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Herbivorous Insects in Agroecosystems: Evolutionary Adaptations and Species Dynamics

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Abstract This study analyzed the biological characteristics, ecological roles, evolutionary adaptation mechanisms and population dynamics of herbivorous insects in agricultural ecosystems, discussed the classification and ecological habits of herbivorous insects, their impact on agricultural production and ecological network functions, and the concept of adaptive evolution unique to agricultural environments, focusing on the evolutionary adaptation mechanisms of herbivorous insects in terms of nutrient utilization, behavioral sensory perception and pesticide resistance. At the same time, the driving factors of their population dynamics were explored, including environmental factors, agricultural management measures and the impact of climate change. Through typical cases such as cotton bollworm, whitefly, *Spodoptera litura*, and rice planthopper, the phenomenon of multi-host adaptation, resistance evolution, population replacement and global expansion of herbivorous insects was analyzed. This study also looks forward to future research directions, such as multi-omics integration to reveal adaptation mechanisms, precision agriculture and population prediction models, biological regulation and ecological agriculture strategies, and adaptive evolution risk assessment under the background of climate change, in order to guide sustainable integrated pest management and provide reference for the stability of agricultural ecosystems and food security.

Keywords Agroecosystems; Herbivorous insects; Evolutionary adaptation; Population dynamics; Pesticide resistance

1 Introduction

Herbivorous insects are the most important biological factors in agricultural ecosystems, and they have a dual role: they are important pests of crops and components of the ecosystem food web. Historically, the yield losses caused by herbivorous insects feeding on crops are extremely significant, and about 20% to 40% of global crop yields are lost to pests each year (Savary et al., 2019). For example, outbreaks of rice planthoppers, armyworms, locusts, etc. will lead to reduced grain production, seriously threatening agricultural production and food security (Hamann et al., 2021). However, from an ecological perspective, herbivorous insects are also part of farmland biodiversity, forming a complex interaction network with host plants and natural enemies, and playing an important role in material circulation and energy flow (Dainese et al., 2019). Some herbivorous insects (such as Lepidoptera larvae) are important food sources for predatory and parasitic natural enemies, thus supporting the realization of biological control in agricultural ecosystems (Wyckhuys et al., 2024).

Since the development of agriculture by humans, the relationship between herbivorous insects and crops has been interdependent. On the one hand, large-scale artificial monoculture provides a rich and concentrated food source for insects that feed on plants, which easily induces a surge in pest populations (Hamann et al., 2021). On the other hand, the lack of diverse landscapes and natural enemy habitats in agricultural ecosystems makes herbivorous insects occupy a dominant position in the ecological niche, and their populations cannot be effectively restricted (Ziesche et al., 2024). In the long-term evolution process, herbivorous insects have formed a variety of unique adaptation mechanisms, enabling them to successfully utilize crop resources and respond to human prevention and control measures. These adaptive evolutionary phenomena include overcoming host plant defenses, evolving resistance to chemical pesticides, and rapidly responding to habitat and climate change in agricultural environments (Gould et al., 2018). Research on the evolutionary adaptability of herbivorous insects

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not only has basic ecological significance, but also directly serves the sustainable management of agricultural pests and provides a scientific basis for ensuring food security.

Given the important position and complex impact of herbivorous insects in agriculture, this study will analyze their evolutionary adaptation mechanisms and species dynamics, introduce the basic characteristics and ecological roles of herbivorous insects in agricultural ecosystems, focus on the evolutionary adaptation mechanisms of herbivorous insects, discuss the species dynamics and population ecology of herbivorous insects in agricultural ecosystems, and summarize the ecological influencing factors of the adaptive evolution and species dynamics of herbivorous insects. This study sorts out the research progress on the evolutionary adaptation and species dynamics of herbivorous insects in recent years, deepens the understanding of the laws of ecological adaptation of pests, and provides scientific support for the formulation of green agricultural pest management strategies.

2 Characteristics and Ecological Role of Herbivorous Insects in Agricultural Ecosystems

2.1 Biological and ecological characteristics of herbivorous insects

Herbivorous insects refer to insect groups that use tissues or products of living plants (including crops) as food sources. There are many species, covering almost all major insect orders (Onstad et al., 2009; Jankielsohn, 2018). In agricultural ecosystems, common herbivorous insects include: moth larvae of Lepidoptera (such as armyworms and cotton bollworms), beetles of Coleoptera (such as corn weevils and sweet potato weevils), Homoptera of Hemiptera (such as planthoppers, aphids, and whiteflies), locusts of Orthoptera, etc. These insects have their own characteristics in morphology and life history. For example, locusts have powerful hind legs that can jump and migrate, planthoppers and whiteflies have piercing and sucking mouthparts to suck plant sap, and moth larvae have chewing mouthparts that specialize in eating leaves or fruits, etc. (Dofuor et al., 2024).

Different groups of herbivorous insects have significantly different host ranges: some are monophagous or oligophagous, feeding on only one or a few closely related plants (such as the rice stem borer, which is mainly a rice pest); others are polyphagous (broad-spectrum) pests that can feed on multiple families of plants (such as cotton bollworms, which can harm dozens of crops such as cotton, corn, and tomatoes). Generally speaking, polyphagous insects are more likely to survive and spread in agricultural landscapes due to their wide food sources, but at the same time they need to evolve complex detoxification and adaptation mechanisms to cope with the defense chemicals of different plants (Crossley et al., 2021). In contrast, monophagous insects often develop highly specialized adaptive traits in their long-term co-evolution with specific hosts, such as feeding behaviors or enzyme systems corresponding to specific herbivorous parts (Horgan, 2024).

2.2 The role of herbivorous insects in agricultural ecosystems

In agricultural ecosystems, the most direct role of herbivorous insects is as pests, affecting crop yield and quality (Fiallo-Olivé et al., 2020). Most herbivorous insects feed on leaves, stems, fruits, seeds or juices of crops, causing crop yield reduction or quality decline. According to statistics, in the absence of prevention and control, the yield loss of major food crops in the world due to insect feeding can reach more than 30% (Savary et al., 2019). Even in modern agriculture, pests still cause huge economic losses and food losses every year. In addition, some herbivorous insects can also act as vectors of pathogens, exacerbating the damage to crops (Fiallo-Olivé et al., 2020).

On the other hand, herbivorous insects are also a key link in the agricultural ecological network (Wyckhuys et al., 2024). They are at the middle level of the food web. On the one hand, they feed on plants and transfer the energy and materials of primary production to higher trophic levels. On the other hand, they provide food sources for predators and parasites (such as parasitic wasps, predatory insects, birds, etc.) at higher trophic levels (Figure 1) (Li et al., 2023; Dofuor et al., 2024). Therefore, the existence of herbivorous insects maintains multiple relationships such as predator-prey and host-parasitoid in farmland ecosystems (Adhikari et al., 2024). If the population of herbivorous insects decreases excessively (for example, extreme use of broad-spectrum pesticides causes the decline of pests and beneficial insects together), some natural enemies may decline due to lack of food, thereby destroying the ecological balance (Wyckhuys et al., 2024).

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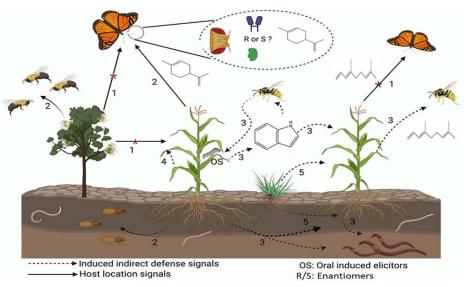


Figure 1 Chemical mechanisms of plant-insect interactions (Adopted from Dofuor et al., 2024)

Image caption: 1) Herbivore are able to distinguish host plants from background signals thus avoiding non-host plants, 2) Herbivore uses host derived signals to locate suitable site for oviposition and feeding (below and above ground); It may be able to distinguish between enantiomer (R or S) in selecting a suitable host, 3) Plant under herbivore feeding indirectly defend itself by emitting volatile compounds that are attractive to natural enemies of the feeding herbivore; Signals from herbivore fed plants can at the same time prime neighboring plants for possible attack; The primed plant emits volatile signals that are attractive to natural enemies (below and above ground), 4) Herbivore fed leaf of a plant can prime neighboring leaves to start emitting biotic stress signals that are capable of recruiting natural enemies, 5) Volatile of certain uninfected plants such as desmodium emit background signals that are able to prime neighboring plant of different species to emit stress related signals for the recruitment of natural enemies (below and above ground) (Adopted from Dofuor et al., 2024)

2.3 Basic concepts of ecological adaptation of herbivorous insects

Adaptive evolution refers to the process in which the frequency of favorable traits in biological populations increases under environmental selection pressure on the basis of genetic variation, thereby improving survival and reproductive success. In the context of agricultural ecosystems, herbivorous insects face special selection pressures, including the combined effects of human factors (pesticides, farming systems, insect-resistant varieties) and environmental factors (single field landscape, irrigation and fertilization patterns, etc.) (Gould et al., 2018). Therefore, their adaptive evolution exhibits some unique characteristics. The first is the rapid adaptation speed. Many studies have shown that the evolutionary response of pests to new environments and new resistance measures can occur in dozens of generations or even shorter (Crossley et al., 2021). The second is the diversity of adaptation mechanisms. The adaptation of herbivorous insects is not limited to a single pathway, but often involves multiple levels of physiology, biochemistry and behavior. In addition, the periodicity of disturbance in agricultural ecosystems also shapes the adaptation pattern of pests. For example, agricultural measures such as crop rotation and fallow will interrupt the continuous host source of pests, which requires pests to have adaptations such as migration or dormancy to survive unfavorable seasons or find new hosts (Lawton et al., 2022).

3 Evolutionary Adaptation Mechanisms of Herbivorous Insects

3.1 Nutritional adaptation evolution

Herbivorous insects can feed on a variety of plant tissues and digest the nutrients in them, which is an important manifestation of their nutritional adaptive evolution. There are significant differences in the utilization strategies of host nutritional resources among different insects, which is largely attributed to evolutionary nutritional adaptation. Insects' tolerance and utilization of plant secondary compounds is one of the core of nutritional adaptation (Crossley et al., 2021). In order to defend against herbivores, many plants synthesize a variety of secondary metabolites (such as alkaloids, phenols, protease inhibitors, etc.) with anti-nutritional or toxic effects. In the process of co-evolution, herbivorous insects have evolved corresponding detoxification and tolerance mechanisms (Skidmore and Hansen, 2017; Salem et al., 2025).



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The nutritional adaptation of herbivorous insects in morphology and behavior is also very obvious. For example, many borers (stem borers, weevils) have evolved hard jaws and specialized digestive tracts to destroy and digest harder tissues in the wood or seeds; pin-mouthed insects are adapted to piercing nutrition, and their saliva contains enzymes to help prevent sieve tube blockage and keep plant nutrients flowing (Dofuor et al., 2024). In addition, some insects co-evolve with symbiotic microorganisms to supplement nutritional adaptability. Symbiotic bacteria in the intestines of locusts and termites can help decompose cellulose; symbiotic bacteria in aphids synthesize essential amino acids to make up for the imbalance of plant sap nutrition (Horgan, 2024).

On an evolutionary time scale, the evolution of the host range of herbivorous insects reflects the trade-offs of nutritional adaptation. Some lineages have chosen a specialized strategy, deeply adapted to the nutritional environment of a single crop, and are highly competitive on this host (e.g., the codling moth is almost exclusively inhabiting apples and related fruit trees); other lineages have adopted a broad-spectrum feeding strategy, acquiring the ability to process a variety of plant secondary metabolites through gene duplication and functional differentiation (Crossley et al., 2021).

3.2 Behavioral and sensory adaptations

In order to find host plants and escape natural enemies and environmental stresses in complex agricultural environments, herbivorous insects have evolved a variety of behavioral and sensory adaptations. These adaptations ensure that pests can effectively complete feeding and reproduction, reflecting the evolutionary adjustment of insects to agricultural ecology from a behavioral ecology perspective. Herbivorous insects have sophisticated host location and selection behavioral adaptations. This relies on their highly sensitive sensory systems, such as smell, vision, and touch. Many insects have a large number of olfactory receptors distributed on their antennae, which can detect plant volatile organic compounds and identify suitable host species from a distance.

Herbivorous insects have evolved a variety of feeding behavior adaptations to circumvent plant defenses and improve feeding efficiency. Some pests adopt a secret feeding method, such as leaf miners and braconid wasp larvae that sneak into the leaf tissue to obtain stable nutrition while avoiding natural enemies and adverse environments. Another example is nocturnal feeding behavior: many Lepidoptera larvae hide during the day and come out to feed at night to avoid predatory natural enemies during the day and high temperature and dry environment (Lawton et al., 2022). Adaptability is also reflected in reproductive and developmental behavior. Oviposition site selection is a key behavior of herbivorous insects to ensure that their offspring can obtain suitable nutrition. In addition, in some insects, clustering helps to enhance resistance to natural enemies or improve the microenvironment. For example, aphids secrete warning pheromones, and other aphids quickly escape when their companions are attacked by predators (Wyckhuys et al., 2024).

3.3 Adaptation and evolution of pesticide resistance

The large-scale application of pesticides has exerted strong selection pressure on herbivorous insect populations, prompting them to develop resistance in a relatively short period of time. This is one of the most interesting areas in the study of evolutionary adaptation of herbivorous insects. Pesticide resistance adaptation and evolution are specifically manifested in the reduced sensitivity of pests to the toxicity of pesticides, so that they can still survive and reproduce at field concentrations (Gould et al., 2018). The evolutionary mechanisms of insect resistance are diverse, mainly including target site mutations, metabolic resistance, and behavioral and physiological resistance.

Many chemical pesticides work by acting on key proteins in the insect nervous system or development process, such as organophosphates and carbamates inhibiting acetylcholinesterase, pyrethroids acting on voltage-gated sodium ion channels, and Bt toxins needing to bind to midgut receptors to exert toxicity. Metabolic resistance means that insects quickly detoxify and eliminate pesticides by enhancing the activity of metabolic enzymes in the body. This usually involves the upregulation or amplification of the expression of multiple genes, especially detoxification enzyme genes, such as P450 monooxygenase, carboxylesterase and glutathione-S-transferase (Guy et al., 2017; Schwander et al., 2019; Crossley et al., 2021; Lin et al., 2024). Behavioral resistance refers to the

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pests reducing their exposure to pesticides by changing their behavior, such as some noctuids moving their feeding parts downward or hiding to avoid the spraying site; or they produce a refusal to feed or inhabit the sprayed plants. Physiological resistance includes, for example, the thickening of the epidermis reduces the penetration of the pesticide and the excretion of toxins by osmotic pumps (Gould et al., 2018).

4 Species Dynamics and Population Ecology of Herbivorous Insects in Agricultural Ecosystems

4.1 Dynamic changes in herbivorous insect populations

The population dynamics of herbivorous insects are the combined result of various density-independent factors (climate, host), density-dependent factors (natural enemies, competition) and human measures (pesticides, tillage) (Ziesche et al., 2024). Typical patterns include: pests increase in warm seasons and host-abundant periods, and decrease in cold or host-deficient periods; unreasonable farming can cause pests to rebound or remain at a high level after a short decline; good ecological regulation can maintain its low-level fluctuations. Understanding these patterns helps predict and warn of pest occurrences. For example, through long-term monitoring and accumulation of data, a statistical model of pest population dynamics and key climate, crop growth period and other factors can be established to predict the peak period and degree of damage of pests in the next season (Lawton et al., 2022). Adjusting agricultural management in accordance with the laws of population ecology, such as actively suppressing insect sources during the low period of pests and protecting natural enemies in the early stage of pest rise, can more effectively stabilize the insect state in farmland and provide a basis for integrated pest management.

4.2 Impact of climate change on the dynamics of herbivorous insect species

Global climate change is increasingly affecting the geographical distribution, seasonal changes and population dynamics of herbivorous insects (Hamann et al., 2021). Among them, rising temperatures, changes in precipitation patterns and frequent extreme weather events are the main climatic factors affecting pest dynamics. Rising temperatures often accelerate the development rate and reproduction cycle of insects, which may lead to an increase in the number of generations of pests and an increase in annual reproduction. Studies predict that under the background of global warming, the annual number of generations of some major pests in temperate regions (such as armyworms and cotton bollworms) can increase from 2 to 3 generations to 3 to 4 generations, significantly increasing their cumulative population size (Deutsch et al., 2018).

Changes in precipitation and humidity also have a significant effect on pest dynamics. Changes in precipitation patterns may affect the overwintering survival and reproduction of pests. For example, in areas with warm winters and heavy rains, pests are more likely to survive the winter, and the initial population density in the early spring of the following year is relatively high, causing early season damage (Lawton et al., 2022). The increase in extreme weather events (such as heat waves, droughts, heavy rains, and cold waves) also has complex effects on pest dynamics. Heat waves may cause large-scale deaths of pests and temporarily suppress the population, but if some individuals adapt to high temperatures and survive, the surviving population may have a stronger tolerance to high temperatures, that is, "selection screening" (Cusumano et al., 2019). In addition, climate change can also change local species dynamics by driving biological invasions.

4.3 Monitoring and prediction methods for the dynamics of herbivorous insect species

Accurate monitoring and prediction of the population dynamics of herbivorous insects is the basis for effective pest early warning and control. Traditional field monitoring methods include: fixed-point surveys, light trapping, sex attractant trapping, yellow board trapping, field retrieval, etc. These methods are easy to operate and low-cost, and are still the main means of routine pest monitoring in the agricultural sector. In recent years, modern technology has been increasingly used in pest monitoring, improving monitoring efficiency and accuracy. Among them, remote sensing technology and Internet of Things monitoring are the most representative progress. Remote sensing monitoring uses high-altitude satellites, drones or aerial cameras to capture the growth and damage characteristics of crops over a large area, thereby inferring the occurrence of pests (Figure 2) (Mpisane et al., 2025).

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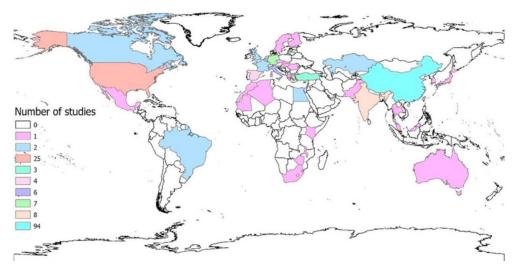


Figure 2 Spatial distribution of studies on the use of remote sensing in the monitoring of insect pests (Adopted from Mpisane et al., 2025)

In addition, molecular ecological methods have also provided new tools for pest monitoring. Environmental DNA (eDNA) detection can determine the presence and abundance of target pests by collecting DNA fragments in soil, air or water, and using specific primers PCR. Population dynamics models and information decision-making systems have become powerful tools for predicting pest conditions. By integrating biological parameters (development rate, reproductive potential, mortality rate, etc.) with weather data, agricultural operations and other factors, and establishing mathematical models (such as logistic growth models, age structure models or artificial neural network models), it is possible to simulate and predict the population trends of pests in the future (Lawton et al., 2022).

5 Ecological Factors Affecting the Adaptive Evolution and Species Dynamics of Herbivorous Insects

5.1 Ecological effects of agricultural management measures

Agricultural management measures not only change the ecology of herbivorous insect populations, but also drive their adaptive evolution. Intensive monoculture and unreasonable use of pesticides tend to simplify the ecosystem, intensify evolutionary pressure, and make pests more likely to break out and evolve resistance (Ziesche et al., 2024). In contrast, diversity management and ecological strategies can inhibit over-adaptation and outbreaks of pests by enhancing system homeostasis and buffering effects (Wyckhuys et al., 2024). Therefore, in order to delay resistance and population replacement, it is necessary to support the promotion of insect-resistant varieties with a "planting resistance management" strategy, such as reasonable rotation and stacking of resistance genes, mixed planting of multiple varieties, etc., to reduce the long-term monopoly of the environment by a single resistance gene (Carrière et al., 2020). In addition, an integrated pest management (IPM) model such as agronomy + biology + chemistry is also adopted to reduce pest damage while protecting ecological service functions.

5.2 Ecological driving role of natural enemies and biological control measures

Natural enemies play an important regulatory role in herbivorous insect populations in agricultural ecosystems and are regarded as "natural plant protection forces". Biological control measures that make full use of natural enemies not only directly suppress the number of pests, but also drive the behavior and adaptive evolution of pests (Wyckhuys et al., 2024). The presence of natural enemies significantly reduces the frequency and peak of pest outbreaks (Dofuor et al., 2024). Natural enemy pressure can also drive pests to produce behavioral and morphological adaptations. It is worth noting that the widespread application of biological control may exert selection pressure on pest populations, prompting them to evolve resistance or avoidance behavior to biological control factors (Gould et al., 2018). Natural enemies and biological control measures can also enhance ecological resilience at the entire agricultural ecological level. Diverse natural enemy communities not only control single pests, but also provide an "insurance" effect against multiple potential pests (Tooker and Giron, 2020).

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5.3 Impact of habitat destruction and ecological landscape change

With the development of modern agriculture, large areas of land have been reclaimed for farmland, natural vegetation fragments have been reduced, and the landscape has become more monotonous, which has brought many impacts on herbivorous insects and their associated organisms. Habitat destruction and landscape change have produced a "double-edged sword" effect on herbivorous insects: on the one hand, the diversity of some sensitive insects has been reduced, and on the other hand, a few pests that have adapted to the agricultural environment have been given an opportunity to take advantage and even become more destructive (Ziesche et al., 2024). Therefore, it is necessary to seek an optimal balance between landscape and habitat management in agricultural production, and to enhance the homeostasis of farmland ecosystems and the natural inhibitory force on pests through habitat restoration and landscape diversification measures, and to slow down the adverse adaptive evolution and population expansion trends. As some researchers pointed out: "Maintaining the complexity of farmland ecological landscapes is the cornerstone of sustainable pest management and farmland health" (Agrawal et al., 2012).

6 Typical case Study Analysis

6.1 Cotton bollworm (Helicoverpa armigera): multi-host adaptation and resistance evolution

The cotton bollworm is an important agricultural pest in the world. One of its notable features is its broad host adaptability and strong ability to evolve resistance (Yang et al., 2022). The cotton bollworm has a very wide host range, and is known to feed on more than 180 plant species, covering a variety of crops such as cotton, corn, soybeans, and tomatoes. This polyphagia stems from its evolutionary pre-adaptation to the chemical defenses of different plants: the cotton bollworm larvae have a variety of detoxification enzymes that can metabolize various plant toxins such as heavy metal phenols in cotton, nicotine in tobacco, and lactones in lettuce. In addition to its broad-spectrum feeding, another outstanding adaptive characteristic of the cotton bollworm is its ability to rapidly evolve resistance to various control measures. The cotton bollworm is one of the first pests found to be resistant to multiple insecticides. So far, it has been reported to be resistant to a variety of insecticides such as organochlorine, organophosphate, carbamate, pyrethroid and Bt protein. Molecular mechanism studies have found that this is mainly due to the kdr (knockdown resistance) mutation of the sodium channel gene in the axon of cotton bollworms, which makes pyrethroids ineffective. At the same time, the activity of carboxylesterase and glutathione transferase in cotton bollworms is also enhanced, which can decompose pyrethroid molecules (Crossley et al., 2021).

6.2 Bemisia tabaci: population replacement, virus transmission and global expansion

Bemisia tabaci is a small piercing-sucking pest that occurs widely in greenhouses and fields. It is known for its fast reproduction rate, strong migration and expansion ability, and serious virus transmission damage. Bemisia tabaci is actually a species complex, which contains a variety of cryptic species with obvious genetic differentiation, among which the Middle East-Asia Minor type I (MEAM1, also known as type B) and the Mediterranean type (MED, also known as type Q) are the most well-known (Xue et al., 2024). Different cryptic species differ in host adaptation and pesticide resistance, so population replacement has occurred worldwide. Another major hazard of whiteflies is their ability to spread a wide spectrum of viruses, which indirectly damages crop health (Fiallo-Olivé et al., 2020). Whiteflies suck phloem sap from plants with their mouthparts, and can carry and spread a variety of plant viruses during feeding, especially persistent circulating Gemini viruses. Whiteflies are highly globally expansive pests. They were originally widespread in tropical and subtropical regions, but through international trade and air migration, they have spread to all parts of the world in the past 30 years and are listed as one of the world's top 100 invasive species (Yang et al., 2022). The reason for their spread is that whiteflies are small in size and can easily spread across borders unintentionally with plant materials such as flowers and vegetables; in addition, they reproduce quickly and can quickly establish populations under protected conditions such as greenhouses after arriving in a new environment.

6.3 Spodoptera frugiperda: rapid adaptation in GM crop systems

Spodoptera litura (also known as Fall Armyworm) is native to the Americas and is a major emerging invasive pest in the world in recent years. Its rapid adaptation and resistance evolution in GM Bt crop systems have attracted



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much attention. Spodoptera litura has extremely strong migration and reproduction capabilities, posing a threat to a variety of food crops such as corn, rice, and sorghum. The rapid adaptation of Spodoptera litura in GM crop systems is also reflected in its migration expansion and ecological habits. There is no history of planting Bt corn in the newly invaded areas of Asia and Africa, but Spodoptera litura still shows strong adaptability: populations have been established in various climate zones, and it can reproduce multiple generations a year and migrate long distances. Spodoptera litura has the potential to become a "super pest": flexible and diverse genomes, high behavioral plasticity, strong reproductive capacity, and outstanding ability to resist environmental and human pressures (Yang et al., 2022).

6.4 Planthoppers and rice farming systems

The population dynamics and evolution of pesticide resistance of rice planthopper pests (such as brown planthopper Nilaparvata lugens and white-backed planthopper Sogatella furcifera) in Asian rice farming systems is a typical example of the "pest-human" game that has lasted for decades (Figure 3) (Chen et al., 2023). These planthoppers are the main piercing-sucking pests in rice fields. They not only directly harm rice but also spread viral diseases. In the 1960s and 1970s, brown planthoppers once became a catastrophic pest due to the large-scale use of broad-spectrum pesticides. Afterwards, its damage was controlled through comprehensive measures such as variety resistance and pesticide management. However, in the 21st century, outbreaks have occurred frequently again, involving complex interactions between population ecology and the evolution of pesticide resistance. Planthopper population dynamics are closely related to rice cultivation systems and regional climate. In terms of chemical control, brown planthoppers have also evolved resistance to commonly used pesticides. This is related to the fact that many generations of planthoppers emerge, the hidden generations encounter fewer pesticides on weeds, and resistance genes are accumulated (Horgan, 2024).

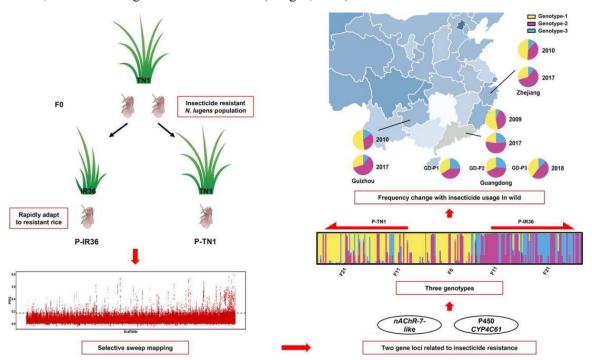


Figure 3 Genetic analysis of brown planthopper's adaptation mechanism to rice varieties and insecticide resistance (Adapted from Chen et al., 2023)

7 Future Research Directions and Implications for Agricultural Management

7.1 Multi-omics and evolutionary ecology integration research

Future research on the evolutionary adaptation of herbivorous insects will increasingly rely on the integration of multi-omics technology and evolutionary ecology. On the one hand, "omics" methods such as genomics, transcriptomics, proteomics, and metabolomics provide powerful tools for in-depth analysis of pest adaptability (McCulloch et al., 2023). On the other hand, combining omics data with evolutionary ecology theory is a major

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trend in the future. This means not only "what genetic variations there are", but also "how these variations are selected and manifested as traits in the ecological environment". In addition, multi-omics integration can also help to clarify the mechanism of complex adaptive traits. For example, drug resistance may involve multiple levels such as target mutations + detoxification enzymes + behavioral changes, which are not easy to fully reveal from a single perspective. By combining genomes, transcriptomics, and metabolomics, a causal chain from genes to phenotypes can be established (Zeng et al., 2023).

7.2 Precision agriculture and population prediction models

The rise of precision agriculture provides new opportunities for monitoring and predicting herbivorous insect populations. Precision agriculture achieves real-time and quantitative management of farmland environment and organisms by integrating sensor technology, data analysis and automated equipment. In the field of pests, the concept of precision agriculture is to accurately predict pest population dynamics and outbreak risks based on environmental variables, pest genotypes and historical data, and formulate customized intervention measures (Mpisane et al., 2025). Specific directions include: real-time monitoring and big data analysis. Use the aforementioned advanced monitoring tools (such as wireless traps, remote sensing drones, and IoT sensors) to collect massive amounts of pest and environmental data, store them in cloud databases, and then find patterns through big data mining and machine learning models. The combination of precision agriculture and intelligent prediction models will push the management of herbivorous insects to a new level: from passive response to active early warning, from extensive prevention and control to customized solutions, and from average levels to differentiated management.

7.3 Biological regulation and ecological agricultural strategies

In order to fundamentally reduce the harm caused by herbivorous insects, agriculture in the future needs to rely more on biological regulation and ecological agricultural strategies, that is, to enhance the resistance and resilience of crops to pests at the ecosystem level (Wyckhuys et al., 2024). Efforts in this regard include: habitat management. Through intentional planning of farmland and surrounding habitats, environmental conditions that are unfavorable to pests but favorable to natural enemies are created. Diversified planting is also one of the key strategies, including rotation, intercropping, interplanting and other methods. Crop rotation disrupts the continuous reproduction chain of pests, and intercropping and interplanting achieve the "repellent-attraction" effect through crop interactions. The construction of ecological compensation areas is a broader habitat management, that is, retaining a certain area of non-agricultural vegetation around farmland as a source of biodiversity. In addition, farming system innovation is also an ecological strategy. Cultivating crop diversity is also a long-term and effective strategy, including screening insect-resistant varieties for mixed planting or creating compound resistant varieties. At a broader level, maintaining the integrity of the regional ecosystem can play a role in source control of agricultural pests.

7.4 Risk assessment of adaptive evolution in the context of climate change

Climate change has brought new uncertainties and risks to the adaptive evolution of herbivorous insects, and it is of great significance to conduct forward-looking risk assessments. On the one hand, warming may accelerate the adaptive process of some pests. For example, higher temperatures will increase the rate of mutation accumulation and generational alternation in pests, making them more susceptible to adaptive mutations to pesticides and resistant varieties. On the other hand, climate change may change the competitive landscape between different pest species, leading to a dynamic rebalance of species, which in turn affects the direction of adaptive evolution (Ziesche et al., 2024). For example, under warm winter conditions, the overwintering survival rate of local pests increases, while some migratory pests can reproduce locally without migrating far, which may intensify the resource competition between local species and immigrant species. In order to cope with the risks of adaptive evolution of pests under climate change, international cooperation needs to be strengthened. Climate change is global, and the risks of pest spread and evolution also cross national borders. For example, the possibility of the African fall armyworm entering southern Europe due to climate change has increased, which requires Europe and Africa to jointly monitor and share resistance management experience (Hamann et al., 2021).



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Conflict of Interest Disclosure

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