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Review

Where do all the pests go? Understanding the genomic mechanisms of crop pest dynamics during the off-season☆

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Agroecosystems provide abundant resources to insects. However, throughout the off-season, insects must overcome resource shortages and adverse climates to survive. This off-season persistence affects pest infestations in subsequent crops or seasons. Key pest species employ diapause, migration, and local-scale dispersal to persist during the off-season. Genomic approaches have advanced our understanding of these survival mechanisms. Clock genes regulate the circadian rhythm and interact with neuropeptides and downstream pathways, such as insulin-like peptides and hormonal factors–like ecdysteroids and juvenile hormones that regulate diapause. Migrant insects must manage processes like energy metabolism, oogenesis, and flight orientation. Local-scale dispersal requires mechanisms to locate, select, and exploit the most suitable host and habitat for survival and reproduction during the off-season. Here, we present advances in genomic research on pest survival during the off-season, focusing on diapause, migration, and local-scale dispersion. Understanding these phenomena is crucial for developing and optimizing effective integrated pest management programs.

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Introduction

Throughout most of the year, agroecosystems provide ample resources to insects, including those considered crop pests. However, resources become scarce when crops are unavailable during the off-season, even in subtropical and tropical regions. Consequently, insects must overcome resource shortages and adverse climatic conditions to survive and reproduce (see Box 1 and Figure 1). These processes involve physiological, metabolic, and behavioral mechanisms that are ultimately regulated at the genomic level [1]. The survival of insect pests during the off-season is a key process to pest management because it affects pest population dynamics and infestations in the next crop season, directly impacting actions such as insect resistance management, biological control, and behavioral strategies. Among the tremendous insect diversity found in agroecosystems, key staple crops are infested by insects from three major insect orders: Lepidoptera, Hemiptera, and Coleoptera. Many pests in these orders can survive the off-season by utilizing diverse strategies, including diapause, migration, and local-scale dispersal (also referred to as short-distance movement) in the agricultural landscape to

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Box 1 Crop pest survival during the off-season concepts.

Crop off-season refers to any period when the preferred crop is unavailable. The off-season varies greatly in agroecosystems, with winter particularly prominent in temperate regions and the dry season in the tropics. Furthermore, the term can also indicate when a specific crop has completed its growth cycle or been harvested, demanding pests that previously infested it in that habitat to find alternative sources of nutrition or new habitat.

Diapause is a complex process that involves physiological and behavioral mechanisms. It suppresses development to ensure survival during unfavorable conditions, synchronizing development and reproduction with resource availability, often crops. This intricate process is a key survival strategy for insects, allowing them to persist in challenging environments.

Migration is a purposeful and intentional movement that occurs at the population level. Migrants typically continue their journey until they reach a suitable destination. Additionally, migration involves round-trip movements, with individuals or future generations returning to their original location.

Local dispersal refers to the local movement of insects between habitats throughout the year. Local dispersal is facultative and refers to the movement of an individual's place of birth and the location where it reproduces and raises its offspring. Furthermore, unlike migration, local dispersal does not involve insects with specific spatial goals but rather entails direct movement and stopping when they encounter a potential host. Sometimes, distinguishing between locally dispersing and migrating insects can be difficult (e.g., moths like *Spodoptera frugiperda* that use wind to disperse and can travel long distances).

Figure 1

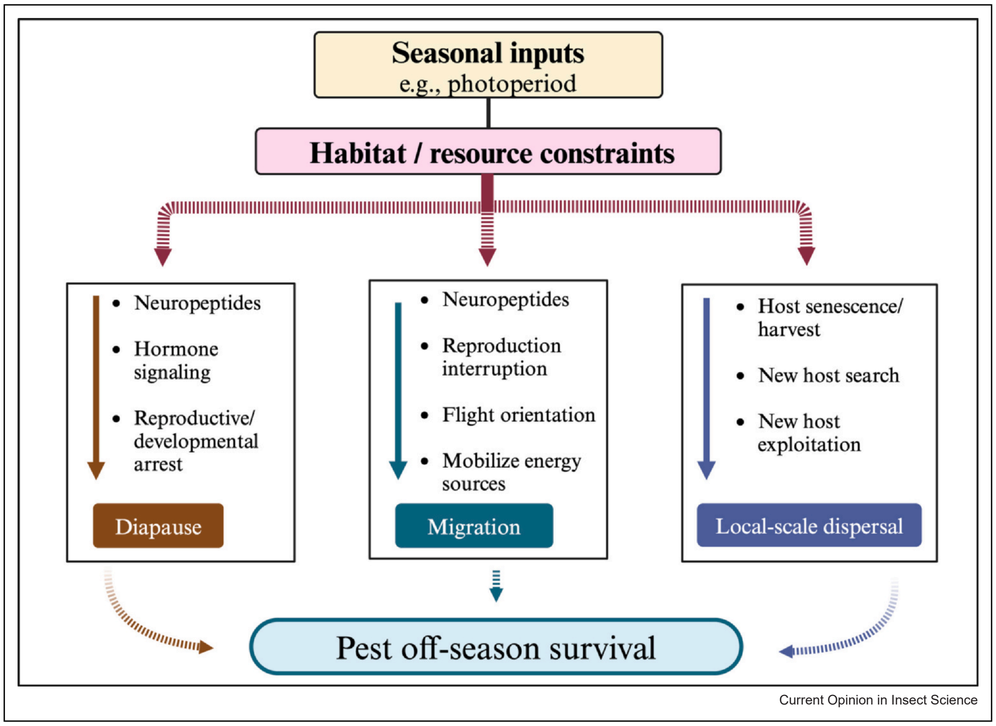


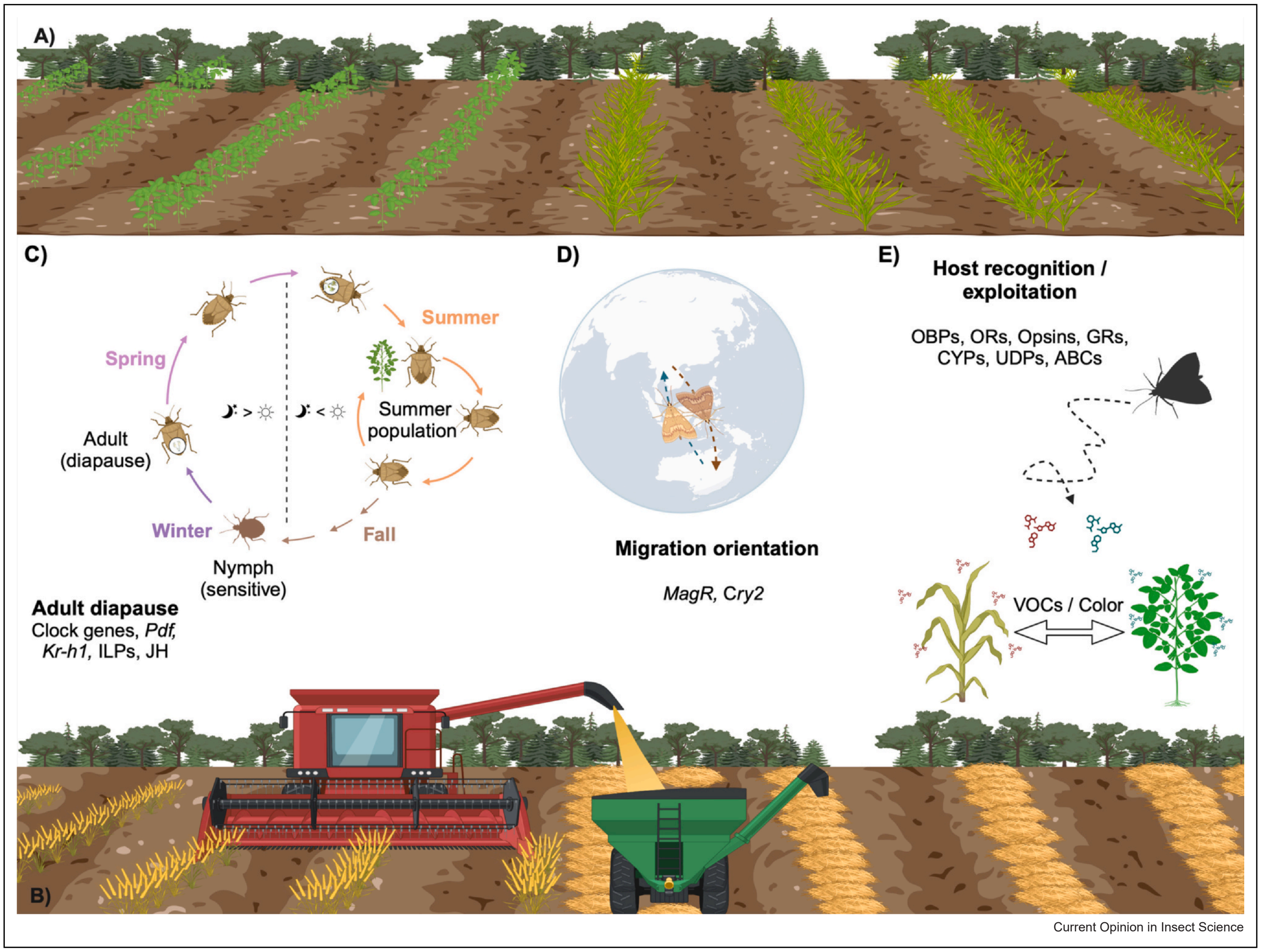
Diagram illustrating how seasonal factors — such as photoperiod, temperature, and rainfall — can significantly impact pest habitats and resource availability. These environmental changes serve as cues that influence whether an organism will enter diapause, migrate, or disperse locally in response to resource shortages. Notably, there is considerable overlap among the environmental factors that shape survival strategies. The variations primarily depend on species, ultimately affecting pest population dynamics during the off-season.

exploit different resources (Box 1, Figures 1 and 2). Genomic approaches have enhanced our understanding of the mechanisms by which insects adapt and survive in adverse conditions. Therefore, we aim to communicate the advancements made over the past 2 years and future opportunities offered by genomic approaches to better understand the evolution and genetic mechanisms of pests' survival during the off-season, focusing on three major topics: diapause, migration, and local-scale dispersal (Figure 1).

Diapause

Diapause is a type of dormancy employed by insects to survive adverse conditions and synchronize their

Figure 2



Overview of agroecosystem landscapes that will be encountered throughout the year by pests. Insects, including those from temperate and tropical areas, mainly use three survival strategies: entering diapause, migrating to a new habitat with favorable conditions, or dispersing on a local scale by moving to adjacent fields and colonizing new hosts or a host in a suitable life stage. **(a)** Crop season has abundant resources that support the development and reproduction of crop pests. **(b)** Crop off-season (crop has completed its growth cycle or been harvested), limiting or preventing the development and reproduction of crop pests. **(c)** Hypothetical stink bug species that survives off-season employ facultative adult diapause coordinated by photoperiod (core clock genes) and is characterized by reproductive halt. During favorable conditions and photoperiod, the species reproduce and develop on crops. Adult diapause is regulated by JH and ILPs. In stink bug diapause, essential genes include clock genes, the neuropeptide gene pigment dispersion factor (pdf), and Krüppelhomolog 1 (Kr-h1), an early JH-response gene. **(d)** Presents a hypothetical lepidopteran insect that migrates and flies long distances to avoid adverse conditions. Insects must orient themselves to migrate in the right direction, avoiding a dead-end migration. Genes like cryptochrome 2 (cry2) and magnoreceptor (MagR) are involved in moth orientation. **(e)** Shows a hypothetical lepidopteran moving between agroecosystems. The dispersal insect must be capable of finding suitable hosts or oviposition sites during movement. Various enzymes and genes are involved in recognizing and using host organisms. OBPs, ORs and opsins identify and select a suitable host. GRs assess nutrient quality, and enzyme families (CYPs, UDP-Glycosyl transferases [UDPs], ABC transporters [ABCs]) process nutrients and detoxify chemicals in the host. VOC = volatile organic compounds.

reproduction with resource availability [1,2,3]. Unlike quiescence, which is a state of dormancy that occurs in direct response to environmental stressors [3], diapause is anticipatory and occurs in response to token stimuli that is a reliable indicator of the approaching, stressful season and that persists for a predetermined amount of time, whether or not the stressful conditions persist. Many key agronomic pests use this adaptation to survive and persist in agroecosystems, including in tropical and subtropical areas, where diapause is common in many insect groups [1,4]. Much progress has been made in recent years regarding the molecular features of diapause. Insects enter diapause by interpreting seasonal and environmental cues, including short daylength, low or high temperatures and humidity, and changes in food quality. Once an internal threshold is exceeded, the organism activates or inactivates endocrine effectors to induce developmental or reproductive arrest. Transcriptomic and reverse genetic studies of insects exposed to environmental conditions that induce diapause revealed the crucial role of photoreceptors, neuropeptides, and neurotransmitters [5,6]. These changes, which either inactivate or activate hormones, lead to a significant decrease in insect metabolism and a halt in development [1]. Functional analyses using RNAi and CRISPR/Cas9 validate the role of crucial genes associated with neural signs, hormones, and metabolic pathways and their impact on diapause phenotypes in insects [1,7] (Supplemental Table S1).

Photoreceptors such as opsins and cryptochrome interpret and transfer photoperiodic information to the circadian clock [8,9,10]. The clock is an endogenous timer that interprets daylength. It relies on negative transcriptional/translational feedback loops that are mainly conserved among insects, with slight differences among insect taxa [6]. The circadian clock's output is sent to the brain through neuropeptides or neurotransmitters [10,11]. One of the best-characterized neuropeptides is the pigment dispersion factor (PDF), which bridges the information from the clock neurons to the neurosecretory cells in several insect groups [10,11,12•]. For instance, in heteropterans, knocking down or knocking out *pdf* disrupts the photoperiod-dependent diapause phenotype [12•,13].

Insects enter diapause during a species-specific developmental time point that can occur during the embryonic, immature, or adult stages (see Supplemental Table S1). Some aphid species undergo embryonic diapause when short-day conditions (SD) trigger a switch from asexual reproduction to sexual reproduction (equivalent to diapause induction), after which the female mates and lays cold-hardy, diapausing eggs ([14,15] and references therein). Evidence shows that melatonin triggers sexual development in pea aphids *Acyrthosiphon pisum* (Hemiptera: Aphididae), with associated genes being more active during short days [16].

The most conspicuous feature of diapause in immature insects is the failure of production and release of neurohormones, such as prothoracicotropic hormone, insulin-like peptides (ILPs), and transforming growth factor beta (TGFβ), which has been extensively validated in lepidopterans (more details in Ref. [1]). The gene Forkhead box O (*FoxO*) encodes a transcription factor identified as the master regulator of diapause induction of the cotton bollworm (CBW), *Helicoverpa armigera* (Lepidoptera: Noctuidae), a pest in the tropics and temperate regions. In CBW diapause-destined pupae, *FoxO* is activated by reactive oxygen species (ROS) and inhibited by AKT protein, a crucial protein in the insulin-signaling pathway [17]. Deleting the *FoxO* gene activates ubiquitin-protease, which decreases *TGFβ* receptor expression, blocking developmental signaling and leading to diapause [18••].

Adult diapause is characterized by arrested reproductive development and is regulated by low levels of juvenile hormone (JH) and ILPs in several insect groups [1]. Females of the bean bug, *Riptortus pedestris* (Hemiptera: Alydidae), enter a facultative diapause in response to short photoperiods (SD) with low levels of JH and ILPs [19]. The Krüppel homolog 1 (*Kr-h1*) gene encodes a zinc finger transcription factor, and its transcription is regulated by Methoprene-tolerant 1 (MET1) and Taiman (TAI) in a JH-dependent fashion [20]. Additionally, under long photoperiods (LD) conditions, RNAi targeting the clock (*Clk*) gene inhibits ovarian development and reduces *Kr-h1* expression, while under SD conditions, RNAi targeting the *Cry-m* (a.k.a. *cry2*, which is light insensitive) transcripts promotes ovarian development and increases *Kr-h1* expression [21]. RNAi against *Met* and *Tai* stops ovarian development and decreases vitellogenin gene expression in the fat body of female linden bugs, *Pyrrhocoris apterus* (Hemiptera: Pyrrhocoridae), raised under conditions that induce reproduction (i.e. long-day conditions or LD) [22].

Some insect species, including many pests, have wide geographic distribution with populations or strains with distinct frequencies of adaptive diapause traits. The European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae), in the United States, presents populations with one or two generations that are mediated by differences in the duration of their postdiapause development [23]. Kozak et al. [24] used the quantitative trait locus approach to show that the circadian clock gene *period* and *pigment dispersion factor receptor* differ in allele frequency among populations with one or two generations. Moreover, studies on two populations of CBW with differing diapause phenotypes have unveiled a chromosomal inversion associated with the control of diapause. This inversion contains three clock genes (*per*, *Clk*, and *cyc*) that show mutations specific to each population, offering insights into the genetic foundations of diapause characteristics of this major pest [25••]. Several other pests, such as the Asian corn borer (ACB), *Ostrinia furnacalis* (Lepidoptera: Crambidae) [26], the Neotropical brown stink bug, *Euschistus heros* (Hemiptera: Pentatomidae) [27], and bird cherry-oat aphid *Rhopalosiphum padi* (Hemiptera: Aphididae) [28], illustrate geographical variation in diapause expression among populations, but we still lack molecular characterization of these differences.

Migration

Long-distance migration is employed to circumvent unfavorable conditions. Seasonal cycles significantly influence migration, enabling organisms to anticipate environmental shifts and engage in migratory behaviors (reviewed in Ref. [29]), which makes migration a type of diapause. Migration significantly impacts an organism's life cycle, including morphological adjustments (wings), a demand for an ample energy supply, and delayed oogenesis. Migration also requires a geographical orientation system to direct flight. Below, we present two examples of important pest groups employing migration.

Wing polyphenism is a key aspect of migration in planthoppers such as the brown planthopper (BPH), *Nilaparvata lugens* (Hemiptera: Delphacidae), and the white-backed planthopper, *Sogatella furcifera* (Hemiptera: Delphacidae) [30,31]. Both species have a northern latitude breeding limit where they cannot survive winter and must migrate [32]. Both species present the long-winged (LW) type that can migrate long distances, while the short-winged type cannot fly. Senescent rice plants increase glucose content, which in turn increases insulin secretion in the feeding BPH, and eventually inhibits FoxO activity, resulting in LW individuals. Conversely, when the glucose content of rice plants is low (rice vegetative stages), there is less insulin secretion, and the FoxO is in the activated state, inducing the resident short-winged individuals [31,33•]. RNAi and CRISPR/Cas9 revealed that the rotund homolog (*Rn*) transcription factor interacts with FoxO in *N. lugens* and that inhibiting *Rn* activity suppresses LW development [34••].

The noctuid moths *Agrotis ipsilon* (Lepidoptera: Noctuidae) and *Mythimna separata* (Lepidoptera: Noctuidae) engage in long-distance flights to avoid unfavorable habitats. Transcriptome analysis of the black cutworm (BCW) *A. ipsilon*, which is distributed throughout the tropics and temperate regions, revealed that moths use carbohydrates to fuel short-distance flights and lipids to fuel long-distance flights [35,36••]. Moreover, oogenesis and sexual maturation are mainly regulated by JH in migrant moths. In temperate and subtropical populations of the oriental armyworm, *M. separata*, moderate flight intensity (no longer than 2 days) stimulates allatotropin gene expression, promoting JH synthesis and reproduction. Meanwhile, the transcript abundance of allatostatin, which inhibits JH synthesis and reproduction, increased when *M. separata* were forced to fly for more than 2 days [37••]. In addition to energy metabolism and reproductive functions, precise navigation and flight directions are essential for migrants. In the BCW and *M. separata*, the magnetoreceptor (*MagR*) gene and the clock gene *cry2* are upregulated in migrant moths [36••,37••]. Moreover, knocking down *MagR* and *cry2* with RNAi impaired the migrant *M. separata* from properly orientating their flight [37••].

Local-scale dispersal

Another survival tactic agricultural pests employ during the off-season is to disperse locally (Box 1). A portion of the population usually initiates local-scale dispersal, seeking new plant hosts throughout the year, but this is less noticeable because the dispersing individuals become integrated with the resident population (discussed in Refs. [38,39]). This is especially relevant for (sub) tropical species that fly to locate primary or alternative hosts. In Brazil, for instance, staple crops such as soybeans and maize have growth cycles that span 3–4 months. These crops can be found in cultivation throughout the year; however, this is influenced by regional differences across the country. Factors like latitude (photoperiod) and climate (rainfall and temperature) are crucial in determining the growing season, nutrient composition, and plant senescence. In this context, local-scale dispersal significantly affects pest dynamics.

After host deterioration/senescence, pests leave their habitat and begin searching for potential hosts. Odorant-binding proteins (OBPs) and chemosensory proteins play a crucial role in transporting external odorant molecules to odorant receptors (ORs) in the sensillum lymph [40]. The function of ORs depends on an essential partner known as the odorant receptor co-receptor (Orco), which is an OR itself [41]. Studies have shown that CRISPR/Cas9 null mutants of *H. armigera* and *Spodoptera litoralis* (Lepidoptera: Noctuidae) lacking the *Or42* and *Orco* genes, respectively, could not detect their host plants [42••,43]. After an odorant binds to a receptive OR, it triggers a cascade that sends signals to the brain; moreover, odorants must be deactivated quickly to prevent overstimulation. There is substantial evidence indicating that various odorant-degrading enzymes such as cytochrome P450s, glutathione S-transferases (GSTs), carboxyl/cholinesterases (CCEs), UDP-glycosyltransferases (UGTs), and aldehyde oxidases play a significant role in resetting the insect olfactory system by breaking down odorant molecules [44].

Vision represents another interface of host recognition for dispersing insects. Insect opsins are part of the G-protein-coupled receptor superfamily and play a crucial role in the visual process, including host selection. Evidence of the significance of vision in host selection was observed in the CBW, where knocking out a long-wavelength sensitive opsin with CRISPR/Cas9 changed the oviposition pattern of female moths [45]. Additionally, knocking out the long-wavelength sensitive opsin and blue-sensitive opsin altered host selection in the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae) [46•].

After interpreting host volatiles and visual cues, chemoreception (collectively called taste) provides information about essential nutrients. Gustatory receptors (GRs) can detect multiple tastants, including carbon dioxide (CO_2), as a cue to identify healthy plants; sugar, which is crucial for assessing the nutritional value; and bitter compounds, used to identify potentially harmful properties of the host [47]. RNA-seq and quantitative reverse transcription polymerase chain reaction have identified specialized genes in adult moths of CBW and tobacco cutworm, *S. litura* (Lepidoptera: Noctuidae), for sensing CO_2 [48,49]. Furthermore, *Gr43a* transcripts, encoding a fructose GR, are mainly located in Asian Corn Borer mouthparts, and targeting this transcript with RNAi caused larvae to lose their preference for fructose [50••]. Chen et al. [51] used the *Xenopus* oocyte expression system to determine that the bitter receptor GR180 from CBW responds to coumarin. They also discovered that *GR180*-null CBW larvae were no longer deterred from consuming coumarin.

After the insect ingests the host plant, the peritrophic matrix protects the midgut epithelium from microorganisms, mechanical damage, and large plant–defensive chemicals [52]. In addition, the plant metabolites are detoxified through oxidation, hydrolysis, and reduction reactions performed by cytochrome P450 monooxygenase proteins (CYP) and CCEs; lipophilic compounds are converted into more hydrophilic forms by GSTs and UGT; and detoxified compounds are excreted the ATP-binding cassette (ABC) [53•]. For example, the 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) is the major benzoxazinoid in maize and rice, and *in vitro* gene expression assay found that fall armyworm (FAW) *Spodoptera frugiperda* (Lepidoptera: Noctuidae) UGT genes are highly expressed in the midgut and fat bodies. The knocking down or out of FAW *UGT33* with RNAi or CRISPR/Cas9 significantly reduces the metabolization of DIMBOA [54,55••].

However, it is worth highlighting that the above-mentioned molecular mechanisms are mostly related to how agricultural pests locate, ingest, and detoxify their preferred hosts. As insects likely use different mechanisms during the off-season, several opportunities exist to understand how insects that disperse locally recognize, select, and develop on nonpreferred hosts. This enhanced understanding can be utilized to develop new control tactics.

Opportunities and future directions

Integrated pest management entails a comprehensive strategy that considers various ecosystem factors. The off-season represents a particularly vulnerable period for pests and an opportunity to manage them. Thus, we present examples of how pests circumvent environmental stresses and lack of host availability during the interseason by entering diapause, migrating, and dispersing locally. This knowledge can help us identify effective strategies and/or targets to manage resistance to insecticides and genetically modified plants, adjust crop rotation, and effectively deploy control tactics, including pheromones, autocidal control with genetically modified insects, and biological control agents.

Although consistent progress has been made (Supplemental Table S1), diapause research in insects is primarily limited to model species, with a significant knowledge gap in nonmodels, such as agricultural pest insects. Nonetheless, gaining a deeper understanding of how clock genes regulate hormone release during diapause is imperative. The molecular and endocrine regulators of diapause in most insect pests that diapause in the embryonic stage are particularly unclear. Additionally, it is crucial to understand how insect pests terminate diapause and resume activities so they can be effectively controlled. Despite the widespread occurrence of diapause in tropical and subtropical species, knowledge of diapause in species found in multiple climate ranges (Supplemental Table S1), such as the CBW, BCW, and aphids, is limited to temperate regions.

Another crucial aspect to consider is the migratory behavior of several pest species, about which little is known at the molecular level. It is essential to understand the factors that lead to migration, the genes that regulate processes such as arrested oogenesis, and what drives the flight orientation of migrants. Furthermore, research regarding the molecular mechanisms that regulate and enable local dispersal is a pivotal aspect and can offer opportunities for crop rotation to avoid pest outbreaks. We urgently need to broaden our understanding of how insects locate and develop on nonpreferred host plants because we know little about how agricultural pests recognize, select, and detoxify secondary metabolites from nonpreferred hosts during the off-season.

Additionally, most insights into pest dynamics during off-seasons have been gathered from temperate regions. We currently have a limited understanding of how pests survive in tropical and subtropical areas during those periods, where resources such as crops are less restricted and climatic conditions are less severe [56]. In this scenario, pests can continue reproducing without significant restrictions because they can find other crops nearby or search for additional, noncrop resources available in the landscape. However, there have been increasingly common reports of behavior changes and host range expansion in agricultural pests during the off-season period [26,57]. Thus, improving our knowledge of the genetic mechanism of host selection and adaptation in agricultural landscapes, especially in regions where agriculture is expanding and/or intensifying, is crucial to predicting new pest invasions and population outbreaks. Finally, climate change demands extra attention since it can alter the overwintering patterns, phenology, and voltinism of significant agricultural pests [4,58,59,60].

Furthermore, few studies on agricultural pests have been associated with changes in insecticide tolerance and allele frequency of the genes related to Bt and insecticide resistance during the off-season. For example, adult stink bugs in Brazil move to other areas and use cotton and maize as alternative hosts during soybean off-season ([27] and references therein). These populations are exposed to insecticides used in these crops to control different pests, and these individuals will colonize the following soybean crops, which can significantly impact the allele frequency of genes associated with insecticide resistance. Similar insights should be considered for populations of polyphagous pests in tropical and subtropical regions that use different crops across years/seasons.

The rapid development of sequencing technologies has opened new possibilities, such as whole-genome resequencing using low-coverage sequencing (see [61]). This approach allows genome exploration of numerous individuals at relatively low financial costs. This opens a window of possibilities for large-scale genomic studies to characterize genetic architectures, reveal genes associated with diapause, migration, and especially local dispersal phenotypes, and provide insights into their molecular regulation that can be subsequently studied. These underutilized approaches bring new insights into how genomic alterations and evolution drive the molecular mechanisms associated with insect survival during the off-season. Furthermore, monitoring these genes and alleles in species and populations may help predict adaptive events, similar to genomic monitoring for resistance. Applying low-coverage whole-genome resequencing across different populations of agricultural pests presents a prime opportunity to better understand the genetic mechanisms that allow insect pests to adapt and survive during the off-season. Uncovering these key genes can lead to finding targets that could be employed in biotechnological programs for regional pest suppression.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.cois.2025.101340.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Denlinger DL: **Insect Diapause**. Cambridge University Press; 2022.
2. Tauber MJ, Tauber CA, Masaki S: **Seasonal Adaptations of Insects**. Oxford University Press; 1986.
3. Danks HV: **Insect Dormancy: An Ecological Perspective**; vol 1: Biological Survey of Canada (Terrestrial Artropods) Ottawa, ON; 1987.
4. Skendžić S, Zovko M, Živković IP, Lešić V, Lemić D: **The impact of climate change on agricultural insect pests**. *Insects* 2021, **12**:440, https://doi.org/10.3390/insects12050440
5. Goto SG: **Molecular mechanisms of photoperiodism**. In *Insect Chronobiology. Entomology Monographs*. Edited by Numata H, Tomioka. Springer; 2023:271-292, https://doi.org/10.1007/978-981-99-0726-7_13
6. Doležel D: **Molecular mechanism of the circadian clock**. In *Insect Chronobiology. Entomology Monographs*. Edited by Numata H, Tomioka. Springer; 2023:49-84, https://doi.org/10.1007/978-981-99-0726-7_4
7. Numata H, Tomioka K: **Insect Chronobiology**. Springer Nature; 2023.
8. van der Kooi CJ, Stavenga DG, Arikawa K, Belušič G, Kelber A: **Evolution of insect color vision: from spectral sensitivity to visual ecology**. *Annu Rev Entomol* 2021, **66**:435-461, https://doi.org/10.1146/annurev-ento-061720-071644
9. Senthilan PR, Grebler R, Reinhard N, Rieger D, Helfrich-Förster C: **Role of rhodopsins as circadian photoreceptors in the *Drosophila melanogaster***. *Biology* 2019, **8**:6, https://doi.org/10.3390/biology8010006
10. Goto SG: **Photoperiodic time measurement, photoreception, and circadian clocks in insect photoperiodism**. *Appl Entomol Zool* 2022, **57**:193-212, https://doi.org/10.1007/s13355-022-00785-7
11. Helfrich-Förster C: **Neuropeptidergic regulation of insect diapause by the circadian clock**. *Curr Opin Insect Sci* 2024, **63**:101198, https://doi.org/10.1016/j.cois.2024.101198
12. • Hasebe M, Kotak T, Shiga S: **Pigment-dispersing factor is involved in photoperiodic control of reproduction in the brown-winged green bug, *Plautia stali*. (2022)**. *J Insect Physiol* 2022, **137**:104359, https://doi.org/10.1016/j.jinsphys.2022.104359.
The study showed via immunohistochemistry that PDF cells are situated in the proximal medulla of the optic lobe. Moreover, RNAi knocked down *pdf*-inhibited oviposition arrest in females transferred from long-day to short-day conditions. Furthermore, it delayed the onset of oviposition in females after switching from short-day to long-day conditions.
13. Kotwica-Rolinska J, Damulewicz JM, Chodakova L, Kristofova L, Doleže D: **Pigment dispersing factor is a circadian clock output and regulates photoperiodic response in the linden bug, *Pyrrhocoris apterus***. *Front Physiol* 2022, **13**:884909, https://doi.org/10.3389/fphys.2022.884909
14. Liu Z, Zhang S, Zhu Y, *et al.*: **Reproduction evaluation and transcription analysis of *Aphis gossypii* under various**

photoperiods. *Insects* 2022, **13**:1105, https://doi.org/10.3390/insects13121105

15. Matsuda N: **Seasonal timer in aphids**. In *Insect Chronobiology. Entomology Monographs*. Edited by Numata H, Tomioka K. Springer; 2023:321-338, https://doi.org/10.1007/978-981-99-0726-7_15

16. Barberà M, Escrivá L, Collantes-Alegre JM, *et al*.: **Melatonin in the seasonal response of the aphid *Acyrthosiphon pisum***. *Insect Sci* 2020, **27**:224-238, https://doi.org/10.1111/1744-7917.12652

17. Zhang X, Wang T, Lin X, Denlinger DL, Xu W: **Reactive oxygen species extend insect life span using components of the insulin-signaling pathway**. *Proc Nat Acad Sci* 2017, **114**:E7832-E7840, https://doi.org/10.1073/pnas.1711042114

18. Zhang X-S, Wang Z-H, Li W-S, Xu W-H: **FoxO induces pupal
•• diapause by decreasing TGFβ signaling**. *Proc Nat Acad Sci* 2022, **119**:e2210404119, https://doi.org/10.1073/pnas.2210404119.

The authors demonstrated that in pupae destined for diapause in *H. armigera*, knocking out *FoxO* prevents them from entering diapause. FoxO activates the ubiquitin-proteasome system (UPS) by increasing the expression of ubiquitin c (Ubc) through direct binding to the Ubc promoter. The activated UPS reduces TGFβ receptor signaling by promoting ubiquitination. This interruption in developmental signaling leads to diapause.

19. Mano G, Goto SG: **Photoperiod controls insulin and juvenile hormone signaling pathways via the circadian clock in the bean bug *Riptortus pedestris* (Hemiptera: Alydidae)**. *Appl Entomol Zool* 2022, **57**:363-377, https://doi.org/10.1007/s13355-022-00795-5

20. Li Y-X, Wang D, Zhao W-L, *et al*.: **Juvenile hormone induces Methoprene-tolerant 1 phosphorylation to increase interaction with Taiman in *Helicoverpa armigera***. *Insect Biochem Mol Biol* 2021, **130**:103519, https://doi.org/10.1016/j.ibmb.2021.103519

21. Dong L, Udaka H, Numata H, Ito C: **Regulation of Krüppel homolog 1 expression by photoperiod in the bean bug, *Riptortus pedestris***. *Physiol Entomol* 2021, **46**:82-93, https://doi.org/10.1111/phen.12347

22. Smykal V, Bajgar A, Provaznik J, *et al*.: **Juvenile hormone signaling during reproduction and development of the linden bug, *Pyrrhocoris apterus***. *Insect Biochem Mol Biol* 2014, **45**:69-76, https://doi.org/10.1016/j.ibmb.2013.12.003

23. Wadsworth CB, Woods WA Jr., Hahn DA, Dopman EB: **One phase of the dormancy developmental pathway is critical for the evolution of insect seasonality**. *J Evol Biol* 2013, **26**:2359-2368, https://doi.org/10.1111/jeb.12227

24. Kozak GM, Wadsworth CB, Kahne SC, *et al*.: **Genomic basis of circannual rhythm in the European corn borer moth**. *Curr Biol* 2019, **29**:3501-3509, https://doi.org/10.1016/j.cub.2019.08.053

25. Jin M, Peng Y, Peng J, *et al*.: **A supergene controls facultative
•• diapause in the crop pest *Helicoverpa armigera***. *Cell Rep* 2024, **43**:114939, https://doi.org/10.1016/j.celrep.2024.114939.

The authors demonstrate that a supergene causes different diapause expressions in two geographical strains of CBW due to a chromosomal inversion. They show that the genes *Clk*, *Cyc*, and *Per* are located within this inversion and that the knockout of these genes independently plays crucial roles in diapause induction.

26. Huang L, Tang J, Chen C, He H, Gao Y, Xue F: **Diapause incidence and critical day length of Asian corn borer (*Ostrinia furnacalis*) populations exhibit a latitudinal cline in both pure and hybrid strains**. *J Pest Sci* 2020, **93**:559-568, https://doi.org/10.1007/s10340-019-01179-5

27. Hickmann F: **Assessing Matting Patterns, Chromosome Composition, Host Suitability, and Diapause Expression of *Euschistus* (Hemiptera: Pentatomidae) Strains and Species**. University of Sao Paulo; 2023:158, https://doi.org/10.11606/T.11.2023.tde-04012024-160736

28. Morales-Hojas R, Gonzalez-Uriarte A, Iraizoz FA, *et al*.: **Population genetic structure and predominance of cyclical parthenogenesis in the bird cherry-oat aphid *Rhopalosiphum padi* in England**. *Evol Appl* 2020, **13**:1009-1025, https://doi.org/10.1111/eva.12917

29. Merlin C, Iiams SE, Lugena AB: **Monarch butterfly migration moving into the genetic era**. *Trends Genet* 2020, **36**:689-701, https://doi.org/10.1016/j.tig.2020.06.011

30. Gao X, Fu Y, Ajayi OE, *et al*.: **Identification of genes underlying phenotypic plasticity of wing size via insulin signaling pathway by network-based analysis in *Sogatella furcifera***. *BMC Genom* 2019, **20**:396, https://doi.org/10.1186/s12864-019-5793-z

31. Lin X, Xu Y, Jiang J, Lavine JM, Lavine LC: **Host quality induces phenotypic plasticity in a wing polyphenic insect**. *Proc Nat Acad Sci* 2018, **115**:7563-7568, https://doi.org/10.1073/pnas.1721473115

32. Tyagi S, Narayana S, Singh RN, Gowda GB: **Molecular insights into wing polymorphism and migration patterns of rice planthoppers**. In *Genetic Methods and Tools for Managing Crop Pests*. Edited by Chakravarthy AK. Springer; 2022:449-460, , https://doi.org/10.1007/978-981-19-0264-2_17

33. Zhang C, Mao M-S, Liu X-D: **Relative contribution of genetic and
• environmental factors to determination of wing morphs of the brown planthopper *Nilaparvata lugens***. *Insect Sci* 2022, **30**:208-220, https://doi.org/10.1111/1744-7917.13037.

The authors established pure-bred lineages of short- and long-winged BPHs in the laboratory. The study found that four wing development-regulated genes, *InR1*, *InR2*, *Akt*, and *FoxO*, were consistently expressed in short-winged adults but nearly silenced in long-winged adults. Furthermore, in unselected lineages of BHPs, all these genes were consistently expressed at similar levels in both short- and long-winged adults, except for *FoxO*.

34. Chen S-J, Zhang J-L, Ma W-J, *et al*.: **FoxO and rotund form a
•• binding complex governing wing polyphenism in planthoppers**. *iScience* 2023, **26**:107182, https://doi.org/10.1016/j.isci.2023.107182.

The authors demonstrate that the gene rotund shows increased cell activation in long-winged (upregulated) compared to short-winged BPHs. Knocking down the rotund gene using RNAi resulted in the transition of long wings to intermediate wings. Furthermore, the activity of the rotund gene is suppressed by binding to the transcription factor FoxO.

35. Arrese EL, Soulages JL: **Insect fat body: energy, metabolism, and regulation**. *Annu Rev Entomol* 2010, **55**:207-225, https://doi.org/10.1146/annurev-ento-112408-085356

36. Jin M, Liu B, Zheng W, *et al*.: **Chromosome-level genome of
•• black cutworm provides novel insights into polyphagy and seasonal migration in insects**. *BMC Biol* 2023, **21**:2, https://doi.org/10.1186/s12915-022-01504-y.

The study employed comparative genomic and transcriptomic analysis. They discovered that the transcript levels of migrating moths indicated downregulation of blue opsin and cycle genes, while the magnetoreceptor and light-insensitive cryptochrome 2 were upregulated. They also observed disrupted adult emergence in *Cry2* CRISPR/Cas9 null mutants.

37. Tong D, Zhang L, Wu N, *et al*.: **The oriental armyworm genome
•• yields insights into the long-distance migration of noctuid moths**. *Cell Rep* 2023, **41**:111843, https://doi.org/10.1016/j.celrep.2022.111843.

The authors assembled a chromosome-level genome. When specific genes related to sensing the Earth's magnetic field (*MagR* and *Cry2*) were silenced in *M. separata*, it affected their flight orientation. Additionally, moderate flight for no more than 2 days increased the expression of the *allatotropin* gene, promoting juvenile hormone (JH) synthesis and reproduction. Conversely, *allatostatin*, which inhibits JH synthesis and reproduction, was significantly upregulated when forced flight lasted over 2 days.

38. Sappington TW: **Migratory flight of insect pests within a year-round distribution: European corn borer as a case study**. *J Integr Agric* 2018, **17**:1485-1505, https://doi.org/10.1016/S2095-3119(18)61969-0

39. Sappington TW: **Aseasonal, undirected migration in insects: 'invisible' but common**. *iScience* 2024, **27**:110040, https://doi.org/10.1016/j.isci.2024.110040

40. Leal WS: **Odorant reception in insects: roles of receptors, binding proteins, and degrading enzymes**. *Annu Rev Entomol* 2013, **58**:373-391, https://doi.org/10.1146/annurev-ento-120811-153635

41. Abendroth JA, Moural TW, Wei H, Zhu F: **Roles of insect odorant binding proteins in communication and xenobiotic adaptation**. *Front Insect Sci* 2023, **3**:1274197, https://doi.org/10.3389/finsc.2023.1274197

42. Guo M, Du L, Chen Q, *et al.*: **Odorant receptors for detecting •• flowering plant cues are functionally conserved across moths and butterflies**. *Mol Biol Evol* 2021, **38**:1413-1427, https://doi.org/10.1093/molbev/msaa300.

This study characterized 44 olfactory receptors (ORs) of *H. armigera in vitro*. The authors found that the OR42 receptor responded to the floral scent phenylacetaldehyde. They also demonstrated the significance of OR42 in host detection and sensing through a CRISPR/Cas9 knockout experiment, providing evidence for the essential role of OR42 in these processes.

43. Koutroumpa FA, Monsempes C, François M-C, *et al.*: **Heritable genome editing with CRISPR/Cas9 induces anosmia in a crop pest moth**. *Sci Rep* 2016, **6**:29620, https://doi.org/10.1038/srep29620

44. Chertemps T, Maïbèche M: **Odor Degradingenzymes and Signal Termination**; In Blomquist GJ, Vogt RG (Eds) Insect *Pheromone Biochemistry and Molecular Biology.* 2021, pp. 619–644. https://doi.org/10.1016/B978–0-12–819628-1.00019–5.

45. Liu X, Cai L, Zhu L, *et al.*: **Knockout of the LW opsin gene interferes with oviposition selection of nocturnal moth, *Helicoverpa armigera***. *J Pest Sci* 2022, **96**:807-817, https://doi.org/10.1007/s10340-022-01513-4

46. Tang Y-H, Bi S-Y, Wang X-D, *et al.*: **Opsin mutants alter host • plant selection by color vision in the nocturnal invasive pest *Tuta absoluta***. *Int J Biol Macromol* 2024, **265**:130636, https://doi.org/10.1016/j.ijbiomac.2024.130636.

The authors demonstrated that CRISPR/Cas9-mediated knockout of the long-wavelength sensitive opsin and blue-sensitive opsin altered female oviposition host selection in the tomato leafminer, *Tuta absoluta*.

47. Montell C: ***Drosophila* sensory receptors–a set of molecular Swiss army knives**. *Genetics* 2021, **217**:1-34, https://doi.org/10.1093/genetics/iyaa011

48. Ning C, Yang K, Xu M, Huang L-Q, Wang C-Z: **Functional validation of the carbon dioxide receptor in labial palps of *Helicoverpa armigera* moths**. *Insect Biochem Mol Biol* 2016, **73**:12e19, https://doi.org/10.1016/j.ibmb.2016.04.002

49. Yang J, Mo B-T, Li G-C, *et al.*: **Identification and functional characterization of chemosensory genes in olfactory and taste organs of *Spodoptera litura* (Lepidoptera: Noctuidae)**. *Insect Sci* 2025, **26**, https://doi.org/10.1111/1744-7917.13350

50. Shi J, He L, Du J, Wang C-Z, Zhao Z: **Mechanism of foraging •• selections regulated by gustatory receptor *43a* in *Ostrinia furnacalis* larvae**. *Pest Manag Sci* 2024, **80**:978-987, https://doi.org/10.1002/ps.7828.

The study aimed to determine the expression level of *Gr43a* gene in *O. furnacalis* at different larval instars and tissues. The authors found that the GR Gr43a is highly expressed in the mouthparts of *Ostrinia furnacalis* larvae during the first and fifth instars. *Gr43a* regulates feeding by discriminating between fructose and sorbitol.

51. Chen Y, Wang P-C, Zhang S-S, *et al.*: **Functional analysis of a bitter gustatory receptor highly expressed in the larval maxillary galea of *Helicoverpa armigera***. *PLoS Genet* 2022, **18**:e1010455, https://doi.org/10.1371/journal.pgen.1010455

52. Barbehenn RV: **Roles of peritrophic membranes in protecting herbivorous insects from ingested plant allelochemicals**. *Insect Biochem Phis* 2001, **7**:86-99, https://doi.org/10.1002/arch.1039

53. Amezian D, Nauen R, Goff GL: **Comparative analysis of the • detoxification gene inventory of four major *Spodoptera* pest species in response to xenobiotics**. *Insect Biochem Mol Biol* 2021, **138**:103646, https://doi.org/10.1016/j.ibmb.2021.103646.

The authors analyzed and compiled information on the detoxification mechanisms of xenobiotics (plant secondary metabolites or insecticides) in four main agricultural pest species: *Spodoptera exigua*, *S. frugiperda*, *S. littoralis*, and *S. litura*.

54. Israni B, Woutersb FC, Luck K, *et al.*: **The fall armyworm *Spodoptera frugiperda* utilizes specific UDP-Glycosyltransferases to inactivate maize defensive benzoxazinoids**. *Front Physiol* 2020, **11**:604754, https://doi.org/10.3389/fphys.2020.604754

55. Wang H, Song J, Benjamin J, Hunt BJ, *et al.*: **UDP- •• glycosyltransferases act as key determinants of host plant range in generalist and specialist *Spodoptera* species**. *Proc Nat Acad Sci* 2024, **121**:e2402045121, https://doi.org/10.1073/pnas.2402045121.

The authors analyzed *Spodoptera* species' genomes and found that generalist species have a consistent number of UGT genes, whereas specialist species have a high level of UGT gene pseudogenization. Employing CRISPR-Cas9 knockouts, they discovered that UGT33 genes enable *S. frugiperda* to feed on poaceous plants, while UGT40 genes facilitate the utilization of cotton. Further functional analyses identified the UGT *SfUGT33F32* as the primary mechanism allowing generalist *S. frugiperda* to neutralize the DIMBOA produced by poaceous plants. However, *Spodoptera picta*, specialized in *Crinum* plants, cannot detoxify DIMBOA due to a nonfunctionalizing mutation in *SpUGT33F34*.

56. Denlinger DL: **Insect diapause: from a rich history to an exciting future**. *J Exp Biol* 2023, **226**:jeb245329, https://doi.org/10.1242/jeb.245329

57. Tougeron K, Brodeur J, le Lann C, van Baaren J: **How climate change affects the seasonal ecology of insect parasitoids**. *Ecol Entomol* 2020, **45**:167-181, https://doi.org/10.1111/een.12792

58. Sampaio F, dos Santos HT, Marchioro CA: **Differences in thermal tolerances between two soybean pests may differently affect their voltinism under climate change**. *Agric Entomol* 2022, **24**:380-389, https://doi.org/10.1111/afe.12501

59. Stoeckli S, Hirschi M, Spirig C, *et al.*: **Impact of climate change on voltinism and prospective diapause induction of a global pest insect–*Cydia pomonella* (L.)**. *PLoS One* 2012, **7**:e35723, https://doi.org/10.1371/journal.pone.0035723

60. Lawton D, Huseth AS, Kennedy GG, *et al.*: **Pest population dynamics are related to a continental overwintering gradient**. *Proc Nat Acad Sci* 2022, **119**:e2203230119, https://doi.org/10.1073/pnas.2203230119

61. Lou RN, Jacobs A, Wilder AP, Therkildsen NO: **A beginner's guide to low-coverage whole genome sequencing for population genomics**. *Molec Ecol* 2021, **30**:5966-5993, https://doi.org/10.1111/mec.16077