






Review

Molecular Diagnostics for Monitoring Insecticide Resistance in Lepidopteran Pests

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Abstract: Chemical control methods to prevent crop damage have long been directly implicated in the selection of lepidoptera insect populations resistant to insecticides. More recently, new products featuring different modes of action (MoA), developed to mitigate the negative effects of control management on both producers and the environment, are rapidly losing efficacy due to the emergence of insect resistance. Among these, certain resistances are associated with molecular changes in the genomes of pest insects that are valuable for developing molecular markers for diagnostic tools, particularly the point mutations. Molecular diagnosis represents an innovative solution for insecticide resistance management (IRM) practices, allowing for the effective monitoring of insecticide resistance. This approach facilitates decision making by enabling the timely alternation between different modes of action (MoAs). In this context, this review focuses on the major lepidopteran pests that affect globally significant crops, discussing the impacts of insecticide resistance. It gathers literature on diagnostic methods; provides a comparative overview of the advantages of different techniques in terms of efficiency, cost, precision, sensitivity, and applicability; and highlights several novel diagnostic tools. Additionally, this review explores the coffee leaf miner, *Leucoptera coffeella*, as an applied model to illustrate potential approaches for more effective and sustainable control strategies.



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1. The Global View of Insecticides in Agriculture

Chemicals were historically the primary method of pest control in global agriculture and remain nowadays at this same status. The use of pesticides allows for less damage of cultivated species, and consequently, increased production. Nonetheless, the use of large quantities of these molecules, estimated at approximately 2 million tons annually [1], implies economical drawbacks. According to data from the Food and Agriculture Organization of the United Nations (FAO) during 2021–2022, Brazil was the leading country in general pesticide use for agriculture, with 719.51 thousand tons, followed by the United States with 417.39 thousand tons and Indonesia with 283.30 thousand tons [2].

Included in this account, insecticides represent a heavy burden to producers, besides having direct consequences on health and the environment, as illustrated in Figure 1. The impacts of insecticides on human health are more severe when workers are directly exposed to the products, considering that the knowledge of health risks is still insufficient for workers to change their handling practices [3]. It is proven that pesticide poisoning can cause effects on the human body such as diarrhea, headaches, and dizziness, and in more severe cases, it can contribute to the development of neurological problems and carcinogenic diseases [4,5]. Beyond human health, the environmental impacts of insecticide application are also severe, as the lack of specificity affects non-target insects that play

important roles in ecosystems, such as pollinators [4] and other animals like birds and fish [6,7]. Additionally, insecticides contaminate water [8], soil [9], and food [10,11], causing damage to the entire trophic chain.

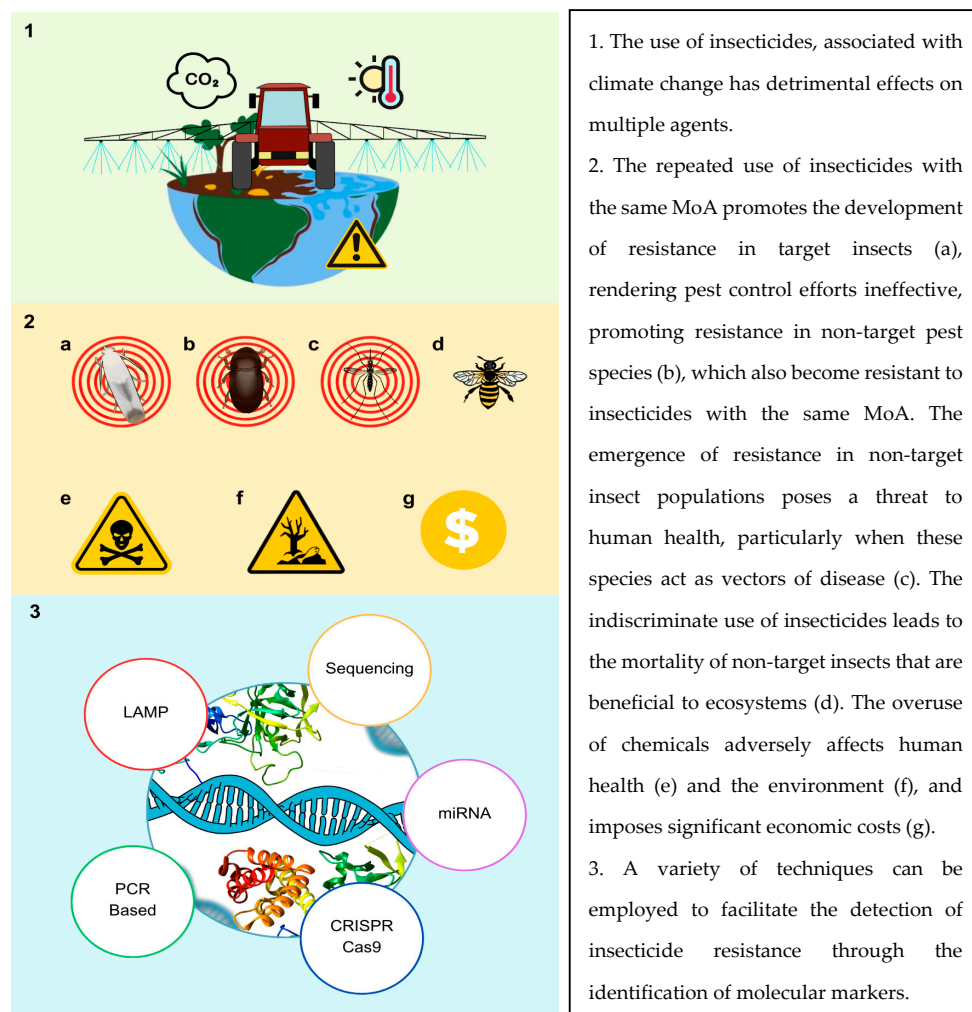


Figure 1. The main physical determinants in the global context of insecticide application, their impact application in One Health precepts, and technologies that can help resolve the problem of insecticide resistance.

The excessive use of insecticides can lead to the development of resistant target insect populations, especially lepidopterans, pests that can cause significant losses in agriculture worldwide [12]. Large broad-spectrum insecticides used to manage lepidopterans over time in association with some characteristics related to their ecology or evolution, like the fast development cycle in most cases [13], and the abundance of horizontal gene transfer (HGT) [14], increase insecticide resistance. This has enormous economic, social, and environmental consequences; in addition, the market pressure for sustainable practices and the reduction of insecticide residues in food has meant that the insecticide resistance in lepidopterans has become an urgent issue [12].

2. The Insecticide Resistance Problem

The first reports of insecticide resistance appeared around 1914, where resistance to sulfur was observed in scale insects [15]. Resistance to insecticides remained at low frequency until the introduction and expansion of synthetic organic insecticides such as DDT, cyclodienes, and organophosphates between the 1940s and 1950s [16]. From the 1960s onwards, insecticide resistance began to be considered an impact factor of the use and

effectiveness of a wide range of chemical compounds. New chemicals were introduced onto the market in an attempt to circumvent the situation, although, in many cases they had the same chemical class as those already existing [17]. In this way, in 1984, the Insecticide Resistance Action Committee (IRAC) was formed together with other organizations in an attempt to establish adequate management of resistance. In 1998, the IRAC began to develop a classification scheme for agricultural chemicals based on the so-called Modes of Action (MoA), a tool that initially classified acaricides, which is currently extended to cover biologicals and insecticides as the main basis for managing resistance [16].

The most recent reports (2020) on the global use of insecticides show this ranking is led by Indonesia, the United States, China, and Brazil, with 116,405 thousand tons, 72,985 thousand tons, 70,126 thousand tons, and 59,587 thousand tons, respectively [2]. Consequently, known resistance in a wide variety of pest insects is closely related to the most cultivated crops in these countries. In Indonesia, the main reports of resistance are in *Spodoptera frugiperda*, with resistance to insecticides in the chemical groups of organophosphates, avermectins, pyrethroids, spinosyns, and diamides, and in *Plutella xylostella*, with resistance detected to organophosphate and pyrethroid insecticides [18]. In Brazil, there are insecticide resistance reports for many of the insects figuring on the top of the agricultural pests and diseases government list, presenting high phytosanitary risk to production [19]. Among these insects, *Bemisia tabaci* is noted, with reports of resistance to tetranortriterpenoids, diamides, carbamates, phenylthiourea, neonicotinoids, and ketoenol [20]; *Helicoverpa armigera* and *S. frugiperda*, with reports of resistance to organophosphates, carbamates, pyrethroids, and oxadiazines [21–23]; and *Tuta absoluta* [24–26] and *P. xylostella* [27–30] to organophosphates. The United States government also has a ranking of the pests and diseases that pose a significant threat to the country's agriculture [31]. Among the listed insects, there are reports of insecticide resistance in *S. litura*, to organophosphates, carbamates, pyrethroids, and oxadiazine [32]; *T. leucotreta*, resistant to benzoylureas [33]; *H. armigera*, resistant to pyrethroids, cyclodienes, and organophosphates [23]; *Tecia solanivora*, resistant to carbamates and organophosphates [34]; and *T. absoluta*, resistant to organophosphates, carbamates, pyrethroids, avermectins, oxadiazine, benzoylureas, and spinosyns [24]. To aggravate the situation, it has been shown that insecticide resistance mechanisms are affected by climate change [35] (Figure 1) and that these changes are related to the increased risk of pest invasion areas worldwide [36–39]. Therefore, the challenge of monitoring resistance is greater than just accounting reports of already installed resistance, which would allow a better control of its development and dissemination. Thus, management techniques and technologies that prioritize environmental concerns are essential for ensuring a more sustainable future, and diagnosing resistance can be a crucial action [40–43]. Besides the agricultural problems posed to crop pests, the consequences of the development of insecticide-resistant insect populations are also closely related to human health. Just as it is an environmental concern, resistance in non-target insect populations is also a critical issue for human health, as there are cases of resistance in insect vectors of important human diseases, such as mosquitoes that transmit dengue, zika, chikungunya, yellow fever, and malaria [44–46]. Finally, other consequences of resistance development are still uncertain, as in non-target insects, such as bees, ants, and termites [47].

Over the past five years, a significant number of studies have been published documenting insecticide resistance in lepidopteran species. Fortunately, the majority of these studies investigated the molecular mechanisms underlying the development of resistance, and numerous diagnostic tools for resistance detection are now in widespread use. To exemplify this, Table 1 presents a review of key studies from the past five years, wherein lepidopteran species classified by the IRAC [48] as resistant to insecticides were evaluated based on the diagnostic methods employed, alongside their respective outcomes. It is important to emphasize that many of these studies, despite successfully characterizing a substantial portion of the molecular basis of resistance, also indicate the need for further in-depth investigations, suggesting that multiple resistance mechanisms may be implicated in the response of a given species to a particular MoA [49,50].

Table 1. Key studies from the past five years of lepidopteran pests resistant to several insecticides, the diagnostic method used to detect insecticide resistance, and their results.

Lepidopteran Species	Major Hosts	Insecticide Resistance Report	Diagnostics Related	Results	Year/Ref.
<i>Chilo suppressalis</i> Asiatic rice borer	Poaceae [51]	Diamides	qRT-PCR	Expression analysis of genes involved in insecticide resistance	2021 [52]
			Sequencing	Mutations detection related to insecticide resistance	2023 [53]
			RNA-seq	Genome-wide analysis and long non-coding RNA (lncRNA) identification associated with insecticide resistance	2023 [54]
		Organophosphates	qRT-PCR	Overexpressed gene detection associated with insecticide resistance	2021 [55]
		Pyrethroids, Organophosphates	Sequencing	Overexpressed genes and mutation detection associated with insecticide resistance	2021 [56]
		Benzamides	Illumina Sequencing + qRT-PCR	Transcriptome analysis and expression analysis of genes involved in insecticide resistance	2023 [57]
		Avermectins	qRT-PCR	Expression analysis of genes involved in insecticide resistance	2022 [58]
<i>Cydia pomonella</i> Codling Moth	Rosaceae and Juglandaceae [59]	Pyrethroids, Organophosphates, Spinosyns	Resequencing and RNA-seq	Mutation detection and transcriptomic and expression analysis related to insecticide resistance	2022 [56]
		Diamides, Pyrethroids	RNA-seq	Expression analysis of genes and mutation detection related to insecticide resistance	2023 [60]
		Pyrethroids	PCR-RFLP	Mutation detection related to insecticide resistance	2020 [61]

Table 1. Cont.

Lepidopteran Species	Major Hosts	Insecticide Resistance Report	Diagnostics Related	Results	Year/Ref.
<i>Helicoverpa armigera</i> Cotton bollworm	Fabaceae, Malvaceae, Asteraceae, Solanaceae, Convolvulaceae, and Scrophulariaceae [62]	Pyrethroids	Illumina sequencing + PCR	Expression analysis of gene and mutation detection associated with insecticide resistance	2023 [49]
			RNA-seq	Genome-wide analysis and long non-coding RNA (lncRNA) identification associated to insecticide resistance	2024 [50]
			CRISPR/Cas9 + qRT-PCR + RNAi	Transcriptional regulation analysis and overexpressed genes associated with insecticide resistance	2023 [63]
		Oxazadines, Semicarbazone, Carbamates	RT-qPCR	Expression analysis of genes involved in insecticide resistance	2021 [64]
<i>Helicoverpa zea</i> Corn earworm	Poaceae, Malvaceae, Fabaceae, and Solanaceae [65]	Pyrethroids	Sequencing	Interspecific introgression detection of genes involved in insecticide resistance	2024 [66]
<i>Leucinodes orbonalis</i> Eggplant fruit borer	Solanaceae [67]	Organophosphates, Diamides, Pyrethroids, Carbamates, Avermectins	qPCR	Expression analysis of genes involved in insecticide resistance	2020 [68]
<i>Lobesia botrana</i> European grapevine moth	Vitaceae [69]	Not specific	RAPD-PCR	Polymorphic gene detection based on sequence characterized amplified region (SCAR) associated with insecticide resistance	2021 [70]
<i>Ostrinia nubilalis</i> European corn borer	Poaceae [71]	Pyrethroids	PCR-RFLP	Mutation detection related to insecticide resistance	2022 [72]

Table 1. Cont.

Lepidopteran Species	Major Hosts	Insecticide Resistance Report	Diagnostics Related	Results	Year/Ref.
<i>Plutella xylostella</i> Diamondback moth	Brassicaceae [73]	Organophosphates	qPCR	Mutation detection related to insecticide resistance	2024 [74]
		Spinosyns	Sequencing	Transcriptome analysis and expression analysis of genes involved in insecticide resistance	2022 [75]
		Diamides Diamides	ddRAD-seq	Expression analysis of genes and mutation detection related to insecticide resistance	2020 [76]
			PacBio and Dovetail Hi-C sequencing	Chromosome level analysis and mutation detection related to insecticide resistance	2021 [77]
<i>Spodoptera exigua</i> Beet armyworm	Solanaceae, Brassicaceae, Alliaceae, Asteraceae, Poaceae, Fabaceae, and more [78]	Diamides	LAMP	Mutation detection related to insecticide resistance	2020 [79]
		Oxazadines	AS-PCR	Mutation detection related to insecticide resistance	2024 [80]
		Organophosphates, Pyrethroids	qRT-PCR and sequencing	Overexpression of transcription factors and mutation detection associated with insecticide resistance	2021 [81]
		Avermectins	Bulked segregant analysis (BSA) + CRISPR/Cas9	Identification of metabolic resistance genes responsible for insecticide resistance	2021 [82]
<i>Spodoptera frugiperda</i> Fall armyworm	Liliaceae, Fabaceae, Brassicaceae, Asteraceae, Cucurbitaceae, Malvaceae, Solanaceae, Poaceae, Chenopodiaceae, and more [83]	Diamides	Pyrosequencing	Mutation detection related to insecticide resistance	2019 [84]
			Illumina sequencing	Post-transcriptional analyses and detection of miRNAs associated with insecticide resistance	2024 [85]
		Organophosphates, Carbamates, Pyrethroids, Avermectins, Benzoylureas, Dimides	Amplicon sequencing	Mutation detection related to insecticide resistance	2024 [86]
		Organophosphates	Whole-genome sequencing	Mutation detection related to insecticide resistance	2020 [87]

Table 1. Cont.

Lepidopteran Species	Major Hosts	Insecticide Resistance Report	Diagnostics Related	Results	Year/Ref.
<i>Spodoptera litura</i> Cotton leafworm	Malvaceae, Fabaceae, Liliaceae, Amaranthaceae, Brassicaceae, Solanaceae, Rutaceae, Araceae, Asteraceae, Convolvulaceae, Euphorbiaceae, Lamiaceae, etc. [88]	Pyrethroids	RNA sequencing	Transcriptome analysis and gene expression detection associated with insecticide resistance	2020 [89]
		Organophosphates, Pyrethroids	qRT-PCR	Overexpressed gene detection associated with insecticide resistance	2024 [90]
<i>Tuta absoluta</i> Tomato leafminer	Solanaceae, Amaranthaceae, Cucurbitaceae, and Fabaceae [91]	Organophosphates	Whole-genome sequencing	Genomic loci detection related to insecticide resistance	2023 [92]
		Diamides	RT-qPCR	Expression analysis of genes involved in insecticide resistance	2023 [93]
			RNA-seq	Expression analysis of genes involved in insecticide resistance	2023 [94]
		Spinosyns	Sequencing	Post-transcriptional analyses and detection of mRNAs associated with insecticide resistance	2021 [95]
		Oxazadines	Sequencing	Mutation detection related to insecticide resistance	2023 [96]
		Avermectins	RNA-seq	Expression analysis of genes involved in insecticide resistance	2021 [97]

3. The Main Forms of Insecticide Resistance

In order to perform diagnosis, the primary question is to determine the most probable mechanism conferring the resistance to a given insect challenged with a specific insecticide. Resistance development is an evolutionary phenomenon arising from a set of dynamic biochemical actions and reactions that are triggered, for example, by the continuous use of chemical products that result in significant metabolic and genetic changes to organism populations over time as a response to selective pressures. As new MoAs and associated technologies emerge, the path to discovery is deepened in terms of understanding the genetic changes responsible for resistance [98]. At present, insect resistance mechanisms are categorized into different groups: cuticular resistance, as well as behavioral, metabolic, sequestration, and “target-site” mutations.

Cuticular resistance occurs due to modifications in the insect’s cuticle that can prevent insecticide penetration. This mechanism involves thickening of the cuticle, which acts as a physical barrier, and changes in cuticle composition, such as increased waxes, which can reduce insecticide absorption [98–102]. Although this mechanism protects the insect from a wide range of insecticides, it generally confers low levels of resistance when considered in isolation [103].

Behavioral resistance, often underestimated due to uncertainty about whether it should be considered a true form of resistance, is defined by the insects’ ability to avoid contact with the toxin [104,105]. Changes in behavior, such as avoiding treated areas or altering feeding patterns, can reduce exposure to the insecticide. This mechanism of resistance has been reported for a wide range of chemical classes, including organochlorines, organophosphates, carbamates, and pyrethroids [106].

Metabolic resistance can be characterized as a detoxification process, meaning the ability to metabolize and/or neutralize chemicals as a defense mechanism, present in insects and plants, through enzymes that degrade or modify toxic compounds, rendering them ineffective [107]. This process involves three main classes of enzymes: (1) cytochrome P450 monooxygenases (P450s), which oxidize organic compounds, making them more water-soluble and more easily excreted; (2) esterases, which hydrolyze esters, often deactivating chemical compounds; and (3) glutathione S-transferases (GSTs), which conjugate chemical compounds with glutathione, facilitating their excretion [108]. The genes that confer metabolic resistance are generally different between insect species, and the production of detoxification enzymes is usually caused by the amplification of these genes [98]. Because this mechanism involves a succession of reactions, metabolic resistance is influenced by various external factors, such as the type and frequency of chemical use, climatic conditions, biological factors, agricultural and management practices, and environmental residues and contamination, which can accelerate, decelerate, or modify how it develops in populations of organisms, similar to cuticular and sequestration resistance processes.

Sequestration resistance is a particular case of metabolic resistance in which insects have the ability to isolate and store insecticide molecules in specific compartments within their bodies without causing harm. This mechanism involves sequestration in vacuoles or organelles and binding to transport or sequestration proteins, which bind and inactivate the insecticides, preventing them from reaching their targets [98,101].

Target-site resistance is relevant for accurately understanding the spread of resistance genes. This mechanism involves changes in the enzymes, receptors, or structural proteins of insects, where chemicals exert their toxic action, preventing the chemical from binding effectively to its target, thereby reducing or eliminating its toxicity [101]. Insect vectors of human diseases have frequently been studied to understand resistance in agricultural pest insects [21,108–110].

The main considered mechanisms are as follows: (1) Genetic mutation, which occurs from mutations that cause changes in the amino acid sequence, potentially altering the structure of the protein involved in binding with insecticide molecules. These can be single-nucleotide polymorphisms (SNPs), insertions, or deletions. (2) Alteration in gene expression, either by overexpressing the amount of the target protein; diluting the chemical

effect; or by underexpressing the amount of the target protein, minimizing the chemical's action sites. (3) Post-transcriptional regulation of genes involved in the resistance processes and its impact on these processes, with research into non-coding RNAs being the main area of development. (4) Post-translational modification, through chemical modifications to the target protein (phosphorylation, methylation, glycosylation) after its synthesis, which can alter its conformation and affinity for the chemical.

Genetic mutations of the target-site knockdown resistance (*kdr*) in the voltage-gated sodium channel (*vgsc*) are extensively studied and result in resistance to pyrethroids and DDT [111,112]. Other commonly described mutations occur in the acetylcholinesterase-1 (*ace-1*) gene, which confer resistance to organophosphates and carbamates [113–116] and mutations in the GABA receptor, commonly known as resistance to dieldrin (*rdl*) mutation, which are associated with resistance to several insecticide groups [115,117,118]. For relatively new insecticide groups, such as diamides, the mutation occurs in ryanodine receptors (RyR) [109,119,120] and is frequently described in lepidopterans [21,119,121,122]. A list compiled in 2020 by IRAC presents the relationship between the MoA of each insecticide and the associated target-site resistance, facilitating access to references [123].

Post-translational modification, gene expression, and post-transcriptional regulation are quite puzzling to understanding in the context of the resistance mechanisms [98,101]. Therefore, a way to shorten this path and allow a greater understanding of the evolution and dissemination of resistance is to seek more direct processes that can be detected, diagnosed, and consequently studied with greater agility.

High sensitivity and viability make the target-site resistance driven by genetic mutation of interest in developing molecular markers [124], as it is primarily characterized by mutations in the coding region of the proteins targeted by an insecticide, and it therefore results in high levels of resistance [125]. Moreover, in many cases, these mutations in the same target gene are responsible for resistance to the same insecticide in different insect species, making molecular markers an excellent monitoring tool [126]. Thus, the identification and localization of genes associated with insecticide resistance are essential for understanding resistance mechanisms and can be effectively achieved with the help of molecular markers, which adds value to resistance management strategies [127].

Therefore, we can conclude that target-site molecular markers are the most promising for developing products for molecular diagnostics with great market potential, as they can be used to overcome the need for time-consuming bioassays and assist in decision making in the field, although this second step remains a challenge [124].

4. The Molecular Insecticide Resistance Diagnostics

Commercially, insecticide resistance diagnostic applications are almost exclusively focused on detecting resistance in human disease vectors [44,128–131]. Except for laboratory services, molecular diagnostics are mostly directed towards detecting phytopathogenic organisms per se, such as bacteria and viruses, via antigen–antibody interaction, gene amplification, or biosensors. A few companies offer services for resistance monitoring using resistance management techniques in the field and laboratory, for which the monitoring of some insects like *P. xylostella* and *Nilaparvata lugens* is already available [132]. Other companies offers services of detecting resistance in genetically modified (GM) plants [133].

In scientific research, molecular methods are already employed for the detection of insecticide resistance in some insect pests (Table 1 and Figure 1). Most of these methods rely on laboratory infrastructure and specialized labor for analysis and execution. For insecticides, it is advantageous to develop target-site molecular markers, as they are more precise, since detecting a point mutation is easily identified via molecular markers compared to identifying and analyzing gene expression in metabolic resistance [124,134]. Moreover, molecular markers can be applied in different regions globally, as many target-site mutations can be very similar or even identical for populations of the same species or even different species [124]. Thus, varieties of methodologies are already applied for studying resistance, with most being based on PCR.

PCR-based diagnostics can be divided into high-tech and low-tech methods. Allele-specific PCR (AS-PCR) and PCR-restriction fragment length polymorphism (PCR-RFLP) are low-tech methodologies that require less laboratory infrastructure and lower costs. However, they have lower specificity and yield and require more time to execute protocols [135]. The TaqMan (Applied Biosystems, Foster City, CA, USA) analysis method is a high-tech PCR with high yield and easy result interpretation, but the cost for analysis is extremely high [135,136]. The TaqMan methodology for real-time quantitative analysis has the advantage of multiplexing [137]. The most recent and promising technology for molecular diagnostics and a high-tech method is Droplet Digital PCR (ddPCR) (Bio-Rad Laboratories, Hercules, CA, USA), a third-generation PCR with extremely high sensitivity and accuracy, with relatively simple execution, but requiring high capital per assay [138]. Besides PCR-based methods, there are only two other methods currently used: isothermal amplification and sequencing.

The loop-mediated isothermal amplification (LAMP) from Eiken Chemical Co., Ltd. (Tokyo, Japan) is the only technique found as a commercial product that [139] offers point of care methodology for field detection without the need for specialized labor [140]. This feature is an advantage of the method, but the methodology is restrictive as it does not provide quantitative information and has low specificity for detecting SNPs [141]. Nanopore, from Oxford Nanopore Technologies (Oxford, UK), is a third-generation sequencing that offers extremely high throughput and deep sequencing capabilities. Sequencing methods are already widely used to detect mutations conferring target-site resistance, and several of these methods are reported in the literature, including Illumina Miseq sequencing (Illumina, San Diego, CA, USA) [142], Sanger sequencing (Applied Biosystems, Foster City, CA, USA) [143], PacBio sequencing (Pacific Biosciences, Menlo Park, CA, USA) [144], pyrosequencing (Qiagen, Hilden, Germany) [21], and ion torrent sequencing (Thermo Fisher Scientific, Waltham, MA, USA) [145]. A promising advantage of this technology is the portability of the Oxford MinION Nanopore device (Oxford Nanopore Technologies (Oxford, UK)) [124], meaning that it could be directly used in the field, even if it requires complex bioinformatics analysis and high initial capital costs, which makes it impractical for use by non-specialized users [146,147].

The choice of technique depends on the nature of the resistance, the organism under study, and the available resources. The integration of these technologies provides a comprehensive understanding of resistance, which is essential for developing effective management and control strategies. The selection of an appropriate technique should primarily be guided by the specific objectives to be achieved. To facilitate this decision-making process, a comparative analysis of the advantages and disadvantages of techniques with similar objectives can be highly effective. In the context of methods aimed at identifying target-site resistance, Table 2 presents a classification of the key advantages and disadvantages associated with various diagnostic approaches.

This analysis is based on studies that have conducted similar comparative evaluations, albeit for different objectives [124,148–152]. These previous works serve as a foundation for understanding the trade-offs between various diagnostic techniques, allowing us to adapt their methodology to the specific aim of identifying target-site resistance.

It is important to emphasize that, although the diagnosis of target-site resistance was the primary objective of this analysis, several additional factors related to each technique must be taken into account. These include the specific characteristics of the species being diagnosed, the logistical considerations surrounding the acquisition of materials and labor, the working conditions under which the experiments will be conducted, and other operational constraints.

Table 2. The main advantages and disadvantages of the different molecular resistance detection methods.

Method	Advantages	Disadvantages
Sanger	Low cost Qualitative High sensitivity and accuracy	Long time taking (10–20 h) Depends on external facilities Depends on careful sample preparation No quantitative information Interpreting complex sequencing data
Pyrosequencing	Low cost Qualitative High sensitivity and accuracy	Long time taking (10–20 h) Depends on external facilities Depends on careful sample preparation No quantitative information Interpreting complex sequencing data
Ion torrent	Short time taking (2.5–4 h) Qualitative High sensitivity and accuracy	High cost Depends on external facilities Depends on careful sample preparation No quantitative information Interpreting complex sequencing data
Illumina Miseq	Qualitative High sensitivity	High cost Long time taking (10–20 h) Depends on external facilities Depends on careful sample preparation No quantitative information Low accuracy Interpreting complex sequencing data
PacBio	Qualitative High sensitivity	High cost Long time taking (10–20 h) Depends on external facilities Depends on careful sample preparation No quantitative information Interpreting complex sequencing data
Oxford MinION Nanopore	Short time taking (2.5–4 h) Portable sequencing device Inexpensive sample preparation, even in low throughput High sensitivity Quantitative and qualitative	High cost Interpreting complex sequencing data
LAMP	Low cost Short time taking (2.5–4 h) Portable sequencing device Low sample preparation Qualitative	No quantitative information Low sensitivity High false-positive rates
Taq-Man	Short time taking (2.5–4 h) Quantitative and qualitative High sensitivity	High cost Depends on external facilities Depends on careful sample preparation No quantitative information

Table 2. Cont.

Method	Advantages	Disadvantages
AS-PCR	Low cost Short time taking (2.5–4 h) Qualitative High sensitivity	Depends on external facilities Depends on careful sample preparation No quantitative information Primer design problematic
ddPCR	Short time taking (2.5–4 h) Absolute quantitative and qualitative High sensitivity	High cost Depends on external facilities Depends on careful sample preparation
RFLP-PCR	Low cost Short time taking (2.5–4 h) Qualitative High sensitivity	Depends on external facilities Depends on careful sample preparation Restriction enzymes expensive

5. Importance of Diagnosing Insecticide Resistance

Resistance monitoring, despite not being considered a common practice [124], is the first step to establish integrated resistance management strategies [153]. To ensure efficient monitoring, diagnosing resistance is the first step in a set of joint actions carried out by the production chain to overcome the challenges of insecticide resistance. According to the United States Environmental Protection Agency (EPA) [43], the incidence of pesticide resistance will continue to increase until all stakeholders effectively perform their roles within the community to achieve efficient management.

It is crucial to set collaborative resistance management programs among public and private entities, research institutions, pest management specialists, farmers, and other involved entities. In this scenario, each party plays a role in the production chain and faces the consequences of productivity loss as well as catastrophic climate effects. Therefore, the adoption of practices that ensure a more sustainable future is increasingly urgent. According to the latest United Nations Conference of the Parties (COP 27), held in Egypt in 2022, the “Food and Agriculture for Sustainable Transformations (FAST)” initiative was created [154], a multilateral partnership aimed at catalyzing and accelerating the transformation of agriculture by 2030 (FAO, 2024).

The adoption of Environmental, Social, and Governance (ESG) criteria by companies and investors has become mandatory for any institution that wants to remain competitive in the market, as incorporating ESG indicators allows for a more comprehensive and sustainable evaluation of a company’s value [155]. ESG criteria serve as a guide to achieving the Sustainable Development Goals (SDGs), or Agenda 2030, developed during the United Nations Sustainable Development Summit in 2015 [156]. ESG criteria are strongly linked to economic development, resulting in motivation and pressure from the business sector to adhere to more responsible and sustainability-focused actions [157]. Thus, sustainable actions, besides being necessary, contribute to economic development both at the business and global levels.

In this context, diagnosing resistance contributes as an action to minimize negative environmental effects, with the potential for a significant positive impact in the pursuit of the SDGs, as it primarily aids in the following factors:

5.1. Mechanisms of Resistance and Their Spread in Populations

It is possible to assert that resistance does not arise inadvertently and incurs a developmental cost for the insect. It is assumed that there may be pre-existing polymorphisms in resistance alleles contributing to its perpetuation [158]. These polymorphisms can be used to develop molecular markers, for example, considered one of the most attractive options for monitoring resistance as they offer greater precision in field decision making [159]. Nevertheless, the link between the genotype and phenotype of resistance can be complex or may

present ambiguous evidence, especially in cases of metabolic resistance [160]. Therefore, a deeper understanding of molecular biology is necessary for this comprehension [158], and diagnosing resistance is likely the first step in this journey.

5.2. Encouraging the Development of Alternative Strategies to Chemical Use

In addition to insecticide resistance, other negative impacts arising from the extensive use of chemicals stimulate the search for alternatives. Integrated pest management (IPM) is highly recommended by IRAC [161]. In this context, IPM is characterized by a set of strategies that contribute to managing resistance. With the detection of resistance, it is possible to choose strategies that are effective in addressing the situation. Biological control, the cultivation of refuge fields, crop rotation, the use of semiochemicals, genetically modified plants, and agroecological systems, among other strategies, are increasingly integrated in the field and contribute to the control of pest species. These strategies can be used in conjunction with chemical applications or even allow for the avoidance of chemical use, as seen in organic farming [162]. By reducing the use of insecticides, these strategies help decrease the selection pressure for resistant organisms [161,163,164].

5.3. Reducing General Insecticide Use

IPM contributes to the reduction of overall insecticide use and is one of the tools used in pest management [161]. However, the reduction of chemical use is still met with reluctance by farmers, as they need to ensure productivity, and culturally, insecticides are still perceived as more advantageous, especially when compared to other management techniques such as the application of biological agents [42].

Thus, field detection of resistance assists farmers in making precise decisions, as excessive use of chemicals in the presence of resistance increases production costs, time, and effort for ineffective pest control. By understanding the resistance present in the field, farmers can not only choose strategies that complement chemical applications but also select chemicals that are truly effective against the target pest at that time, depending on the MoA to which the species in question is resistant. Knowing which chemicals are effective eliminates the need for a variety of products for application. Additionally, with products focused on specific control, the application window for chemicals is extended, and the dosage is reduced, contributing to effective management.

5.4. Reduction of Production Costs

A direct consequence of reducing insecticide use is the reduction in production costs. In the United States, a study on the profitability of insecticide applications in soybeans indicated that application was profitable in only 39% of the cases evaluated and was not profitable when insect pressure in the field was low [40]. In contrast, when an insecticide is highly effective, applying it at lower pest densities is recommended, as low efficacy increases control costs [41]. The logic behind using chemical insecticides loses reliability when the insecticide does not control the target species, especially if the low efficacy is due to the presence of insect resistance. Thus, the application becomes even less profitable, regardless of pest density and/or pressure in the field. Diagnosing insecticide resistance enables the establishment of a rational application strategy with appropriate insecticides, ensuring lower production costs and consequently higher profitability and revenue.

5.5. Embassy of the Creation of Resistance Monitoring Programs

Monitoring programs are already being implemented around the world, but they are mostly limited to pests affecting major crops [43]. However, resistance also impacts smaller production chains, which can become significant as different production chains may share common pest species, and consequently, they require the use of insecticides with the same MoA. They also share the environmental and human health consequences resulting from the indiscriminate application of chemicals. Diagnosing resistance is the first step toward developing a series of actions that need to be carried out jointly by public and

private entities affected by and contributing to the issue of chemical resistance. Programs that integrate these actions are necessary to change the current paradigm in resistance management [43], ensuring proper, effective, and sustainable management.

5.6. Developing New Technologies

The diagnosis of resistance, by providing deeper insights into its development and dissemination, forms the foundation for understanding its molecular and metabolic characteristics, thereby facilitating the creation of new technologies. Obtaining these data enables the development of more precise technologies that contribute to increased sustainability overall. An innovative example is the new product Calantha™, featuring Ledprona technology (GreenLight Biosciences, Boston, Massachusetts, USA), which introduces a novel MoA for insecticides. This technology uses RNA interference (RNAi) for silencing, which has a reduced likelihood of resistance development compared to other MoAs. It offers greater specificity in pest control and lowers the chances of affecting non-target insects [161,165]. Molecular diagnostics of a resistance mechanism provides the foundation for developing products that can silence the resistance mechanism itself, making the insect susceptible again and contributing to more effective pest management rather than creating and releasing new chemical products. Therefore, diagnosis not only allows for the detection of resistant populations but also represents the first step towards understanding the physical and chemical reactions that precede and follow the assessed event, especially if it is a genetic event that can be characterized as a molecular marker.

6. Consequences of Insecticide Resistance Affecting a Lepidopteran Key Pest of Coffee

Coffee, one of the most consumed beverage worldwide, is significantly affected by the increase in resistance to chemical insecticides [166]. Cultivated in approximately 12.5 million agricultural properties managed primarily by smallholder farmers, with 95% of producing farms being 5 hectares or smaller [167], global production is led by South America (Brazil, 39%; Colombia, 7%) and Vietnam (16%) [168].

Despite genuine initiatives to avoid chemical insecticide control in the coffee crop [169], reports of resistance development in important pests in coffee production are becoming increasingly frequent. Frequent use of chemicals with the same MoA contributes to the development of resistance. Organophosphate insecticides are the most cited when related to resistance due to being one of the most widely applied groups of insecticides globally [170], as observed in Table 1.

The coffee leaf miner (CLM) (*Leucoptera coffeella*) is a major coffee pest in Brazil, causing losses of up to 70% of production [171]. Chemical control practices are inevitable due to the pressure of this highly aggressive pest. There are various reports of insecticide resistance in CLM populations to organophosphates [172], diamides [173], avermectins, and pyrethroids [174].

Resistance is implicated in fitness cost, as showed by Amaral Rocha [172], where not exposing CLM populations to chlorpyrifos rapidly reverted resistance in seven generations to a susceptibility status. This observation indicates that the correct management of chlorpyrifos and other chemicals may be used to reverse the resistance process, causing reduction of applications, improving the efficiency in the field, and prolonging the viability of this chemical to insecticide rotation.

Applying similar MoA chemicals can induce cross-selection, as suggested by Fragozo et al. [175], to the interplay between organophosphates, inducing the evolution of the resistance in different populations of the CLM. It is interesting to notice that the producers often believe they are managing two species with the same application. In reality, they are contributing to the development of resistance. To illustrate this, another severe pest of coffee is a coleopteran, the coffee berry borer (CBB) (*Hypothenemus hampei*), which causes losses of approximately USD 500 million annually [176]. CBB lodges inside fruits and seeds, contributing to the difficulty of management, since the insecticide does not reach the pest properly. Many of the insecticides used to control the CBB are also registered to control the

CLM in Brazil [177]. Since the CLM has a rapid development cycle [178], it is possible that this practice accelerates the resistance evolution process in the CLM.

Detecting and monitoring insecticide resistance is essential for decision making in the field. Specifically, for the CLM, the economic damage thresholds (EDTs) and economic thresholds (ETs) of the species are 14% and 11% of mined leaves, respectively [178]. Diagnosing the resistance mechanisms of this species is crucial, especially because these levels are reached quickly when environmental conditions are favorable, with the insect taking only 14.1 days to complete its development cycle [179]. Also, due to its short development cycle, the recommended interval for applying chemicals to this species is 15 to 20 days [179], and applications are made at a very high cost, using various application methods, with the most expensive being aerial applications by plane or drone [178]. The factor that most influences the cost of application is the price of insecticides, which represents 71.45% for the control cost for the species [178]. Additionally, it has been reported that the species is in a phase of colonization and that climate change is contributing to the increase in areas with potential invasion by *L. coffeella* [180], and consequently, cases of resistance are likely to increase. Thus, diagnosing CLM resistance quickly and efficiently will primarily contribute to a greater profit of the application, as it will allow the producer to benefit from an effective MoA product, as well as make the best decision regarding the timing of these chemicals (15 to 20 days) and the application method. It is interesting to note that resistance can be reverted after some insect generations, enabling chemicals previously considered inefficient to be applied within the correct dosage and application frequency recommendations. These factors contribute to cost reduction and even to the reduction of chemical applications, as non-functional products, i.e., those that are not effective for control due to insect resistance, should not be applied. In this way, only effective products would be used, and possibly in longer application windows, contributing to increased sustainability in the field.

Resistance monitoring programs are seldom offered to adequately support the small producers, who are heavily affected by the poor dissemination of new technologies due to communication failures between rural producers and the government [181]. Thus, there is an urgent need for the development of technologies that address molecular resistance diagnostics to management and monitoring, particularly for smallholders, who face socioeconomic challenges related to the access and cost of these practices [182]. Also, it is necessary to overcome the challenges of delivering and gaining acceptance of new technology by farmers in the specialty coffee market and providing alternatives to organic coffee producers.

7. Perspectives on the Molecular Diagnostics of Insecticide Resistances

Molecular diagnostics plays a critical role in the management of diseases that pose a threat to global public health [183]. Emerging methodologies that are both specific and sensitive [80,183,184] represent innovative and promising techniques that can also be applied in molecular diagnostics for monitoring insecticide resistance. Among the new technologies applicable to diagnostics, the following stand out: (1) nanopore sequencing, a third-generation sequencing technology that is simple, real-time, and long-read, which does not rely on PCR. This method allows for the detection of mutations in RNA and DNA through a nano-sized protein or synthetic pore [185,186]. (2) CRISPR-Cas technology (Caribou Biosciences, Inc., Berkeley, CA, USA), originally designed for genome editing, possesses DNA/RNA detection capabilities and can distinguish single-nucleotide mutations [187]. It has been used to confirm the function of a target-site mutation related to insecticide resistance in a hemipteran insect [188], as well as to identify metabolic resistance genes responsible for insecticide resistance in *S. exigua* [82]. (3) LAMP technology, when combined with other methodologies such as nanopore sequencing, can identify highly scalable, multi-gene regions, as in LAMP-ORE [189], as well as allele-specific amplification (asLAMP), which enables the detection of mutations conferring insecticide resistance, as observed in *S. exigua*. (4) DNA microarray technology, which utilizes DNA and RNA probes via hybridization, is not only useful in gene expression studies but is also capable of

detecting mutations [184,190] and identifying differentially expressed miRNAs associated with detoxification pathways, as seen in *S. frugiperda* [85].

Robust, precise, and cost-effective technologies that contribute to the management for lepidopteran pests ensure advancement of several markets affected by these insects, increasing more sustainable production and, consequently, the pursuit of the SDGs. However, an important challenge for the agricultural sector is the acceptability and adoption of new technologies by rural producers. Given the need for a swift transition to increasingly sustainable and productive agriculture, this challenge should be considered urgent. Several factors, including social, emotional, attitudinal, cognitive, and the technology itself and its ease of use, affect acceptability and adoption [191]. Access to new technologies and the associated costs are also factors that impact the adoption of new practices [192].

Undoubtedly, molecular diagnostic technologies with a high degree of accuracy, sensitivity, and ease of application have the potential to be adopted (Figure 1). However, factors unrelated to the technology itself also need to be considered to ensure its acceptability. The increasing market demand for high-quality, traceable products and food, coupled with the need for greater sustainability in agriculture, should, before justifying the development of new diagnostic technologies, be of importance to the technology adopter. Therefore, it is necessary that the benefits of applying molecular resistance diagnostics be demonstrated.

It is important to highlight that the path to developing these technologies for lepidopterans and other orders of insects is still long. Filling the knowledge gaps of resistance mechanisms and understanding the main metabolic mechanisms remains a challenge. For this, molecular markers play a pivotal role and will be the means for creating increasingly precise molecular diagnostic tools for insecticide resistance.

8. Conclusions

It is possible to summarize a series of positive factors regarding the application and development of molecular diagnostics for insecticide resistance in agriculture. The most impactful factor is certainly the reduction in costs and the decreased application of insecticides in the management for lepidopterans, stemming from improved decision making in the field. These factors are considered most impactful due to the challenge of adopting and accepting new technologies by farmers, the first entity to whom resistance diagnostics will positively affect. However, for this to happen, the diagnostics must be accepted and adopted. Demonstrating cost reduction and even adding value to more sustainable products may be crucial.

The adoption of new technologies is also the role of monitoring programs, which should unite actions from public institutions, private entities, and all involved stakeholders, contributing to the advancement of resistance management. Once adopted, the reduction in insecticide application triggers a series of positive consequences. In addition to increased profitability, molecular diagnostics for insecticide resistance may provide a shorter path to a broad understanding of resistance mechanisms in lepidopterans, as they can rely on diagnostic tools based on molecular markers.

Detecting mutations and analyzing gene expression are the main techniques applied to explore the insecticide resistance universe, especially because insect responses to chemicals are highly complex, and the development of insecticide resistance is likely attributable to multiple resistance mechanisms. The identification of an increasing number of molecular markers, along with in-depth studies on the specificity of these markers in relation to their direct involvement in resistance, enhances the prospects of ultimately elucidating the underlying mechanisms governing resistance development and its persistence. To this end, some diagnostic methodologies applied mainly to human diseases were shown as techniques with great potential for application in the agricultural sector, especially those that can be applied to diagnose target-site resistance, as this mechanism has several characteristics that render its detection more practical compared to other resistance mechanisms.

With advancements in new technologies, resistance management will become much more dynamic and agile, risks to human and environmental health will be mitigated due

to reduced indiscriminate use of chemicals, and this will positively impact the pursuit of the objectives set by the 2030 Agenda.

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