Effects of Crop Diversity on Pests and Natural Enemies in Agricultural Fields: Postprint

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Abstract

Crop diversity planting has an ancient and longstanding history in China, and continues to play a significant role in modern agricultural production. In recent years, utilizing diversity planting for pest control has become a hotspot in agricultural research worldwide. Crop diversity planting directly influences the occurrence, damage, and behavior of agricultural pests. Numerous studies have demonstrated that crop diversity planting can reduce pest populations and damage levels to varying degrees. However, some studies have indicated that crop diversity planting not only fails to mitigate pest damage but may even exacerbate it. Diversity planting affects not only the population densities of natural enemy insects but also their parasitism or predation rates, and influences their activity capacity by altering their orientation, searching, and dispersal behaviors. This paper synthesizes recent research findings on the effects of crop diversity planting on agricultural pests and their natural enemies, and discusses the prospects and current challenges in this field. Additionally, this paper introduces seven hypotheses concerning the mechanisms by which crop diversity planting influences insects (physical barrier hypothesis, optomotor response hypothesis, host plant odor masking hypothesis, repellent chemical substance hypothesis, altered plant odor composition hypothesis, natural enemy hypothesis, and resource density hypothesis) and one theory (suitable/unsuitable landing theory). While these hypotheses and theories can partially elucidate the mechanisms through which diversity planting affects insects, none can comprehensively explain the ecological mechanisms underlying pest control through diversity planting.

Full Text

Effect of Diversified Cropping on Insect Pests and Natural Enemies in Agroecosystems

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Abstract

Diversified cropping has an ancient and longstanding history in China and continues to play a vital role in modern agricultural production. In recent years, leveraging crop diversity for pest control has become a global research priority in agriculture. Diversified cropping systems directly influence the occurrence, damage levels, and behavior of agricultural pests. Numerous studies have demonstrated that crop diversification can reduce pest populations and mitigate damage to varying degrees. However, other research indicates that diversified cropping may fail to reduce pest damage or even exacerbate it. Beyond affecting natural enemy populations, diversification influences parasitism and predation rates while modifying the activity patterns of beneficial insects through impacts on their orientation, foraging, and dispersal behaviors. This paper synthesizes recent findings on how diversified cropping affects insect pests and their natural enemies in agroecosystems and discusses future research directions and current challenges. We also introduce seven hypotheses (physical obstruction, visual camouflage, host plant odor masking, repellent chemicals, altered plant odor profiles, enemy hypothesis, and resource concentration hypothesis) and one theoretical framework (appropriate/inappropriate landing theory) that attempt to explain the mechanisms through which diversified cropping influences insects. While these hypotheses and theories partially elucidate the underlying mechanisms, none comprehensively explains the ecological dynamics of pest control through crop diversification.

Keywords: Crop; Diversified cropping; Insect pest; Natural enemy; Agroecosystem; Population behavior

1.1 Effects of Diversified Cropping on Pest Occurrence and Damage

Several studies have shown that rational intercropping can reduce pest populations and damage levels. Numerous successful examples of pest control through intercropping have been documented (Table 1). It is generally believed that one reason intercropping mitigates pest damage is that diversified plantings create unfavorable microenvironments for pests while restricting their free movement among different crop species. More importantly, diversification may influence insect populations in four key ways: (1) attracting pests to crops with lower economic value or lighter damage, (2) interfering with host-finding behavior, (3) repelling pests through odor-producing plants, particularly in vegetable intercropping systems that may enhance natural enemy efficacy, and (4) providing nectar, pollen, or sheltered, humid ground-level habitats that support predatory natural enemies. Table 1 summarizes reported effective diversified cropping patterns for pest control, covering major food crops like maize (*Zea mays*) and wheat (*Triticum aestivum*), economic crops such as sugarcane (*Saccharum sinense*) and legumes, and vegetables including cabbage (*Brassica oler-*

acea), tomato (*Solanum lycopersicum*), and cucumber (*Cucumis sativus*). Target pests are highly diverse, ranging from stem borers, cotton bollworm (*Helicoverpa armiger*), and Japanese beetle (*Popillia japonica*) to aphids (Aphidoidea), flea beetles (*Phyllotreta striolata*), and termites (*Microtermes* spp.). Notably, pests such as stem borers and diamondback moth (*Plutella xylostella*), which are difficult to control with conventional pesticides, are particularly amenable to biodiversity-based management. Moreover, a single crop combination can sometimes control multiple pest species simultaneously. These findings demonstrate the considerable potential of diversified cropping for pest control and natural enemy conservation, offering cost savings for pest management while protecting ecological systems and beneficial insects—making it a crucial direction for future pest control strategies.

However, some studies indicate that intercropping does not reduce pest damage and may even intensify it. For example, European corn borer (*Ostrinia nubilalis*) caused less early-season damage but more late-season damage in maize-potato (*Solanum tuberosum*) intercrops compared to maize monocultures [41]. Banana (*Musa paradisiaca*) intercropped with legumes [*Canavalia ensiformis*, *Mucuna pruriens*, *Tephrosia vogelii*] showed no effect on banana weevil (*Cosmopolites sordidus*) populations or damage levels [42]. Alfalfa weevil (*Hypera postica*) densities did not differ significantly between alfalfa (*Medicago sativa*) monocultures and alfalfa-smooth bromegrass (*Bromus inermis*) intercrops [37]. Intercropping snap beans (*Phaseolus vulgaris*) with winter wheat increased populations of the tarnished plant bug (*Lygus lineolaris*) and the flea beetle *Systena frontalis* [19]. In oat (*Avena sativa*)-faba bean (*Vicia faba*) mixtures, peak populations of bird cherry-oat aphid (*Rhopalosiphum padi*) were higher than in monocultures [43]. Leek moth (*Acrolepia assectella*) laid equal numbers of eggs on cabbage (host plant) grown in monoculture versus cabbage intercropped with red clover (*Trifolium pratense*, a non-host) [44]. Strip intercropping with soybean or maize did not significantly reduce planthopper populations [*Sogatella furcifera*, *Nilaparvata lugens*, *Laodelphax striatellus*] [45]. Fruit-cotton intercropping [jujube (*Zizyphus jujuba*)-cotton, almond (*Amygdalus communis*)-cotton, walnut (*Juglans regia*)-cotton] led to severe aphid outbreaks [*Acyrthosiphon gossypii*, *Aphis gossypii*, *A. atrata*] [46]. Sugarcane intercropped with soybean did not reduce adult populations of the green weevil (*Hypomeces squamosus*); the richer host environment may have even facilitated movement from soybean to sugarcane at different growth stages [47].

1.2 Effects of Diversified Cropping on Pest Behavior

The impact and mechanisms of diversified cropping largely depend on pest biology and behavioral responses. Therefore, understanding how diversification affects pest behavior is essential for effective pest management. Many studies show that diversified cropping primarily influences pest (herbivorous insect) settlement and reproduction by interfering with orientation, mating, oviposition, and dispersal behaviors, thereby affecting crop damage levels [48]. The authors have previously published a detailed review on how crop diversification affects phytophagous insect behavior [48], so this topic will not be elaborated further here.

2.1 Effects of Diversified Cropping on Natural Enemy Populations and Parasitism/Predation Rates

Diversified cropping can significantly increase natural enemy populations. For instance, compared to carrot (*Daucus carota*) and onion (*Allium cepa*) monocultures, higher numbers of the predatory ground beetles *Bembidion* spp. and rove beetle *Aleochara bipustulata* were trapped in onion-carrot intercrops [32]. During the larval stage of the cabbage root fly (*Delia brassicae*), predator catches (ground beetles Carabidae and rove beetles Staphylinidae) were twice as high in brassica-non-brassica intercrops as in brassica monocultures, yet predation impact on egg numbers was equivalent [49]. Sugarcane-maize intercropping significantly increased predatory ladybird beetle (Coccinellidae) densities [18], while pepper (*Capsicum annuum*)-sugarcane intercropping significantly increased parasitoid populations attacking the South American leafminer [*Diglyphus isaea*, *Opius* sp., *Hemiptarsenus varicornis*] [35]. In squash (*Cucurbita moschata*)-maize-pea (*Pisum sativum*) mixtures, parasitoid catches were more than double those in squash monocultures [38]. Intercropping tomato with cauliflower (*Brassica oleracea* var. *botrytis*) significantly increased *Cotesia plutellae* populations [34]. Intercropping wheat varieties with different resistance levels increased average aphid parasitoid numbers [*Aphidius avenae*, *Aphidius gifuensis*] [25]. Cabbage intercropped with broad bean and wild mustard (*Brassica kaber*) supported six predator species and eight parasitoid species, compared to only three predators and three parasitoids in monoculture [50].

Diversified cropping also enhances predation and parasitism rates. Onion and guar (*Cyamopsis tetragonoloba*) proved optimal intercrops for managing eggplant (*Solanum melongena*) pests, with acetone extracts from onion leaves and guar flowers significantly increasing parasitism by *Trichogramma chilonis* (from 50.3% in controls to 82.7% and 74.3%, respectively) and predation by *Chrysoperla carnea* (from 59.1% to 92.1% and 89.7%) [51]. Maize intercropped with sweet potato (*Ipomoea batatas*) increased parasitism of Asian corn borer (*Ostrinia furnacalis*) eggs by *Trichogramma chilonis* [52]. In maize-chickpea (*Cicer arietinum*) intercrops, parasitism of stem borers by *Cotesia flavipes* increased with higher chickpea planting ratios [10]. In squash-maize-pea mixtures, 33% of melonworm (*Diaphania hyalinata*) eggs and 59% of larvae were parasitized, compared to 11% and 29% in squash monocultures [38]. Summer maize intercropped with prostrate mung bean (*Vigna radiata*) significantly increased parasitism of Asian corn borer by *Trichogramma ostriniae* [53], and pepper-sugarcane intercropping significantly enhanced parasitism of South American leafminer by *Diglyphus isaea*, *Opius* sp., and *Hemiptarsenus varicornis* [35].

Some studies, however, show no effects of diversification on natural enemy numbers or parasitism/predation rates. For example, predation and parasitism rates did not differ significantly between cabbage-clover intercrops and cabbage monocultures [29]. Strip intercropping with soybean or maize also failed to increase populations of planthopper egg parasitoids [*Anagrus nilaparvatae*, *Anagrus paranilaparvatae*, *Anagrus longitubulosas*] [45].

2.2 Effects of Diversified Cropping on Natural Enemy Behavior

Diversified cropping influences natural enemies primarily by affecting their mobility, orientation, searching behavior, and dispersal, which in turn impacts predation and parasitism rates. Cage experiments with sorghum (*Sorghum bicolor*)-pigeon pea (*Cajanus cajan*) intercrops showed that the minute pirate bug *Orius tantillus* was significantly more active on sorghum flowers than on other plant parts or on pigeon pea, resulting in stronger predation on cotton bollworm larvae on sorghum [54]. In maize monocultures, the spotted lady beetle *Coleomegilla maculata* exhibited high predation rates on European corn borer egg masses, but rates declined in maize-bean-squash intercrops because beetles spent more time searching on plants without egg masses (beans and squash), reducing foraging efficiency. Even with equal egg mass densities per plant, increased ineffective search time in intercrops significantly lowered predation rates and accelerated beetle emigration from intercropped fields [55]. Predatory ground beetles and rove beetles were more active in cabbage monocultures than in cabbage-clover intercrops [29]. When cereal crops are intercropped with molasses grass (*Melinis minutiflora*), volatiles released by the grass attract the stem borer parasitoid *Cotesia sesamiae*, significantly increasing parasitism rates [12,56]. In soybean-tall maize intercrops, the parasitoid *Pediobius foveolatus* (an enemy of the Mexican bean beetle) immigrated less and emigrated more than in soybean monocultures, with maize height being the primary factor reducing parasitoid immigration [57].

3 Hypotheses on Mechanisms of Diversified Cropping Effects on Insects

Seven hypotheses have been proposed to explain how diversified cropping reduces populations of host-specific pests: (1) physical obstruction, (2) visual camouflage, (3) masking of host plant odors, (4) repellent chemicals, (5) altering host plant odor profiles, (6) enemy hypothesis, and (7) resource concentration hypothesis.

The physical obstruction hypothesis posits that tall non-host plants in intercrops conceal host plants, disrupting visual orientation and field dispersal of pests, thereby reducing herbivore numbers on host plants. The visual camouflage hypothesis suggests that pest landing during flight is determined by two visual stimuli: a direct color response (typically to green) and an optomotor response that causes landing on plants in the flight path. Other green plants or weeds above the background create competing visual stimuli, shortening the distance to the host plant background and creating camouflage. Host plants become less conspicuous when surrounded by non-host foliage, reducing pest landings. The host plant odor masking hypothesis proposes that volatiles from non-host plants mask host plant odors, preventing pests from locating hosts and thereby protecting the crop [58]. The repellent chemicals hypothesis contends that odors from non-host plants strongly repel host-seeking pests, reducing the number orienting toward host plants [32]. The altered plant odor profile hypothesis suggests that host plants absorb soil chemicals they cannot synthesize, which modify their physiological state and affect pest populations. The enemy hypothesis argues that diversified cropping supports more abundant and effective parasitoids and predators, suppressing herbivore outbreaks [59] because diverse plantings provide better survival conditions, diverse pollen and nectar sources across time periods, and alternative foods that retain natural enemies when primary pests are scarce. The resource concentration hypothesis posits that pests prefer to settle and reproduce on concentrated host plant patches; diversified habitats containing both host and non-host crops create spatially dispersed host plants with varying sizes, colors, and odors that make it difficult for pests to land, remain, and reproduce [59].

Finch et al. [60] evaluated these seven hypotheses and proposed the appropriate/inappropriate landing theory. This theory suggests that host plant volatiles trigger landing by flying pests. When host plants are surrounded by bare soil, pests land directly on hosts since most insects avoid landing on brown surfaces like exposed soil, resulting in "appropriate landings" that aggregate pests on host plants. When non-host plants surround hosts, the ground is covered by both plant types, preventing flying insects from distinguishing hosts from non-hosts and causing "inappropriate landings" on non-hosts. Subsequent decisions to remain and oviposit are based on visual cues and non-volatile compounds, with non-host plants interfering with these behaviors and reducing pest numbers.

While these hypotheses and theories partially explain how diversified cropping affects pests, none fully elucidates the ecological mechanisms of pest control through crop diversification.

4 Challenges and Future Directions

Growing recognition of the urgent need to conserve biodiversity has substantially advanced research on crop diversification effects on insects in recent years, both in depth and breadth. Notably, increasing numbers of studies are attempting to clarify the mechanisms underlying diversification effects on pests and natural enemies [24]. However, several areas require strengthening:

First, effective field experimental evidence is lacking to demonstrate that reduced pest numbers in diversified systems actually increase crop yields, though some researchers are beginning to explore this [40]. Second, while many factors influence how diversified cropping affects insects, most studies focus on only one or two aspects. Comprehensive analyses are needed to identify primary versus secondary factors and clarify their respective roles. Third, global climate change is an undeniable reality that affects plant physiological functions, signaling molecules, and volatiles, significantly impacting crop yields. Ozone alters plant primary and secondary metabolism, affecting pest feeding preferences, behavior, growth, and development, which in turn influences natural enemy fitness [61]. Climate change will inevitably affect pests and natural enemies in diversified systems, yet research on this topic remains scarce. Fourth, the scale of diversified plantings and surrounding environmental features such as vegetation, buildings, and light or heat sources substantially influence pests and natural enemies, but these aspects have received insufficient attention, particularly regarding accurate quantitative evaluation techniques. With advancing research technologies, tools like remote sensing, drones, and image processing can measure and assess field environments, enabling integrated analysis of environmental and crop factors. Incorporating habitat diversity factors alongside genetic and species diversity will yield more systematic and comprehensive understanding and facilitate development of precisely tailored multi-level diversity strategies for improved natural enemy conservation, environmental protection, and pest control. Fifth, quantitative research on biodiversity effects is needed. Pest control through diversification can be slow or delayed, with different plant growth stages affecting various pest and natural enemy life stages differently. These effects are often quantitative, requiring systematic surveys of multiple factors and computer modeling to identify optimal spatiotemporal planting patterns that maximize diversification benefits. Sixth, diversified cropping should be integrated with other environmentally friendly pest management technologies. Multiple pest species may threaten a given region and season, and single tactics may not provide adequate control. Combining biodiversity-based approaches with physical and biological controls will be necessary to achieve effective chemical pesticide reduction and high-quality, high-yield production goals.

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