11 Conclusions

Research on the monarch butterfly has progressed from classical natural history and ecological observations to an integrative genomic, functional, and eco-physiological understanding of this iconic species. Chromosome-scale genome assemblies, population resequencing, and functional genomic tools have enabled identification of genes and pathways associated with migratory behavior, circadian rhythms, chemical defense, and sex-chromosome evolution (Satterfield et al., 2015). Studies of host-plant interactions and metabolomics have revealed how cardenolide sequestration and chemical stress responses mediate survival, predator avoidance, and parasite resistance, highlighting the complex interplay between genotype, phenotype, and environment (Agrawal et al., 2012; 2024; 2025). Simultaneously, ecological and population genomic analyses underscore how microbiomes, parasite pressures, and environmental changes shape adaptive variation and influence conservation priorities (de Roode et al., 2008; Dale et al., 2014; Sanaei et al., 2024).

Despite these advances, significant gaps remain in fully elucidating the proximate and ultimate mechanisms underlying monarch adaptation. Key opportunities include causal mapping of migration-related alleles, single-cell and spatial genomics to resolve cell-type specific regulatory networks, pan-genome analyses of structural variants and neo-sex chromosome evolution. Additional metabolomic profiling to link host-plant chemistry with physiological stress responses. Integrative experimental designs combining genotype, metabolome, microbiome, milkweed chemistry, and parasite exposure (Dreisbach et al., 2023; Agrawal et al., 2025) offers a pathway to connect molecular mechanisms with ecological function. By leveraging these multi-dimensional approaches, future research can provide mechanistic insights into migration, chemical defense, and adaptation while directly informing conservation strategies to enhance monarch resilience in the face of habitat loss, climate change, and shifting ecological pressures.

Acknowledgments

I thank colleagues and mentors at Kansas State University and Central College for insightful discussions that helped shape the ideas synthesized in this review. I am also grateful to the anonymous reviewer for their thoughtful and constructive feedback, which improved the clarity and scope of the manuscript. I thank the researchers in the monarch biology, genomics, and chemical ecology communities whose foundational and ongoing work made this synthesis possible. No specific funding sources directly supported the preparation of this manuscript.

Conflict of Interest Disclosure

The author declares no conflicts of interest.

References

Agrawal A.A., Petschenka G., Bingham R.A., Weber M.G., and Rasmann S., 2012, Toxic cardenolides: chemical ecology and coevolution of specialized plant-herbivore interactions, Annual Review of Ecology, Evolution, and Systematics, 43: 59-80.

Agrawal A.A., Böröczky K., Haribal M., Hastings A.P., White R.A., Jiang R.W., and Duplais C., 2021, Cardenolides, toxicity, and the costs of sequestration in the coevolutionary interaction between monarchs and milkweeds, Proceedings of the National Academy of Sciences, 118(16): e2024463118. https://doi.org/10.1073/pnas.2024463118

Agrawal A.A., Hastings A.P., and Duplais C., 2024, Testing the selective sequestration hypothesis: Monarch butterflies preferentially sequester plant defences that are less toxic to themselves while maintaining potency to others, Ecology Letters, 27(1): e14340. https://doi.org/10.1111/ele.14340

Agrawal A.A., Hastings A.P., Lenhart P.A., Blecher M., Duplais C., Petschenka G., Hawlena D., Wagschal V., and Dobler S., 2024, Convergence and divergence among herbivorous insects specialized on toxic plants: revealing syndromes among the cardenolide feeders across the insect tree of life, The American Naturalist, 204(3): 201-220. https://doi.org/10.1086/731277

Agrawal A.A., Hastings A.P., Patrick E.T., Knight A.C., and Dreisbach T.A., 2025, Metabolomic variation in milkweeds shapes herbivore defense, performance, and parasite resistance, Ecology Letters.

Agrawal A.A., Salminen J.P., and Fishbein M., 2012, The coevolution of plant defenses and insect herbivores, Ecology, 93(3): 1-10.

Altizer S., and Oberhauser K., 1999, Effects of the protozoan parasite Ophryocystis elektroscirrha on the survival and reproduction of monarch butterflies, Journal of Invertebrate Pathology, 74(1): 61-68. https://doi.org/10.1006/jipa.1999.4853

Altizer S., Hobson K.A., Davis A.K., De Roode J.C., and Wassenaar L.I., 2015, Do healthy monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected monarch butterflies overwintering in Mexico, PLOS ONE, 10(11): e0141371. https://doi.org/10.1371/journal.pone.0141371