

The genomics of adaptation in migratory insects

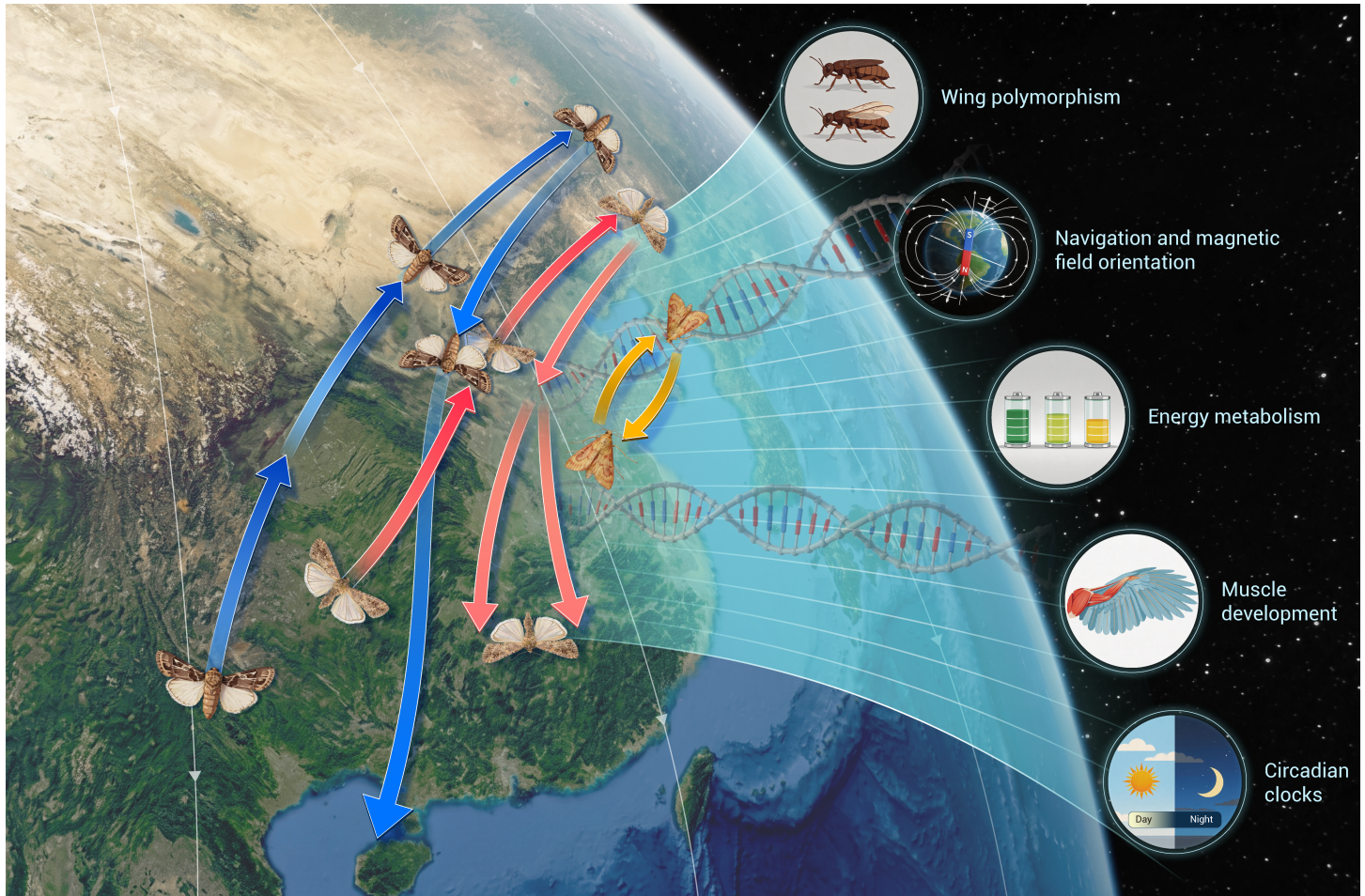
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Research into insect migration mechanisms supports population monitoring, outbreak prediction and pest control.
- Genomic approaches uncover the molecular basis underlying insect migration.
- Integrating advances in genomics and ecology is essential for migration-related research.
- Migratory insect genomics has progressed rapidly in recent years and shows great application potential.
- Rapidly evolving insect migration genomics reveal key mechanisms of this important biological phenomenon.

The genomics of adaptation in migratory insects

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Insect migration is a complex, large-scale biological phenomenon with profound ecological, evolutionary, and physiological significance. Numerous agricultural and non-agricultural insect species exhibit seasonal or multigenerational migratory behaviors. Resolving the mechanistic underpinnings of these behaviors is essential for understanding population dynamics, predicting outbreak risks, and improving pest management strategies. The rapid development and decreasing cost of high-throughput sequencing technologies have enabled the generation of high-quality reference genomes for an increasing number of migratory insects. These genomic resources offer unprecedented opportunities to investigate the molecular and evolutionary processes underlying migration. Despite these advances, critical gaps remain, including incomplete understanding of the genetic architecture and regulatory networks governing migratory traits. Additionally, challenges associated with assembling and annotating highly heterozygous insect genomes, the limited application of telomere-to-telomere and pan-genome approaches, and difficulties in linking genomic variation to migratory behavior under natural conditions still hinder our understanding. Furthermore, functional validation of candidate genes and translation of genomic knowledge into practical monitoring and pest management strategies remain limited. Integrative reviews that synthesize progress across genomics, molecular biology, population genetics, and ecology are crucial for facilitating systematic investigations of migration-related traits across multiple biological scales. This review aims to provide a comprehensive synthesis of recent advances in genomics research of migratory insects, hence, offering a comprehensive overview of the rapidly advancing genomic and molecular foundations of insect migration, thereby contributing to a deeper understanding of the mechanisms that drive one of the most remarkable biological phenomena in nature.

INTRODUCTION

Migration is defined as a persistent and purposeful movement across substantial distances, typically seasonal in occurrence and distinct from dispersal or foraging behavior. As an adaptive life-history strategy, migration enhances survival and reproductive success by responding to fluctuating ecological conditions.^{1,2} The initiation of migratory behavior arises from complex interactions between intrinsic factors, such as developmental stage and physiological state, and extrinsic environmental cues, including photoperiod, temperature, and resource availability. These cues activate regulatory pathways that drive broad adaptive modifications, including shifts in circadian rhythms, reprogramming of metabolic processes, and the development of specialized morphological traits. Collectively, these changes constitute the migratory syndrome, which integrates behavioral (timing and navigation), physiological (energy mobilization and hormonal regulation), and morphological (wing polymorphism and body size) components.²⁻⁵

Classical research on insect migration established the foundation for understanding its ecological and evolutionary roles, emphasizing orientation mechanisms, flight biomechanics, and trade-offs between migration and reproduction.⁶⁻⁸ A defining feature of migration in many insects is that it precedes reproduction, thereby maximizing the likelihood of successful colonization. Numerous species complete their migratory journeys over multiple generations, sometimes spanning continents, as demonstrated by migratory lepidopterans, such as the monarch butterfly (*Danaus plexippus*), and locusts.⁹⁻¹¹ These studies collectively reveal that migration is not random dispersal but a genetically and physiologically programmed life-history strategy

shaped by natural selection. At broader scales, migratory insects influence ecosystems by promoting long-distance gene flow, redistributing pollination and biological control services, and facilitating pathogen transmission.¹²⁻¹⁴

Despite extensive behavioral and physiological studies, the genetic and molecular bases of migratory traits remain incompletely resolved. Key questions persist regarding the heritability of migratory phenotypes, gene regulatory networks controlling flight endurance and orientation, and the role of environmental variation in shaping the genomic architecture associated with migration. Recent genomic studies have begun to uncover the molecular foundations of these processes. For instance, studies in the *Nilaparvata lugens* (brown planthopper) and *Locusta migratoria* (migratory locust) have revealed the involvement of insulin signaling, energy metabolism pathways, and hormonal regulation in migration and phase transition.^{15,16} Similarly, comparative genomic analyses in *Helicoverpa armigera* have highlighted gene family expansions and metabolic adaptations linked to long-distance flight capacity.¹⁷ However, findings on the regulatory architecture, evolutionary origins, and functional validation of migration-associated genes remain poorly understood, particularly in non-model migratory insects. While genomic studies of migratory insect pests have advanced rapidly, the field still lacks a cohesive synthesis of disparate results to elucidate the mechanisms by which genomic adaptation governs insect migratory life histories.

It has been over 15 years since the first genome of a migratory insect was published,¹⁸ ushering in a new era of migration genomics. This review summarizes the current progress in the genomic research of migratory insects, focusing on three major themes: (1) genomic features of migratory insects, (2) genomic insights associated with key migratory behaviors, and (3) ecological genomics and population dynamics in migratory insects. We also highlight the promise of emerging genomic technologies, outline outstanding challenges, and discuss future research directions. Ultimately, this review aims to provide a comprehensive understanding of the genetic and evolutionary bases of insect migration and the mechanisms by which migratory insects adapt to rapidly changing environments in an era of global climate uncertainty.

TECHNOLOGICAL LEAPS IN MIGRATION GENOMICS OF INSECTS

Over the past two decades, rapid technological advances have fundamentally transformed the study of migratory insects. Once largely constrained to morphological and physiological observations, migration research now leverages genomics, transcriptomics, and population-scale datasets to elucidate the molecular foundations of migratory behavior. The advent of long-read sequencing technologies, high-contiguity genome assemblies, and large-scale population resequencing has enabled unprecedented resolution of genome structure, function, and evolutionary dynamics. Collectively, these technological breakthroughs have not only deepened our understanding of the genetic architecture underlying insect migration but have also established a robust framework for investigating ecological adaptation, pest population dynamics, and evolutionary diversification.

High-resolution genome sequencing and assembly

The transition from phenotype-based investigations to whole-genome analyses represents a fundamental paradigm shift in the study of insect migration. The increasing availability of high-quality reference genomes has now enabled these traits to be examined at the molecular and genomic levels. This shift was initiated by the sequencing of the first lepidopteran genome, *Bombyx mori*, which demonstrated the feasibility of large-scale

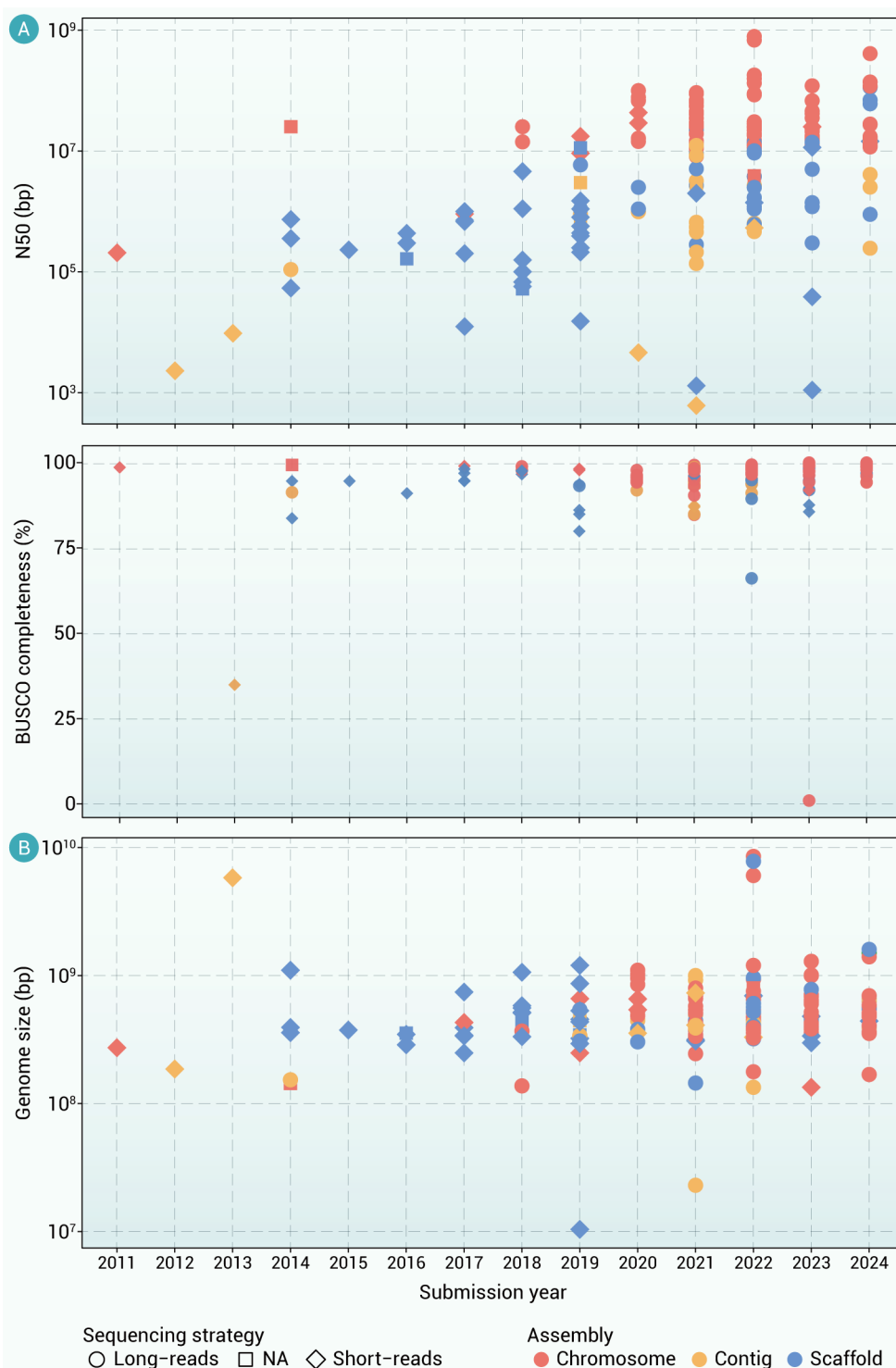


Figure 1. Trends in genome sequencing and assembly of migratory insects (A) Contig or scaffold N50 size. (B) BUSCO completeness. (C) Genome size. Assembly level and sequencing strategies are shown based on submission dates to the NCBI (National Center for Biotechnology Information) and ENA (European Nucleotide Archive) databases. The data highlight the significant improvement in genome assembly quality associated with the adoption of long-read sequencing technologies.

the transformation of migratory insect research. The emergence of long-read sequencing platforms, including PacBio HiFi and Oxford Nanopore Technologies (ONT), in combination with Hi-C scaffolding and telomere-to-telomere (T2T) assembly strategies, has fundamentally improved genome completeness and accuracy. Long-read assemblies achieve an average contig N50 of 5.49 Mb (Figure 1A), nearly five-fold greater than that of short-read assemblies,²⁵ thereby enabling more reliable gene annotation and robust detection of structural variation. These innovations have facilitated the resolution of repetitive elements, telomeres, and centromeres, features that are particularly important in large, complex, or highly heterozygous insect genomes such as those of locusts and dragonflies.²⁶ Concomitant improvements in assembly strategies have substantially increased the proportion of chromosome-level genome assemblies, especially through the integration of long-read sequencing with Hi-C-based scaffolding (Figure 1). Notably, more than 130 of the approximately 190 currently available migratory insect genomes (>68%) have been generated using long-read technologies (Figure 1), enabling comparative genomic analyses at the structural and chromosomal levels.

Advancements in sequencing and assembly technologies have therefore substantially expanded our capacity to investigate insect migration, although important technical and analytical challenges remain. Sequencing the entire genomes of migratory insects provides a crucial blueprint for exploring migration at the molecular level. This approach enhances our understanding of migration as it reveals integrated networks of genes that regulate metabolism, sensory systems, neuroendocrine control, stress response, and muscle physiology. Sequencing not only identifies specific genes but also reconstructs migratory histories

insect genomics.^{19,20} A major milestone followed with the publication of the *D. plexippus* (monarch butterfly) genome,¹⁸ which provided the first genomic blueprint of a long-distance migratory insect and uncovered genetic pathways associated with circadian regulation, orientation, and energy metabolism. Subsequent landmark genome projects further advanced the field. The *L. migratoria* genome,²¹ then the largest insect genome sequenced, yielded critical insights into flight muscle metabolism and energy allocation. Similarly, genomic studies of agricultural pests such as *H. armigera* have revealed key genetic determinants underlying flight endurance, dispersal capacity, and host adaptation.²²⁻²⁴ Collectively, these efforts established a robust foundation for comparative genomic analyses across diverse migratory insect taxa.

As previously articulated, technological advancements have been central to

and demographic patterns, effectively linking movement ecology with evolutionary concepts. Population genomics reconceptualizes migration as a simultaneous demographic, evolutionary, and genetic process.⁹ Additionally, the possibility of massively parallel sequencing facilitates population-scale whole-genome resequencing, thereby enabling comparative analyses between migratory and non-migratory individuals, as well as among populations exhibiting distinct migratory strategies.

Emerging sequencing tools such as single-cell RNA-seq and spatial transcriptomics allow researchers to analyze gene expression at the cellular level, uncovering previously hidden cellular heterogeneity in tissues associated with flight, metabolism, or sensory functions.²⁷ These techniques facilitate deep phenotyping, enabling scientists to connect cell-type-specific gene regulation with migratory functions, thereby advancing our understanding beyond

bulk tissue measures. As a result, advancements in sequencing technologies have transformed insect migration research from a descriptive field into a mechanistic and predictive science. This transformation allows for: the genome-wide identification of genes and regulatory networks linked to migration; comparative and population genomic analyses that reconstruct migratory evolution and pathways; the integration of multi-omic data (such as expression, sequence variation, and cell-specific expression) into models of migratory biology; and the identification of convergent genetic strategies across diverse migratory lineages. These aforementioned methods rely on extensive genomic data and accurate assemblies, both products of enhanced sequencing techniques. Without high-resolution genomic variations and thorough population sampling, detecting subtle molecular signatures linked to complex behaviors like migration becomes extremely challenging.

Despite these remarkable advances, important technical limitations remain. Many migratory insects possess large, highly repetitive, and heterozygous genomes, which continue to challenge even long-read sequencing platforms.^{28,29} High heterozygosity can lead to haplotig duplication, inflated genome size estimates, and misrepresentation of allelic variation as paralogous sequences. Repetitive elements, which often harbor genes involved in adaptation and regulatory evolution, remain difficult to assemble accurately, resulting in assembly gaps.³⁰ Structural variants such as inversions and translocations (features potentially critical for maintaining migratory phenotypes) are also frequently underdetected.³¹ Furthermore, incomplete and erroneous assemblies can result in annotation errors, complicating downstream functional inference. These challenges are particularly common in non-model species lacking high-quality reference genomes and population-level validation datasets. Continued improvements in sequencing chemistry, phasing algorithms, trio-binning strategies, and validation using independent long-range technologies will be necessary to achieve fully accurate representations of complex migratory insect genomes. These advances, however, collectively mark the onset of a new genomic era in migration research, characterized by integrative, high-resolution datasets that increasingly enable direct links between genomic variation, ecological adaptation, and migratory performance.

Genomic resource availability

In parallel with advances in sequencing technologies, large-scale genomic initiatives have substantially expanded the availability of insect genomic resources. Programs such as the i5K initiative,³² the Darwin Tree of Life Project,³³ and the Earth BioGenome Project have accelerated the generation of high-quality reference genomes across insects, including numerous migratory species. As of April 2025, more than 7,000 insect genome sequencing projects, encompassing over 60 migratory species have been registered in the National Center for Biotechnology Information (NCBI) database. Of these, more than 815 insect genomes have been published in peer-reviewed journals,³⁴ representing a substantial increase from the 401 complete assemblies available in 2019.³⁵ A growing proportion of migratory insect genomes are now publicly available at chromosome, scaffold, and contig levels, reflecting a clear trend toward higher assembly quality in recent years (Figure 2). These sequenced migratory species span seven insect orders, including Lepidoptera, Orthoptera, Hemiptera, Diptera, Odonata, Coleoptera, and Neuroptera. Notably, more than 64% of the available migratory insect genomes belong to Lepidoptera, one of the most diverse and ecologically significant insect orders. Within Lepidoptera, genomic resources are particularly enriched for moth families such as Noctuidae (19 species), Pyralidae (9 species), and Nymphalidae (6 species), reflecting both their agricultural importance and experimental tractability (Table S1). In contrast, Hemipteran migratory species, including members of Aphididae (4 species), remain comparatively underrepresented. The phylogenetic distribution of available migratory insect genomes remains uneven across orders and families, with certain lineages, most notably Noctuidae, exhibiting disproportionately high genomic coverage relative to others (Figure 2).

The availability of whole-genome data is critical because, instead of relying on superficial physiological traits, these data anchor studies in actual genomic architecture, allowing researchers to identify key loci and regulatory networks that are consistently associated with migratory phenotypes.

Nevertheless, the rapid accumulation of high-quality reference genomes

provides an increasingly robust foundation for comparative genomic analyses, enabling deeper insights into the evolutionary, ecological, and mechanistic bases of migratory adaptation.

Multi-omics and regulatory insights into insect migration

While genome sequencing provides a structural framework, transcriptomic and epigenomic approaches elucidate the functional and regulatory dynamics underlying insect migration. Comparative transcriptomic analyses between migratory and resident populations have revealed complex gene expression programs that govern flight muscle development, energy metabolism, and circadian regulation. In particular, the differential expression of genes involved in lipid mobilization, mitochondrial function, and oxidative phosphorylation ensures sustained energy production during long-distance flight.³⁶ Endocrine signaling pathways play central roles in linking environmental cues to physiological state transitions associated with migration. Insulin signaling regulates nutrient allocation and wing morph differentiation, juvenile hormone (JH) controls reproductive delay and migration timing, and adipokinetic hormone (AKH) promotes the mobilization of energy reserves during prolonged flight.^{3,37} Together, these hormonal pathways integrate intrinsic developmental programs with extrinsic environmental factors such as temperature, photoperiod, and food availability to coordinate the onset, duration, and termination of migratory behavior.

Beyond transcriptional regulation, emerging epigenomic studies highlight the importance of reversible chromatin modifications in maintaining migratory plasticity. DNA methylation patterns and histone modifications have been associated with migration-related gene expression changes, influencing behavioral flexibility and metabolic reprogramming.^{38,39} These epigenetic mechanisms likely facilitate rapid and reversible transitions between migratory and sedentary states, enabling insects to respond adaptively to fluctuating environmental conditions. As sequencing technologies continue to advance and costs decline, the integration of single-cell transcriptomics and spatial epigenomics is expected to provide unprecedented resolution of tissue and cell-type-specific regulatory networks that underpin migration-related traits.

Even though genomic and transcriptomic data provide essential insights into regulatory architecture, migration is ultimately expressed at the physiological and biochemical levels. Proteomic and metabolomic approaches are therefore increasingly necessary to capture the functional state of migratory insects. Quantitative proteomics enables direct assessment of flight muscle protein composition, mitochondrial enzyme abundance, and stress-response pathways, which may not correlate linearly with transcript levels.⁴⁰ Similarly, metabolomic profiling reveals dynamic shifts in lipid reserves, carbohydrate utilization, and oxidative metabolites that underpin sustained flight endurance.⁴¹ Lipidomics has proven particularly informative in migratory Lepidoptera and Orthoptera, where energy storage and mobilization strategies determine flight performance and reproductive trade-offs.⁴² Integrating genomics with proteomics, metabolomics, and hormonal profiling will thus provide a more complete systems-level understanding of the migratory phenotype, linking gene regulation to biochemical output and ecological performance.

Comparative and functional genomics of migratory traits

Comparative and functional genomic approaches have generated critical insights into the evolutionary origins and maintenance of migratory behavior across insect lineages. The increasing availability of high-quality genome assemblies has enabled the identification of both conserved and lineage-specific genetic features associated with migration. Notably, recurrent expansions of gene families involved in chemosensation, detoxification (e.g., cytochrome P450s), lipid metabolism, and immune responses have been documented in migratory insects.^{3,43,44} These expansions likely enhance environmental adaptability, allowing migrants to exploit diverse host plants and tolerate novel chemical and microbial challenges encountered along migratory routes. At the genomic scale, islands of differentiation and regions of reduced recombination frequently overlap with loci linked to migratory traits. Such genomic architectures may contribute to the maintenance of distinct migratory phenotypes by limiting gene flow between migratory and resident populations.^{9,45} These differentiated regions are often enriched for genes

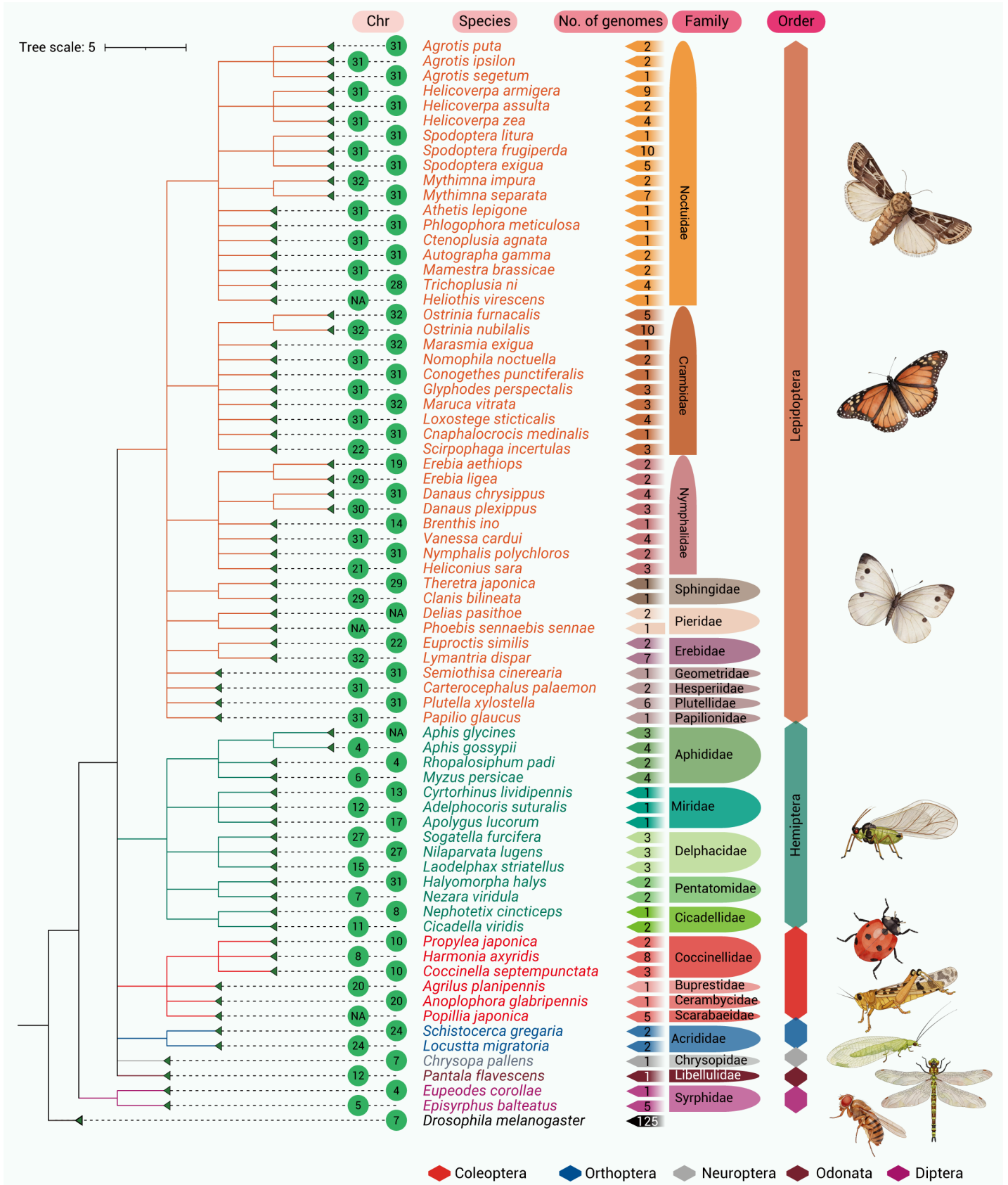


Figure 2. Phylogenetic framework of migratory insects showing genome representation across major lineages The tree illustrates the phylogenetic relationships among migratory insect taxa, with annotations summarizing the current genomic landscape as of April 2025. The phylogeny is primarily reconstructed based on high-quality genome assemblies retrieved from the NCBI database. The second column denotes species-level clusters, highlighting the diversity of sequenced migratory species within each lineage. The third column indicates the total number of available genome assemblies per species, reflecting the extent of genomic coverage and population-level representation. The fourth column represents clusters at the family level, enabling comparative insights into evolutionary diversification across families. When available, chromosome numbers are also indicated, offering a comparative view of karyotypic variation among taxa. Collectively, this figure provides an overview of the taxonomic breadth, phylogenetic relationships, and chromosomal assembly status of sequenced migratory insects, emphasizing the increasing genomic resources that facilitate evolutionary and functional genomic studies in migratory behavior.

involved in circadian regulation, flight muscle development, and sensory orientation, suggesting that they represent core genomic components of the migratory syndrome.

Integrative studies combining functional genomics, transcriptomics, and population-level resequencing have further advanced our understanding of migratory evolution. Gene network analyses reveal coordinated regulation of pathways governing energy storage and mobilization, while genome-wide association studies (GWAS) have identified allelic variants associated with flight endurance and environmental plasticity. Comparative analyses across *Danaus*, *Spodoptera*, and *Helicoverpa* species indicate convergent evolution of molecular strategies that support long-distance dispersal and multigenerational migration. Beyond advancing fundamental knowledge, these genomic insights are increasingly informing applied research: they enable the identification of molecular targets for disrupting migration or reproduction in major agricultural pests and guide conservation strategies by highlighting genetic diversity critical for the persistence of endangered migratory species.^{3,46,47} In summary, the past decade has witnessed transformative advances in the genomics of insect migration. The combined power of long-read sequencing, population-scale resequencing, and functional genomic analyses now permits dissection of the molecular machinery underlying migration with unprecedented resolution. These integrative datasets increasingly inform that migration is not a single trait but a multi-coordinated suite of physiological, behavioral, metabolic, and regulatory adaptations collectively termed the "migratory syndrome". Nevertheless, translating genomic associations into experimentally validated mechanisms and field-applicable management strategies remains underexploited and an important next frontier.

GENOMIC INSIGHTS ASSOCIATED WITH KEY MIGRATORY SYNDROME AND BEHAVIORS

Advances in insect genomics have yielded important insights into the evolutionary adaptations and ecological significance of migratory behavior, uncovering the molecular mechanisms underlying navigation and environmental responsiveness. The migratory phenotype in insects comprises a coordinated suite of adaptive traits spanning multiple biological levels, including morphology (e.g., wing size and shape), development, sensory processing (e.g., circadian rhythms, skylight polarization cues, and magnetic sensing), physiology (e.g. energy metabolism and reproductive regulation), and behavior (e.g. orientation, navigation, and flight endurance).

A notable characteristic of insect migration is that individuals are typically inexperienced migrants, completing at most a single migratory journey within their lifetime.⁴⁸ Consequently, successful migration relies heavily on heritable traits embedded within the genetic architecture of populations, as well as on genetic correlations among key components of the migratory syndrome. These inherited genomic features enable the precise coordination of morphology, physiology, and behavior required for long-distance movement across variable environments. In this section, we highlight selected migratory traits that have been examined using genomic approaches, emphasizing how comparative genomics, functional genomics, and population-level analyses have advanced our understanding of the genetic bases underlying migratory syndromes and behaviors.

Wing polymorphism

Intraspecific divergence in migratory behavior is frequently associated with variation in wing morphology, making wing polymorphism a central component of the migratory syndrome.⁴⁹ Wing polymorphism is the presence of alternate winged versus wing-reduced or wingless variants, which is a common adaptation that allows insects to balance dispersal and reproductive strategies. While short-winged or wingless morphs usually devote most of their energy to reproduction and local persistence, long-winged morphs have a fully developed flying mechanism and muscles, which facilitate migration and colonization of new environments. Within a single species, genetically and environmentally mediated variation in wing form often arises in response to seasonal migratory demands. Species that undertake long-distance migration commonly exhibit discrete wing morphs, including long-winged forms optimized for sustained flight and short-winged or wingless forms adapted to sedentary lifestyles.⁵⁰ These alternative morphs confer distinct fitness advantages: long-winged individuals facilitate dispersal and

colonization, whereas short-winged morphs often exhibit enhanced reproductive output in stable, resource-rich environments. For instance, facultatively wing-dimorphic species, such as aphids, respond to environmental conditions such as crowding, resource depletion, and temperature by producing dispersive morphs that are perfectly matched to local migratory or reproductive opportunities.⁵¹

A suite of conserved endocrine and signaling pathways regulates wing morph determination, often integrating environmental cues into developmental decisions and the genetic architecture underlying wing polymorphism varies across taxa, ranging from single-locus Mendelian control to complex polygenic regulation. Population genomic evidence supports this diversity. For example, migratory *Spodoptera exigua* populations from Shandong, a critical hub within a larger seasonal migration route,⁵² exhibit larger wings and greater flight capacity than their non-migratory counterparts from southern Xinjiang. High-quality genome assemblies and population genomic analyses of more than 300 individuals revealed pronounced genetic structure and differentiation between these populations, consistent with divergent selection on migratory traits (Li et al., 2024, unpublished data).

Furthermore, mechanistic insights into wing polymorphism have been most comprehensively characterized in a few insects including the brown planthopper (BPH) (*N. lugens*) and aphids. Studies integrating genomics and transcriptomics revealed that wing morph determination is governed by a phosphorylation-regulated network dominated by the insulin/insulin-like signaling (IIS) pathway.⁴ The zinc-finger transcription factor Zfh1 was identified as a key regulator of long and short-wing morphs, acting through transcriptional control of FoxO. A refined molecular model proposes parallel regulation by the Zfh1-FoxO transcriptional pathway, which suppresses long-wing development, and the IIS-FoxO pathway, which promotes long-wing morphogenesis via post-translational modification.⁵³ Consistent with this framework, insulin receptor 1 (InR1) and insulin receptor 2 (InR2) play antagonistic roles in determining wing dimorphism in *N. lugens*⁵⁴ (Figure 3). In aphids, wing polymorphism is influenced by a complex interaction of hormonal signals, including ecdysone, dopamine, and insulin signaling pathways.⁵¹ Additionally, key developmental regulators such as vestigial and REPTOR2 play significant roles in this process. These pathways translate environmental signals, such as maternal perception of crowding, into diverse developmental outcomes through changes in gene expression and morphogenesis.

Beyond hemipterans, genomic studies also implicate discrete genomic regions in wing reduction in other migratory insects. In the New Zealand stonefly *Zelandoperla fenestrata* Clade 1, genotyping-by-sequencing (GBS) identified multiple highly differentiated loci between fully winged and vestigial-winged individuals, indicating that wing reduction is controlled by small, strongly differentiated genomic regions.⁵⁵ Emerging evidence further suggests that epigenetic mechanisms also contribute to the mechanisms linking environmental variation to wing polymorphism. Distinct DNA methylation patterns have been detected between wing morphs in the white-backed planthopper (*Sogatella furcifera*), indicating that epigenetic regulation may modulate wing development in response to environmental cues.⁵⁶ The findings suggest that epigenetic regulation may function as a flexible interface between environmental cues and genetically encoded developmental programs underlying migration-related traits. In many migratory insects, inexperienced migrants may initiate migration, implying that environmentally induced epigenetic modifications may prime transcriptional networks that regulate dispersal morphology and physiology. Further to mention, reverse DNA methylation and chromatin remodeling can allow rapid adjustment of gene expression without altering underlying DNA sequences, enabling populations to respond quickly to fluctuating ecological changes. Consequently, migratory phenotypes may arise from the interaction between stable genomic architectures and environmentally responsive epigenetic states rather than from fixed genetic differences alone.

Notably, the IIS-FoxO regulatory core is present in various hemimetabolous insects; however, significant taxon-specific differences exist in the regulation of wing polymorphism. In planthoppers and related Hemiptera, there is an indicative integration of nutrient-sensing IIS signaling with transcriptional control modules (including FoxO, Rtn, and MAD proteins) that facilitate the development of environmentally responsive wing morphs through the graded regulation of growth and morphogenic genes.⁵⁷

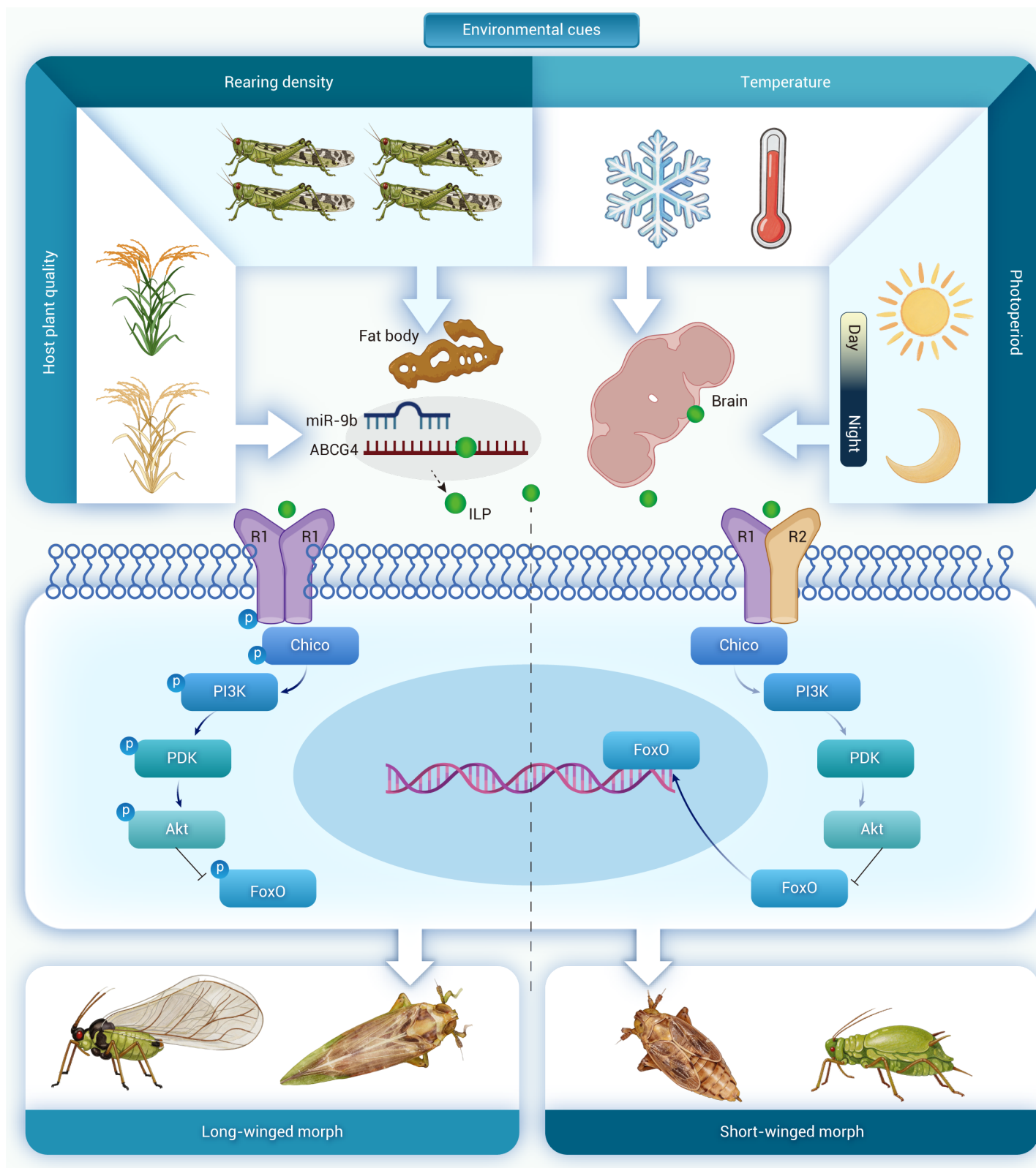


Figure 3. A diagrammatic model for interpreting wing-polymorphism regulation in the representative species of migratory insects Environmental cues, including host plant quality, rearing density, temperature, and photoperiod, stimulate secretory brain cells to release insulin-like peptides (ILPs). ILPs activate insulin receptor 1 (R1) in wing buds, initiating the insulin/insulin-like signaling (IIS) cascade involving PI3K–Akt phosphorylation, which suppresses FoxO transcription factor activity and promotes cell growth and development associated with the long-winged morph. In contrast, interaction between R1 and insulin receptor 2 (R2) reduces IIS signaling strength, allowing FoxO to remain transcriptionally active, thereby favoring developmental programs associated with the short-winged morph. Differential activation of R2 is proposed to occur under distinct environmental conditions, modulating signaling balance between dispersal and reproduction. Components showing reduced or inactive signaling are indicated by dashed arrows. The diagrammatic model is largely based on Zhang et al. (2019).¹²⁹

Conversely, aphids exhibit intricate plastic responses in which maternal and transgenerational cues, combined with hormonal effectors (such as ecdysone and insulin), interact with epigenomic states to produce winged

offspring. Notably, the same genotype can generate divergent morphs, with epigenetic changes emerging as significant modulators of this plasticity.⁵¹ Additionally, viral manipulation models demonstrate how biotic agents can

exploit insect genetic networks, thereby adding an ecological dimension to our understanding of how wing morphs and migratory potential are influenced beyond the realm of endogenous genetics.⁵⁸ Therefore, while the IIS–FoxO axis is a frequent locus of control in hemimetabolous groups, epigenetic mechanisms and upstream environmental sensing (e.g., maternal cues, photoperiod) vary among taxa, pointing to both shared and lineage-specific regulatory architectures of wing polymorphism.

From an evolutionary perspective, an important question is whether migratory traits evolved independently across insect orders or arose through modification of conserved ancestral pathways. As previously articulated from comparative genomic studies, insulin/insulin-like signaling, circadian clock networks, and lipid metabolic pathways are deeply conserved across insects and appear to be repeatedly co-opted to regulate dispersal capacity, reproductive timing, and energy allocation. This pattern supports a “conserved molecular toolkit with convergent deployment,” whereby shared pathways are independently tuned across lineages to produce similar migratory phenotypes. Collectively, these findings demonstrate that wing polymorphism arises from the interaction of genetic architecture, environmental signals, epigenetic regulation, and developmental axis integration across taxa. Despite these advances, a comprehensive understanding of wing polymorphism across migratory insects remains incomplete. Future studies integrating high-quality genome assemblies, GWAS, and functional validation will be essential for resolving the molecular basis and evolutionary dynamics of wing morph determination.

Navigation and magnetic field orientation

Long-distance migratory insects, including monarch butterflies, moths, dragonflies, and locusts, rely on an integrated suite of environmental cues to navigate across vast spatial scales. Navigation, the ability to determine and maintain a route toward a distant destination, depends on orientation mechanisms that allow insects to perceive directional information from their environment. These cues include solar position, polarized skylight, and the Earth's magnetic field. The geomagnetic sensing represents a key orientation mechanism in migratory insects.^{59,60} Although the precise sensory mechanisms remain under investigation, behavioral experiments indicate that several migratory species can detect and respond to changes in magnetic field parameters. In many species, geomagnetic information is integrated with a time-compensated sun compass to achieve directional accuracy. Monarch butterflies, for example, combine solar cues with circadian timing mechanisms to maintain consistent migratory headings, with JH-regulated physiological processes contributing to migratory readiness in diurnal migrants.⁶¹ At the molecular level, cryptochromes (CRYs)—core components of the circadian clock have emerged as key mediators of magnetosensitivity. Experimental and comparative genomic studies implicate CRYs in magnetic field detection in insects, particularly in *Drosophila melanogaster* and *D. plexippus*.⁶² In migratory moths, type-2 cryptochrome (cry2) and putative magnetoreceptors (MagR) are proposed to function in perceiving geomagnetic fields, supporting orientation in both diurnal and nocturnal migrants.^{43,63,64} Comparative transcriptomic and genomic studies in non-model migratory insects, such as noctuid moths, locusts, and dragonflies, suggest that CRY-based magnetosensitivity is broadly conserved yet shows lineage-specific molecular adaptation. Variation in CRY copy number, expression patterns, and protein interactions points to a shared sensory framework that is functionally tuned for either nocturnal or diurnal migration. Rather than a single universal mechanism, magnetoreception likely arises from evolutionary modifications of a conserved molecular module across migratory lineages. The integration of magnetic orientation with other navigation systems enables insects to maintain course under varying environmental conditions.⁶⁵ During overcast conditions when solar cues are unavailable, geomagnetic information provides a reliable backup reference.⁶⁶ Similarly, at dawn and dusk when solar position is ambiguous, polarized skylight patterns and magnetic cues together provide complementary directional information.^{65,67} This multimodal orientation system ensures navigational robustness across the diverse conditions encountered during long-distance migration.⁶⁵ Together, these findings highlight a conserved molecular framework linking geomagnetic sensing to circadian and hormonal regulation as summarized in an integrative model of insect navigation (Figure 4).

Adaptation to host environments

Migratory insects traverse vast geographic ranges and encounter highly heterogeneous environments, including variation in host plant availability, climatic factors, and anthropogenic pressures such as pesticide exposure. Consequently, exceptional ecological and physiological plasticity is essential for their survival and reproductive success. Successful colonization across such environments requires coordinated adaptation at multiple biological levels. Genomic evidence indicates that environmental adaptation in migratory insects can be broadly organized into four interrelated mechanisms: (i) sensory system diversification, (ii) metabolic and detoxification capacity expansion, (iii) structural genomic variation, and (iv) phenotypic plasticity mediated by regulatory networks.^{68–70} Chemosensory gene families represent the frontline of environmental adaptation, enabling insects to detect and evaluate host plants, oviposition sites, and conspecifics across geographically distinct habitats. Comparative genomics has highlighted extensive expansion of chemosensory gene families in several migratory species, suggesting strong selective pressure for sensory diversification.^{64,71} In the Oriental armyworm, *Mythimna separata*, gustatory receptor (GR) genes are markedly expanded, particularly within clades encoding bitter receptors, suggesting enhanced capacity to detect and utilize a broad spectrum of host plants during migration.⁶⁴ This expansion likely enhances the species' capacity to assess host plant suitability across its extensive migratory range, which spans diverse agroecosystems from tropical to temperate zones. By discriminating among a broader spectrum of plant secondary metabolites, migrants can avoid toxic hosts while capitalizing on nutritionally suitable plants encountered along migration routes. Such sensory diversification facilitates host switching, a critical capability when migrants arrive in regions where their natal host plants may be absent or phenologically mismatched. Upon detecting potential hosts, migratory insects must often contend with plant chemical defenses and anthropogenic pesticides encountered in agricultural landscapes. Adaptation to these challenges is mediated by metabolic plasticity and enhanced detoxification capacity. Many migratory species have evolved resistance to both synthetic insecticides and biopesticides, enabling successful feeding on treated crops encountered along migratory pathways.^{72,73} This resistance is not merely a passive consequence of pesticide exposure but reflects active genomic and transcriptional responses that facilitate host range expansion. For instance, populations of the fall armyworm (*Spodoptera frugiperda*) invading eastern hemisphere regions exhibit upregulated metabolic genes when feeding on alternative hosts, with Zambian lineages showing particularly pronounced transcriptional plasticity on both maize and rice.⁷⁴

Beyond gene expression plasticity, structural genomic variation provides essential raw material for adaptive evolution in migratory insects. Copy number variations (CNVs), duplications, deletions, and rearrangements of genomic segments can generate rapid phenotypic change by altering gene dosage or creating novel gene functions. In the fall armyworm, comprehensive genomic analyses have identified numerous CNVs associated with selective sweeps across geographic regions.⁷⁵ Notably, duplications encompassing detoxification genes and toxin-resistance loci have been directly linked to insecticide resistance phenotypes, demonstrating a causal relationship between structural variation and adaptive success. These CNVs are not randomly distributed but cluster in genomic regions under strong selection, suggesting that structural variation is an active mechanism of environmental adaptation rather than merely mutational noise. For migratory insects that encounter novel selective pressures across their ranges, such structural plasticity may accelerate adaptation relative to species with more static genomes.⁷⁴

Adaptation to heterogeneous environments also manifests through phenotypic plasticity, the ability of a single genotype to produce different phenotypes in response to environmental conditions. Wing polymorphism exemplifies this phenomenon, with many migratory insects exhibiting both fully winged (macropterous) and flight-capable forms and reduced-wing (brachypterous) forms optimized for local reproduction, as previously mentioned. This polymorphism is under complex genomic control, with recent studies identifying conserved genetic architectures regulating wing development across diverse insect orders.^{76,77} Similarly, adaptive resemblance, such as the leaf-like wing patterns observed in several migratory

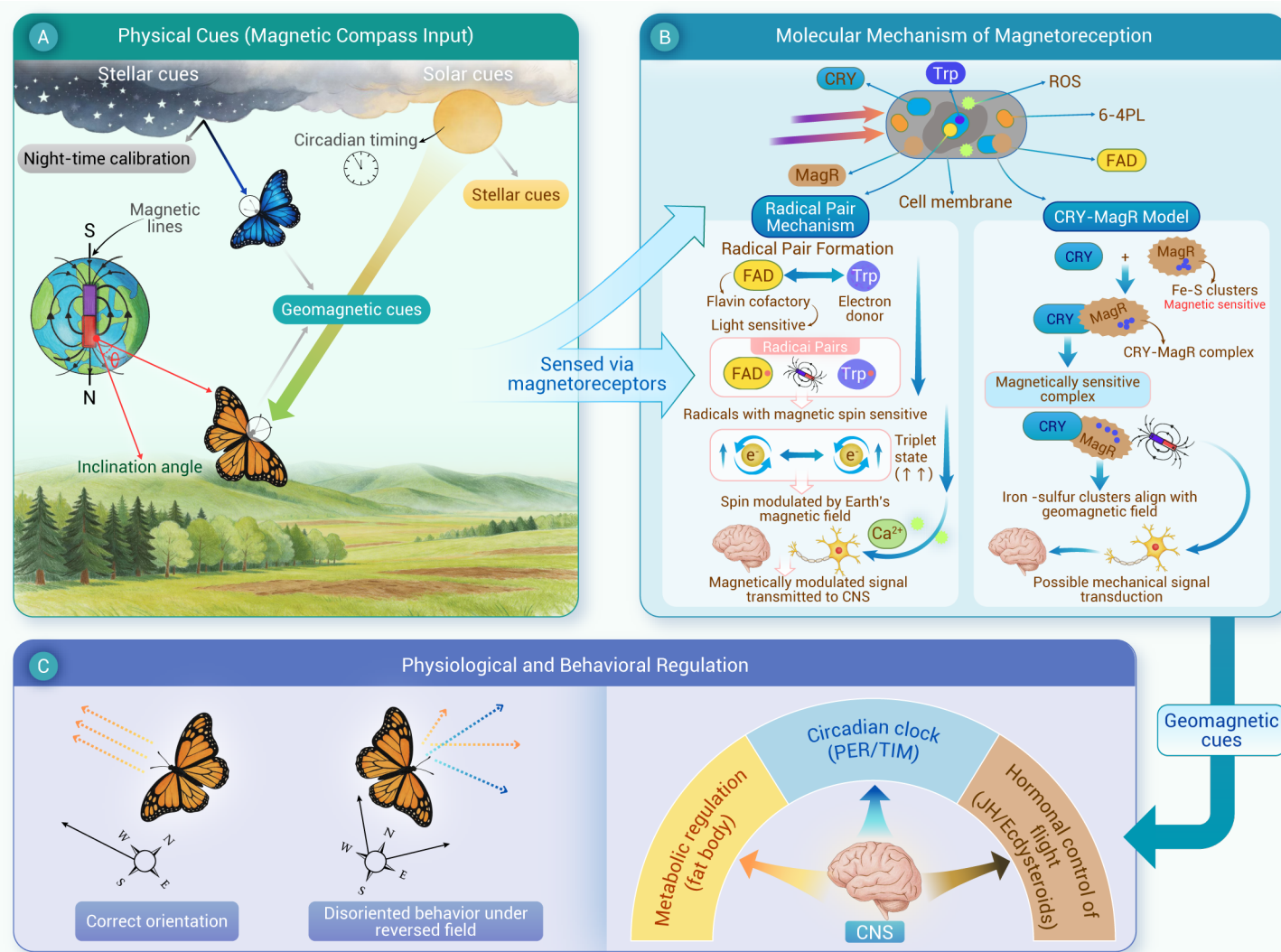


Figure 4. Diagrammatic illustration integrating the geomagnetic cues in migratory insects (A) Migratory insects such as butterflies, moths, and locusts utilize the Earth's magnetic field as a compass. Magnetic field lines and inclination angles provide reliable directional guidance during long-distance migrations. This magnetoreception is often light-dependent, with solar and stellar inputs interacting synergistically to enhance orientation accuracy.^{48,121} (B) At the molecular level, two primary models have been proposed to explain magnetosensation. Firstly, the radical pair mechanism mediated by cryptochromes (CRY) in the eyes or antennae involves light-induced electron transfer between flavin adenine dinucleotide (FAD) and conserved tryptophan (Trp) residues. This generates radical pairs whose spin dynamics are sensitive to geomagnetic fields, allowing directional detection under specific light conditions.^{54,122} Secondly, the CRY-MagR model, which proposes a magnetoreceptive complex formed by CRY and a magnetosensitive protein called Magnetoreceptor (MagR), which contains iron-sulfur clusters. These clusters may respond directly to geomagnetic fields, providing a light-independent or complementary detection mechanism.¹³⁰ In both models, processed magnetic information is transmitted to the insect's nervous system. (C) Magnetoreception integrates with physiological pathways to regulate behavioral outputs. Under normal geomagnetic conditions, this integration supports correct orientation whereas reversed magnetic fields can induce disoriented behavior. The circadian clock, modulated by PER/TIM oscillations coordinates with geomagnetic input and visual cues to maintain time-compensated navigation. Additionally, magnetically influenced pathways may extend to metabolic regulation via the fat body and hormonal control of migratory flight through juvenile hormone (JH) and ecdysteroids, enabling adaptive behavioral responses in variable environments.^{48,131}

moth lineages, enhances crypsis during daytime resting periods, reducing predation risk during migratory stopovers.⁷⁸ In monarch butterflies, such morphological adaptations likely contribute to migratory success by minimizing mortality during the prolonged overwintering period when individuals are concentrated and vulnerable.

Perhaps the most dramatic examples of adaptive plasticity in migratory insects involve reversible, environmentally-cued transformations. The desert locust (*Schistocerca gregaria*) possesses one of the largest insect genomes sequenced to date, enriched for genes associated with phase polyphenism, the ability to reversibly alter morphology, physiology, and behavior in response to population density.^{79,80} At low densities, locusts exist as cryptic, solitary individuals; upon crowding, they transform within hours into gregarious, swarming phenotypes characterized by distinct coloration, enhanced flight capacity, and aggregation behavior.⁸¹ This genomic flexibility, encoded by extensive regulatory networks responding to serotonin and other crowding signals, underpins the swarm formation and long-distance migration that make locusts among the most destructive agricultural pests globally.

Similarly, migratory insects exhibit sophisticated responses to seasonal

environmental cues. In the European corn borer (*Ostrinia nubilalis*) and other temperate migrants, shifts in allele frequencies at loci associated with temperature tolerance and diapause initiation have been documented across latitudinal gradients.^{70,82,83} These genomic signatures reflect rapid adaptation to climatic variability, with populations evolving locally-optimized timing of diapause termination and migration initiation. Such photoperiodic and thermal responses ensure that migrants arrive at destination habitats when resources are available and conditions are favorable for reproduction. Together, these studies demonstrate that adaptation to host environments in migratory insects is driven by an integrated interplay of sensory expansion, metabolic regulation, structural variation, and phenotypic plasticity. Genomic approaches continue to uncover how these mechanisms, operating at different temporal and organizational scales, collectively enable migrants to detect, evaluate, exploit, and thrive across the diverse and rapidly changing ecological landscapes they encounter. By establishing this structured framework, we can appreciate that environmental adaptation is not a monolithic phenomenon but rather a multifaceted suite of capabilities, each shaped by distinct selective pressures and implemented through specific genomic

architectures.

Energy metabolism and flight resilience in migratory insects

Efficient energy metabolism underpins the endurance required for long-distance insect migration, and recent genomic and transcriptomic studies have begun to elucidate the molecular basis of this adaptation. Accumulating evidence indicates that lipid metabolism constitutes the dominant energetic pathway supporting sustained flight. For example, in *Agrotis ipsilon*, genes involved in fatty acid degradation, lipid digestion, and oxidative phosphorylation are significantly enriched, with key enzymes such as ECIL1, CPT2, and ACADS exhibiting expression patterns correlated with flight duration.⁴³ Across migratory insect taxa, convergent genomic signatures further support the central role of lipid-based energy metabolism. In locusts, lineage-specific expansions of genes encoding perilipins, fatty acid-binding proteins, Prdx6s, and enoyl-CoA hydratase enhance lipid mobilization efficiency and antioxidant capacity, thereby sustaining prolonged aerobic flight.^{21,84} Consistently, population-level transcriptomic analyses in *H. armigera* demonstrate that long-distance migratory individuals show elevated expression of oxidative phosphorylation and energy production genes relative to sedentary counterparts.³⁶ Together, these findings indicate that adaptive remodelling of lipid transport, oxidation, and mitochondrial energy pathways through both gene expansion and regulatory modulation represents a core genomic signature of migratory flight resilience in insects. Despite these advances, key gaps remain. Future studies integrating metabolomic and transcriptomic profiling across distinct migration phases, applying functional validation of candidate energy-metabolism genes via CRISPR or RNAi, and evaluating life-history trade-offs between migratory investment and reproduction will be essential for a mechanistic understanding of insect migratory adaptation.

Muscle development and structural adaptation in migratory insects

Flight muscle development is a key component of the migratory syndrome, enabling the sustained flight performance required for long-distance movement.⁸⁵ Notable genomic studies have revealed that selection on muscle-related gene networks underpins the physiological divergence between migratory and non-migratory morphs. In migratory insects such as the monarch butterfly, a 21-kb genomic segment within the collagen IV α -1 gene shows strong differentiation, with specific allelic variants linked to enhanced flight muscle architecture and endurance, crucial for long-distance migration.⁷⁶ Collagen alpha genes are vital for maintaining the structural integrity of tissues, supporting organ function, facilitating wound healing, and contributing to various developmental and physiological processes in the bodies of living organisms.⁸⁶⁻⁸⁸ Similarly, the chromosome-level genome of *L. migratoria* showed lineage-specific expansions of gene families associated with muscle development and neurophysiological coordination, proposing a broad genomic reconfiguration supporting sustained locomotor activity.²¹

Recent transcriptomic and proteomic evidence extends these insights, identifying conserved molecular pathways involved in muscle remodeling. In *M. separata*, multi-omics integration uncovered upregulation of proteasome components and collagen α subunits, indicating active protein turnover and muscle tissue restructuring during migratory flight.⁶⁴ The convergence of collagen-related gene upregulation across *M. separata* and *D. plexippus* implies an evolutionary parallel in structural adaptation, possibly reflecting a shared requirement for muscle resilience and elasticity across independent migratory lineages. Further transcriptomic analyses, such as those in *Episyrphus balteatus*, substantiate this pattern by linking differential expression of muscle structure and energy metabolism genes to migratory activity.³

All of these findings demonstrate that migratory insects have undergone convergent genomic adaptations in muscle-related gene families, particularly those involved in collagen synthesis, protein recycling, and mitochondrial efficiency, forming a molecular foundation for flight tolerance. Despite these advances, future research should integrate high-resolution functional genomics, single-cell transcriptomics, and gene-editing approaches to dissect how structural protein networks in collagen and proteasome-related gene families contribute to flight resilience, plasticity, and energy efficiency across migratory taxa. Expanding comparative studies beyond model species will also be crucial for identifying whether these molecular signatures represent convergent or lineage-specific adaptations to migration.

Temporal orchestration: circadian modulation in migratory insects

Circadian clocks are endogenous time-regulating systems that coordinate biological processes to match the 24-hour daily light-dark cycle. Circadian rhythms of physiology and behavior, and cycles of moulting are critical aspects of insect biology which organize the biological systems of insects to adapt to a daily and seasonally changing environment.^{89,90} At the heart of the molecular circadian clock in animals including migratory insects is a transcription-translation feedback loop (TTFL) that takes about 24 hours to complete. This loop involves the rhythmic expression of core clock genes and proteins, such as period (*per*), cryptochrome (*cry*), timeless (*tim*), clock (*clk*), and cycle (*cyc*) which regulate own transcription through inhibitory and triggering interactions.^{91,92} Generally, in nocturnal migrants such as moths, circadian regulation ensures synchronized take-off at dusk and optimizes nighttime migratory behavior, likely via melatonin-mediated signaling pathways and photoreceptor input to the central clock.⁹³⁻⁹⁵ The flexibility of circadian outputs in adapting to changing latitudinal gradients and differing photoperiods accentuates the evolutionary resilience of these internal clocks, allowing migratory insects to anticipate and respond effectively to environmental cues encountered across diverse geographic landscapes.

Remarkably, in migratory insects, circadian adjustment plays pivotal roles associated with migration, including reproductive timing (egg laying and hatching), pupation, and adult eclosion.⁹⁶ Recent population genomic studies of migratory pest lepidopterans indicate that loci regulating circadian rhythms are key determinants of migratory propensity and timing. The repeated recruitment of these circadian pathways across diverse taxa underscores their fundamental evolutionary role in facilitating migration.^{97,98} Comparative genomics in diverse migratory taxa, such as the monarch butterfly among Lepidoptera and migratory locusts among Orthoptera, has highlighted strong correlations between circadian regulation and migratory behaviors.^{16,99} In-depth molecular and bioinformatic analyses have revealed that many migratory insects contain a conserved set of core clock genes, including orthologues of *tim*, *per*, *clk*, *cycle*/*Bmal1*, and both light-sensitive and mammalian-type cryptochromes (*cry-d* and *cry-m*) originally characterized in *Drosophila* and mammals.^{91,100,101} For instance, *D. plexippus*, *Antheraea pernyi*, and *B. mori* all possess functionally conserved PER proteins starring critical domains such as the nuclear localization signal (NLS), PAS domains, cytoplasmic localization domain (CLD), and nuclear export signal (NES).^{91,102,103} Fascinatingly, *A. pernyi* harbours three sex-linked *per* genes, although only one (*ApperZ*) is essential for circadian function.¹⁰⁴

In monarchs, circadian genes have been directly linked to the coordination of migration-related outputs with environmental cues such as photoperiod and geomagnetic fields, facilitating orientation, timing, and energy management during long-distance flights.^{46,91} The regulation of seasonal polyphenisms in migratory insects such as diapause in the European corn borer and the switch between migratory and resident strategies arises from the integration of circadian and photoperiodic cues. This integration is reflected at the genomic level, where allelic variation in circadian clock and phototransduction genes correlates with seasonal phenotypic changes, demonstrating a co-opted molecular framework for annual timekeeping.¹⁰⁵ From these findings, it is suggested that across migratory insects, the evolutionary conservation and diversification of circadian clock genes support a highly adaptive temporal framework, enabling precise modulation of migration-related phenotypes over vast ecological and geographical ranges. Future studies should focus on how circadian gene variation influences migration-related traits at the molecular, physiological, and behavioral levels. Functional validation of circadian clock-related loci and their associations with environmental factors could provide comprehensive insights into the evolutionary adaptation of migration in diverse insect species.

ECOLOGICAL AND EVOLUTIONARY GENOMICS OF MIGRATION

Population structure, gene flow, and geographic expansion

Migration profoundly shapes insect population structure by modulating gene flow, demographic connectivity, and spatial patterns of genetic differentiation across heterogeneous landscapes. Through ecological genomics, it is now possible to quantify how migratory behavior simultaneously maintains population connectivity and facilitates regional divergence under distinct ecological pressures.⁶⁹ Population-scale genomic analyses, including whole-

genome resequencing, SNP-based clustering, and demographic modeling, have revealed how migration drives recurrent cycles of expansion, admixture, and local adaptation.

Biotypes and colonization dynamics

Migratory insects often expand beyond their original ranges through genetically distinct or behaviorally specialized biotypes capable of exploiting diverse ecological niches. Population genomic analyses have demonstrated that such biotypes contribute to successful colonization and regional persistence. In the BPH, whole-genome resequencing of 360 individuals revealed clear genetic differentiation among Australian, Asian, South Asian, and East Asian populations, reflecting adaptation to region-specific environmental conditions and host landscapes.⁹ These patterns highlight how migration can promote both connectivity and structured divergence at continental scales. Similarly, genome-wide SNP analyses of 280 *S. frugiperda* individuals showed that while native populations in the Americas form distinct genetic clusters, invasive populations in Africa and Asia exhibit relative genetic homogeneity.⁷⁴ This pattern is consistent with rapid geographic expansion accompanied by substantial gene flow facilitated by high migratory capacity. Early global sampling of 101 *D. plexippus* genomes likewise identified distinct regional clusters across Central/South America, the Pacific, and the Atlantic, with the North American population displaying comparatively lower divergence.⁷⁶ These findings collectively illustrate how migration shapes both structured differentiation and large-scale connectivity.

Reconstruction of dispersal routes and invasion history

Genomic data have also enabled reconstruction of ancestral origins and dispersal pathways. Comparative analyses identified Asia as the ancestral range of BPH and South America as the origin of the bella moth (*Utetheisa ornatrix*).^{9,106} In BPH, gene flow signatures further revealed contrasting seasonal movement patterns, including multigenerational round-trip migration in East Asia and predominantly one-way movements toward Indochina and South Asia, likely reflecting climatic drivers of regional dispersal.⁹ Additionally, studies on *S. frugiperda*'s mitochondrial and nuclear markers (COI, Tpi) suggested an origin from Florida and the Greater Antilles,^{107,108} while mitogenome and whole-genome analyses indicated multiple introductions into Africa, potentially from South America.^{109,110} High-resolution genomic comparisons further demonstrated that invasive eastern-hemisphere populations most closely resemble North and Central American corn-strain lineages, supporting a primary origin in this region.⁷⁴ The identification of a genetically distinct Zambian lineage suggests an independent African introduction event, underscoring the complexity of invasion histories.⁷⁴ However, parallel patterns have been observed in *Tuta absoluta*, where genome-wide SNP analyses revealed three regional clusters, Andean, central South American, and North (Colombia-Costa Rica), consistent with a northward expansion from the Andes likely facilitated by human-mediated transport and environmental shifts.¹¹¹ These studies demonstrate how migration reshapes population genetic architecture through repeated episodes of expansion, admixture, and local adaptation.

Demographic connectivity and genetic diversity

Comparative population-genomic metrics further indicate that migratory lineages often maintain elevated heterozygosity relative to sedentary counterparts, reflecting recurrent admixture, large effective population sizes, and high demographic connectivity across landscapes.⁴⁵ Such patterns suggest that migration buffers against genetic drift while preserving adaptive potential, enabling rapid responses to environmental variability. That said, migration does not happen in a vacuum. Insects today are navigating a world reshaped by human activity, shifting climates, fragmented habitats, and altered landscapes, which are all taking a toll. Increasing environmental pressures, including climate change and habitat fragmentation, are likely to alter patterns of connectivity among migratory insect populations. Changes in migratory timing, shifting geographic ranges, and the loss or modification of seasonal habitats may reduce movement and gene flow between populations, promoting greater genetic differentiation at regional scales. As a result, the genomic patterns typically associated with highly connected migratory systems may gradually shift toward more fragmented population structures,

potentially changing the balance between the maintenance of adaptive genetic variation and the effects of genetic drift.

Evolutionary divergence between migratory and resident lineages

Beyond shaping spatial population structure, migration also represents a recurrent evolutionary transition between mobility and sedentariness. Comparative genomics between migratory and resident lineages provides critical insight into how migratory capacity is gained, maintained, or secondarily lost. These transitions are typically associated with targeted selection on specific physiological pathways rather than extensive genome-wide divergence, reflecting the modular and repeatable nature of migratory evolution.¹¹² Genomic comparisons across independently evolved migratory systems reveal convergent patterns of pathway-level adaptation. In the globe skimmer dragonfly (*Pantala flavescens*), genome sequencing identified expansions in gene families associated with muscle performance and oxidative stress regulation, suggesting selection on pathways that enhance sustained flight and metabolic resilience.^{113,114} Such findings support the view that selection on functional modules, rather than diffuse genomic differentiation, underpins repeated evolutionary origins of long-distance migration. In the monarch butterfly (*D. plexippus*), population genomic analyses have demonstrated that migratory and non-migratory populations have diverged repeatedly through independent dispersal events.^{18,115,116} Subsequent fine-scale genomic comparisons refined this pattern by identifying three highly differentiated genes, FBXO45, DPOGS206536, and collagen $\alpha 1$, that collectively distinguish migratory North American monarchs from non-migratory populations.⁹⁰ These results illustrate that migratory capacity may be maintained through strong selection on a narrow set of loci, rather than broad genome-wide divergence, reinforcing the concept of a focused genomic architecture underlying migration. Parallel patterns have been documented in other migratory lepidopterans. In the Oriental armyworm (*M. separata*), comparative genomic and transcriptomic analyses between migratory (gregarious) and resident (solitary) populations revealed differential regulation of pathways involved in protein processing, hormonal signaling, and neurotransmitter metabolism.⁶⁴ Similarly, in the black cutworm, transcriptomic comparisons between short and long-distance fliers identified dynamic modulation of energy metabolism pathways, indicating that metabolic gene expression is flexibly tuned to migratory intensity and flight duration.⁴³ These findings highlight the complementary roles of fixed genetic differentiation and gene expression plasticity in sustaining phenotypic divergence between migratory and resident forms. In locusts, functional diversification at the post-transcriptional level further underscores the evolutionary refinement of migratory capacity. The identification of two Hif-1 α splice variants (Hif-1 $\alpha 1$ and Hif-1 $\alpha 2$) revealed specialization in redox homeostasis during prolonged aerobic flight, with Hif-1 $\alpha 2$ specifically regulating reactive oxygen species balance.¹¹⁷ This example demonstrates how alternative splicing and regulatory modification, rather than solely sequence-level mutations, contribute to the persistence and optimization of migratory performance. At the population scale, migratory lineages frequently exhibit higher heterozygosity relative to sedentary counterparts, as observed across lepidopteran species.⁴⁵ Elevated genetic diversity likely reflects large effective population sizes and recurrent admixture associated with migration, providing a reservoir of standing variation that facilitates rapid adaptive shifts. These findings demonstrate that evolutionary divergence between migratory and resident forms is characterized by recurrent, pathway-focused selection embedded within a broader framework of demographic connectivity.

Life history regulation and reproductive trade-offs in migratory systems

At the organismal level, the persistence of migration depends on tight integration between locomotor capacity and reproductive timing. Migration is energetically demanding, and successful long-distance movement requires coordinated allocation of resources between flight and reproduction. Genomic and transcriptomic analyses increasingly reveal how endocrine regulation and gene expression plasticity mediate the flight-reproduction trade-off central to migratory life histories.¹¹⁸ A central regulator of this trade-off is JH, which governs reproductive maturation in many insects. In migratory species, JH signaling is dynamically modulated in response to flight demands and environmental cues. For example, in the Oriental armyworm,

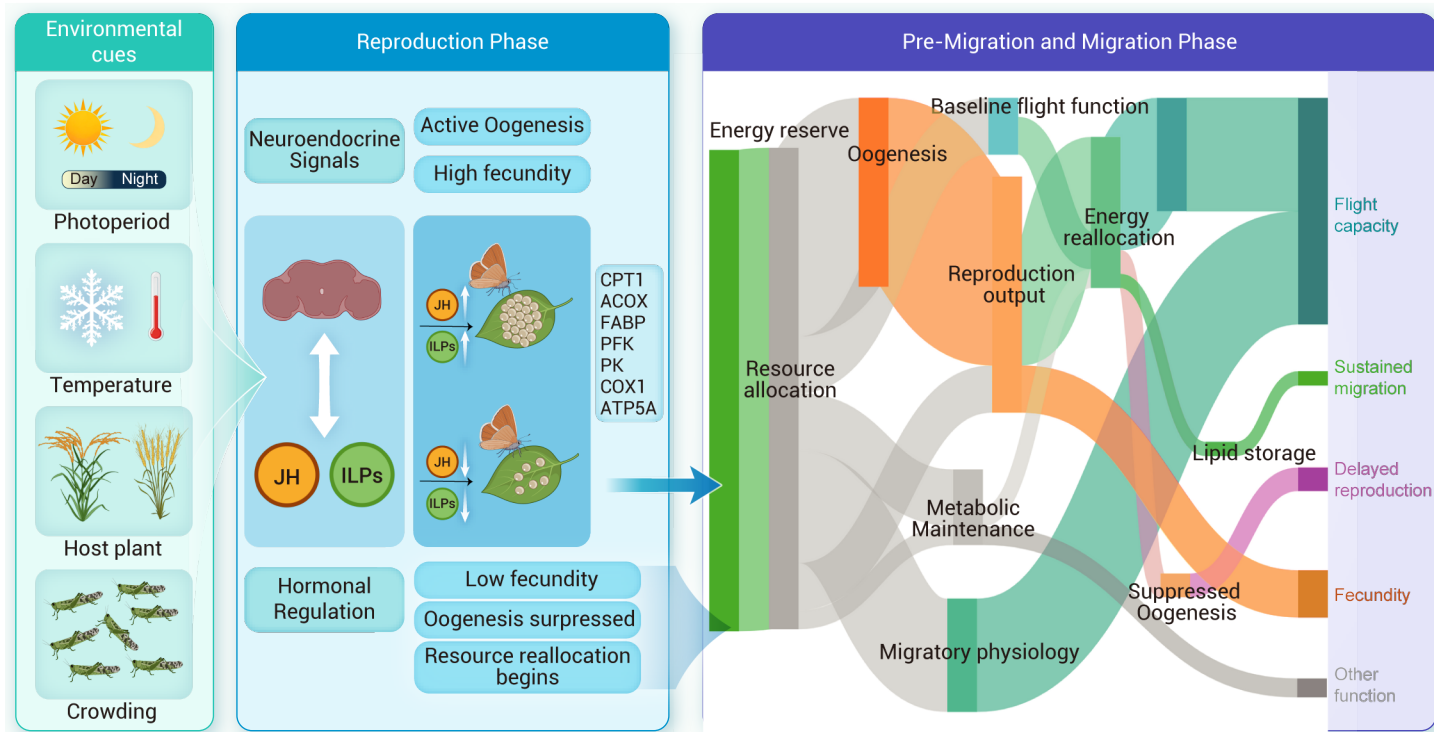


Figure 5. Environmental regulation of reproductive and migratory trade-offs in migratory insects The key environmental factors such as photoperiod, temperature, host plant quality, and population density (insect crowding) are detected and integrated by the insect central nervous system (CNS), triggering neuroendocrine signalling cascades. These external cues modulate the expression and activity of reproductive hormones, such as juvenile hormone (JH) and insulin-like peptides (ILPs), which play central roles in regulating fecundity. Under favorable environmental conditions, elevated levels of JH and ILPs promote reproductive investment, resulting in increased oogenesis and egg deposition. Conversely, under stress or migration-inducing cues, reduced hormonal activity leads to a downregulation of reproductive output. This suppression facilitates an energy reallocation trade-off, whereby resources are diverted from reproduction toward physiological processes essential for migration, including flight muscle development and energy reserve accumulation. The model highlights how migratory insects fine-tune reproductive investment versus migratory capacity in response to environmental variability, a critical adaptation for balancing survival and reproductive success across variable environments.

expression of the allatotropin gene (*at*), which stimulates JH synthesis, is suppressed in long-distance fliers, resulting in delayed reproductive maturation.⁶⁴ Conversely, expression of allatostatin (*ast*), an inhibitor of JH synthesis, is upregulated following prolonged flight, further supporting endocrine regulation of the flight-reproduction balance.⁶⁴ These transcriptional shifts demonstrate how hormonal pathways are plastically adjusted to prioritize migratory performance over immediate reproductive investment. A similar regulatory framework operates in the black cutworm, where JH degradation is mediated by expanded copies of the JH epoxide hydrolase (*JHEH*) gene in migratory populations.^{43,119} Together with other genes involved in JH synthesis and turnover, including *JHAMT2* and *JHEH5*, these regulatory components modulate circulating hormone levels to optimize energy allocation between sustained flight and reproduction.^{43,119} Such fine-tuned endocrine modulation illustrates how genomic variation and transcriptional control reinforce life-history trade-offs associated with migration. In the monarch butterfly, migration is coupled to a pronounced reproductive diapause.⁷⁶ During fall migration, reproductive development is suspended, extending longevity and promoting lipid accumulation required for overwintering and long-distance travel. This diapause program integrates environmental cues such as photoperiod and temperature with endocrine signaling pathways, demonstrating how neuroendocrine networks synchronize migratory timing with reproductive delay.

Environmental factors during development can also influence migratory and reproductive phenotypes through gene expression plasticity. Larval crowding and nutritional limitation have been shown to induce significant transcriptomic shifts in pathways related to development and metabolism (Figure 5).¹²⁰ These environmentally induced regulatory responses likely contribute to phenotypic plasticity that coordinates migration and reproduction under fluctuating ecological conditions. Therefore, migration is sustained not only by structural genomic adaptations but also by dynamic endocrine and transcriptional regulation. Neuroendocrine pathways also modulate hormone synthesis, degradation, and signaling in response to environmental

and physiological inputs, ensuring precise synchronization between migratory behavior and reproductive timing. Figure 5 summarizes the regulatory interactions underlying this life-history balance.

Understanding these mechanisms provides crucial insight into how migratory insects maintain fitness across energetically challenging journeys and rapidly changing environments, with important implications for both ecological theory and applied pest management.

APPLICATIONS AND IMPLICATIONS

Gaining deep insights into how migratory insects cope with environmental variability, physiological stress, and ecological challenges across vast geographic ranges is possible through the study of their adaptations. By uncovering the genetic blueprints of notable migratory species such as monarch butterflies, locusts, and migratory moths, researchers have identified key mechanisms related to navigation, environmental sensing, physiological changes, and adaptation during long-distance migrations. These findings not only enhance our understanding of insect biology and ecology but also possess significant implications for agricultural pest control, conservation, and evolutionary biology. For example, elucidating the genetic foundations of pesticide resistance and migration can inform more effective pest management strategies, while conservation efforts can be better tailored to protect essential habitats and migratory routes.

Pest management

Certain insects, such as locusts, bollworms, and armyworms, are well-known for their remarkable ability to traverse vast distances and feed on a wide variety of plants, leading to significant damage to crops and natural ecosystems. Gaining insights into the genetic mechanisms underlying their migratory behaviors, reproductive strategies, and environmental adaptations can greatly improve pest management practices. Research into the genomes of migratory insects has unveiled innovative approaches for managing and controlling pest populations more effectively and sustainably. Advanced

sequencing technologies have pinpointed specific genes and regulatory networks that are crucial for navigation, flight endurance, and responses to environmental stimuli.^{46,68} By targeting these genes and pathways through methods like RNA interference or gene editing, new pest management strategies that disrupt migratory patterns can be developed, thereby mitigating the adverse effects of these pests on agriculture. This genetic-based approach offers a more precise and efficient pest management solution, reducing the dependence on chemical pesticides. Furthermore, understanding the genetic foundations of environmental adaptability in migratory insects empowers scientists to anticipate potential shifts in pest distribution and formulate adaptive management strategies.^{9,98} Predicting future expansions and outbreaks of insect pests is essential for implementing preventive measures and control strategies, which is crucial for ensuring global food security amid changing climate conditions. Thus, integrating genomic insights with traditional pest management practices holds great promise for enhancing agricultural productivity and safeguarding ecosystems from the devastating impacts of migratory insect pests.

Understanding migration patterns

The analysis of migratory insect genomes has revealed genetic factors that govern navigation, timing, and environmental adaptability during migration, as well as the genetic differences and similarities among populations in various locations.¹²¹ These genetic insights contribute to our understanding of how insects perceive and respond to changing environments, coordinate their movements over extensive distances, and adapt to a range of habitats, including their patterns of expansion.^{12,78,122} In locusts for instance, genome sequencing has uncovered genes that regulate phase polyphenism, a crucial genetic mechanism for their mass migration events, which are influenced by changes in population density and environmental conditions.²¹ Additionally, the migration of the monarch butterfly is closely tied to the availability of milkweed plants, essential for their larval development. Genomic research has shed light on how migratory patterns have been affected by alterations in land use and climate impacting the availability of these plants.¹²³ By combining ecological data with genomic surveillance, we can better predict invasion threats, migration patterns, and population dynamics.

Conservation and biodiversity

Genome research plays a vital role in insect conservation and biodiversity by offering detailed insights into the genetic diversity, population structure, and evolutionary history of insect species. By sequencing the genomes of endangered or ecologically significant insects, researchers can identify genetic factors that influence adaptability, resilience, and reproductive success. This information is crucial for developing targeted conservation strategies, including habitat restoration, captive breeding programs, and measures to enhance genetic diversity.

Population genomics is increasingly being utilized in conservation initiatives to identify at-risk populations and guide management plans.¹²⁴ For example, studies on the monarch butterfly have revealed reduced genetic diversity in declining populations, which has informed targeted conservation efforts.¹²⁵ Genomic studies have identified how changes in land use and climate affect the availability of milkweed plants, which in turn impacts the survival of the monarch butterflies.¹²⁶ This knowledge is vital for conservation efforts aimed at preserving migratory routes and breeding grounds. By mapping the genetic diversity of migratory populations, it is possible to identify critical habitats that require protection to ensure the survival of these species.

Moreover, there is a growing trend to employ genomic markers associated with diapause, photoperiod sensitivity, and temperature tolerance to predict how populations may respond to climate stressors.^{105,127} For species like locusts, which can rapidly expand their range in response to environmental cues, these predictive models are essential. Given that insects have demonstrated remarkable abilities to adapt to changing environments, it is essential to conserve ecologically important and resilient species.

FUTURE DIRECTIONS AND CHALLENGES

Genomic studies in migratory insects present exciting prospects and significant challenges for the future. With the many achievements attained through genomic research, challenges, however, still persist, including the

complexity of analyzing large genomic datasets from diverse populations and the difficulty of linking genetic variations to specific migratory behaviors.¹¹⁸ There have been remarkable advancements in genomic studies on migratory butterflies, moths, and dragonflies. However, studies on general migration by other groups of insects, such as social insects (e.g., honey bees) with a shift from a statary to a migratory phase within colonies, characterized by greater scout activity are still lacking,¹²⁸ despite their impact on ecosystem services, food security, and biodiversity. Accurate results from genomic analyses usually require large sample sizes from a broader range of locations, which are tedious and costly to achieve. The transient nature of migratory insect populations complicates sample collection and long-term studies.² Genome annotation in insects has been frequently hindered by suboptimal assembly quality, which often stems from high levels of genetic variability within species, presenting a significant challenge in accurately piecing together and interpreting insect genomic data. Some sequencing projects are still far from being realized due to difficulty in assembling insect genomes and limited financial support. The development and use of insect tags are uncommon, hence posing difficulty in monitoring insect movements using traceable tags due to their small sizes. Practically, the field application of genome-based innovative migratory pest control strategies for the direct benefit of farmers is still uncommon.

To overcome some of these challenges, novel techniques and tools are continuously being developed; hence, further research is required to gain more insights using the available advanced resources for genomic research to better understand the biology of migratory insects. Third-generation sequencing technologies, such as ONT and PacBio, capable of generating long reads exceeding 10 kb in length, offer a solution to the limitations of short-read sequencing. Several high-quality insect genomes have already been sequenced and made public using either PacBio technology alone or a hybrid approach combining technologies such as PacBio and Illumina data. Furthermore, the extensive application of pan-genomics, population genomics, and comparative genomics has illuminated a number of areas, including the evolution of certain insect adaptations. However, investigations on T2T genomes and pan-genome analysis techniques in insects are still less advanced than in plants and other animals. By resolving intricate repetitive areas with substantial evolutionary importance, such as telomeres and filaments, T2T genomes have the potential to enhance genome quality. Pan-genomics, on the other hand, makes it possible to examine variation and domestication features among strains in more details, as well as the evolutionary paths of species lineages. As a result, it is anticipated that T2T research and pan-genomics will emerge as important areas of study in insect genomics, establishing new trends in the study of insect evolution.

Even though there are still challenges faced, with the available sequencing technologies in the field of genomic research, there is however, great optimism that these challenges will be managed as improvements are continuously being made.

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AUTHOR CONTRIBUTIONS

Hongran Li, Nimlin Dickson Gabuin, and Alexander Yesaya contributed equally to this work. Hongran Li was primarily responsible for drafting the manuscript. Hongran Li, and Alexander Yesaya mainly contributed to the preparation of figures. Nimlin Dickson Gabuin contributed to both manuscript writing and figure preparation. VIGAN Chess-Kadousté contributed to data collection, literature review, and provided support for the development of research ideas. Yutao Xiao, and Kongming Wu as corresponding authors, conceived and designed the overall review framework, supervised the review process, and revised the manuscript. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

No new data were created or analyzed in this study.

SUPPLEMENTAL INFORMATION

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