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Genomic Analysis of Earwigs and Their Ecological Adaptation: From Genome Assembly to Molecular Mechanisms of Environmental Adaptation

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Abstract The earwig, *Forficula auricularia*, serves as a significant model organism for studying maternal care, sexual selection, sociality, and host-parasite interactions. Despite its importance, genetic research on this species has been limited due to a lack of comprehensive genomic resources. This study synthesizes recent advancements in the genomic analysis of earwigs, focusing on genome assembly, annotation, and the molecular mechanisms underlying their ecological adaptation. High-quality genome assemblies have been developed using advanced sequencing technologies, revealing extensive genetic diversity and adaptive traits. These genomic resources have facilitated the identification of key genes and pathways involved in environmental adaptation, including responses to temperature, humidity, and other ecological stressors. Comparative genomic studies have further elucidated the evolutionary processes and genetic architecture that enable earwigs to thrive in diverse environments. This study highlights the potential of genomic tools to enhance the understanding of earwig biology and their adaptive strategies, providing a valuable foundation for future research in evolutionary ecology and conservation genetics.

Keywords *Forficula auricularia*; Genome assembly; Ecological adaptation; Genetic diversity; Evolutionary processes

1 Introduction

Earwigs, belonging to the order Dermaptera, are a diverse group of insects with over 2,000 described species distributed globally, predominantly in tropical and subtropical regions (Kamimura et al., 2023). They are known for their distinctive forceps-like cerci and exhibit a range of interesting biological characteristics, including maternal care, viviparity, and epizoic relationships with other small animals (Liu et al., 2022; Meunier, 2023). Earwigs play significant ecological roles, acting as both pests and beneficial biological control agents in various ecosystems (Meunier, 2023). Their distribution and habitat preferences are influenced by various factors, including climatic conditions and historical biogeographical events, such as the breakup of Gondwana (Fattorini, 2022).

Genomic analysis has become a crucial tool in understanding the ecological adaptation of earwigs. The sequencing of mitochondrial genomes has revealed extensive gene rearrangements and intraspecific variations, providing insights into the molecular diversity and evolutionary processes within the Dermaptera (Chen, 2022; Liu et al., 2022). DNA barcoding and phylogenomic studies have further elucidated the phylogenetic relationships and evolutionary history of earwigs, challenging previous taxonomic classifications and highlighting the complexity of their genetic makeup (Wipfler et al., 2020; Kamimura et al., 2023). These genomic studies are essential for understanding how earwigs adapt to their environments, including their roles in pest control and their responses to ecological pressures (Stuart et al., 2019; Núñez-Pascual et al., 2022).

This study synthesizes current knowledge on the genomic analysis of earwigs and their ecological adaptation. By examining genome assembly techniques, gene rearrangements, and molecular mechanisms underlying environmental adaptation, this study provides a comprehensive understanding of the genetic factors that contribute to the ecological success of earwigs and covers various aspects of earwig genomics, including mitochondrial and nuclear genome sequencing, phylogenetic analyses, and the implications of these findings for taxonomy, biogeography, and ecological roles. Through the synthesis, this study aims to highlight the importance of genomic research in uncovering the adaptive strategies of earwigs and their potential applications in ecological and evolutionary studies.

2 Genome Assembly of Earwigs

2.1 Methods for genome sequencing and assembly

The genome assembly of earwigs, specifically *Forficula auricularia*, has been achieved using advanced sequencing technologies (Figure 1). The hybrid genome assembly was constructed using nanopore long-reads and 10x chromium link-reads. This combination allowed for a comprehensive assembly with a final length of 1.06 Gb and a GC content of 31.03% (Bhattarai et al., 2022a; 2022b). The assembly process involved the use of the MAKER2 pipeline for annotating 12 876 protein-coding genes and 21 031 mRNAs, ensuring a high-quality genomic resource for further studies (Bhattarai et al., 2022a; 2022b).

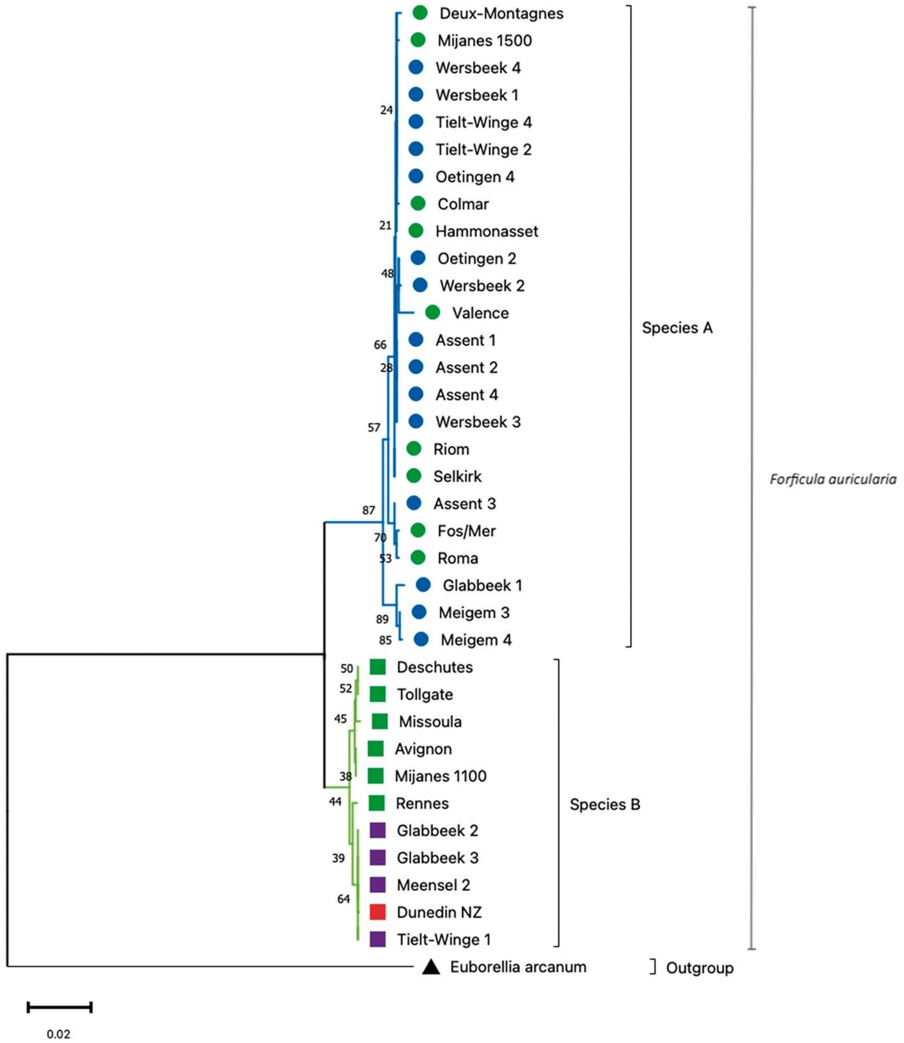

Figure 1 The phylogenetic relationships of *F. auricularia* obtained from different geographic regions inferred from COI and COII using a Neighbour-Joining method and Maximum Composite Likelihood approach in MEGA11. All ambiguous positions were removed for each nucleotide sequence pair (pairwise deletion). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1 000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. Species labeled with the colored squares are subspecies B. The red square (Dunedin NZ) is the one for which the genome is reported in this article. Green squares are the species categorized as subspecies B by Wirth et al. (1998) and the purple squares are others for which the nucleotide sequences were downloaded from NCBI. Species labeled with colored circles belong to subspecies A. Green circles represent subspecies A inferred by Wirth et al. (1998) and blue are other species for which nucleotide sequences were downloaded from NCBI. *E. arcanum* is the outgroup labelled with a black triangle (Adopted from Bhattarai et al., 2022b)

The phylogenetic analysis of *Forficula auricularia* (European earwig) conducted by Bhattarai et al. (2022b) reveals two major subspecies groups, which align with the findings of previous studies such as Wirth et al. (1998). One clade consists of 24 individuals, including subspecies A, while the second group, subspecies B, includes the genome analyzed in this study from Dunedin, New Zealand. By utilizing mitochondrial genes COI and COII, along with phylogenetic methods like Neighbour-Joining and Maximum Composite Likelihood, the study provides reliable evolutionary insights. It highlights the genetic diversity within *F. auricularia* populations across different geographic regions, reinforcing the subspecies differentiation. These findings underscore the importance of genomic resources in understanding earwig adaptation and contribute to broader discussions on insect evolution and local environmental pressures, especially in the case of subspecies B in New Zealand.

2.2 Challenges in earwig genome assembly

One of the primary challenges in assembling the earwig genome is the high repeat content, which constitutes 64.62% of the genome. This high repeat content can complicate the assembly process, leading to potential gaps and misassemblies (Bhattarai et al., 2022a; 2022b). Additionally, the presence of extensive gene rearrangements, as observed in the mitochondrial genomes of Haplodiplatyidae, adds another layer of complexity to the assembly process (Liu et al., 2022). These rearrangements can result in difficulties in accurately annotating and aligning the genomic sequences.

2.3 Comparative analysis of earwig genomes with other insect species

Comparative genomic analyses have revealed significant insights into the evolutionary adaptations of earwigs. For instance, the genome of *Forficula auricularia* has been compared with other insect genomes to identify unique and conserved genetic elements. The benchmarking of Universal Single-Copy Orthologs (BUSCO) scores, which are approximately 90% for eukaryotic, insect, and arthropod orthologs, indicates a high level of completeness and accuracy in the earwig genome assembly (Bhattarai et al., 2022a; 2022b).

Furthermore, studies on other insect genomes, such as the spruce budworm (*Choristoneura fumiferana*) and the eastern fence lizard (*Sceloporus undulatus*), have provided valuable comparative data. For example, synteny analysis with the *Bombyx mori* genome revealed the presence of a neo-Z chromosome in the spruce budworm, highlighting the evolutionary dynamics of sex chromosomes in insects (Picq et al., 2018). Similarly, the high-quality chromosome-level genome assembly of the eastern fence lizard has facilitated synteny and whole-genome association mapping analyses, which can be applied to earwig genomic studies to understand chromosome evolution and adaptation mechanisms (Westfall et al., 2021).

3 Genomic Features of Earwigs

3.1 Gene family expansions and their functions

Gene family expansions play a crucial role in the evolutionary adaptation of organisms to their environments. In the case of earwigs, the sequencing and analysis of their genomes have revealed significant gene rearrangements and expansions. For instance, the mitochondrial genomes of the earwig species *Haplodiplatys aotouensis* showed extensive gene rearrangement events, particularly in protein-coding genes (PCGs) and transfer RNA (tRNA) genes (Liu et al., 2022). These rearrangements and expansions are indicative of the evolutionary pressures and adaptations that earwigs have undergone.

Moreover, gene family expansions have been observed in other species as a response to environmental pressures. For example, the pinewood nematode *Bursaphelenchus xylophilus* exhibited expansions in gene families associated with xenobiotic detoxification pathways, such as flavin monooxygenase (FMO) and cytochrome P450 (CYP450) (Zhang et al., 2020). These expansions likely facilitate the nematode's adaptation to its host's defense chemicals. Similarly, such expansions in earwigs could be linked to their unique ecological niches and survival strategies.

3.2 Identification of genes involved in environmental adaptation

Identifying genes involved in environmental adaptation is essential for understanding how earwigs thrive in diverse habitats. Comparative genomic studies have highlighted the role of specific genes in adaptation to environmental stressors. For instance, in the damselfly *Ischnura elegans*, genes associated with heat shock proteins (HSP40 and HSP70), ion transport (V-ATPase), and visual processes (long-wavelength-sensitive opsin) were identified as crucial for adaptation to varying climatic conditions (Dudaniec et al., 2018). These findings underscore the importance of stress response and physiological adaptation genes in environmental adaptation.

In earwigs, similar genomic analyses could reveal genes that enable them to cope with environmental challenges. The high-quality genome assembly of the European earwig *Forficula auricularia* provides a valuable resource for such investigations, with 12,876 protein-coding genes annotated (Bhattarai et al., 2022a). Future studies could focus on identifying genes with signatures of positive selection and their roles in environmental adaptation, similar to the approach used in other insect species (Colgan et al., 2021; Soudi et al., 2022).

3.3 Molecular pathways associated with stress response

Molecular pathways associated with stress response are critical for the survival of organisms in fluctuating environments. In earwigs, the identification of such pathways can provide insights into their resilience and adaptability. Studies on other species have shown that stress response pathways often involve heat shock proteins, detoxification enzymes, and other protective mechanisms. For example, the mangrove plant *Aegiceras corniculatum* exhibited expansions in gene families related to oxidative phosphorylation and phenylalanine metabolism, which are essential for coping with intertidal stressors (Ma et al., 2021).

In earwigs, the presence of genes involved in similar pathways could be indicative of their ability to withstand environmental stress. The genomic resources available for *Forficula auricularia*, including the annotated protein-coding genes, offer a foundation for exploring these molecular pathways (Bhattarai et al., 2022a). Additionally, the study of gene-environment associations in other species, such as the recent invasive Aedes aegypti populations, has highlighted the role of heat-shock proteins and other stress-related genes in local adaptation (Soudi et al., 2022). These findings can guide future research on the molecular mechanisms underlying stress response in earwigs.

4 Molecular Mechanisms of Ecological Adaptation

4.1 Mechanisms of temperature tolerance and adaptation

Temperature tolerance and adaptation are critical for the survival of species in varying climates. Genomic studies have revealed that specific genetic variations are associated with temperature adaptation. For instance, in the Chinese wingnut (*Pterocarya stenoptera*), adaptive divergence is influenced by temperature seasonality and annual temperature, with 801 candidate SNPs identified that correlate with these environmental factors (Li et al., 2020). Similarly, in lacertid lizards, 200 genes were found to be under positive diversifying selection, many of which are involved in physiological adaptations to climate, including temperature (Valero et al., 2021). These findings highlight the role of specific genes and genetic variations in enabling species to tolerate and adapt to temperature changes.

4.2 Adaptations to arid and humid environments

Adaptations to arid and humid environments involve complex genetic changes that enable species to survive under extreme conditions. In cactophilic *Drosophila* species, high rates of gene gains and positive selection were observed in species adapted to arid environments, with genes related to metabolism and stress response playing significant roles (Rane et al., 2019). In white spruce (*Picea glauca*), genomic studies identified 285 genes associated with drought tolerance, including those involved in anatomical and growth responses to aridity (Depardieu et al., 2021). These genetic adaptations are crucial for species to manage water scarcity and maintain physiological functions in arid environments.

4.3 Behavioral and physiological traits linked to genetic adaptations

Behavioral and physiological traits are often linked to genetic adaptations that enhance survival in specific environments. In bumblebees (*Bombus terrestris*), recent adaptations were found to affect neurobiology, wing development, and response to xenobiotics, which are critical for their interaction with the environment (Colgan et al., 2021). In the rufous-capped babbler (*Cyanoderma ruficeps*), genetic adaptations to high elevation environments were associated with changes in beak size and physiological functions such as haematopoiesis and metabolism, which are essential for coping with low temperatures and hypoxia (Lu et al., 2023). These examples illustrate how genetic adaptations can drive behavioral and physiological changes that improve the fitness of organisms in their respective habitats.

5 Evolutionary Genomics of Earwigs

5.1 Phylogenetic analysis of earwigs and related species

The phylogenetic position and inner relationships of *Dermaptera*, commonly known as earwigs, have been a subject of extensive research. Recent studies have provided significant insights into the phylogenetic relationships within this order. For instance, the first mitochondrial genomes of the family *Haplodiplatyidae* revealed intraspecific variation and extensive gene rearrangement events, which are crucial for understanding the molecular diversity and mitogenomic evolution of earwigs (Liu et al., 2022). Comparative mitogenomic analysis of two earwig species, *Apachyus feae* and *Diplatys flavicollis*, highlighted variable mitogenomic structures and extensive gene rearrangements, further contributing to the phylogenetic understanding of Dermaptera (Figure 2) (Chen, 2022).

Figure 2 Relative synonymous codon usage (RSCU) of PCGs in six species of earwigs (Adopted from Chen, 2022)

Chen (2022) investigates the protein-coding genes (PCGs) and relative synonymous codon usage (RSCU) in six species of earwigs. Differences in sequencing completeness were noted, with *A. feae* having fully annotated PCGs, while *D. flavicollis* lacks certain genes like *ND2* and *COX2*. Both species primarily use standard ATN start codons, though *A. feae* employs special codons for ATP8 and COX3. Most PCGs terminate with standard TAN codons, except for *A. feae*'s ND4 and CYTB, which end with incomplete stop codons. The RSCU analysis reveals codon preference variations among species, with *A. feae* favoring TCT (Ser) and other species like *E. metallica* and *D. flavicollis* showing a preference for leucine codons. These findings contribute to understanding the mitochondrial gene evolution and codon bias in earwigs.

5.2 Insights into adaptive evolution from genome data

Genomic data have provided valuable insights into the adaptive evolution of earwigs. The genome assembly and annotation of the European earwig, *Forficula auricularia*, have facilitated detailed genetic investigations, revealing a high-quality hybrid genome assembly with significant repeat elements and protein-coding genes (Bhattarai et al., 2022b). This genomic resource is instrumental in studying the molecular mechanisms underlying the ecological and physiological adaptations of earwigs. Furthermore, the de novo whole-genome sequencing and assembly of the yellow-throated bunting, although not an earwig, demonstrated the importance of adaptive genes in coping with environmental stressors, which can be paralleled in earwig studies to understand their adaptation to diverse ecological niches (Hu et al., 2022).

5.3 Convergent evolution in ecological niches

Convergent evolution, where different species independently evolve similar traits, is evident in the ecological niches occupied by earwigs. The adaptation to new environments often involves complex genomic changes, as seen in the study of woody plants colonizing the land-sea interface, which identified pre-adaptive genomic features that facilitated the invasion of new habitats (Guo et al., 2022). Similarly, the genomic analysis of *Sarcophaga peregrina*, a species with significant ecological and medical importance, revealed expanded and positively selected genes related to its unique biological characteristics, such as ovoviviparous reproduction and carrion-feeding adaptations (Ren et al., 2020). These findings underscore the role of convergent evolution in shaping the ecological adaptations of earwigs and related species.

6 Case Study: Adaptation of a Specific Earwig Species in a Particular Environment

6.1 Selection of the case study species and environmental context

For this case study, we selected the European earwig, *Forficula auricularia*, as the focal species. This species is widely distributed across Europe and is known for its adaptability to various environmental conditions. The European earwig is an important model organism for studies on maternal care, sexual selection, sociality, and host-parasite interactions (Bhattarai et al., 2022a). The environmental context for this study involves examining the earwig's adaptation to temperate climates, characterized by seasonal variations in temperature and humidity.

6.2 Genome analysis and ecological adaptation in the case study species

The genome of *Forficula auricularia* has been sequenced and assembled to a high quality, providing a comprehensive resource for genetic studies. The genome assembly is 1.06 Gb in length with 31.03% GC content, consisting of 919 scaffolds with an N50 of 12.55 Mb. The genome annotation revealed 12,876 protein-coding genes and 21,031 mRNAs (Bhattarai et al., 2022a). This genomic resource allows for detailed investigations into the genetic basis of ecological adaptation.

Studies on other species have shown that genomic adaptations often involve genes related to environmental interactions, such as those involved in neurobiology, development, and response to environmental stressors (Li et al., 2020; Colgan et al., 2021; Valero et al., 2021). In the case of the European earwig, similar genomic analyses can be conducted to identify candidate genes and pathways that contribute to its adaptation to temperate climates. For instance, genes involved in temperature regulation, water balance, and light response are likely to be crucial for the earwig's survival and reproduction in its environment (Li et al., 2020).

6.3 Discussion of unique adaptive traits observed in the species

The European earwig exhibits several unique adaptive traits that have likely contributed to its success in temperate environments. One notable trait is its maternal care behavior, which includes guarding and cleaning eggs, as well as feeding and protecting nymphs. This behavior enhances offspring survival in variable environmental conditions (Bhattarai et al., 2022a). Additionally, the earwig's ability to tolerate a wide range of temperatures and humidity levels is likely underpinned by specific genetic adaptations.

Comparative studies on other insects and vertebrates have identified key genes and pathways involved in environmental adaptation, such as those related to stress response, detoxification, and morphological changes (Rellstab et al., 2020; Valero et al., 2021; Schaal and Wuitchik, 2023). In the European earwig, similar mechanisms may be at play, with genes involved in stress response and detoxification playing a crucial role in coping with environmental fluctuations and pollutants (Weigand et al., 2018).

7 Future Directions in Earwig Genomic Research

7.1 Potential for genomic editing and functional studies

The advent of CRISPR/Cas9 technology has revolutionized the field of genome editing, providing a powerful tool for precise genetic modifications. This technology can be leveraged to study gene function in earwigs, enabling researchers to knock out or knock in specific genes to observe phenotypic changes and understand their roles in ecological adaptation. For instance, the CRISPR/Cas9 system has been successfully used in various organisms, including the water flea *Daphnia pulex*, to study gene function related to environmental responses (Hiruta et al., 2018). Additionally, the development of CRISPR-based tools such as base editing and high-fidelity variants like xCas9 and Cas12a can further enhance the precision and efficiency of genomic edits in earwigs (Manghwar et al., 2019; 2020). These advancements open up new possibilities for functional genomics studies in earwigs, allowing for the dissection of genetic pathways involved in their unique ecological adaptations.

7.2 Broader implications for understanding insect ecological adaptation

The application of CRISPR/Cas9 in earwig research can provide broader insights into the genetic basis of ecological adaptation in insects. By enabling targeted gene disruption and precise genetic modifications, researchers can investigate the roles of specific genes in adaptation to environmental stressors, reproductive strategies, and social behaviors. For example, studies on the fall armyworm *Spodoptera frugiperda* have demonstrated the utility of CRISPR/Cas9 in identifying genes involved in development and stress responses, which can be extrapolated to understand similar mechanisms in earwigs (Zhu et al., 2020). Furthermore, the ability to perform genome-wide CRISPR screens can help identify key regulatory genes and pathways that contribute to the ecological success of earwigs in diverse environments (Concordet and Haeussler, 2018; Ansai and Kitano, 2022). These findings can enhance our understanding of insect evolution and inform conservation strategies for maintaining ecological balance.

7.3 Recommendations for future genomic and ecological studies

To advance earwig genomic research, several recommendations can be made. First, the establishment of a comprehensive genomic database for earwigs, including high-quality genome assemblies and annotations, is essential. This will provide a reference for designing CRISPR/Cas9 experiments and interpreting genetic data. Second, the development of efficient CRISPR/Cas9 delivery systems tailored to earwigs, such as ribonucleoprotein complexes or viral vectors, will facilitate successful gene editing (Hiruta et al., 2018; Shan et al., 2020). Third, integrating CRISPR/Cas9 with other omics approaches, such as transcriptomics and proteomics, can provide a holistic view of gene function and regulation in response to environmental changes (Zhang et al., 2018; Min et al., 2022). Finally, collaborative efforts between geneticists, ecologists, and evolutionary biologists will be crucial to translate genomic findings into ecological and evolutionary contexts, thereby enriching our understanding of earwig biology and their adaptation mechanisms (Tavakoli et al., 2021).

8 Concluding Remarks

The genomic analysis of earwigs has provided significant insights into their ecological adaptation mechanisms. Studies have shown that environmental pressures drive genetic diversity and adaptation in various species, including insects, plants, and vertebrates. For instance, research on bumblebees revealed extensive genetic diversity and recent adaptation to environmental changes, highlighting key processes such as neurobiology and wing development. Similarly, the genomic study of rubber rabbitbrush identified environmental variables like precipitation and elevation as drivers of local adaptation, supported by both genomic and phenotypic data. In amphibians, genomic data have elucidated the molecular mechanisms of adaptation and speciation, despite challenges in genome assembly. Furthermore, functional genomics in lacertid lizards demonstrated the role of specific genes in physiological and morphological adaptations to climate. These findings collectively underscore the importance of genomic studies in understanding the adaptive potential and resilience of species to environmental changes.

The insights gained from genomic studies have profound implications for conservation and ecological research. Understanding the genetic basis of adaptation can inform conservation strategies by identifying key genetic variants that contribute to resilience against environmental stressors. For example, the study on Ethiopian indigenous chickens highlighted the importance of integrating ecological niche modeling with genomic analyses to identify environmental drivers of adaptation, which can guide sustainable breeding programs. Similarly, the genomic analysis of the Chinese wingnut provided valuable information on the genetic basis of local adaptation, which is crucial for the conservation of non-model species. These approaches can be applied to other species to develop targeted conservation strategies that enhance their adaptive potential in the face of climate change and habitat loss.

The genomic study of earwigs represents a significant step forward in understanding the molecular mechanisms underlying their ecological adaptation. By leveraging advanced genomic techniques and integrating them with ecological data, researchers can uncover the genetic basis of adaptation and resilience in earwigs and other species. This knowledge is essential for predicting how species will respond to future environmental changes and for developing effective conservation strategies. As genomic technologies continue to advance, they will provide even deeper insights into the complex interactions between genetics and the environment, ultimately contributing to the preservation of biodiversity and ecosystem stability.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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