (2009). Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control, 51*(2), 294–305. https://doi.org/10.1016/j.biocontrol.2009.05.016

MacLeod, A., Wratten, S. D., Sotherton, N. W., & Thomas, M. B. (2004). 'Beetle banks' as refuges for beneficial arthropods in farmland: Long-term changes in predator communities and habitat. *Agricultural and Forest Entomology, 6*(2), 147–154. https://doi.org/10.1111/j.1461-9563.2004.00215.x

Martins, C. B. C., Almeida, L. M., Zonta-de-Carvalho, R. C., Castro, C. F., & Pereira, R. A. (2009). *Harmonia axyridis*: A threat to Brazilian Coccinellidae? *Revista Brasileira de Entomologia, 53*(4), 663–671. https://doi.org/10.1590/S0085-56262009000400018

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., & Nowakowski, M. (2002). The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation, 106*(2), 259–271. https://doi.org/10.1016/S0006-3207(01)00252-X

Men, X., Ge, F., Yardim, E., & Parajulee, M. (2004). Evaluation of winter wheat as a potential relay crop for enhancing biological control of cotton aphids. *BioControl, 49*(6), 701–714. https://doi.org/10.1007/s10526-004-5278-z

Messelink, G. J., Lambion, J., Janssen, A., & Van Rijn, P. C. J. (2021). Biodiversity in and around greenhouses: Benefits and potential risks for pest management. *Insects, 12*(10), 933. https://doi.org/10.3390/insects12100933

Michaud, J. P. (2002). Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology, 31*(5), 827–835. https://doi.org/10.1603/0046-225X-31.5.827

Miliczky, E. R., & Horton, D. R. (2005). Densities of beneficial arthropods within pear and apple orchards affected by distance from adjacent native habitat and association of natural enemies with extra-orchard host plants. *Biological Control, 33*(3), 249–259. https://doi.org/10.1016/j.biocontrol.2005.03.002

Morandin, L. A., Long, R. F., & Kremen, C. (2014). Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment, 189*, 164–170. https://doi.org/10.1016/j.agee.2014.03.030

Niu, J.-Z., Hull-Sanders, H., Zhang, Y.-X., Lin, J.-Z., Dou, W., & Wang, J.-J. (2014). Biological control of arthropod pests in citrus orchards in China. *Biological Control, 68*, 15–22. https://doi.org/10.1016/j.biocontrol.2013.06.005

Obrycki, J. J., Harwood, J. D., Kring, T. J., & O'Neil, R. J. (2009). Aphidophagy by Coccinellidae: Application of biological control in agroecosystems. *Biological Control, 51*(2), 244–254. https://doi.org/10.1016/j.biocontrol.2009.05.009

Ortiz-Martínez, S., Staudacher, K., Baumgartner, V., Traugott, M., & Lavandero, B. (2020). Intraguild predation is independent of landscape context and does not affect the temporal dynamics of aphids in cereal fields. *Journal of Pest Science, 93*(1), 235–249. https://doi.org/10.1007/s10340-019-01142-4

Osawa, N. (1991). *Ecological studies on the ladybird beetle Harmonia axyridis Pallas in a natural population* [Ph.D. thesis]. Kyoto University.

Osawa, N. (2000). Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): Resource tracking and population characteristics. *Population Ecology, 42*(2), 115–127. https://doi.org/10.1007/PL00011990

Osawa, N. (2011). Ecology of *Harmonia axyridis* in natural habitats within its native range. *BioControl, 56*(4), 613–621. https://doi.org/10.1007/s10526-011-9382-6

Pan, H., Liu, B., Jaworski, C. C., Yang, L., Liu, Y., Desneux, N., … Lu, Y. (2020a). Effects of aphid density and plant taxa on predatory ladybeetle abundance at field and landscape scales. *Insects, 11*(10), 695. https://doi.org/10.3390/insects11100695

Pan, H., Xiu, C., Liu, B., Wyckhuys, K. A. G., & Lu, Y. (2020b). Whorl-stage maize provides a microclimate refuge for predatory ladybeetles. *Biological Control, 142*, 104162. https://doi.org/10.1016/j.biocontrol.2019.104162

Park, Y.-L., & Obrycki, J. J. (2004). Spatio-temporal distribution of corn leaf Aphids (Homoptera: Aphididae) and lady beetles (Coleoptera: Coccinellidae) in Iowa cornfields. *Biological Control, 31*(2), 210–217. https://doi.org/10.1016/j.biocontrol.2004.06.008

Parolin, P., Bresch, C., Desneux, N., Brun, R., Bout, A., Boll, R., & Poncet, C. (2012). Secondary plants used in biological control: A review. *International Journal of Pest Management, 58*(2), 91–100. https://doi.org/10.1080/09670874.2012.659229

Payton Miller, T. L., & Rebek, E. J. (2018). Banker plants for aphid biological control in greenhouses. *Journal of Integrated Pest Management, 9*(1), 9. https://doi.org/10.1093/jipm/pmy002

Pell, J. K., Baverstock, J., Roy, H. E., Ware, R. L., & Majerus, M. E. N. (2008). Intraguild predation involving *Harmonia axyridis*: A review of current knowledge and future perspectives. *BioControl, 53*(1), 147–168. https://doi.org/10.1007/s10526-007-9125-x

Pfister, S. C., Schirmel, J., & Entling, M. H. (2017). Aphids and their enemies in pumpkin respond differently to management, local and landscape features. *Biological Control, 115*, 37–45. https://doi.org/10.1016/j.biocontrol.2017.09.005

Raak-van Den Berg, C. L., van Wielink, P., de Jong, P. W., Gort, G., Haelewaters, D., Helder, J., & van Lenteren, J. C. (2014). Invasive alien species under attack: Natural enemies of *Harmonia axyridis* in the Netherlands. *BioControl, 59*(2), 229–240. https://doi.org/10.1007/s10526-014-9561-3

Rakotomalala, A. A. N. A., Ficiciyan, A. M., & Tscharntke, T. (2023). Intercropping enhances beneficial arthropods and controls pests: A systematic review and meta-analysis. *Agriculture, Ecosystems & Environment, 356*, 108617. https://doi.org/10.1016/j.agee.2023.108617

Riddick, E. W. (2017). Spotlight on the positive effects of the ladybird *Harmonia axyridis* on agriculture. *BioControl, 62*(3), 319–330. https://doi.org/10.1007/s10526-016-9758-8

Rizzo, M. E., Salvo, A., Rocca, M., & Greco, N. (2023). Spatial and temporal cooccurrence among Neotropical native coccinellids and the exotic *Harmonia axyridis. Phytoparasitica, 51*(1), 89–99. https://doi.org/10.1007/s12600-022-01040-z

Rocca, M., Díaz Lucas, M. F., & Greco, N. M. (2022). Effect of spatiotemporal association and trophic interactions between aphidophagous coccinellids toward aphid control. *Environmental Entomology, 51*(1), 44–51. https://doi.org/10.1093/ee/nvab127

Rondoni, G., Athey, K. J., Harwood, J. D., Conti, E., Ricci, E., & Obrycki, J. J. (2015). Development and application of molecular gut-content analysis to detect aphid and coccinellid predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) in Italy. *Insect Science, 22*(6), 719–730. https://doi.org/10.1111/1744-7917.12165

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., & Asís, J. D. (2020). Natural enemies and pollinators in traditional cherry orchards: Functionally important taxa respond differently to farming system. *Agriculture, Ecosystems & Environment, 295*, 106920. https://doi.org/10.1016/j.agee.2020.106920

Roy, H. E., Adriaens, T., Isaac, N. J. B., Kenis, M., Onkelinx, T., San Martin, G., … Maes, D. (2012). Invasive alien predator causes rapid declines of native European ladybirds. *Diversity & Distributions, 18*(7), 717–725. https://doi.org/10.1111/j.1472-4642.2012.00883.x

Roy, H. E., & Brown, P. M. J. (2015). Ten years of invasion: *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Britain. *Ecological Entomology, 40*(4), 336–348. https://doi.org/10.1111/een.12203

Roy, H. E., Brown, P. M. J., Adriaens, T., Berkvens, N., Borges, I., Clusella-Trullas, S., … Zhao, Z. (2016). The harlequin ladybird, *Harmonia axyridis*: Global perspectives on invasion history and ecology. *Biological Invasions, 18*(4), 997–1044. https://doi.org/10.1007/s10530-016-1077-6

Roy, H. E., Brown, P. M. J., Rothery, P., Ware, R. L., & Majerus, M. E. N. (2008). Interactions between the fungal pathogen Beauveria bassiana and three species of coccinellid: *Harmonia axyridis*, *Coccinella septempunctata* and *Adalia bipunctata*. *BioControl, 53*(1), 265–276. https://doi.org/10.1007/s10526-007-9122-0

Sasaji, H. (1971). *Fauna Japonica, Coccinellidae (Insecta: Coleoptera)*. Academic Press of Japan.

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution, 30*(9), 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Seko, T., Abe, J., Miura, K., & Hikawa, M. (2017). The contribution of a beneficial insectary plant *Scaevola aemula* to survival and long-term establishment of flightless *Harmonia axyridis* in greenhouses. *BioControl, 62*(2), 221–231. https://doi.org/10.1007/s10526-017-9790-3

Serée, L., Chiron, F., Valantin-Morison, M., Barbottin, A., & Gardarin, A. (2022). Flower strips, crop management and landscape composition effects on two aphid species and their natural enemies in faba bean. *Agriculture, Ecosystems & Environment, 331*, 107902. https://doi.org/10.1016/j.agee.2022.107902

Shields, M. W., Johnson, A. C., Pandey, S., Cullen, R., González-Chang, M., Wratten, S. D., & Gurr, G. M. (2019). History, current situation and challenges for conservation biological control. *Biological Control, 131*, 25–35. https://doi.org/10.1016/j.biocontrol.2018.12.010

Sicsú, P. R., Macedo, R. H., & Sujii, E. R. (2015). Oviposition site selection structures niche partitioning among coccinellid species in a tropical ecosystem. *Neotropical Entomology, 44*(5), 430–438. https://doi.org/10.1007/s13744-015-0313-6

Simon, S., Bouvier, J.-C., Debras, J.-F., & Sauphanor, B. (2010). Biodiversity and pest management in orchard systems. A review. *Agronomy for Sustainable Development, 30*(1), 139–152. https://doi.org/10.1051/agro/2009013

Sloggett, J. J., Magro, A., Verheggen, F. J., Hemptinne, J.-L., Hutchison, W. D., & Riddick, E. W. (2011). The chemical ecology of *Harmonia axyridis. BioControl, 56*(4), 643–661. https://doi.org/10.1007/s10526-011-9376-4

Song, B., Tang, G., Sang, X. S., Zhang, J., Yao, Y., & Wiggins, N. (2013). Intercropping with aromatic plants hindered the occurrence of *Aphis citricola* in an apple orchard system by shifting predator–prey abundances. *Biocontrol Science and Technology, 23*(4), 381–395. https://doi.org/10.1080/09583157.2013.763904

Spellman, B., Brown, M. W., & Mathews, C. R. (2006). Effect of floral and extrafloral resources on predation of *Aphis spiraecola* by *Harmonia axyridis* on Apple. *BioControl, 51*(6), 715–724. https://doi.org/10.1007/s10526-005-5252-4

Steenberg, T., & Harding, S. (2009). Entomopathogenic fungi recorded from the harlequin ladybird, *Harmonia axyridis. Journal of Invertebrate Pathology, 102*(1), 88–89. https://doi.org/10.1016/j.jip.2009.07.002

Straub, C. S., Finke, D. L., & Snyder, W. E. (2008). Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control, 45*(2), 225–237. https://doi.org/10.1016/j.biocontrol.2007.05.013

Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances, 6*(45), eaba1715. https://doi.org/10.1126/sciadv.aba1715

Thomas, C. F. G., & Marshall, E. J. P. (1999). Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems & Environment, 72*(2), 131–144. https://doi.org/10.1016/S0167-8809(98)00169-8

Thomine, E., Rusch, A., Supplisson, C., Monticelli, L. S., Amiens-Desneux, E., Lavoir, A.-V., & Desneux, N. (2020). Highly diversified crop systems can promote the dispersal and foraging activity of the generalist predator *Harmonia axyridis. Entomologia Generalis, 40*(2), 133–145. https://doi.org/10.1127/entomologia/2020/0894

Thomine, E., Rusch, A., & Desneux, N. (2023). Predators do not benefit from crop diversity but respond to configurational heterogeneity in wheat and cotton fields. *Landscape Ecology, 38*(2), 439–447. https://doi.org/10.1007/s10980-022-01574-x

Thomine, E., Mumford, J., Rusch, A., & Desneux, N. (2022). Using crop diversity to lower pesticide use: Socio-ecological approaches. *Science of the Total Environment, 804*, 150156. https://doi.org/10.1016/j.scitotenv.2021.150156

Tiede, J., Iuliano, B., & Gratton, C. (2022). Agriculturally intensified landscapes are associated with reduced body condition of lady beetles. *Landscape Ecology, 37*(7), 1921–1936. https://doi.org/10.1007/s10980-022-01458-0

Tooker, J. F., O'Neal, M. E., & Rodriguez-Saona, C. (2020). Balancing disturbance and conservation in agroecosystems to improve biological control. *Annual Review of Entomology, 65*(1), 81–100. https://doi.org/10.1146/annurev-ento-011019-025143

Tourniaire, R., Ferran, A., Giuge, L., Piotte, C., & Gambier, J. (2000). A natural flightless mutation in the ladybird, *Harmonia axyridis. Entomologia Experimentalis et Applicata, 96*(1), 33–38. https://doi.org/10.1046/j.1570-7458.2000.00676.x

Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M. H., Najar-Rodriguez, A. J., & Jacot, K. (2016). Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *Journal of Applied Ecology, 53*(4), 1169–1176. https://doi.org/10.1111/1365-2664.12653

Tschumi, M., Albrecht, M., Entling, M. H., & Jacot, K. (2015). High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings. Biological Sciences, 282*(1814), 20151369. https://doi.org/10.1098/rspb.2015.1369

Uyi, O., Lahiri, S., Ni, X., Buntin, D., Jacobson, A., Reay-Jones, F. P. F., … Toews, M. D. (2022). Host plant resistance, foliar insecticide application and natural enemies play a role in the management of *Melanaphis sorghi* (Hemiptera: Aphididae) in grain sorghum. *Frontiers in Plant Science, 13*, 1006225. https://doi.org/10.3389/fpls.2022.1006225

Van Lenteren, J. C., Alomar, O., Ravensberg, W. J., & Urbaneja, A. (2020). Biological control agents for control of pests in greenhouses. In M. L. Gullino, R. Albajes, & P. C. Nicot (Eds.), *Integrated Pest and Disease Management in Greenhouse Crops* (pp. 409–439). Springer International Publishing. https://doi.org/10.1007/978-3-030-22304-5_14

Vandereycken, A., Brostaux, Y., Joie, E., Haubruge, E., & Verheggen, F. J. (2013a). Occurrence of *Harmonia axyridis* (Coleoptera: Coccinellidae) in field crops. *European Journal of Entomology, 110*(2), 285–292. https://doi.org/10.14411/eje.2013.042

Vandereycken, A., Durieux, D., Joie, E., Sloggett, J. J., Haubruge, É., & Verheggen, F. J. (2013b). Is the multicolored Asian ladybeetle, *Harmonia axyridis*, the most abundant natural enemy to aphids in agroecosystems? *Journal of Insect Science, 13*(158), 1–14. https://doi.org/10.1673/031.013.15801

Wan, H. H., Song, B., Tang, G., Zhang, J., & Yao, Y. C. (2015). What are the effects of aromatic plants and meteorological factors on *Pseudococcus comstocki* and its predators in pear orchards? *Agroforestry Systems, 89*(3), 537–547. https://doi.org/10.1007/s10457-015-9789-7

Wan, N.-F., Ji, X.-Y., Deng, J.-Y., Kiær, L. P., Cai, Y.-M., & Jiang, J.-X. (2019). Plant diversification promotes biocontrol services in peach orchards by shaping the ecological niches of insect herbivores and their natural enemies. *Ecological Indicators, 99*, 387–392. https://doi.org/10.1016/j.ecolind.2017.11.047

Wang, J., Li, S., Yuan, W., Hatt, S., Fang, Y., Jin, Z., & Wang, S. (2025). Ecological wisdom: Functional plant *Cosmos bipinnata* enhances fitness traits of predator *Harmonia axyridis* strengthening biological control in greenhouse production. *Agricultural Communications, 3*(3), 100097. https://doi.org/10.1016/j.agrcom.2025.100097

Wang, J., Yang, Y., Li, Y., Jin, Z., Desneux, N., Han, P., … Li, S. (2022). Direct and indirect effects of banker plants on population establishment of *Harmonia axyridis* and aphid control on pepper crop. *Frontiers in Plant Science, 13*, 1083848. https://doi.org/10.3389/fpls.2022.1083848

Wang, S., Michaud, J. P., Tan, X. L., Zhang, F., & Guo, X. J. (2011). The aggregation behavior of *Harmonia axyridis* in its native range in Northeast China. *BioControl, 56*(2), 193–206. https://doi.org/10.1007/s10526-010-9325-7

Wang, Y., Yao, F., Soares, M. A., Basiri, S. E., Amiens-Desneux, E., Campos, M. R., … Desneux, N. (2020). Effects of four non-crop plants on life history traits of the lady beetle *Harmonia axyridis. Entomologia Generalis, 40*(3), 243–252. https://doi.org/10.1127/entomologia/2020/0933

With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K., & Fisher, J. L. (2002). Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications, 12*(1), 52–65. https://doi.org/10.1890/1051-0761(2002)012[0052:TEOLSO]2.0.CO;2

Wolf, S., Romeis, J., & Collatz, J. (2018). Utilization of plant-derived food sources from annual flower strips by the invasive harlequin ladybird *Harmonia axyridis. Biological Control, 122*, 118–126. https://doi.org/10.1016/j.biocontrol.2018.04.008

Wu, C., Hatt, S., Xiao, D., Wang, S., Wang, S., Guo, X., & Xu, Q. (2024). Functional plants supporting predatory ladybirds in a peach orchard agroecosystem. *Arthropod-Plant Interactions, 18*(4), 713–721. https://doi.org/10.1007/s11829-024-10069-2

Wyckhuys, K. A. G., Abram, P. K., Barrios, E., Cancino, J., Collatz, J., Fancelli, M., … Elkahky, M. (2025). Orchard systems offer low-hanging fruit for low-carbon, biodiversity-friendly farming. *Bioscience, 2025*, biae140. https://doi.org/10.1093/biosci/biae140

Xiu, C.-L., Pan, H.-S., Ali, A., & Lu, Y.-H. (2017). Extrafloral nectar of *Hibiscus cannabinus* promotes adult populations of *Harmonia axyridis. Biocontrol Science and Technology, 27*(8), 1009–1013. https://doi.org/10.1080/09583157.2017.1364697

Xu, Q., Wang, S., Li, S., & Hatt, S. (2020). Conservation Biological Control in Organic Greenhouse Vegetables. In Y. Gao, H. M. T. Hokkanen, & I. Menzler-Hokkanen (Eds.), *Integrative Biological Control* (*Vol. 20*, pp. 133–144). Springer International Publishing. https://doi.org/10.1007/978-3-030-44838-7_8

Xu, Q., Wu, C., Xiao, D., Jin, Z., Zhang, C., Hatt, S., … Wang, S. (2023). Ecological function of key volatiles in *Vitex negundo* infested by *Aphis gossypii*. *Frontiers in Plant Science, 13*, 1090559. https://doi.org/10.3389/fpls.2022.1090559

Yan, F., Zhou, Z., Wang, S., Cao, Y., & Li, K. (2012). The effect of hedgerows on the distribution of *Harmonia axyridis* Pallas in agroforestry systems. *Shengtai Xuebao*. *Acta Ecologica Sinica, 32*(7), 2230–2238. https://doi.org/10.5846/stxb201105160639

Yang, L., Xu, L., Liu, B., Zhang, Q., Pan, Y., Li, Q., … Lu, Y. (2019). Non-crop habitats promote the abundance of predatory ladybeetles in maize fields in the agricultural landscape of northern China. *Agriculture, Ecosystems & Environment, 277*, 44–52. https://doi.org/10.1016/j.agee.2019.03.008

Yang, L., Zeng, Y., Xu, L., Liu, B., Zhang, Q., & Lu, Y. (2018). Change in ladybeetle abundance and biological control of wheat aphids over time in agricultural landscape. *Agriculture, Ecosystems & Environment, 255*, 102–110. https://doi.org/10.1016/j.agee.2017.12.013

Yang, Q., Li, Z., Ouyang, F., Men, X., Zhang, K., Liu, M., … Ge, F. (2023). Flower strips promote natural enemies, provide efficient aphid biocontrol, and reduce insecticide requirement in cotton crops. *Entomologia Generalis, 43*(2), 421–432. https://doi.org/10.1127/entomologia/2022/1545

Yang, Q., Men, X., Zhao, W., Li, C., Zhang, Q., Cai, Z., … Ouyang, F. (2021). Flower strips as a bridge habitat facilitate the movement of predatory beetles from wheat to maize crops. *Pest Management Science, 77*(4), 1839–1850. https://doi.org/10.1002/ps.6209

Zhang, X., Ouyang, F., Su, J., Li, Z., Yuan, Y., Sun, Y., … Ge, F. (2022). Intercropping flowering plants facilitate conservation, movement and biocontrol performance of predators in insecticide-free apple orchard. *Agriculture, Ecosystems & Environment, 340*, 108157. https://doi.org/10.1016/j.agee.2022.108157

Zhou, H., Yu, Y., Tan, X., Chen, A., & Feng, J. (2014). Biological control of insect pests in apple orchards in China. *Biological Control, 68*, 47–56. https://doi.org/10.1016/j.biocontrol.2013.06.009

Zhu, Y. (2023). *Assessing the role of Hibiscus cannabinus and Ricinus communis in ecological control of Aphis craccivora and impact on ecological adaptation of Harmonia axyridis* [Thesis]. Tarim University.

Manuscript received: May 27, 2025
Revisions requested: August 15, 2025
Final revised version received: October 7, 2025
Manuscript accepted: October 31, 2025